

# Animal-derived foods in our diets: nutrition, health and social implications

**Edited by**

Jeff Wood, Ian Givens and Carlotta Giromini

**Published in**

Frontiers in Animal Science



**FRONTIERS EBOOK COPYRIGHT STATEMENT**

The copyright in the text of individual articles in this ebook is the property of their respective authors or their respective institutions or funders. The copyright in graphics and images within each article may be subject to copyright of other parties. In both cases this is subject to a license granted to Frontiers.

The compilation of articles constituting this ebook is the property of Frontiers.

Each article within this ebook, and the ebook itself, are published under the most recent version of the Creative Commons CC-BY licence. The version current at the date of publication of this ebook is CC-BY 4.0. If the CC-BY licence is updated, the licence granted by Frontiers is automatically updated to the new version.

When exercising any right under the CC-BY licence, Frontiers must be attributed as the original publisher of the article or ebook, as applicable.

Authors have the responsibility of ensuring that any graphics or other materials which are the property of others may be included in the CC-BY licence, but this should be checked before relying on the CC-BY licence to reproduce those materials. Any copyright notices relating to those materials must be complied with.

Copyright and source acknowledgement notices may not be removed and must be displayed in any copy, derivative work or partial copy which includes the elements in question.

All copyright, and all rights therein, are protected by national and international copyright laws. The above represents a summary only. For further information please read Frontiers' Conditions for Website Use and Copyright Statement, and the applicable CC-BY licence.

ISSN 1664-8714  
ISBN 978-2-8325-7400-3  
DOI 10.3389/978-2-8325-7400-3

**Generative AI statement**

Any alternative text (Alt text) provided alongside figures in the articles in this ebook 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.

**About Frontiers**

Frontiers is more than just an open access publisher of scholarly articles: it is a pioneering approach to the world of academia, radically improving the way scholarly research is managed. The grand vision of Frontiers is a world where all people have an equal opportunity to seek, share and generate knowledge. Frontiers provides immediate and permanent online open access to all its publications, but this alone is not enough to realize our grand goals.

**Frontiers journal series**

The Frontiers journal series is a multi-tier and interdisciplinary set of open-access, online journals, promising a paradigm shift from the current review, selection and dissemination processes in academic publishing. All Frontiers journals are driven by researchers for researchers; therefore, they constitute a service to the scholarly community. At the same time, the *Frontiers journal series* operates on a revolutionary invention, the tiered publishing system, initially addressing specific communities of scholars, and gradually climbing up to broader public understanding, thus serving the interests of the lay society, too.

**Dedication to quality**

Each Frontiers article is a landmark of the highest quality, thanks to genuinely collaborative interactions between authors and review editors, who include some of the world's best academicians. Research must be certified by peers before entering a stream of knowledge that may eventually reach the public - and shape society; therefore, Frontiers only applies the most rigorous and unbiased reviews. Frontiers revolutionizes research publishing by freely delivering the most outstanding research, evaluated with no bias from both the academic and social point of view. By applying the most advanced information technologies, Frontiers is catapulting scholarly publishing into a new generation.

**What are Frontiers Research Topics?**

Frontiers Research Topics are very popular trademarks of the *Frontiers journals series*: they are collections of at least ten articles, all centered on a particular subject. With their unique mix of varied contributions from Original Research to Review Articles, Frontiers Research Topics unify the most influential researchers, the latest key findings and historical advances in a hot research area.

Find out more on how to host your own Frontiers Research Topic or contribute to one as an author by contacting the Frontiers editorial office: [frontiersin.org/about/contact](https://frontiersin.org/about/contact)

# Animal-derived foods in our diets: nutrition, health and social implications

## Topic editors

Jeff Wood — University of Bristol, United Kingdom

Ian Givens — University of Reading, United Kingdom

Carlotta Giromini — University of Milan, Italy

## Citation

Wood, J., Givens, I., Giromini, C., eds. (2026). *Animal-derived foods in our diets: nutrition, health and social implications*. Lausanne: Frontiers Media SA.  
doi: 10.3389/978-2-8325-7400-3

# Table of contents

05	<b>Editorial: Animal-derived foods in our diets: nutrition, health and social implications</b> Jeff Wood, Carlotta Giromini and Ian Givens
08	<b>Processed meat consumption and associated factors in Chile: A cross-sectional study nested in the MAUCO cohort</b> Jenny Ruedlinger, Vicente Cid-Ossandón, Andrea Huidobro, Vanessa Van De Wyngard, Claudio Vargas and Catterina Ferreccio
22	<b>The role of meat in iron nutrition of vulnerable groups of the UK population</b> Susan Fairweather-Tait
32	<b>Valorizing meat by-products for human consumption: understanding consumer attitude formation processes</b> Georgia Lavranou, Maeve Henchion, Mary B. McCarthy and Seamus J. O'Reilly
47	<b>Meat industry by-products: a bio-refinery approach to the production of safe, value added products for sustainable agriculture applications</b> Stephen L. Woodgate
54	<b>Milled rapeseeds and oats decrease milk saturated fatty acids and ruminal methane emissions in dairy cows without changes in product sensory quality</b> Anni Halmemies-Beauchet-Filleau, Seija Jaakkola, Tuomo Kokkonen, Anu M. Turpeinen, D. Ian Givens and Aila Vanhatalo
71	<b>Health effects of ruminant trans fatty acids with emphasis on type 2 diabetes</b> Yanqing Xu, Michael E. R. Dugan, Cletos Mapiye and Payam Vahmani
80	<b>Benefits, perceived and actual risks and barriers to egg consumption in low- and middle-income countries</b> Chhavi Tiwari, Mulubrhan Balehegn, Adegbola T. Adesogan and Sarah L. McKune
91	<b>Pleasure, quality or status? an analysis of drivers of purchase of fresh pork in China</b> Maartje D. G. H. Mulders, Klaus G. Grunert, Susanne Pedersen, Karen Brunsø and Yanfeng Zhou
102	<b>Oleic acid concentration in bovine adipose tissues: impact on human health, sensory attributes, and genetic regulation</b> Stephen B. Smith
109	<b>From feed to fork: immunity, performance and quality of products from farm animals fed sugarcane products</b> Nee Edirisinghe, Matthew Flavel, Dodie Pouniotis, Rosita Zakaria, Kosta Fremiella Lim and Daniel Anthony Dias



- 120 **Animal-derived foods: consumption, composition and effects on health and the environment: an overview**  
J. D. Wood, C. Giromini and D. I. Givens
- 133 **Enrichment of ruminant meats with health enhancing fatty acids and antioxidants: feed-based effects on nutritional value and human health aspects – invited review**  
Eric N. Ponnampalam, Michelle Kearns, Ali Kiani, Sarusha Santhiravel, Payam Vahmani, Sophie Prache, Frank J. Monahan and Cletos Mapiye
- 152 **Animal breeding and feeding tools may close human nutrition gaps**  
Björg Egelandssdal, Vladana Grabez-Ågren, Liv Torunn Mydland, Anna Haug and Egil Prestløkken
- 174 **Change of dietary patterns on CO<sub>2</sub> emissions under the African swine fever in South Korea**  
Sungtae Eun



## OPEN ACCESS

EDITED AND REVIEWED BY  
Christine Janet Nicol,  
Royal Veterinary College (RVC),  
United Kingdom

## \*CORRESPONDENCE

Jeff Wood  
✉ jeff.wood@bristol.ac.uk

RECEIVED 16 January 2025

ACCEPTED 27 January 2025

PUBLISHED 06 February 2025

## CITATION

Wood J, Giromini C and Givens I (2025)  
Editorial: Animal-derived foods in our diets:  
nutrition, health and social implications.  
*Front. Anim. Sci.* 6:1561770.  
doi: 10.3389/fanim.2025.1561770

## COPYRIGHT

© 2025 Wood, Giromini and Givens. This is an  
open-access article distributed under the terms  
of the [Creative Commons Attribution License](#)  
(CC BY). The use, distribution or reproduction  
in other forums is permitted, provided the  
original author(s) and the copyright owner(s)  
are credited and that the original publication  
in this journal is cited, in accordance with  
accepted academic practice. No use,  
distribution or reproduction is permitted  
which does not comply with these terms.

# Editorial: Animal-derived foods in our diets: nutrition, health and social implications

Jeff Wood<sup>1\*</sup>, Carlotta Giromini<sup>2</sup> and Ian Givens<sup>3</sup>

<sup>1</sup>Bristol Veterinary School, University of Bristol, Bristol, United Kingdom, <sup>2</sup>Department of Veterinary Medicine and Animal Science, University of Milan, Milan, Italy, <sup>3</sup>Institute for Food, Nutrition and Health, University of Reading, Reading, United Kingdom

## KEYWORDS

meat, milk, fish, eggs, nutrition, health, environment

## Editorial on the Research Topic

**Animal-derived foods in our diets: nutrition, health and social implications**

Animal-derived foods (ADFs), including meat and meat products, milk and dairy products, fish and eggs, contribute vital nutrients to the diets of people around the world and low intakes have been linked to conditions such as stunted growth, poor bone development and anaemia. At the same time there is concern that some ADFs may pose a risk to health. There is also increasing worry about the environmental cost of some modes of ADF production and with the welfare of the animals involved. The aim of this Research Topic was to assemble a collection of research reports and reviews which give the reader insights into these important topics. Fourteen papers were published which included five reports on original research. Broadly, the papers have covered the whole food chain from the diet of the animal to food quality, human health, consumer attitudes, and food by-products.

Egelandstad et al. highlighted the fact that animal breeding and feeding have been mainly focused on profitability and yield rather than improving the nutritional quality of ADFs. They proposed that sustainable food production from animals should be within the 'One Health' for animals and humans concept. Edirisinghe et al. reviewed the feed to fork concept for the use of sugarcane products as feeds for animals (pigs, poultry, ruminants and fish). They concluded that sugarcane products had promise for promoting growth in pigs, poultry and fish, in part by modulating inflammatory responses and enhancing immune cell activities. They also highlighted beneficial effects on meat tenderness but concluded that more research was needed. Another review examined the enrichment of ruminant meat with health benefiting fatty acids by appropriate animal diets (Ponnampalam et al.). They concluded that high quality pasture was superior for producing ruminant meat enriched with health enhancing fatty acids, notably those of the n-3 PUFA family. The paper of Halmemies-Beauchet-Filleau et al. showed that milled rapeseeds and oats in the diet of dairy cows not only reduced saturated fatty acids in the milk fat by 16-20%, increased *cis*-MUFA by about 50% but also reduced methane production by the cows by 20%. In addition, the organoleptic quality of the milk, butter, and cheese produced was not compromised by the modified lipid profile.

The paper of Eun demonstrated that changing dietary patterns in a region of South Korea, resulting from an outbreak of African Swine Fever, resulted in a reduction of

household carbon dioxide emissions. This illustrated the fact that human dietary change can have a direct impact on the environment. The review by Wood et al. compared the environmental impact of ADFs when expressed per 100g of protein produced vs. the traditional per kg of food product. The former is a more realistic comparison but still disregards other beneficial nutrients present in many ADFs. Both comparisons showed ruminant meat to be linked with the highest environmental impact among foods.

Wood et al. also highlighted the substantial variation that exists in the nutritional composition of the different ADFs which is often ignored when plant-based alternative foods are proposed as a replacement. Smith highlighted the health benefits of oleic acid in the diet and what animal related diet and genotype factors influence its concentration in beef. They also concluded that there is little correlation between concentrations of fatty acids and the flavour of beef unless there are differences in the diet of the animal which can contribute to flavour (e.g. grass vs. grains).

Various aspects of the associations between ADFs and human health were covered in eight of the contributing papers. Wood et al. reviewed associations with chronic diseases in some depth with key conclusions that milk/dairy products have a broadly neutral association with CVD with some evidence that fermented dairy has been associated with a reduced risk of type 2 diabetes. A key conclusion was that higher intakes of processed meat are associated with increased risk of CVD, colorectal cancer and possibly dementia. This supports the current dietary guidance that consumption of processed meat should be low. There is still no clear understanding of what are the damaging components of processed meat and which processed meats pose the greatest problems. Ruedlinger et al. reported on a cross-sectional study in Chile examining processed meat consumption in the MAUCO cohort. Processed meat consumption is increasing and this study found that high consumption of it was associated with frequent consumption of other unhealthy foods and alcohol and was associated with increased risk of CVD. No association was found between self-reported cancer and processed meat, but the cohort does reside in a region with a high mortality rate for colon cancer. It is notable that Fairweather-Tait highlighted that haem iron, typically present in red meat, has a bioavailability consistently higher than non-haem iron present in plants and cereals and discusses the implications of this for vegetarian and vegan diets. It is recommended that vulnerable groups such as teenage girls and women of child-bearing age should have careful monitoring of their iron status. Xu et al. reviewed the health effects of naturally occurring trans fatty acids in foods from ruminants with focus on evidence from mainly observational studies suggesting their association with reduced risk of type 2 diabetes. It was concluded that this benefit has not been seen in some animal studies or human clinical trials although so far, the number of such studies is low. Nutritional issues in low- and middle-income countries (LMIC) were reviewed by Tiwari et al. with a focus on the benefits of ADFs, and eggs in particular, for improving nutrition, health and growth of young children. Whilst the evidence for the benefits of eggs is strong, there are few studies in LMIC, where there are social and cultural barriers to egg consumption. A key conclusion is that governments should develop policies that make eggs more

affordable and have education targets to counter sociocultural factors which restrict egg consumption.

Additional aspects of consumer attitudes relating to food quality were considered by other contributing papers. Mulders et al. examined the factors which drive fresh pork purchase in China. They concluded that buying fresh meat is mostly driven by the anticipated pleasure and less by perceptions of quality, safety and healthiness. Lavranou et al. reported on the attitudes of Irish consumers towards hypothetical food products derived from beef offal sources which have been shown to contain worthwhile amounts of high-quality protein. Overall, they found that consumers who had been given benefit information regarding health and the environment of consuming the protein-containing products from beef offal had a more positive attitude toward the products. However, interestingly, the provision of benefit- and risk-orientated information at the same time also had a positive effect on deliberative evaluations. It was concluded that the results have implications for the development of new products and for strategies concerning sustainable food production and consumption.

The recycling of meat processing by-products is covered in two papers. The work of Lavranou et al. clearly represent a route by which products at the end of the meat processing chain can be usefully used. This subject of dealing with meat processing by-products was tackled in depth by Woodgate. Their review gives a history of the so-called rendering process and how it was impacted by the bovine spongiform encephalopathy (BSE) epidemic in Europe. It concluded that rendering is now regarded as an essential part of the food chain that correctly prioritises human and animal health and can now produce safe and environmentally sustainable products which benefit society.

Some papers in the Research Topic noted differences between countries and regions of the world in the conclusions from studies and in the approaches taken by governments. Wood et al. showed that the harmful effects of some ADFs on health have mainly been observed in high-income rather than LMIC. This could be due to differences in intakes. In some high-income countries, governments have considered the use of legislation to reduce the production of ADFs.

We are certain that this special Frontiers Research Topic has stimulated the production of excellent contributions that are concerned with many of the issues in the pathway of food production from animals through food processing, choice, consumption, human health and environmental impacts plus the final step of dealing with the end products of meat processing. The papers also confirm the high degree of diversity both within and between ADFs. This and related nutrition and health characteristics of these foods need to be fully accounted for in decisions concerning their replacement by plant-based alternatives. As always, there are issues that need further research, but the papers have highlighted many of these topics which will aid future thought and research planning.

## Author contributions

JW: Writing – original draft. CG: Writing – original draft. IG: Writing – original draft.

## 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.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

## Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.



## OPEN ACCESS

EDITED BY  
Jeff Wood,  
University of Bristol, United Kingdom

REVIEWED BY  
Stefaan De Smet,  
Ghent University, Belgium  
Joanne Karam,  
Modern University for Business and  
Science, Lebanon

\*CORRESPONDENCE  
Catterina Ferreccio  
cferrec@med.puc.cl

SPECIALTY SECTION  
This article was submitted to  
Public Health and Nutrition,  
a section of the journal  
Frontiers in Public Health

RECEIVED 03 June 2022  
ACCEPTED 01 August 2022  
PUBLISHED 18 August 2022

CITATION  
Ruedlinger J, Cid-Ossandón V,  
Huidobro A, Van De Wyngard V,  
Vargas C and Ferreccio C (2022)  
Processed meat consumption and  
associated factors in Chile: A  
cross-sectional study nested in the  
MAUCO cohort.  
*Front. Public Health* 10:960997.  
doi: 10.3389/fpubh.2022.960997

COPYRIGHT  
© 2022 Ruedlinger, Cid-Ossandón,  
Huidobro, Van De Wyngard, Vargas  
and Ferreccio. This is an open-access  
article distributed under the terms of  
the [Creative Commons Attribution  
License \(CC BY\)](https://creativecommons.org/licenses/by/4.0/). The use, distribution  
or reproduction in other forums is  
permitted, provided the original  
author(s) and the copyright owner(s)  
are credited and that the original  
publication in this journal is cited, in  
accordance with accepted academic  
practice. No use, distribution or  
reproduction is permitted which does  
not comply with these terms.

# Processed meat consumption and associated factors in Chile: A cross-sectional study nested in the MAUCO cohort

Jenny Ruedlinger<sup>1,2</sup>, Vicente Cid-Ossandón<sup>1,2</sup>,  
Andrea Huidobro<sup>2,3</sup>, Vanessa Van De Wyngard<sup>1,2</sup>,  
Claudio Vargas<sup>2,4</sup> and Catterina Ferreccio<sup>1,2\*</sup>

<sup>1</sup>Facultad de Medicina, School of Medicine, Pontificia Universidad Católica de Chile, Santiago, Chile,  
<sup>2</sup>Advanced Center for Chronic Diseases, Universidad de Chile and Pontificia Universidad Católica de  
Chile, Santiago, Chile, <sup>3</sup>Facultad de Medicina, School of Medicine, Universidad Católica del Maule,  
Talca, Chile, <sup>4</sup>Departamento de Matemáticas y Ciencias de la Computación, Facultad de Ciencias,  
Universidad de Santiago de Chile, Santiago, Chile

Processed meat consumption is increasing in Latin America. While in developed countries processed meat consumption has been associated with cardiovascular diseases and cancer, our region lacks data associated to its consumption and health impact. We characterized processed meat intake and associated factors in a population-based cohort of a Chilean agricultural county, MAUCO. We analyzed baseline dietary data of 7,841 participants, 4,358 women and 3,483 men (38–77 years), who answered an adapted Mediterranean index food frequency questionnaire. Eight percent of the participants presented high processed meat consumption ( $\geq 5$  times per week). We explored associations of processed meat consumption with participant characteristics using multinomial logistic regression models. Main factors associated with higher consumption were being men, younger and currently employed, and having a high intake ( $>4$  times per week) of red meat (Odds ratio, 2.71, 95% CI 2.10–3.48), butter/cream (1.96, 1.60–2.41), whole-fat dairy products (1.32, 1.04–1.67) and a high intake ( $\geq 1$  time per day) of sugary snacks/sweets (2.49, 2.04–3.03) and sugary drinks (1.97, 1.63–2.38). Processed meat consumption associated to chronic diseases, particularly cardiovascular disease (Prevalence ratio, 2.28, 95% CI 1.58–3.29). Obesity mediated this association in a proportion of 5.0%, whereas for diabetes the proportion was 13.9%. In this population, processed meat was associated with other unhealthy dietary and lifestyle factors, as well as with chronic diseases, particularly cardiovascular disease.

## KEYWORDS

processed meat, meat consumption, Latin American, Mediterranean diet, population-based cohort, chronic diseases, cancer

## Introduction

Worldwide daily consumption of red meat (beef, lamb and pork) is greater than what was recommended by the World Cancer Research Fund (WCRF) in 2018 (350–500g of weekly intake) (1) and even more than suggested as optimal by The Global Burden of Disease Study (GBD) (18–27 g per day) (2). Although both processed meat (i.e., meat transformed through salting, curing, fermentation, smoking, or other processes in order to enhance flavor or improve preservation) and red meat (unprocessed) have been associated with chronic diseases in different populations, the risk is clearer and stronger for processed meat (2–7), which represents a popular form of meat consumption. The associated health conditions are cardiovascular diseases like stroke (7) and coronary heart disease (5), cancer like renal cell carcinoma (8), breast (9–11), gastric (12, 13) and colorectal (14, 15), and type 2 diabetes (16, 17), including mortality due to these and all-causes (3, 4, 18, 19). High processed meat consumption is also associated to overweight and obesity (19), metabolic syndrome (20, 21), and hypertension (22, 23). Moreover, the International Agency for Research on Cancer classified processed meat as “carcinogenic to humans” (Group 1) on the basis of sufficient evidence for colorectal cancer, although a positive association was also reported for stomach cancer (6). Despite recent controversies questioning the evidence behind current international recommendations of limiting red meat and processed meat consumption (24), these risks continue to be warned as the quality of the evidence improves (25, 26).

Average processed meat consumption is well above the suggested intake (2) even in low-income settings in Latin America (27) and some regions of Africa and Asia (2). Low socioeconomic status has been related to higher processed meat consumption, particularly in Chile and Argentina (28), and also in high-income countries in Europe (29). In Latin America, processed meat consumption varies between Southern, Central, Tropical and Andean regions, ranging from 6.2 g/day to 24.8 g/day (28). Among the Organization for Economic Cooperation and Development countries, Chile has one of the highest red meat intakes per year (30). This increased from 81.2 to 89.1 kg/per capita between 2008 and 2013 (31), with pork being the most consumed (31, 32). In Chilean adolescents, in particular, processed meat intake is higher than unprocessed red meat (33).

As shown, most evidence of the health effects of processed meat consumption come from Asian, European and US populations. Given the high and growing consumption of processed meat in Latin America as well as the sustained increase of the chronic diseases associated to it -reported elsewhere (2, 34–38)- an assessment of the magnitude and impact of this preventable risk factor is urgently needed in Latin America. In Chile, processed meat intake has received little attention, even though previous studies showed the

country had the highest consumption among 8 Latin American countries (28).

The MAUCO Cohort is located in the agricultural Molina County in the Maule Region, 200 km south of the capital city of Santiago. This population is characterized by the fact that in recent decades it has gone from being undernourished to suffering from excess caloric intake, and has one of the highest national rates of cardiovascular disease, stomach cancer and gallbladder cancer. In addition, poverty rates here dropped significantly in a short period of time (2009–2011) which implied advances in terms of sanitation. As the county economy is agriculture based, pesticide exposure is of particular interest in this population, as well as the study of other environmental risk factors in the development of chronic diseases (39). Here we present the frequency of processed meat consumption and its associated sociodemographic, health and lifestyle factors in this population-based cohort.

## Materials and methods

### Study design and setting

We conducted a cross-sectional analysis of baseline dietary data of all participants enrolled in the Maule cohort (MAUCO), from the agricultural county of Molina in the Maule Region, central Chile (39). This region is characterized for presenting one of the highest incidence rates for gastric cancer in men and women per 100,000 (regional 46.3 and 17.7 vs. 34.1 and 12.8 nationwide, respectively) (40), one of the highest mortality rates for colon cancer per 100,000 (regional 8.6 vs. 7.19 nationwide) (41) and a prevalence of cardiovascular risk factors above national average (42). MAUCO seeks to analyze the natural history of chronic diseases in Chile. Details of cohort recruitment and study protocols have been described elsewhere (39). In brief, selection criteria were: to be a resident of Molina for at least 6 months and without plans to move for the next 3 years, aged 38 to 74 years, and being able to consent autonomously. Individuals with a diagnosis of terminal illness were excluded (43). We included the 7,841 participants enrolled in the cohort between December 2014 and December 2019 and who had answered the question on consumption of processed meat. Written informed consent was obtained from all participants.

### Dietary assessment

Baseline dietary assessment of the regularly consumed foods in the last 12 months was based on a food frequency questionnaire which included items from a Mediterranean diet survey (44). This Mediterranean diet was designed based on traditional food consumption habits in the European



Mediterranean region with modifications to incorporate Chilean dietary habits. This “Chilean Mediterranean Diet Index” (Chilean MDI) was the first Mediterranean diet quality index to be adapted and validated specifically for use in Chile (45). The MAUCO food frequency questionnaire, adapted from the Chilean MDI, was applied in person by trained field staff. For each item, four to six consumption frequencies were available, depending on the food item. For example, response options ranged from “none” to “>3 time per day” for vegetables and to “>8 times per week” for whole-fat dairy products. With the exception of processed meat, the consumption frequency of all other dietary items was categorized into two levels based on recommendations for the Mediterranean diet (44–46). [Box 1](#) summarizes the foods and cut-points used.

## Sociodemographic, lifestyle, anthropometric and health variables

All participants answered surveys about sociodemographics, lifestyle (i.e., tobacco and alcohol consumption), personal and family medical history, health status, and employment history, among others. Participants provided fasting blood, and received a hepatobiliary ultrasound exam, anthropometry and other physical (blood pressure, tooth count) and laboratory tests (glycemia, triglycerides, cholesterol, alanine aminotransferase, aspartate aminotransferase, among others). Metabolic syndrome score was constructed considering abdominal obesity, high Triglycerides, low HDL cholesterol, high blood pressure and high fasting glucose, according to ATP III criteria (47).

For the present analysis, the following variables were included: sex (male, female), age (years, 38–74), schooling (years completed); self-identified ethnicity (Chilean/Latin, other nationalities or ethnic groups); health insurance (public, private/other); employment status (occupied/employed, not employed); smoking status (current, former/never); drinking pattern (binge drinking:  $\geq 3$  drinks for women or  $\geq 4$  drinks for men per occasion; abstainers/other drinking patterns); number of chronic conditions ( $\geq 2$  or  $< 2$ ), including diabetes (self-report or fasting glycemia  $\geq 126$  mg/dl or use of hypoglycemic drugs), cardiovascular disease (self-reported history of heart disease, heart failure, stroke or other, excluding hypertension), cancer (self-reported history), digestive symptoms (biliary colic, gastroesophageal reflux and gastritis symptoms in the last 12 months), non-infectious digestive diseases (self-reported history of gastric ulcer, irritable bowel syndrome, inflammatory bowel disease or other) and hypertension (use of hypotensive drugs or measured systolic blood pressure  $\geq 130$  mm Hg or diastolic blood pressure  $\geq 80$  mm Hg); remaining teeth ( $< 20$  or  $\geq 20$ ); waist circumference (cm); body mass index (BMI:  $> 30$  kg/m<sup>2</sup>;  $\leq 30$  kg/m<sup>2</sup>); Ultrasound-detected (48) fatty liver (any degree: yes; no) and gallbladder disease including cholecystectomy or

gallstones (yes; no); metabolic syndrome (47) (yes; no); fasting blood glucose  $\geq 126$  mg/dl (yes; no); Low-Density Lipoprotein cholesterol (LDL)  $> 160$  mg/dL (yes; no); triglycerides  $\geq 200$  mg/dL (yes; no); High-Density Lipoprotein cholesterol (HDL)  $\leq 40$  mg/dL in men,  $\leq 50$  mg/dL in woman (yes; no); Aspartate Aminotransferase (AST)  $> 48$  UI/L (yes; no); and Alanine Aminotransferase (ALT)  $> 55$  UI/L (yes; no).

## Statistical analysis

To characterize processed meat consumption we analyzed baseline sociodemographic, lifestyle and health characteristics of participants across categories of intake. We present this data as prevalence for categorical variables or as mean  $\pm$  standard deviation (SD) for continuous variables; reporting p-Values for trend. We obtained odds ratios (OR) and 95% confidence intervals (CI) by logistic regression using processed meat consumption as the explained variable dichotomized into  $< 1$  time per week (reference) vs.  $\geq 1$  times per week, adjusted by age, sex and schooling.

We also conducted multinomial logistic regression models to explore associations between sociodemographic, lifestyle and dietary variables with processed meat consumption as the outcome variable in four levels ( $< 1$  time per week as reference; 1 time per week; 2–4 times per week; and  $\geq 5$  times per week). In order to keep most participants in this analysis, we conducted multiple imputation of missing values using MICE (Multiple Imputation by Chained Equations). We created 100 imputed databases. To impute the missing values of each variable, we specified a predictive mean matching model using the 27 variables described. In each imputed dataset we performed a stepwise procedure with backward/forward direction to determine the best multinomial model to explain the outcome (processed meat consumption frequency). According to Akaike information criterion, where the variables that remain in the final model are registered in each of the 100 databases. for the final model, we considered the variables that remained in at least 60% of the models through stepwise ([Supplementary Table S1](#)). Finally, five imputed databases were created with MICE and a multinomial model was fitted with the selected variables; all the results of the analysis were aggregated with rubin's rule applying the corresponding transformations (49). We use this method under the assumption that the missing observations of the covariates are missing at random (MAR). We explore this by assessing the relationship between variables and missingness for each variable using the chi-square or kruskal wallis test, as appropriate. Given the relationships we observed (see [Supplementary Table S2](#)) and since in epidemiological research missingness appears to be typically MAR (50). We consider our assumption to be feasible. Results were expressed as OR. All models were adjusted by sex, age, schooling, employment status and red meat consumption.

## BOX 1

Dietary items in food frequency questionnaire and cut-off points used.

**I. Items categorized according to frequency of intake**

- 1 **Vegetables** (1 serving = 1 cup) raw or cooked, consumed as salads, stews, soups made of natural vegetables, and hot side dishes (servings per day:  $\geq 1 / < 1$ ).
  - 2 **Fruits** (1 serving = 1 cup), including raw, cooked or dried fruits as dried peaches, raisins, dried figs, others (servings per day:  $> 2 / \leq 2$ ).
  - 3 **Legume** (1 serving = 1 plate), as soups, stews and salads, including lentils, chickpeas, beans, and dried or dehydrated peas (servings per week:  $> 2 / \leq 2$ ).
  - 4 **Nuts** (1 serving = 1 handful) such as walnuts, almonds, hazelnuts, cashews, pistachios, peanuts, seeds, etc. (servings per week:  $> 2 / \leq 2$ ).
  - 5 **Whole grain cereals** (1 serving = 1 cup or 2 slices of bread or 6 cookies/crackers), considering brown rice and whole-wheat pasta, whole-wheat bread, whole-grain breakfast cereals, whole-wheat cookies or crackers, and all kinds of dough or dishes made with whole-grain cereals (servings per day:  $\geq 2 / < 2$ ).
  - 6 **White meat** including poultry, chicken, turkey and lean pork (times per week:  $\leq 4 / > 4$ ).
  - 7 **Red meat** considering beef, lamb and fatty pork (times per week:  $\leq 4 / > 4$ ).
  - 8 **Fish or seafood** (times per week:  $> 2 / \leq 2$ ).
  - 9 **Skimmed/fermented dairy products** including skimmed, low-fat or fermented milk, all kind of yogurt, cultured milk, cottage cheese and fresh cheese (times per week:  $> 4 / \leq 4$ ).
  - 10 **Whole-fat dairy products** such as milk and yogurt (times per week:  $\leq 4 / > 4$ ).
  - 11 **Butter or cream** (times per week:  $\leq 4 / > 4$ ).
  - 12 **Olive oil** (teaspoons per day:  $\geq 3 / < 3$ ).
  - 13 **Avocados** (units per week:  $> 3 / \leq 3$ ).
  - 14 **Sugary snacks/sweets** including candies, cookies, chocolates, and desserts with sugar like jelly, pies, cakes (times per day:  $< 1 / \geq 1$ ).
  - 15 **Sugary drinks** (times per day:  $< 1 / \geq 1$ ).
  - 16 **Sugar** (teaspoons per day:  $< 4 / \geq 4$ ).
  - 17 **Fried foods** (times per week:  $\leq 1 / > 1$ ).
  - 18 **Fresh green chili pepper** (times per week:  $< 5 / \geq 5$ ).
  - 19 **Fresh red chili pepper** (times per week:  $< 5 / \geq 5$ ).
  - 20 **Dried red chili pepper** such as chili powder, chili paste or Chilean smoked chili pepper known as merken (tablespoons per week:  $< 5 / \geq 5$ ).
- II. Processed Meat** Meat products transformed through salting, curing, fermentation, smoking, or other processes, e.g., bacon, ham, sausages (including Chilean products as paté, longanizas and other meat by-products) and pre-made hamburgers. Participants were categorized into five groups (weekly frequency: non-consumers,  $< 1$ , 1, 2–4 and  $\geq 5$  times per week).

To better understand whether the association between chronic diseases and processed meat consumption is influenced by the presence of obesity, we explored separately the different chronic conditions in the subgroups of high and low processed meat consumers with and without obesity. We reported prevalence ratio adjusted by age, sex, schooling, smoking and binge drinking using logistic regression. To further confirm if obesity was mediating these associations, we run a mediation analysis in the same subgroup of participants. We reported Average Causal Mediation Effect (ACME), Average Direct Effect (ADE) and proportion mediated, all estimated with R using package 'mediation' with non-parametric bootstrap.

Analyses for the multiple imputation routine were also performed in R 4.0.3 and MICE Package 3.13.0. All other data analyses were performed using stata (StataCorp. 2019. Stata Statistical Software: Release 16. StataCorp LLC, College Station, TX, USA). The level of significance of each risk estimate was set at 0.05.

## Results

### Participants

The study sample included 7,841 MAUCO participants with information about processed meat consumption at baseline; 55%

women, a mean age of  $53.5 \pm 9.7$  years, with  $8.8 \pm 4$  years of schooling.

### Sociodemographic, lifestyle, health and dietary characteristics in relation to processed meat consumption

The proportion of participants with missing data are reported in [Supplementary Table S3](#). A high intake of processed meat ( $\geq 5$  times per week) was reported by 8% of the participants (7% of women and 9% of men); 33% reported non-consumption, 21% reported  $< 1$  time per week, 19.2% 1 time per week and 18.6% 2–4 times per week. [Table 1](#) shows the prevalence (adjusted by age, sex and schooling) of sociodemographic, lifestyle, and health characteristics of MAUCO participants according to their distribution across the five processed meat consumption categories. Participants who ate processed meat more frequently tended to be male, younger, currently employed and with a greater proportion of smokers and binge drinkers. Regarding health conditions, those who ate processed meat more frequently were more likely to be obese and to have **two** or more chronic conditions, fatty liver, metabolic syndrome and elevated levels of fasting blood glucose, triglycerides and

TABLE 1 Profile of participants by weekly frequency of processed meat consumption.

Baseline characteristics		Overall	Frequency of processed meat consumption					P trend <sup>z</sup>
			None <i>n</i> = 2,596 (33%)	<1/week <i>n</i> = 1,651 (21%)	1/week <i>n</i> = 1,504 (19%)	2–4/week <i>n</i> = 1,459 (19%)	≥5/week <i>n</i> = 631 (8%)	
Sociodemographics								
Sex	Men	44.4	33.3	46.0	48.1	55.6	51.3	<0.0001
Age	Years, mean±SD	53.5 ± 9.7	55.3 ± 9.4	54.2 ± 9.6	52.5 ± 9.6	51.5 ± 9.6	51.9 ± 9.9	<0.0001
	Years, ≤55	58.9	50.9	57.1	63.4	68.0	65.5	<0.0001
Ethnicity	Chilean/Latin	97.0	97.0	96.8	97.3	96.8	97.3	0.77
Schooling	Years, mean±SD	8.8 ± 4.0	8.6 ± 4.1	8.9 ± 4.1	8.9 ± 4.0	8.9 ± 3.8	8.9 ± 3.8	0.65
Health insurance	Public	85.5	84.2	84.3	85.9	88.6	85.4	0.05
Lifestyle								
Work	Occupied/employed	80.8	78.6	79.5	81.3	81.0	91.6	<0.0001
Tobacco	Current smoker	29.6	28.2	29.0	28.8	29.8	34.8	0.0019
Alcohol	Binge drinking <sup>a</sup>	19.4	16.2	19.3	20.3	21.0	21.9	0.0004
Health								
Chronic diseases	≥2 <sup>b</sup>	37.4	37.9	35.0	38.6	39.0	45.7	0.0022
Teeth	Remaining teeth <20	44.0	46.5	45.4	46.8	45.9	48.9	0.2
Anthropometry	Waist circumference, cm	98.9 ± 11.05	98.3 ± 11.2	98.6 ± 11.2	99.0 ± 10.9	99.6 ± 10.8	100.3 ± 10.8	<0.0001
	Body mass index >30 kg/m <sup>2</sup>	39.9	37.8	38.5	42.3	41.4	44.8	0.0017
Ultrasound exam	Fatty liver (any degree)	48.4	45.0	47.7	50.1	50.9	53.9	<0.0001
	Gallbladder disease <sup>c</sup>	32.3	32.6	32.2	31.3	33.0	31.3	0.68
Laboratory tests	Fasting blood glucose ≥126 mg/dL	8.5	8.5	7.5	7.9	9.5	10.5	0.04
	LDL >160 mg/dL	9.9	9.7	11.2	9.4	9.6	9.1	0.34
	Triglycerides ≥200 mg/dL	25.1	24.9	24.5	23.3	26.0	30.0	0.0078
	HDL ≤40 mg/dL or ≤50 mg/dL <sup>d</sup>	52.6	52.9	52.6	51.3	53.3	52.5	0.9
	AST >48 UI/L	6.1	4.9	6.6	5.5	7.7	6.2	0.14
	ALT >55 UI/L	10.6	9.5	10.6	10.9	11.4	12.5	0.03
	Metabolic syndrome <sup>e</sup>	48.5	48.8	47.4	46.2	48.9	54.3	0.0138

Analysis in 7,841 MAUCO participants. Values are presented as percentages unless otherwise indicated. Prevalence estimated by logistic regression model. For continuous variables multiple linear regression. Adjusted by age, schooling and sex. Missing data were excluded (see [Supplementary Table S3](#)); <sup>a</sup>≥3 drinks for women or ≥4 drinks for men per occasion; <sup>b</sup>number of chronic conditions, including diabetes, cardiovascular disease, cancer, digestive symptoms, non-infectious digestive diseases and hypertension; <sup>c</sup>Including gallstones and cholecystectomy; <sup>d</sup>≤50 mg/dL in women, ≤40 mg/dL in men; <sup>e</sup>≥3 of the following: abdominal obesity, high triglycerides, low HDL cholesterol, high blood pressure and high fasting glucose; LDL, low-density lipoprotein cholesterol; HDL, high-density lipoprotein cholesterol; AST, Aspartate aminotransferase, ALT, Alanine Aminotransferase; <sup>z</sup>p for trend according to logistic regression model.

ALT enzyme. Some of these associations were also evident in the logistic model with processed meat consumption as a dichotomized variable (<1/≥1 per times per week), presented in [Table 2](#).

[Table 3](#) shows that participants who ate processed meat more frequently were also more likely to have a higher intake of other foods, such as red meat, butter or cream, sugary snacks and sweets, sugary drinks, refined sugar and fried foods, and a lower intake of vegetables. Consumption of a variety of chili peppers was also associated with processed meat intake. Some of these foods were also associated in the logistic model with processed meat consumption as a dichotomized variable (<1/≥1 times per week), presented in [Table 4](#).

In the multinomial logistic regression model with processed meat consumption as the outcome (4 frequency levels), male sex, lower age and being currently occupied or employed were independently associated with higher consumption. Among dietary options, high processed meat was associated with red meat, whole-fat dairy products, butter or cream, sugary snacks or sweets and sugary drinks ([Table 5](#)). On the other hand, a low intake of legumes, fish or seafood and avocados showed an inverse association to processed meat consumption. Other variables like binge drinking, fried foods and low intake of vegetables were associated to processed meat consumption but did not show a clear positive trend.

[Table 6A](#) shows the prevalence of self-reported chronic conditions among participants divided into four groups of

**TABLE 2** Sociodemographic and health factors associated with processed meat consumption at least once a week.

	Baseline characteristic ( <i>n</i> )	PMC ≥1/week (%) <i>n</i> = 3,594	Odds ratio (95% CI) <sup>†</sup>
Sex	Men (3,483)	53.3	1.82 (1.66–2.0)
	Women (4,358)	39.8	1
Health insurance	Public (6,450)	46.5	1.24 (1.08–1.42)
	Other (1,095)	42.8	1
Employment	Occupied/employed (5,046)	49.7	1.35 (1.16–1.56)
	Not employed (1,197)	32.1	1
Alcohol intake	Binge drinking <sup>a</sup> (1,520)	56.5	1.26 (1.12–1.43)
	Abstainer or another drinking pattern (6,313)	43.3	1
Chronic diseases	≥2 <sup>b</sup> (2,102)	40.0	1.14 (1.01–1.28)
	<2 or none (3,433)	41.8	1
Body mass index	>30 kg/m <sup>2</sup> (2,970)	47.1	1.19 (1.08–1.31)
	≤30 kg/m <sup>2</sup> (4,457)	43.7	1
Ultrasound fatty liver	Yes (any degree) (3,579)	47.2	1.22 (1.11–1.34)
	No (3,823)	42.9	1
ALT	>55 UI/L (788)	53.0	1.17 (1.00–1.36)
	≤55 UI/L (6,607)	44.1	1

Analysis in 7,841 MAUCO participants. <sup>†</sup>Odds ratios and 95% confidence intervals obtained by logistic regression using processed meat consumption (PMC) as the explained variable dichotomized into <1/week (reference, including non-consumers) vs. ≥1 times per week. Age, sex and schooling-adjusted.; Missing data were excluded (see [Supplementary Table S3](#)); <sup>a</sup>≥3 drinks for women or ≥4 drinks for men per occasion; <sup>b</sup>number of chronic conditions, including diabetes, cardiovascular disease, cancer, digestive symptoms, non-infectious digestive diseases and hypertension; ALT, Alanine Aminotransferase.

high and low processed meat consumers with and without obesity. As expected, hypertension and diabetes were more prevalent in obese participants among both high consumers and low consumers; similarly, cardiovascular disease and digestive symptoms were more prevalent in the obese among low consumers. However, when comparing high consumers vs. low consumers within the same obesity group, the prevalence of cardiovascular disease was 2-fold higher in high consumers vs. low consumers, in both the obese group and in the non-obese group. To further confirm if obesity was mediating these effects and to what degree, we performed a mediation analysis in the same subgroup of participants. [Table 6B](#) shows that association

between high processed meat consumption and diabetes was partly mediated through obesity in a proportion of 13.9%. This mediation was also evident for cardiovascular disease and digestive symptoms, but to a lesser degree (proportions of 5.0 and 3.0%, respectively).

## Discussion

A more frequent consumption of processed meat was associated with male sex, younger age, being employed, binge drinking, a higher consumption frequency of red meat, butter or cream, sugary snacks/sweets, sugary drinks, fried foods, legumes and fish or seafood, and a low intake of vegetables. Participants with higher processed meat consumption were also more likely to be obese and to have multiple chronic conditions, fatty liver, metabolic syndrome, and elevated levels of fasting blood glucose, triglycerides and ALT enzyme. Regarding chronic diseases, when analyzing the conditions separately, the association of processed meat consumption with diabetes and hypertension appear influenced by obesity, while the association with cardiovascular disease was still evident when evaluating the obese and non-obese subgroups. To our knowledge, this is the first population-based cohort study to address associations between processed meat consumption and sociodemographic, lifestyle and health factors in Chile. The Latin American Study of Nutrition and Health (ELANS), conducted in 2014–2015 using 24-h recall in eight Latin American countries (Argentina, Brazil, Chile, Colombia, Costa Rica, Ecuador, Peru, and Venezuela), found that Chile had the highest processed meat consumption; in the region, processed meat intake was higher among men and showed a trend toward higher consumption at low socioeconomic status (28). Processed meat intake was also assessed in Chile in 2010 by a nationwide dietary survey (population ≥2 years of age) (33); geographical distribution was reported, with lower processed meat consumption in the north and higher consumption in the central (which included Maule Region, where the MAUCO cohort is located) and southern zones.

## Interpretation of findings

According to the last Chilean dietary survey (2010) (33), the population had a median processed meat consumption of 26.4 g/day; intake among respondents with similar characteristics to our participants in terms of age, sex, region, and rurality, ranged from 19 to 32 g/day. However, these figures are 10 years old, and since then the consumption of animal protein has increased in Chile (51). In our study, more than 25% of participants consumed processed meat twice or more per week. Translating portions to grams per day, we conservatively estimate that our participants in the highest intake category (≥5 times per week)

TABLE 3 Intake of other foods with increasing consumption of processed meat.

Food item(intake category)*	Overall	Frequency of processed meat consumption					P trend <sup>z</sup>
		None <i>n</i> = 2,596 (33%)	<1/week <i>n</i> = 1,651 (21%)	1/week <i>n</i> = 1,504 (19%)	2–4/week <i>n</i> = 1,459 (19%)	≥5/week <i>n</i> = 631 (8%)	
Vegetables <1 time/day	34.1	31.2	34.6	33.3	33.6	36.2	0.009
Fruits ≤ 2 servings/day	95.3	94.0	95.7	96.2	95.6	96.0	0.11
Legumes ≤2 servings/week	82.3	84.6	84.8	84.0	80.8	68.6	<0.0001
Nuts ≤2 servings/week	89.3	87.7	89.8	91.6	89.6	85.6	0.19
Whole grain cereals <2 servings/day	98.3	98.4	98.9	98.5	97.8	97.2	0.008
White meat >4 times/week	4.1	4.5	2.9	3.2	3.8	8.3	0.0002
Red meat >4 times/week	11.7	8.7	7.7	10.5	16.2	27.5	<0.0001
Fish or seafood ≤2 times/week	94.5	93.9	95.9	96.1	94.5	88.0	<0.0001
Skimmed/fermented dairy products ≤4 times/week	81.4	80.0	82.4	83.2	81.4	76.9	0.08
Whole-fat dairy products >4 times/week	15.3	14.7	14.0	15.3	14.6	21.2	0.0004
Butter or cream >4 times/week	21.4	15.9	19.6	22.6	26.2	34.2	<0.0001
Olive oil <3 teaspoons/day	99.3	99.3	99.4	99.5	99.2	99.6	0.48
Avocados ≤3 units/week	86.0	85.4	87.3	88.4	85.3	79.1	0.0003
Sugary snacks/sweets ≥1 time/day	22.6	21.5	17.1	19.2	24.7	45.3	<0.0001
Sugary drinks ≥1 time/day	35.5	28.7	28.6	39.5	42.5	49.0	<0.0001
Sugar ≥4 teaspoons/day	38.4	35.7	37.0	38.0	41.9	42.2	0.0003
FGC pepper ≥5 times/week	7.8	6.2	5.7	6.8	6.6	23.5	<0.0001
FRC pepper ≥5 times/week	5.1	3.9	3.1	4.9	4.3	14.3	<0.0001
DRC pepper ≥5 tablespoons/week	6.9	5.4	4.4	6.4	6.9	18.8	<0.0001
Fried foods >1 time/week	20.7	16.5	20.0	21.7	25.8	22.0	<0.0001

Analysis in 7,841 MAUCO participants. Values are presented as percentages. Prevalence estimated by logistic regression model, adjusted by age, schooling and sex; Missing data were excluded (see [Supplementary Table S3](#)); \*Only one category is presented; FGC, Fresh green chili; FRC, Fresh red chili; DRC, dried red chili. <sup>z</sup>p for trend according to logistic regression model.

are likely eating processed meat in the upper limit reported in 2010, i.e., 32 g/day. This is 10 times the daily amount of 0–4 g/day suggested to reduce the risk of chronic disease mortality and morbidity (2), including cancer (7). Although specific data on processed meat intake for the Maule Region is not available, Maule is the second largest processed meats producer in Chile (52), and is located in the Central macrozone which has one of the highest processed meat consumptions in the country (33). Interestingly, the lowest intake is in the Northern macrozone of Chile, which has lower cancer and cardiovascular disease mortality than the Central macrozone (53).

In MAUCO, 33% of participants reported being non-consumers of processed meat. This is similar to what was reported in Swiss population in 2014–2015 (54) and lower than what was reported for the countries in ELANS study, including Chile where 40% of the sample reported not consuming processed meat (28). Men ate more processed meat than women in MAUCO, which is consistent with previous reports in Chile (33), and in other populations in Latin America (28), Europe (3, 54–56), Australia (57) and the US (58). Younger people ate more processed meat, also previously reported in Chile (28, 33),

other Latin American countries (28, 59), the US (56, 60), and Europe (61), while studies in Switzerland and Ireland found opposite trends (54, 62). However, it should be noted that given the age range of MAUCO participants (38–74 years), it was not possible to assess consumption in younger segments of the adult population. We did not find an association of processed meat consumption with schooling, a marker of socioeconomic status in Chile; this could be explained by its low variability in our sample, with an interquartile range of 6. On the other hand, being employed, a marker of higher current income, was associated with higher processed meat consumption. The association between socioeconomic status and processed meat intake is not clear in the international literature: In some high-income European countries, lower socio-economic groups are higher processed meat consumers (29, 61); in Switzerland, lower intake of processed meat was associated with higher education but not with income (54); in Latin America, although a higher consumption at lower socioeconomic status seems to be the current trend (28), older reports from Chile and Colombia show the opposite (33, 63). Overall, global meat consumption is rising (64) and processed meat consumption is particularly high with



**TABLE 4** Frequency of intake of other foods associated with processed meat consumption at least once a week.

<b>Foods items: [reference]</b>	<b>PMC ≥1/week (%) n = 3,594</b>	<b>Odds ratio (95% CI)<sup>†</sup> Ref: &lt;1/week</b>
Vegetables, servings/day <1 [≥1]	49.6	1.12 (1.01–1.24)
Fruits, servings/day ≤2 [>2]	46.2	1.28 (1.03–1.61)
Legumes, servings/week ≤2 [>2]	44.4	0.73 (0.64–0.82)
Red meat, times/week >4 [≤4]	62.3	2.05 (1.75–2.38)
Butter or cream, times/week >4 [≤4]	55.2	1.69 (1.50–1.90)
Sugary snacks/sweets, times/day ≥1 [<1]	53.0	1.43 (1.28–1.60)
Sugary drinks, times/day ≥1 [<1]	58.5	1.87 (1.69–2.07)
Sugar, teaspoons/day ≥4 [<4]	49.7	1.19 (1.08–1.31)
FGC pepper, times/week ≥5 [<5]	56.6	1.65 (1.38–1.97)
FRC pepper, times/week ≥5 [<5]	60.4	1.76 (1.41–2.21)
DRC pepper, servings/week ≥5 [<5]	60.6	1.80 (1.49–2.18)
Fried foods, times/week >1 [≤1]	56.9	1.42 (1.26–1.60)

Analysis in 7,841 MAUCO participants. <sup>†</sup>Odds ratios and 95% confidence intervals obtained by logistic regression using processed meat consumption (PMC) as the explained variable dichotomized in <1/week (reference, including non-consumers) vs. ≥1 times per week. Age, sex and schooling-adjusted. Missing data were excluded (see [Supplementary Table S3](#)). FGC, Fresh green chili; FRC, Fresh red chili; DRC, dried red chili.

respect to an optimal intake (2), and is increasing in some low- and middle-income countries (29), even regardless of per capita family income in countries like Brazil (59).

Meat in general is a dietary source of several micronutrients, so a modest intake can be important for health and disease prevention (65). In the case of processed meat, however, no level of intake can confidently be associated with a lack of risk according to WCRF (1), especially in relation to cancer. Our findings of processed meat consumption being associated with poorer health are in accordance with the literature. Micha et al. (5) reported 42% higher risk of coronary heart disease and 19% higher risk of diabetes per 50 g/day. Chen et al. reported 11% higher risk of stroke per 50 g/day (7). In the US, processed meat was associated with incident cardiovascular disease (66). A recent meta-analysis of sixteen studies covering 10 countries reported that high consumers of processed meat had 35% higher risk of metabolic syndrome (20).

We found an association between processed meat consumption and obesity based on waist circumference or BMI, which is consistent with reports in Chile and elsewhere (55, 67–70). Additionally, we found an association of processed meat consumption with diabetes and hypertension, however, when stratifying by obesity (presence or absence) this association was not observed. On the other hand, a higher prevalence of cardiovascular disease was observed for high consumers, regardless of obesity status. We then confirm that the association of processed meat with diabetes was partly mediated by obesity (13.9%), as were cardiovascular disease and

digestive symptoms, but to a lesser degree. A previous study in Chilean population reported that fatty and processed meats (≥1 vs. <1 portion/week) were associated with abdominal obesity (OR 1.30), and with metabolic syndrome components, including high blood glucose (OR 1.41) and high triglycerides (OR 1.19) (68). The association of processed meat intake with diabetes, partly mediated by obesity, has been reported in other populations (16, 17).

We also found a positive trend between processed meat consumption and elevated ALT enzyme (>55 UI/L) and fatty liver, the latter concordant with previous reports (71). The prospective cohort Nurses' Health Study II, with 77,795 women, reported that red meat consumption -unprocessed and processed- was associated with increased risk of non-alcoholic fatty liver disease (72).

In MAUCO, current smoking and binge drinking had a positive trend across processed meat categories. This has also been reported in European and Asian studies (62, 73, 74), while a meta-analysis including four studies in Europe and the US found an association of processed meat with current smoking but not with alcohol drinking (75). Another lifestyle behavior that has been related with high processed meat intake is low physical activity, with studies showing evidence of association in Switzerland (54), France (55) and Spain (70). In MAUCO, the prevalence of low physical activity (<30 min of physical activity 3 times/week), although high (>90%), was very similar across the five categories of intake (data not shown).

Higher amounts of processed meat are consumed in low quality diets, usually classified as western-type patterns and associated with several chronic conditions (76–78). Moreover, some processed meat products such as pre-made hamburgers, sausages and ham, are considered ultra-processed foods (79), a category that also includes carbonated soft drinks, chocolate, pastries, confectionery, mass-produced packaged breads, and margarines, among others, and that has already been associated with chronic conditions like cancer (80) and hypertension (73). In our study, a high intake of red meat, butter or cream, sugary snacks and sweets, sugary drinks, sugar, fried foods and chili peppers were associated with higher frequency of processed meat consumption. These findings are consistent with reports from the EPIC cohort (3) and NHANES III (81). Sugary drinks and sugars have also been associated with processed meat intake and unhealthy dietary patterns (62, 69, 82), making it challenging to identify the risk attributed to each food item. In MAUCO, chili pepper consumption was associated with higher processed meat consumption, as reported in the US population, where consumers of hot red chili pepper were more likely to be younger, male, to smoke cigarettes, drink alcohol, and consume meat (83). Nevertheless, a regular consumption of chili peppers appears to be more related to Mediterranean dietary patterns rather than to western types (84).

Although an inverse relation between processed meat and healthy foods is commonly reported (55, 62, 69), we observed



TABLE 5 Sociodemographic and diet factors associated with processed meat consumption.

Variables [reference]	Processed meat consumption		
	Odds Ratio (95% CI) <sup>†</sup>		
	1/week	2–4/week	≥5/week
Male [female]	1.30 (1.13–1.49)	1.72 (1.49–1.98)	1.37 (1.11–1.69)
Age (years)	0.98 (0.97–0.99)	0.97 (0.96–0.98)	0.98 (0.97–0.99)
Public health insurance [other]	1.16 (0.97–1.38)	1.44 (1.19–1.74)	1.09 (0.84–1.41)
Occupied/employed [not employed]	1.16 (0.94–1.45)	1.08 (0.89–1.32)	1.91 (1.28–2.83)
Binge drinking <sup>a</sup> [abstainer or other drinking pattern]	1.19 (1.02–1.39)	1.23 (1.05–1.43)	1.19 (0.95–1.49)
Vegetables, servings/day <1 [≥1]	1.00 (0.88–1.14)	1.16 (1.02–1.33)	1.22 (1.00–1.48)
Legumes, servings/week ≤2 [>2]	0.94 (0.80–1.12)	0.77 (0.65–0.90)	0.50 (0.41–0.62)
Nuts, servings/week ≤2 [>2]	1.33 (1.07–1.65)	1.16 (0.94–1.44)	1.25 (0.93–1.69)
Red meat, times/week >4 [≤4]	1.26 (1.01–1.57)	1.83 (1.51–2.21)	2.71 (2.10–3.48)
Fish or seafood, times/week ≤2 [>2]	1.35 (0.99–1.84)	0.99 (0.74–1.30)	0.60 (0.43–0.83)
Whole-fat dairy products, times/week >4 [≤4]	1.04 (0.88–1.23)	0.96 (0.80–1.15)	1.32 (1.04–1.67)
Butter or cream, times/week >4 [≤4]	1.37 (1.17–1.59)	1.56 (1.34–1.81)	1.96 (1.60–2.41)
Sugary snacks/sweets, times/day <1 [≥1]	0.91 (0.78–1.06)	1.17 (1.00–1.35)	2.49 (2.04–3.03)
Sugary drinks, times/day <1 [≥1]	1.64 (1.44–1.87)	1.72 (1.50–1.96)	1.97 (1.63–2.38)
FGC pepper, times/week <5 [≥5]	1.00 (0.77–1.30)	0.93 (0.71–1.23)	2.42 (1.82–3.23)
DRC pepper, tablespoons/week <5 [≥5]	1.22 (0.93–1.59)	1.25 (0.96–1.66)	2.52 (1.87–3.39)
Fried foods, times/week ≤1 [>1]	1.20 (1.03–1.40)	1.46 (1.26–1.70)	1.13 (0.90–1.40)

Multinomial model among 7,841 MAUCO participants; data imputed with MICE (Multiple Imputation by Chained Equations); <sup>†</sup>Reference category was <1 time per week, including non-consumers; <sup>a</sup>≥3 drinks for women or ≥4 drinks for men per occasion; FGC, Fresh green chili; FRC, Fresh red chili; DRC, dried red chili.

this only for vegetables, and not for legumes, fish, seafood or avocados. This unexpected finding could be partially explained by the fact that in Chile men have a higher intake of legumes than women (28, 85), particularly in the Maule Region, which has the highest compliance with legume national recommendations (86) (≥2 times per week) (85). Additionally, although current recommendations advise against mixing legumes with processed meats, this is one of the most popular ways of consuming them in the country. The positive association of processed meat with fish and avocado in our study could be related to the higher price of these food items, considering that high processed meat consumers were more likely to be employed.

## Nutritional relevance of the findings and potential health impacts

Despite the fact that MAUCO participants are from a population with particularities in terms of location, exposures and sociodemographic changes, they have also been impacted by the so-called nutrition transition affecting the entire country. Although the direction of causation cannot be established in this study, the associations of higher processed meat consumption and chronic health conditions are in line with the international evidence, suggesting that a high consumption

could promote obesity and associated diseases. However, due to the cross-sectional nature of the study design and the potential confounding role of other dietary factors (69), the results should be interpreted carefully. The findings of this study contribute to a better understanding of other relevant factors that go along with the consumption of processed meat in this population, as well as a better comprehension of this exposure in Chile. This will be useful information for future regulation efforts.

## Strengths and limitations of the study

MAUCO is a Chilean cohort with a comprehensive and detailed measurement collection. At baseline, participants answered health and risk factor surveys (exploring diet, alcohol, physical activity and health history, among others) including adapted nationally and internationally validated instruments. MAUCO constitutes an opportunity to address specific health needs of Chile's population in the context of accelerated development and nutritional transition (87); hence, the information obtained from this study will also be relevant for other Latin American populations. The food frequency questionnaire used for the dietary assessment was elaborated from a Mediterranean

TABLE 6A Association of chronic diseases and processed meat consumption by obesity status in MAUCO participants.

	A	B	C	D	Prevalence Ratio (95% CI) <sup>†</sup>			
	High consumers with obesity <i>n</i> = 252	High consumers without obesity <i>n</i> = 317	Low consumers with obesity <i>n</i> = 1,572	Low consumers without obesity <i>n</i> = 2,508	A/B Obesity effect in high PMC	A/C PMC effect in obese	C/D Obesity effect in low PMC	B/D PMC effect in non-obese
Age, years, mean±SD	51.8 ± 10.0	52.5 ± 9.9	55.1 ± 9.4	54.7 ± 9.5				
Sex, women	52.8	46.1	65.1	60.1				
Schooling, years, mean±SD	8.7 ± 3.9	9.0 ± 3.7	8.2 ± 4.2	9.0 ± 4.1				
Current smoker	34.5	38.3	23.7	29.1				
Binge drinking <sup>a</sup>	21.4	26.8	15.5	15.8				
Hypertension <sup>b</sup> ( <i>n</i> = 2,457)	58.6	43.0	62.5	47.9	2.09 (1.47–3.00)	1.05 (0.80–1.39)	1.87 (1.63–2.15)	0.90 (0.70–1.16)
Diabetes <sup>c</sup> ( <i>n</i> = 735)	21.4	13.3	20.6	12.6	1.91 (1.20–3.03)	1.30 (0.94–1.80)	1.75 (1.47–2.08)	1.22 (0.85–1.75)
Cancer <sup>d</sup> ( <i>n</i> = 178)	3.6	2.5	3.8	4.1	1.50 (0.57–3.99)	1.22 (0.59–2.52)	0.87 (0.62–1.21)	0.68 (0.30–1.47)
Cardiovascular disease <sup>e</sup> ( <i>n</i> = 298)	15.5	12.7	10.1	6.3	1.40 (0.69–2.79)	2.03 (1.19–3.45)	1.58 (1.22–2.05)	2.42 (1.45–4.02)
Digestive symptoms <sup>f</sup> ( <i>n</i> = 1,912)	46.0	46.3	45.0	38.4	0.99 (0.95–1.03)	1.02 (0.96–1.08)	1.06 (1.01–1.10)	1.12 (1.03–1.20)
Non-infectious digestive diseases <sup>g</sup> ( <i>n</i> = 599)	11.1	11.4	11.6	14.1	0.93 (0.60–1.45)	1.03 (0.68–1.54)	0.82 (0.68–0.99)	0.88 (0.62–1.24)

Data presented as percent prevalence unless otherwise specified. Prevalences are unadjusted. <sup>†</sup>Prevalence ratio and 95% confidence intervals obtained by logistic regression are adjusted by age, sex, schooling, smoking and binge drinking. Obesity, body mass index >30 kg/m<sup>2</sup>; <sup>a</sup>≥3 drinks for women or ≥4 drinks for men per occasion; <sup>b</sup>use of hypotensive drugs or measured systolic blood pressure ≥130 mm Hg or diastolic blood pressure ≥80 mm Hg; <sup>c</sup>self-report or glycemia ≥126 mg/dL or use of hypoglycemic drugs; <sup>d</sup>self-reported; <sup>e</sup>self-reported: history considering heart disease, heart failure, stroke or other, and excluding hypertension; <sup>f</sup>biliary colic, gastroesophageal reflux and gastritis symptoms; <sup>g</sup>gastric ulcer, irritable bowel syndrome, inflammatory bowel disease or other. PMC, Processed meat consumption.

index (Chilean-MDI) with the advantage of being adapted and validated specifically for use in Chilean population (45).

Among the limitations of this study is that MAUCO is located in a Chilean agricultural county similar to the majority of small counties in the country but some results may not be applicable to residents of large urban areas in Chile (43). In addition, as the main objective of MAUCO is to study the natural history of chronic diseases in adult population from 38 years of age, the representativeness of the results in terms of processed meat intake is limited, as younger segments of the adult population were not included. With respect to diet, processed meat consumption was obtained in terms of weekly frequency, which is often accompanied with serving size estimations to have a better measurement of intake (88); we did not directly assess serving size, but we estimated it based on national nutrition surveys. Finally, being a cross-sectional analysis, it is not possible to

establish causal relationship and reverse causality cannot be ruled out.

Future directions of this study include prospectively evaluating the association of processed meat consumption with incidence of chronic conditions, and identifying mediators or potentiators of the damage.

In conclusion, in this population, in addition to male sex and lower age, high processed meat intake was associated with other foods consumed at frequencies considered unhealthy, and with risky alcohol intake, unhealthy weight, and chronic diseases, particularly cardiovascular disease. However, no association was found between self-reported cancer and processed meat. Since this cohort resides in a region with a high incidence rate for gastric cancer and one of the highest mortality rates for colon cancer, future prospective studies are warranted in order to assess this association.

TABLE 6B Mediation analysis of the relationship between processed meat consumption and chronic diseases using obesity as a mediator.

	Prevalence ratio (95% CI) <sup>†</sup>		ACME	ADE	Proportion mediated by obesity
	PMC→CD*	PMC→CD*			
	Obesity not in model	Obesity in model			
Hypertension <sup>a</sup> (n = 2,457)	1.02 (0.85–1.23)				
Diabetes <sup>b</sup> (n = 735)	1.32 (1.04–1.68)	1.28 (1.00–1.63)	0.00541	0.03348	13.9% (3.0–57.0%)
Cancer <sup>c</sup> (n = 178)	0.89 (0.53–1.51)				
Cardiovascular disease <sup>d</sup> (n = 298)	2.28 (1.58–3.29)	2.22 (1.54–3.21)	0.00399	0.07661	5.0% (0.8–12.0%)
Digestive symptoms <sup>e</sup> (n = 1,912)	1.07 (1.02–1.12)	1.07 (1.02–1.13)	0.00220	0.07000	3.0% (0.7–13.0%)
Non-infectious digestive diseases <sup>f</sup> (n = 599)	0.93 (0.71–1.21)				

Obesity, Body mass index >30 kg/m<sup>2</sup>. <sup>†</sup> Prevalence ratio and 95% confidence intervals obtained by logistic regression are adjusted by age, sex, schooling, smoking and binge drinking. \*Prevalence ratio for CD between high PMC and low PMC; <sup>a</sup> use of hypotensive drugs or measured systolic blood pressure ≥130 mm Hg or diastolic blood pressure ≥80 mm Hg; <sup>b</sup> self-report or glycemia ≥126 mg/dL or use of hypoglycemic drugs; <sup>c</sup> self-reported; <sup>d</sup> self-reported: history considering heart disease, heart failure, stroke or other, and excluding hypertension; <sup>e</sup> biliary colic, gastroesophageal reflux and gastritis symptoms; <sup>f</sup> gastric ulcer, irritable bowel syndrome, inflammatory bowel disease or other. PMC, Processed meat consumption; CD, Chronic disease; ACME, Average causal mediation effect; ADE, Average direct effect.

## Data availability statement

The datasets presented in this article are not readily available because they are available from the corresponding author upon reasonable request. Requests to access the datasets should be directed to CF, [cferrec@med.puc.cl](mailto:cferrec@med.puc.cl).

## Ethics statement

The studies involving human participants were reviewed and approved by the Ethics Committee of the School of Medicine at Pontificia Universidad Católica de Chile on 21 March 2019 (project 181010022). In addition, the MAUCO study protocol was approved by Ethics Committees at Pontificia Universidad Católica de Chile and the Maule Regional Service of the Chilean Ministry of Health. The patients/participants provided their written informed consent to participate in this study.

## Author contributions

JR: formal analysis, methodology, funding acquisition, investigation, and writing the manuscript. VC: data curation, formal analysis, and methodology. AH and VV: funding acquisition, investigation, and review & editing the manuscript. CV: formal analysis and methodology. CF: formal analysis, methodology, funding acquisition, investigation, supervision, review, and editing the manuscript. All authors contributed to the article and approved the submitted version.

## Funding

This research was funded by Fondo Nacional de Desarrollo Científico y Tecnológico (FONDECYT Postdoctoral), Grant

Number 3190842 and Fondo de Financiamiento de Centros de Investigación en Áreas Prioritarias (FONDAP) (Grant Number 15130011).

## Acknowledgments

The authors would like to thank the MAUCO study group, MAUCO collaborators and the daily work of the MAUCO field team. We thank Estela Blanco for manuscript edition and her valuable suggestions. We express our sincere gratitude to the MAUCO participants for their contribution to the study.

## 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.

## Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fpubh.2022.960997/full#supplementary-material>

## References

- World Cancer Research Fund/American Institute for Cancer Research. *Diet, Nutrition, Physical Activity and Cancer: A Global Perspective. Continuous Update Project Expert Report*. (2018). Available online at: <https://www.wcrf.org/diet-and-cancer/> (accessed July 20, 2022).
- GBD 2017 Diet Collaborators. Health effects of dietary risks in 195 countries, 1990–2017: a systematic analysis for the global burden of disease study 2017. *Lancet*. (2019) 393:1958–72. doi: 10.1016/S0140-6736(19)30041-8
- Rohrmann S, Overvad K, Bueno-de-Mesquita HB, Jakobsen MU, Egeberg R, Tjønneland A, et al. Meat consumption and mortality - results from the European prospective investigation into cancer and nutrition. *BMC Med*. (2013) 11:63. doi: 10.1186/1741-7015-11-63
- Zheng Y, Li Y, Satija A, Pan A, Sotos-Prieto M, Rimm E, et al. Association of changes in red meat consumption with total and cause specific mortality among US women and men: two prospective cohort studies. *BMJ*. (2019) 365:l2110. doi: 10.1136/bmj.l2110
- Micha R, Wallace SK, Mozaffarian D. Red and processed meat consumption and risk of incident coronary heart disease, stroke, and diabetes mellitus: a systematic review and meta-analysis. *Circulation*. (2010) 121:2271–83. doi: 10.1161/CIRCULATIONAHA.109.924977
- Bouvard V, Loomis D, Guyton KZ, Grosse Y, Ghisassi F, El Benbrahim-Tallaa L, et al. Carcinogenicity of consumption of red and processed meat. *Lancet Oncol*. (2015) 16:1599–600. doi: 10.1016/S1470-2045(15)00444-1
- Chen GC, Lv DB, Pang Z, Liu QF. Red and processed meat consumption and risk of stroke: a meta-analysis of prospective cohort studies. *Eur J Clin Nutr*. (2013) 67:91–5. doi: 10.1038/ejcn.2012.180
- Zhang S, Wang Q, He J. Intake of red and processed meat and risk of renal cell carcinoma: a meta-analysis of observational studies. *Oncotarget*. (2017) 8:77942–56. doi: 10.18632/oncotarget.18549
- Pouchieu C, Deschasaux M, Hercberg S, Druesne-Pecollo N, Latino-Martel P, Touvier M. Prospective association between red and processed meat intakes and breast cancer risk: modulation by an antioxidant supplementation in the SUVIMAX randomized controlled trial. *Int J Epidemiol*. (2014) 43:1583–92. doi: 10.1093/ije/dyu134
- Inoue-Choi M, Sinha R, Gierach GL, Ward MH. Red and processed meat, nitrite, and heme iron intakes and postmenopausal breast cancer risk in the NIH-AARP diet and health study. *Int J Cancer*. (2016) 138:1609–18. doi: 10.1002/ijc.29901
- Anderson JJ, Darwis NDM, Mackay DF, Celis-Morales CA, Lyall DM, Sattar N, et al. Red and processed meat consumption and breast cancer: UK Biobank cohort study and meta-analysis. *Eur J Cancer*. (2018) 90:73–82. doi: 10.1016/j.ejca.2017.11.022
- Ferro A, Rosato V, Rota M, Costa AR, Morais S, Pelucchi C, et al. Meat intake and risk of gastric cancer in the Stomach cancer Pooling (StoP) project. *Int J Cancer*. (2020) 147:45–55. doi: 10.1002/ijc.32707
- De Stefani E, Boffetta P, Ronco AL, Deneo-Pellegrini H, Correa P, Acosta G, et al. Processed meat consumption and risk of cancer: a multisite case-control study in Uruguay. *Br J Cancer*. (2012) 107:1584–8. doi: 10.1038/bjc.2012.433
- Händel MN, Rohde JF, Jacobsen R, Nielsen SM, Christensen R, Alexander DD, et al. Processed meat intake and incidence of colorectal cancer: a systematic review and meta-analysis of prospective observational studies. *Eur J Clin Nutr*. (2020) 74:1132–48. doi: 10.1038/s41430-020-0576-9
- Mehta SS, Arroyave WD, Lunn RM, Park YMM, Boyd WA, Sandler DP, et al. Prospective analysis of red and processed meat consumption and risk of colorectal cancer in women. *Cancer Epidemiol Biomarkers Prev*. (2019) 29:141–50. doi: 10.1158/1055-9965.EPI-19-0459
- Fan M, Li Y, Wang C, Mao Z, Zhou W, Zhang L, et al. Dietary protein consumption and the risk of type 2 diabetes: a dose-response meta-analysis of prospective studies. *Nutrients*. (2019) 11:2783. doi: 10.3390/nu1112783
- Pan A, Sun Q, Bernstein AM, Schulze MB, Manson JE, Willett WC, et al. Red meat consumption and risk of type 2 diabetes: 3 cohorts of US adults and an updated meta-analysis. *Am J Clin Nutr*. (2011) 94:1088–96. doi: 10.3945/ajcn.111.018978
- Sinha R, Cross AJ, Graubard BI, Leitzmann MF, Schatzkin A. Meat intake and mortality: a prospective study of over half a million people. *Arch Intern Med*. (2009) 169:562–71. doi: 10.1001/archinternmed.2009.6
- Larsson SC, Orsini N. Red meat and processed meat consumption and all-cause mortality: a meta-analysis. *Am J Epidemiol*. (2013) 179:282–9. doi: 10.1093/aje/kwt261
- Kim Y, Je Y. Meat consumption and risk of metabolic syndrome: results from the Korean population and a meta-analysis of observational studies. *Nutrients*. (2018) 10:390. doi: 10.3390/nu10040390
- Gallardo-Alfaro L, Bibiloni MDM, Mascaró CM, Montemayor S, Ruiz-Canela M, Salas-Salvadó J, et al. Leisure-time physical activity, sedentary behaviour and diet quality are associated with metabolic syndrome severity: the PREDIMED-plus study. *Nutrients*. (2020) 12:1013. doi: 10.3390/nu12041013
- Schwingshackl L, Schwedhelm C, Hoffmann G, Knüppel S, Iqbal K, Andriolo V, et al. Food groups and risk of hypertension: a systematic review and dose-response meta-analysis of prospective studies. *Adv Nutr*. (2017) 8:793–803. doi: 10.3945/an.117.017178
- Lajous M, Bijon A, Fagherazzi G, Rossignol E, Boutron-Ruault MC, Clavel-Chapelon F. Processed and unprocessed red meat consumption and hypertension in women. *Am J Clin Nutr*. (2014) 100:948–52. doi: 10.3945/ajcn.113.080598
- Johnston BC, Zeraatkar D, Han MA, Vernooij RWM, Valli C, El Dib R, et al. Unprocessed red meat and processed meat consumption: dietary guideline recommendations from the Nutritional Recommendations (NutriRECS) Consortium. *Ann Intern Med*. (2019) 171:756–64. doi: 10.7326/M19-1621
- Qian F, Riddle MC, Wylie-Rosett J, Hu FB. Red and processed meats and health risks: how strong is the evidence? *Diabetes Care*. (2020) 43:265–71. doi: 10.2337/dci19-0063
- World Cancer Research Fund International. *Red and Processed Meat Still Pose Cancer Risk, Warn Global Health Experts*. (2019). Available online at: <https://www.wcrf.org/latest/news-and-updates/red-and-processed-meat-still-poses-cancer-risk-warn-global-health-experts> (accessed August 1, 2021).
- GBD 2019 Risk Factors Collaborators. Global burden of 87 risk factors in 204 countries and territories, 1990–2019: a systematic analysis for the Global Burden of Disease Study 2019. *Lancet*. (2020) 396:1223–49. doi: 10.1016/S0140-6736(20)30752-2
- Kovalskys I, Rigotti A, Koletzko B, Fisberg M, Gómez G, Herrera-Cuenca M, et al. Latin American consumption of major food groups: Results from the ELANS study. *PLoS ONE*. (2019) 14:e0225101. doi: 10.1371/journal.pone.0225101
- Clonan A, Roberts KE, Holdsworth M. Socioeconomic and demographic drivers of red and processed meat consumption: implications for health and environmental sustainability. *Proc Nutr Soc*. (2016) 75:367–73. doi: 10.1017/S0029665116000100
- OECD. *Meat Consumption*. (2020). Available online at: <https://data.oecd.org/agroutput/meat-consumption.htm> (accessed September 1, 2021).
- Instituto Nacional de Estadísticas Chile. *Producción Pecuaria. Período 2008 – 2013 y primer semestre 2014*. (2013). Available online at: <https://inec.cl/> (accessed September 1, 2021).
- Llorca-Jaña M, Nazer R, Morales D, and Navarrete-Montalvo J. Milk and meat consumption and production in Chile, c. 1930–2017: a history of a successful nutrition transition. *Historia Agraria*. (2020) 82:1–40. doi: 10.26882/histagrar.082e051
- Ministry of Health & Government of Chile. *Survey of Food Consumption in Chile (ENCA)*. (2010). Available online at: <https://www.minsal.cl/encabasededatos/> (accessed October 1, 2021).
- GBD 2016 Causes of Death Collaborators. Global, regional, and national age-sex specific mortality for 264 causes of death, 1980–2016: a systematic analysis for the Global Burden of Disease Study 2016. *Lancet*. (2017) 390:1151–210. doi: 10.1016/S0140-6736(17)32152-9
- Bray F, Ferlay J, Soerjomataram I, Siegel RL, Torre LA, Jemal A. Global cancer statistics 2018: GLOBOCAN estimates of incidence and mortality worldwide for 36 cancers in 185 countries. *CA Cancer J Clin*. (2018) 68:394–424. doi: 10.3322/caac.21492
- Global Burden of Disease Cancer Collaboration, Fitzmaurice C, Akinyemiju TF, Al Lami FH, Alam T, Alizadeh-Navaei R, et al. Global, regional, and national cancer incidence, mortality, years of life lost, years lived with disability, and disability-adjusted life-years for 29 cancer groups, 1990 to 2016: a systematic analysis for the global burden of disease study. *JAMA Oncol*. (2018) 4:1553–68. doi: 10.1200/JCO.2018.36.15\_suppl.1568
- NCD Risk Factor Collaboration (NCD-RisC). Worldwide trends in diabetes since 1980: a pooled analysis of 751 population-based studies with 4.4 million participants. *Lancet*. (2016) 387:1513–30. doi: 10.1016/S0140-6736(16)0618-8
- Popkin BM, Reardon T. Obesity and the food system transformation in Latin America. *Obes Rev*. (2018) 19:1028–64. doi: 10.1111/obr.12694

39. Ferreccio C, Roa JC, Bambs C, Vives A, Corvalán AH, Cortés S, et al. Study protocol for the Maule Cohort (MAUCO) of chronic diseases, Chile 2014–2024. *BMC Public Health*. (2016) 16:122. doi: 10.1186/s12889-015-2454-2
40. Ministry of Health & Government of Chile. *Puesta Al Día De La Situación Epidemiológica Del Cáncer En Chile*. (2018). Available online at: <http://epi.minsal.cl/> (accessed December 1, 2021).
41. Ríos JA, Barake MF, Arce MJ, López-Köstner F, Labbe TP, Villena, J. Situación actual del cáncer de colon en Chile: una mirada traslacional. *Rev Med Chile*. (2020) 148:858–67. doi: 10.4067/S0034-98872020000600858
42. Palomo I, Icaza G, Mujica V, Núñez L, Leiva E, Vásquez M, et al. Prevalencia de factores de riesgo cardiovascular clásicos en población adulta de Talca, Chile, 2005. *Rev Med Chile*. (2007) 135:904–12. doi: 10.4067/S0034-98872007000700011
43. Ferreccio C, Huidobro A, Cortés S, Bambs C, Toro P, Van De Wyngaert V, et al. Cohort profile: the Maule Cohort (MAUCO). *Int J Epidemiol*. (2020) 49:760–61. doi: 10.1093/ije/dyaa003
44. Leighton F, Polic G, Strobel P, Pérez D, Martínez C, Vásquez L, et al. Health impact of Mediterranean diets in food at work. *Public Health Nutr*. (2009) 12:1635–43. doi: 10.1017/S136898009990486
45. Echeverría G, Urquiaga I, Concha MJ, Dussailant C, Villarroel L, Velasco N, et al. Validación de cuestionario autoaplicable para un índice de alimentación mediterránea en Chile. *Rev Med Chile*. (2016) 144:1531–43. doi: 10.4067/S0034-98872016001200004
46. Willett WC, Sacks F, Trichopoulos A, Drescher G, Ferro-Luzzi A, Helsing E, et al. Mediterranean diet pyramid: a cultural model for healthy eating. *Am J Clin Nutr*. (1995) 61:1402S–6S. doi: 10.1093/ajcn/61.6.1402S
47. Grundy SM, Brewer HB, Cleeman JI, Smith SC, Lenfant C. Definition of metabolic syndrome. *Circulation*. (2004) 109:433–8. doi: 10.1161/01.CIR.0000111245.75752.C6
48. Rumack C, Wilson S, Charboneau JW, Levine D. *Diagnostic Ultrasound*. Saunders, PA: General Adult (2014).
49. Marshall A, Altman DG, Holder RL, Royston P. Combining estimates of interest in prognostic modelling studies after multiple imputation: current practice and guidelines. *BMC Med Res Methodol*. (2009) 9:57. doi: 10.1186/1471-2288-9-57
50. Moons KG, Donders RA, Stijnen T, Harrell FE Jr. Using the outcome for imputation of missing predictor values was preferred. *J Clin Epidemiol*. (2006) 10:1092–101. doi: 10.1016/j.jclinepi.2006.01.009
51. Whitton C, Bogueva D, Marinova D, and Phillips CJC. Are we approaching peak meat consumption? Analysis of meat consumption from 2000 to 2019 in 35 countries and its relationship to gross domestic product. *Animals*. (2021) 11:3466. doi: 10.3390/ani11123466
52. Instituto Nacional de Estadísticas Chile. *Encuestas Intercensales Agropecuarias 2017–2018*. (2018). Available online at: <https://www.inec.cl/> (accessed August 1, 2021).
53. Ministry of Health Government of Chile - Department of Statistics and Information in Health. *Mortalidad por Causa, Según Sexo y Región*. (2019). Available online at: <https://deis.minsal.cl/> (accessed February 1, 2022).
54. Sych J, Kaelin I, Gerlach F, Wróbel A, Le T, FitzGerald R, et al. Intake of processed meat and association with sociodemographic and lifestyle factors in a representative sample of the Swiss population. *Nutrients*. (2019) 11:2556. doi: 10.3390/nu11112556
55. Diallo A, Deschasaux M, Latino-Martel P, Hercberg S, Galan P, Fassier P, et al. Red and processed meat intake and cancer risk: results from the prospective NutriNet-Santé cohort study. *Int J Cancer*. (2018) 142:230–7. doi: 10.1002/ijc.31046
56. Pot GK, Prynn CJ, Almoosawi S, Kuh D, Stephen AM. Trends in food consumption over 30 years: evidence from a British birth cohort. *Eur J Clin Nutr*. (2015) 69:817–23. doi: 10.1038/ejcn.2014.223
57. Birrell CL, Neale EP, Probst YC. Usual intake of meat in Australians: secondary analysis of the 2011–12 national nutrition and physical activity survey using the NCI method. *J Hum Nutr Diet*. (2020) 33:505–17. doi: 10.1111/jhn.12745
58. Zeng L, Ruan M, Liu J, Wilde P, Naumova EN, Mozaffarian D, and Zhang FF. Trends in processed meat, unprocessed red meat, poultry, and fish consumption in the United States, 1999–2016. *J Acad Nutr Diet*. (2019) 119:1085–98.e12. doi: 10.1016/j.jand.2019.04.004
59. de Carvalho AM, César CLG, Fisberg RM, Marchioni DM. Meat consumption in São Paulo-Brazil: trend in the last decade. *PLoS ONE*. (2014) 9:e96667. doi: 10.1371/journal.pone.0096667
60. Daniel CR, Cross AJ, Koebeck C, Sinha R. Trends in meat consumption in the USA. *Public Health Nutr*. (2011) 14:575–83. doi: 10.1017/S13689800100102077
61. Linseisen J, Kesse E, Slimani N, Bueno-De-Mesquita HB, Ocké MC, Skeie G, et al. Meat consumption in the European Prospective Investigation into Cancer and Nutrition. (EPIC) cohorts: results from 24-hour dietary recalls. *Public Health Nutr*. (2002) 5:1243–58. doi: 10.1079/PHN20020402
62. Lenighan YM, Nugent AP, Li KF, Brennan L, Walton J, Flynn A, et al. Processed red meat contribution to dietary patterns and the associated cardio-metabolic outcomes. *Br J Nutr*. (2017) 118:222–8. doi: 10.1017/S0007114517002008
63. Khandpur N, Cediel G, Obando DA, Jaime PC, Parra DC. Sociodemographic factors associated with the consumption of ultra-processed foods in Colombia. *Rev Saude Publica*. (2020) 54:19. doi: 10.11606/s1518-8787.2020054001176
64. Godfray H, Aveyard P, Garnett T, Hall JW, Key TJ, Lorimer J, et al. Meat consumption, health, and the environment. *Science*. (2018) 361:eam5324. doi: 10.1126/science.aa5324
65. Mann NJ. A brief history of meat in the human diet and current health implications. *Meat Sci*. (2018) 144:169–79. doi: 10.1016/j.meatsci.2018.06.008
66. Zhong VW, Van Horn L, Greenland P, Carnethon MR, Ning H, Wilkins JT, et al. Associations of processed meat, unprocessed red meat, poultry, or fish intake with incident cardiovascular disease and all-cause mortality. *JAMA Intern Med*. (2020) 180:503–12. doi: 10.1001/jamainternmed.2019.6969
67. Rouhani MH, Salehi-Arbargouei A, Surkan PJ, Azadbakht L. Is there a relationship between red or processed meat intake and obesity? A systematic review and meta-analysis of observational studies. *Obes Rev*. (2014) 15:740–8. doi: 10.1111/obr.12172
68. Echeverría G, McGee EE, Urquiaga I, Jiménez P, D'Acuña S, Villarroel L, et al. Inverse associations between a locally validated Mediterranean diet index, overweight/obesity, and metabolic syndrome in Chilean adults. *Nutrients*. (2017) 9:862. doi: 10.3390/nu9080862
69. Fogelholm M, Kanerva N, Männistö S. Association between red and processed meat consumption and chronic diseases: the confounding role of other dietary factors. *Eur J Clin Nutr*. (2015) 69:1060–5. doi: 10.1038/ejcn.2015.63
70. Gómez-Donoso C, Martínez-González MÁ, Martínez JA, Sayón-Orea C, de la Fuente-Arrillaga C, Bes-Rastrollo M. Adherence to dietary guidelines for the Spanish population and risk of overweight/obesity in the SUN cohort. *PLoS ONE*. (2019) 14:e0226565. doi: 10.1371/journal.pone.0226565
71. Noureddin M, Zelber-Sagi S, Wilkens LR, Porcel J, Boushey CJ, Le Marchand L, et al. Diet associations with nonalcoholic fatty liver disease in an ethnically diverse population: the multiethnic cohort. *Hepatology*. (2020) 71:1940–52. doi: 10.1002/hep.30967
72. Kim MN, Lo CH, Corey KE, Luo X, Long L, Zhang X, et al. Red meat consumption, obesity, and the risk of non-alcoholic fatty liver disease among women: evidence from mediation analysis. *Clin Nutr*. (2022) 41:356–64. doi: 10.1016/j.clnu.2021.12.014
73. Mendonça RD, Lopes ACS, Pimenta AM, Gea A, Martínez-González MA, Bes-Rastrollo M. Ultra-processed food consumption and the incidence of hypertension in a Mediterranean cohort: the seguimiento universidad de Navarra Project. *Am J Hypertens*. (2017) 30:358–66. doi: 10.1093/ajh/hpw137
74. Shimazu T, Kuriyama S, Hozawa A, Ohmori K, Sato Y, Nakaya N, et al. Dietary patterns and cardiovascular disease mortality in Japan: a prospective cohort study. *Int J Epidemiol*. (2007) 36:600–9. doi: 10.1093/ije/dym005
75. Grosso G, Micek A, Godos J, Pajak A, Sciacca S, Galvano F, et al. Health risk factors associated with meat, fruit and vegetable consumption in cohort studies: a comprehensive meta-analysis. *PLoS ONE*. (2017) 12:e0183787. doi: 10.1371/journal.pone.0183787
76. Fung TT, Schulze M, Manson JE, Willett WC, Hu FB. Dietary patterns, meat intake, and the risk of type 2 diabetes in women. *Arch Intern Med*. (2004) 164:2235–40. doi: 10.1001/archinte.164.20.2235
77. Pestoni G, Riedl A, Breuninger TA, Wawro N, Krieger JP, Meisinger C, et al. Association between dietary patterns and prediabetes, undetected diabetes or clinically diagnosed diabetes: results from the KORA FF4 study. *Eur J Nutr*. (2020) 60:2331–41. doi: 10.1007/s00394-020-02416-9
78. Medina-Remón A, Kirwan R, Lamuela-Raventós RM, Estruch R. Dietary patterns and the risk of obesity, type 2 diabetes mellitus, cardiovascular diseases, asthma, and neurodegenerative diseases. *Crit Rev Food Sci Nutr*. (2018) 58:262–96. doi: 10.1080/10408398.2016.1158690
79. Monteiro CA, Cannon G, Levy RB, Moubarac JC, Louzada ML, Rauber F, et al. Ultra-processed foods: what they are and how to identify them. *Public Health Nutr*. (2019) 22:936–41. doi: 10.1017/S1368980018003762
80. Fiolet T, Srour B, Sellem L, Kesse-Guyot E, Allès B, Méjean C, et al. Consumption of ultra-processed foods and cancer risk: results from NutriNet-Santé prospective cohort. *BMJ*. (2018) 360:k322. doi: 10.1136/bmj.k322
81. Kappeler R, Eichholzer M, Rohrmann S. Meat consumption and diet quality and mortality in NHANES III. *Eur J Clin Nutr*. (2013) 67:598–606. doi: 10.1038/ejcn.2013.59



82. Wang D, Karvonen-Gutierrez CA, Jackson EA, Elliott MR, Appelhans BM, Barinas-Mitchell E, et al. Western dietary pattern derived by multiple statistical methods is prospectively associated with subclinical carotid atherosclerosis in midlife women. *J Nutr.* (2020) 150:579–91. doi: 10.1093/jn/nxz270
83. Chopan M, Littenberg B. The association of hot red chili pepper consumption and mortality: a large population-based cohort study. *PLoS ONE.* (2017) 12:e0169876. doi: 10.1371/journal.pone.0169876
84. Bonaccio M, Di Castelnuovo A, Costanzo S, Ruggiero E, De Curtis A, Persichillo M, et al. Chili pepper consumption and mortality in Italian adults. *J Am Coll Cardiol.* (2019) 74:3139–49. doi: 10.1016/j.jacc.2019.09.068
85. Ramírez-Alarcón K, Labraña AM, Martorell M, Martínez-Sanguinetti MA, Nazar G, Troncoso-Pantoja C, et al. Caracterización del consumo de legumbres en población chilena: resultados de la Encuesta Nacional de Salud 2016-2017. *Rev Med Chile.* (2021) 149:98–707. doi: 10.4067/s0034-98872021000500698
86. Olivares S, Zacarías I, González CG, Villalobos E. Proceso de formulación y validación de las guías alimentarias para la población chilena. *Rev chil nutr.* (2013) 40:262–8. doi: 10.4067/S0717-75182013000300008
87. Albala C, Vio F, Kain J, Uauy R. Nutrition transition in Chile: determinants and consequences. *Public Health Nutr.* (2002) 5:123–8. doi: 10.1079/PHN2001283
88. Shim JS, Oh K, Kim HC. Dietary assessment methods in epidemiologic studies. *Epidemiol Health.* (2014) 36:e2014009. doi: 10.4178/epih/e2014009





## OPEN ACCESS

## EDITED BY

Ian Givens,  
University of Reading, United Kingdom

## REVIEWED BY

Paolo Silacci,  
Agroscope, Switzerland  
Patrick Tounian,  
Hôpital Armand Trousseau, France

## \*CORRESPONDENCE

Susan Fairweather-Tait  
✉ s.fairweather-tait@uea.ac.uk

## SPECIALTY SECTION

This article was submitted to  
Product Quality,  
a section of the journal  
Frontiers in Animal Science

RECEIVED 11 January 2023

ACCEPTED 04 April 2023

PUBLISHED 19 April 2023

## CITATION

Fairweather-Tait S (2023) The role of meat  
in iron nutrition of vulnerable groups of the  
UK population.  
*Front. Anim. Sci.* 4:1142252.  
doi: 10.3389/fanim.2023.1142252

## COPYRIGHT

© 2023 Fairweather-Tait. This is an open-  
access article distributed under the terms of  
the [Creative Commons Attribution License](#)  
(CC BY). The use, distribution or  
reproduction in other forums is permitted,  
provided the original author(s) and the  
copyright owner(s) are credited and that  
the original publication in this journal is  
cited, in accordance with accepted  
academic practice. No use, distribution or  
reproduction is permitted which does not  
comply with these terms.

# The role of meat in iron nutrition of vulnerable groups of the UK population

Susan Fairweather-Tait\*

Norwich Medical School, University of East Anglia, Norwich, Norfolk, United Kingdom

Iron deficiency is a common public health problem in the UK. This review examines the role of meat in iron nutrition, focusing on the most vulnerable groups of the UK population. Meat contains haem iron which is absorbed by a different pathway to non-haem iron found in cereals and vegetables. A summary of absorption data from studies using isotopically-labelled haem iron shows that, although there is a wide degree of variation, haem iron bioavailability is consistently higher than non-haem iron. The importance of meat alternatives, such as plant protein, insects, and biofortified crops as a supply of bioavailable iron, and the use of food iron fortification is reviewed. Finally, the consequences of excluding meat from the diet in relation to dietary iron requirements is discussed.

## KEYWORDS

iron deficiency, iron intake from meat, iron bioavailability, meat alternatives, haem iron

## Introduction

Iron deficiency is a long-standing public health problem in the UK, especially in teenage girls, women of child-bearing age, and elderly men and women ([Public Health England, 2020](#)). Low iron stores are quite common, especially in teenage girls, and a smaller number have iron deficiency anaemia caused by an imbalance between dietary iron supply and physiological requirements. Approximately one fifth of the UK daily intake of iron in adults is provided from meat and meat products. Meat is also considered to be an important source of iron because it contains haem iron which is more bioavailable than non-haem iron from plants, and it enhances non-haem iron absorption from foods consumed at the same meal. On the other hand, meat is reported to have adverse effects on human health, although the impact of different types and quantities of meat is somewhat controversial ([Johnston et al., 2019](#)). In relation to iron nutrition, the consequences of avoiding meat have been examined by measuring the iron status of vegetarians and vegans, but confounding is a well-known weakness of cross-sectional data. Randomised controlled trials provide evidence of causality, but interventions have to be long enough in duration to enact a change in iron status, therefore data of this type are very limited. The drive to consume less meat, for environmental, health, economic and other reasons, has led to a growing number of meat replacement products entering the market. These include protein sources derived from soy and other plants, as well as traditional

foods that are novel to the UK, such as insects. Globally, a number of iron-biofortified staple crops have been developed, including beans, cereals and potatoes, and these are being introduced into agricultural practice. However, the problem of low iron bioavailability in high phytate/polyphenol foods remains a practical constraint, and dietary advice to improve iron bioavailability is needed to ensure that iron deficiency does not become widespread in children and women who consume meat-free diets.

## Iron deficiency in the UK

Population groups that are at risk of iron deficiency include infants (over 6 months of age), toddlers and young children, adolescents, women of child-bearing age, and pregnant women. The reasons for their vulnerability are the high iron requirements for growth and, in the case of women, losses associated with menstruation and/or the demands of pregnancy. According to the latest figures available from the National Diet and Nutrition Survey (Public Health England, 2020) low haemoglobin concentrations, indicative of anemia, are present in 9% of girls aged 11-18 years, 7% of women aged 18-64 years, and 17% of men and women over 65 years (Table 1). A higher percentage of girls and women have low iron stores (low plasma ferritin), 24% in girls aged 11-18 years, and 15% in women aged 18-64 years, but only 2% of the elderly have a low plasma ferritin concentration. There are two possible explanations for the apparent discordance in the elderly: either iron deficiency is not the cause of anaemia, or ferritin (an acute phase protein) may be raised due to chronic inflammation (as often found in older people) and therefore does not accurately reflect iron stores.

## Contribution of meat to the iron intake of vulnerable groups of the UK population

The NDNS shows that between 2008 and 2019 there was a small reduction in iron intakes in all age groups except men aged 75 years and over. The greatest reduction was in girls aged 4-10 years (-1.4 mg/d), boys aged 11-18 years (-1.1 mg/d), men aged 65-74 years (-1.1 mg/d), and women aged 75 years and over (-1.5 mg/d).

The sources of dietary iron by food group are shown in Figure 1 for adults aged 19-65 years. Cereals made the greatest contribution to total iron intake (37-53%, depending on age group), with high fibre breakfast cereals, some of which are fortified with iron, contributing 8-15%, followed by meat and meat products (14-19%, depending on age group). The food group entitled 'beef, veal and dishes' contribute one quarter, and 'chicken, turkey and dishes' contribute another quarter of the iron intake from meat in most age groups. Burgers, kebabs and sausages were consumed in higher amounts in children and teenagers, whereas older people tended to consume more meat pies and pastries. Median consumption of red and processed meat was significantly lower in 2016-2019 than 2014-2016 for men aged 19-64 years and adults aged 65 years and over. Since 2008, there has been a reduction in mean meat consumption in all age groups of 13 g/day, 23 g/day and 19 g/day for ages 11-18 years, 19-64 years and 65 years and over, respectively. The latest data shows that mean consumption in all age or sex groups met the UK recommendation of no more than 70g per day (Scientific Advisory Committee on Nutrition, 2010).

## Iron content of meat

It is generally assumed that 40% of the total iron in meat is in the form of haem iron (Monsen et al., 1978; Monsen and Balintfy, 1982), but the haem iron content of meat is, in fact, very variable, depending on the origin of the meat, and the method of cooking (Gandemer et al., 2020). Pretorius et al. (2016) reported values for the iron content of pooled samples of raw homogenized muscle from carcasses of 4 types of meat. The total haem iron content (mg/100 g fresh weight) for lamb, beef, pork and chicken was 1.32, 1.21, 0.71 and 0.58 mg/100g respectively, with haem iron (%) being reported to be 81, 77, 88 and 74% of total iron respectively. Lombardi-Boccia et al. (2002) analyzed the haem and non-haem iron content of a range of different meats before and after cooking (Table 2). The haem iron content was highest in beef, followed by lamb, pork and chicken. When chicken and turkey were cooked in the oven at 180°C for 50 min, there was a substantial loss of haem iron, ranging from 22-43%. In contrast, when cooked in a pan, the losses were lower, ranging from 1-24%. The decrease in haem iron is the result of the oxidative cleavage of the porphyrin ring which releases iron from the haem complex, which may only occur at relatively high temperatures i.e. above 85°C (Han et al., 1993).

TABLE 1 Haemoglobin (Hb) and plasma ferritin (PF) concentrations in different age groups (NDNS years 7-8, 2014/15-2015/16) .

Age (y)	Mean Hb (SD) g/L	% below threshold	Mean PF (SD) µg/L	% below threshold
4-10	128 (7.8)	3	31 (23.9)	9
11-18 (M)	144 (9.7)	1	57 (53.5)	2
11-18 (F)	132 (11.7)	9	28 (17.0)	24
19-64 (M)	149 (11.3)	3	153 (164.2)	1
19-64 (F)	133 (9.8)	7	59 (51.5)	15
65+	136 (13.4)	17	149 (134.9)	2

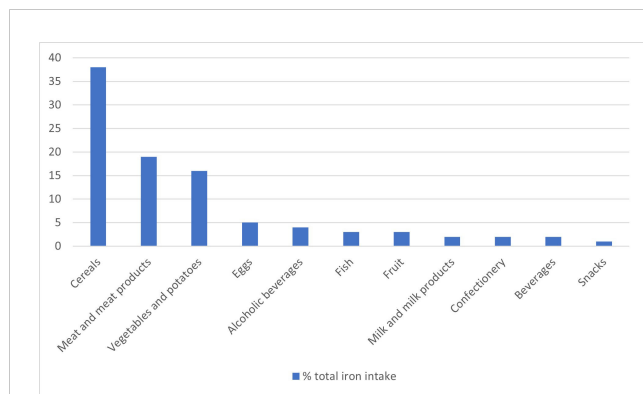


FIGURE 1

Contribution of food groups to total dietary intake of iron.

Pourkhalili et al. (2013) examined the effect of different cooking methods on the haem iron content of lamb meat. The lean raw meat was boiled at 97°C for 90 min, pan fried in oil for 20 min (internal temperature 85°C), or grilled above a flame for 10 min (internal temperature not higher than 86°C). The greatest losses occurred with boiling, and lowest losses were with grilling. An important finding from this study was that the four analytical methods, modified from Hornsey (1956), used to measure haem iron gave different results, and the authors concluded that a haem extraction solution comprised of 90% acetone, 18% water and 2% hydrochloric acid was the most appropriate because it correlated better with results for haem iron content calculated from the difference between total iron and non-haem iron.

Gel filtration can be used to examine the distribution of iron compounds in raw meat. Clement et al. (1972) examined different types of raw meat and found that beef steak had a higher iron concentration (30 µg/g) than chicken (4.7 µg/g in breast compared with 9.0 µg/g in leg meat, which contains more myoglobin). Apart from haemoglobin and myoglobin, the other main component is ferritin (beef steak, chicken breast and chicken leg contain 3.6, 2.4 and 1.9 µg/g respectively). In veal muscle, 15–20% of the total iron was reported to be present as ferritin (Layrisse, 1973). In addition to haem iron in haemoglobin and myoglobin, ferritin, haemosiderin, and a small quantity of low molecular weight iron compounds, are

present in meat (Latunde-Dada and Neale, 1986). The % of total iron present as haem in beef, lamb, pork and chicken were reported to be 77, 68, 55 and 42%, respectively. In pigeon, haem iron was 79% and 45% of total iron in breast meat and liver respectively, ferritin was 6% and 26% of total iron in breast meat and liver respectively, and haemosiderin was 14% and 25% of total iron in breast meat and liver respectively. As with haem iron, cooking changes the bioavailability of other forms of iron in meat, presumably through changes in both the solubility and composition of the different iron compounds (Latunde-Dada and Neale, 1986), therefore data obtained from raw meat is of limited use when predicting the potential contribution of different types of meat to iron nutrition.

It is important to take into account haem iron intake when assessing the impact of diet in relation to risk of iron deficiency because of its higher bioavailability (see following section). However, this is a challenging task due to the lack of analytical data on the haem iron content of foods and the discrepancy in quoted values. The haem iron values proposed by Monsen et al. (1978) and Monsen (1988) were 30–40% of iron in pork and liver, and 50–60% in beef, lamb and chicken. Schriker et al. (1982) quote 49%, 57% and 62% in pork, lamb and beef respectively. In addition, the haem iron content can vary between muscles in the same animal and according to the cooking method used (Schriker et al., 1982). In view of the lack of data on haem iron in meat, Cross et al. (2012) developed a haem iron database based on meat type, cooking method and doneness level. Meats with the highest level of haem iron, regardless of cooking method, were hamburgers (mean 10.3 µg/g) and steak (mean 9.3 µg/g). Pork had values in the range of 3.4–7.5 µg/g. Chicken had the lowest haem values but varied according to the cut of meat (mean for chicken breast 2.4 µg/g). The method used to measure total iron was inductively coupled plasma-atomic emission spectrometry (ICP-AES). Haem iron was extracted with acidified acetone (Hornsey, 1956) and analyzed by flame atomic absorption spectrometry. The remaining solid material was subjected to a total acid digestion and analyzed by ICP-AES to provide the non-haem iron. Interestingly, there was no clear effect of cooking method on haem iron, as has been reported previously. However, the extraction solution for haem iron (acetone:H<sub>2</sub>O:HCl) was 80:10:10, which differed from the 90:18:2 composition recommended by Pourkhalili et al. (2013), and the absence of certified reference materials introduces some uncertainty in the data.

TABLE 2 Haem and non-haem iron content (mg/100g) of different types of cooked meat (Lombardi-Boccia et al 2002).

Meat	Total iron	Haem iron
Beef sirloin	3.59	2.64
Lamb chop	3.20	2.25
Veal fillet	1.58	1.33
Pork chop	0.79	0.56
Chicken leg	1.20	0.42
Rabbit	0.60	0.31
Pork loin	0.46	0.21
Chicken breast	0.58	0.16

## Iron absorption from meat

Dietary iron is predominantly inorganic (non-haem) iron which has a well-established mechanism of absorption; ferric iron in the digestate is reduced to ferrous iron, transported across the apical membrane of the intestinal enterocyte by divalent metal-ion transporter 1 (DMT1), and either stored as ferritin in the cell or exported to the circulation *via* ferroportin 1 (FPN1) where it binds to plasma transferrin (Anderson and Frazer, 2017). Meat contains haem iron, either as haemoglobin in red blood cells or myoglobin in muscle cells, comprised of one ferrous atom bound to four globin

molecules. Meat also contains variable amounts of ferritin and haemosiderin, both of which are less well absorbed than haem iron (Martínez-Torres et al., 1976). As is the case with non-haem iron, the efficiency of absorption of iron from ferritin is inversely related to iron status; mean absorption of radio-isotopically ferritin iron was 0.9% in normal subjects, 2.5% in subjects with moderate iron deficiency, and 5.7% in subjects with marked iron deficiency (Layrisse et al., 1975).

## Haem iron absorption

The mechanism of absorption of haem iron has not yet been fully characterized (Fairweather-Tait and Sharp, 2021). It is believed to bind to the enterocyte brush border intact and then endocytosed, although the molecular details of the process are unknown, and the possibility of a haem transporter cannot be discounted. Within the enterocyte the iron is released from haem through the action of heme oxygenase and is either stored as ferritin or exported from the cells *via* FPN1 i.e. by the same pathway as non-haem iron (Anderson and Frazer, 2017). There are a limited number of studies investigating haem iron absorption, the majority of which were carried out several decades ago. The main limitation is that the iron has to be isotopically labelled with radio- or stable isotopes of iron in order to undertake metabolic studies.

Although the findings from different studies cannot be directly compared, an overview of the data generated from the studies undertaken using radio-isotopically labelled haem iron is given in Table 3. There is an inverse relationship between dose of haem iron and percentage absorption. Pizarro et al. (2003) reported that the absorption of radio-isotopically labelled haem iron by healthy women was both dose-related and saturable over the range tested (0.5–100 mg). At levels of haem iron typically found in a portion of meat (approximately 1 mg), mean absorption ranges from 20.7–37.3%, but at higher intakes (e.g. 5–10 mg iron) the efficiency of absorption is greatly reduced i.e. 11–16%.

As with non-haem iron, the iron status of individuals (often categorized according to serum ferritin concentration) affects iron absorption. Haem iron absorption from a burger and chips meal containing 1.2 mg radio-isotopically labelled haem iron was inversely correlated to serum ferritin concentration, with mean values of 22–25% in 57 healthy men and women (Roughead and Hunt, 2000). Haem iron absorption is upregulated when iron requirements are raised, as occurs in iron deficiency, although to a much lesser extent than non-haem iron (Cook, 1990). A summary is provided by Cook (1990) for a large set of data obtained from studies measuring haem and non-haem iron absorption from a hamburger, french fries and a milk shake meal (containing 1.4 mg haem iron and 3.4 mg non-haem iron), the two forms of iron being labelled with different radioisotopes of iron. Iron replete men absorbed 2.5% of non-haem iron compared with 26% of haem iron. However, when iron stores were depleted, absorption increased nearly 10-fold (increased to 22%) for non-haem iron, whereas haem iron absorption only doubled (increased to 47%), indicating that the adaptive response for non-haem iron is much greater than for haem iron.

As discussed earlier, cooking changes the forms of iron in meat, and the method used impacts on iron bioavailability. For example, absorption of haem iron from radio-isotopically labelled beef was 23.4 (SEM 1.0)% but when it was fried, the value fell to 19.4 (SEM 1.2)%, and when it was overcooked absorption fell to 14.5 (SEM 1.2)% (Martínez-Torres et al., 1986).

Haem iron absorption is around 50% lower when the globin chains are removed during digestion (Turnbull et al., 1962). One possible explanation is that the released heme polymerises into large aggregates that are poorly soluble at physiological pH (Gaitán et al., 2011). Haem iron is better absorbed with food than on its own (Table 3) which may be because peptides released from food bind the liberated haem to form monomeric haem products that are readily absorbed by the mucosal cells (Conrad et al., 1966).

When deriving Dietary Reference Values (DRVs) for iron, EFSA reviewed studies on haem iron absorption in whole diets and cited the study by (Hallberg et al., 1997) in which radio-isotopically labelled rabbit haemoglobin was used to label four high bioavailability meals per day (total iron intake 13 mg/day) for five days. The mean absorption of haem iron was 35% in 12 male blood donors and 23% in 19 non-blood donors, with an overall absorption of 28.6% (Table 3). EFSA used this and other evidence to reach a conclusion that the absorption of haem iron from a Western-style diet is approximately 25% (EFSA NDAPanel, 2015).

## Effect of meat on non-haem iron absorption

A number of dietary components influence the bioavailability of non-haem iron, either positively or negatively. The most common mechanism is chemical binding between the constituent and iron released from digested food, which either prevents iron from being taken up by the iron transporter protein in the duodenal mucosal cells (reducing bioavailability), or prevents iron from forming insoluble hydroxides with the increase in pH in the duodenum (increasing bioavailability). A recently conducted literature search listed inhibitors of absorption as phytic acid/phytates, polyphenols/tannins, proteins from soya beans, milk, eggs and calcium, and enhancers as ascorbic acid, lactic acid, alcohol (which stimulates iron uptake by inhibition of hepcidin expression), the presence of haem iron, and the so-called 'meat factor' in flesh from mammals, birds and fish, (Milman, 2020).

The enhancing effect of meat on non-haem iron absorption has been known for many years and this attribute has been used, for example, as a strategy to optimize iron absorption in children (Etcheverry et al., 2006). Cook and Monsen (1976) found that substituting egg ovalbumin in a semi-synthetic meal with beef, lamb, pork, chicken, liver and fish caused a two to four-fold increase in iron absorption by human volunteers, whereas no increase was observed with milk, cheese, or egg. Hurrell et al. (2006) reported that freeze-dried beef and chicken muscle increased iron absorption by 180% and 100%, respectively, relative to egg albumin, and suggested that the enhancing effect of muscle tissue on iron absorption was mainly protein related. A recent scoping review

TABLE 3 Absorption of isotopically-labelled haem iron.

Dose	Format	Subjects	% absorption	Reference
0.5 mg	Rabbit <sup>a</sup> rbc (capsules)	13F	<sup>b</sup> 31.1	Gaitán et al., 2012
10 mg			16.4	
20 mg			14.5	
50 mg			5.8	
8 mg	Pork	11F	50.1 ± 14.8	Young et al., 2010
5 mg	Rabbit rbc (capsules)	15F	<sup>b</sup> 13.9 (8.7-22.1)	Gaitán et al., 2011
5mg		11F	11.1 (6.2-19.8)	
0.7 mg	Beefburger, bun, fries, apple juice	6M, 6F	<sup>c</sup> 22 (20, 25)	Roughead et al., 2005
0.5mg	Rabbit rbc (capsules)	14F	<sup>c</sup> 27.1 (22.4-32.7)	Pizarro et al., 2003
3 mg			13.2 (11.6-15.0)	
15 mg			14.6 (13.3-16.0)	
30 mg			7.4 (5.6-9.8)	
1.2 mg	Beefburger, bun, fries, milk shake, tomato ketchup	27M, 30F	<sup>b</sup> 25(18-34)	Roughead and Hunt, 2000
1.8 mg	5 days of high iron bioavailability meals	31M	28.6 (14.9-43.5)	Hallberg et al., 1997
1.1 mg	Hamburger (115 g beef), roll, fries, milkshake	6M, 4F	22.1	Hallberg et al., 1993
1.4 mg	Hamburger (113 g beef),	100M	20.6	Lynch et al., 1989
	roll, fries, milkshake	30F	31.6	
0.28 mg	Potato, gravy, rabbit rbc	9F	<sup>b</sup> 20.6 (15.5-27.4)	Bezwooda et al., 1983
1.12 mg		9F	19.0 (14.2-25.3)	
2.24 mg		8F	19.6 (14.4-26.8)	
4.48 mg		8F	19.5 (14.2-26.8)	
1.0 mg	Lunch and dinner, rabbit haemoglobin	8M	37.3 (SEM 2.8)	Björn-Rasmussen et al., 1974
0.5 mg	Veal hamburger	6M, 6F	20.72	Layrisse et al., 1973
		9M, 4F	17.95	
2-3 mg	Veal hamburger	4M, 7F	<sup>c</sup> 23.2 (19.9-26.9)	Layrisse et al., 1975
2-4 mg	Veal hamburger	64M, 43F	<sup>b</sup> 21.5 (13.4-34.4)	Martínez-Torres et al., 1976
3 mg	Haemoglobin	5M, 6F	12.0 (6.9-20.9)	

<sup>a</sup>Red blood cells.<sup>b</sup>Geometric mean (-SD, +SD).<sup>c</sup>Geometric mean (-SE, +SE).

that systematically mapped studies on the meat factor (Consalez et al., 2022) concluded from data extracted from 77 eligible studies that the addition of muscle tissue and muscle tissue fractions to single plant-based meals steadily increased absorption of iron. There were no clear differences between red meat, poultry and fish in promoting the meat factor effect, and no evidence that milk and egg products contain the meat factor.

Attempts to fully characterise the meat factor (or factors) have been unsuccessful to date. In addition to the well-known gastric acid-promoting effect of meat (McArthur et al., 1988), proposed candidates include amino acids (Martínez-Torres and Layrisse, 1970), peptides (Taylor et al., 1986; Hurrell et al., 2006), and protein hydrolysates (Li et al., 2017). Evidence from *in vitro* Caco-2 cell studies suggest that glycosaminoglycans (GAG) may

enhance non-haem iron bioavailability (Huh et al., 2004). However, an *in vivo* stable isotope study investigating the effect of GAG (3-10 times the quantity present in 150 g beef muscle) from fish and chicken muscle reported that it had no effect on iron absorption from a semi-synthetic meal of egg albumin, corn oil, maltodextrin and water. Using an initial *in vitro* screening approach, Armah et al. (2008) separated fractions from cooked beef after it had undergone simulated gastric and intestinal digestion and tested their effect on iron uptake into Caco-2 cells using an <sup>55</sup>Fe label. Mass spectrometric techniques were used to identify the active fractions, and L-alpha-glycerophosphocholine (L-alpha) was found to be the compound present in the most active fraction. The effect of L-alpha on iron absorption *in vivo* was determined in a human stable isotope study measuring non-heme iron absorption



from 2 meals of vegetarian lasagne, each containing 10 mg iron. Absorption was significantly increased from 3.4% to 5.6% by the addition of 100mg ascorbic acid to the meal, and from 3.5% to 4.9% by the addition of 46 mg L-alpha to the meal. However, in a different study, the enhancing effect of L-alpha was not observed when 70 mg L-alpha was added to maize porridge, although ascorbic acid did increase iron absorption (Troesch et al., 2009). Although phospholipids might have an enhancing effect on non-heme iron absorption, it is clear that there is no single component of meat that can be identified as the meat factor, and that the enhancing effect of meat on non-haem iron absorption is probably a combination of factors.

## The potential contribution of meat alternatives and fortified/biofortified plant foods towards iron nutrition

Alternatives to meat, such as the soy protein Tofu, have been consumed as traditional foods for a long time, and more recently, other meat alternatives, including textured vegetable protein and mycoprotein (Quorn) have entered the market (Thavamani et al., 2020). The acknowledgement that diets containing high intakes of meat have a negative impact on the environment and adverse consequences for human health (Godfray et al., 2018) has stimulated the search for alternative sources of protein to replace meat. Many plant-based meat alternatives have been developed in recent years, including cultured meat, plant protein concentrates, and insect products. Iron is one of the key nutrients in meat and although some plant-based meat analogues are reported to have a higher content of iron than meat (Bryngelsson et al., 2022) others may not (Ismail et al., 2020), and, in fact, the bioavailability of iron is the overriding factor when assessing the quality of a meat alternative in relation to iron nutrition.

Phytate, widely found in plant foods but not meat, dramatically reduces iron absorption; many high iron plant foods, such as pulses, wholegrains and some green leafy vegetables (kale, spinach) contain high levels of phytate (Milman, 2020). An example of a novel plant protein that contains high levels of both iron and phytate is duckweed (*Wolffia globosa*), a traditional food consumed in Asian countries. A human intervention study in healthy men and women, in which diets containing duckweed were consumed for 6 months, reported no detrimental effect on iron status (Yaskolka Meir et al., 2019). Duckweed is currently under consideration for approval as a novel food by the Advisory Committee on Novel Foods and Processes ([https://acnfp.food.gov.uk/ACNFPMeeting\\_June2021](https://acnfp.food.gov.uk/ACNFPMeeting_June2021)).

Like many plant foods, edible insects have a lower ecological footprint than meat, and are an alternative to meat as they contain high levels of protein and iron. Iron occurs predominantly in non-haem forms, bound to ferritin and transferrin and other transport and storage proteins (Mwangi et al., 2018). In a stable isotope absorption study undertaken in iron-depleted women, Mwangi et al. (2022) found that iron absorption from intrinsically labelled house crickets (*Acheta domesticus*) added to maize porridge was low (~3%) which they suggested might be due to the presence of chitin

and other inhibitors in the cricket biomass. A study of similar design examined iron absorption from mealworm larvae (*Tenebrio molitor*) and found it was similar to maize porridge (~5%); processing of the *T. molitor* biomass to reduce the chitin content did not increase iron bioavailability (Hilaj et al., 2022). The authors conclude that *T. molitor* iron is absorbed from the common nonheme iron pool and could therefore be a useful source of dietary iron.

One of the strategies for addressing the long-standing global problem of iron deficiency has been food iron fortification, but there have been several technical challenges, notably the low bioavailability of iron compounds that can be added to foods without causing adverse organoleptic changes (Hurrell, 2022). Micronutrient deficiencies and the move towards lower meat consumption have led to the development of breeding programmes for biofortified staple food crops. The goal is to generate food crops with a higher iron content, although bioavailability is another important consideration (La Frano et al., 2014). It has been shown, for example, that the phytic acid content of plant foods such as biofortified beans has a strongly negative impact on iron absorption (Petty et al., 2014). Absorption from biofortified purple potatoes was lower than from biofortified yellow potatoes, presumably because of the presence of polyphenols which inhibit iron absorption. Conversely, the absorption of iron from biofortified sweet potatoes, which do not contain phytate or polyphenols, was high (Jongstra et al., 2020).

## Vegetarian and vegan diets

Iron is listed as one of the nutrients of concern in a plant-based diet (Craig et al., 2021). A systematic review of the intake and adequacy of vegan diets was recently published (Bakaloudi et al., 2021) and, in general, the intake of iron in vegan diets is no lower than other categories of diet, presumably because of the high iron content of widely consumed vegan foods such as green-leafy vegetables, grains, nuts and beans. Neufingerl and Eilander (2021) undertook a systematic review and analysed data from 38 studies that reported on iron intake (30 assessed intake from foods only). The mean iron intake was higher in vegans (21.0 mg/d) compared to vegetarians (15.3 mg/d) and meat eaters (13.9 mg/d), independent of supplement intake. Fabricius et al. (2021) used a risk-benefit assessment approach to estimate the health impact of substituting unprocessed red meat by pulses in the Danish diet, including the impact of substitution on adequacy of iron intake. There was a small decrease in the proportion of individuals below the average requirement in men and post-menopausal women (men: 32–30%), women >51: 35–33%), but no change for menstruating women (women <52: 75%); no predictions were made about changes in iron status, which would, of course, be an extremely challenging task because of the overriding effect of bioavailability. A modelling study on the unintended consequences of switching from animal- to plant-based foods, based on data from NHANES 2018–2018, predicted that dietary requirements for iron are met with flexitarian, vegetarian and vegan diets comprised of either traditional or novel plant-based foods (Tso and Forde, 2021).



The systematic review by Neufingerl and Eilander (2021) examined data on iron stores (serum/plasma ferritin concentration) in vegans, vegetarian and omnivores, from 17 studies (10 of which excluded supplement users). Iron status was higher in meat-eaters (55.5 µg/L) than in vegetarians (33.8 µg/L) and vegans (31.3 µg/L) and was lowest in vegetarian women (24.3 µg/L). However, mean haemoglobin values were similar and adequate across the three dietary patterns (i.e., 139/136/140 g/L for meat-eater, vegans and vegetarians, respectively). Another meta-analysis of 24 cross-sectional studies found that vegetarians are more likely to have lower iron stores than non-vegetarians, the results being more pronounced in men than premenopausal women (Haider et al., 2018). However, caution must be used when interpreting data from cross-sectional studies because associations are not necessarily causal. Potential confounders include the observation that people who eat more vegetables tend to have healthier diets overall, and could have other healthier lifestyle factors, such as having a higher socioeconomic and educational status, smoking less, being more physically active, and having a lower BMI. In addition, the length of time for iron stores to become depleted varies between individuals, depending on the size of body iron stores at the onset of the dietary change, their physiological requirements and capacity to absorb iron, which may be related to genotype.

There are very few randomized controlled trials on the effects of eliminating meat from the diet on iron status, and most of them were too short to demonstrate an effect on ferritin or haemoglobin. Wells et al. (2003) carried out a 12-week dietary intervention in older men undertaking resistive training. Total iron intake was similar between the group consuming a vegetarian or a beef-containing diet but at the end of the 12 weeks, although serum ferritin had decreased in both groups, the meat-consuming group had an increased haemoglobin and haematocrit compared with the vegetarian group. Another RCT investigating the effect of meat on iron status was a study in New Zealand toddlers, aged 12–20 months at baseline (Szymlek-Gay et al., 2009). The children were given red meat, iron-fortified milk or cow's milk for 20 weeks. Serum ferritin and body iron were significantly higher in the fortified milk group and serum ferritin was significantly higher in the red meat group than the cow's milk group. The authors concluded that an increased intake of red meat prevents the decline in iron status observed in toddlers not given additional iron.

## Food fortification and biofortification

Iron fortification of foods has been undertaken for a very long time, with differing degrees of success. The first major challenge is the development of technical solutions to allow highly bioavailable forms of iron to be added to foods without adverse organoleptic changes; the second is the physiological response to infection and inflammation which causes a rise in hepcidin and instigates a barrier to iron absorption (Hurrell, 2022).

A more sustainable solution to the widespread problem of iron deficiency is to increase the nutrient density of foods by

conventional plant or animal breeding, agronomic management, or genetic engineering. This is known as biofortification. Iron is amongst the most common micronutrients in plant crop biofortification programmes. Whilst there are successful examples of meat biofortified with both vitamin D (Neill et al., 2021) and selenium (D'Amato et al., 2020), there have been no attempts to increase its already high iron content. Therefore, the focus is on producing biofortified plant food crops.

Plant breeding programmes have managed to double the iron content of common beans, but the high phytic acid content of beans reduces iron bioavailability and impedes the effectiveness of bean iron biofortification, highlighting the importance of reducing the phytic acid content of food crops (Petry et al., 2015). Potatoes are low in phytic acid and this may be one of the reasons why the iron bioavailability of iron in yellow fleshed potato (containing 0.33 mg iron/100g fresh weight) was found to be remarkably high; the geometric mean absorption from a meal was 28.4% (95% CI 23.5%, 34.2%). The geometric mean absorption of iron from biofortified purple flesh potato (containing 0.69 mg iron/100g fresh weight) was much lower, namely 13.3% (95% CI 10.6%, 16.6%), probably due to the presence of polyphenols (Jongstra et al., 2020). The higher iron content of the biofortified potato meant that the total iron absorbed was similar between the two species of potato, a good illustration of the advantage conferred by biofortification.

## Dietary requirements

In 1998, the World Health Organization and the Food and Agriculture Organization proposed dietary iron bioavailability values for setting DRVs of 15, 10 or 5%, depending on the composition of the diet (Food Agriculture Organization of the United Nations, & World Health Organization, 1988). The highest bioavailability value is for diversified diets with generous amounts of meat and/or foods rich in ascorbic acid. The lowest bioavailability is for diets based on cereals, tubers and legumes with little or no meat or ascorbic acid-containing fruits and vegetables.

Craig et al. (2021) published guidelines for health professionals in relation to plant-based diets in which they stated that vegetarians, and especially vegans, should consume a well-balanced diet, regularly use fortified foods and/or supplements, and pay special attention to calcium, iron, vitamin D, and vitamin B12. When the US Dietary Reference Intakes (DRIs) were derived, approximately 20 years ago, there were separate recommendations for iron intake by vegetarians (Institute of Medicine, 2003). The DRIs for iron are derived factorially whereby physiological requirements, estimated from the sum of iron losses plus iron needed for growth, are converted into dietary intakes with an assumed dietary iron absorption of 18%. However, for plant-based diets they assume that absorption is lower, at around 10%, so they estimate that dietary iron requirements for vegetarians are 1.8 times higher than omnivores. The evidence to support this includes (1) a radioisotope study by Hunt and Roughead (1999) in which non-haem absorption was measured over 2 days and where there was a 6-

fold difference in absorption from a lacto-ovo-vegetarian diet compared with a nonvegetarian diet, and (2) a longer-term trial which found a two-fold difference in iron absorption between low bioavailability Western-style diets (mainly vegetarian) and high bioavailability diets (containing meat) consumed for a period of 2 weeks (Cook et al., 1991).

In 2015, EFSA published updated Dietary Reference Values for iron (EFSA NDA Panel, 2015) in which they concluded that the bioavailability of iron from European vegetarian diets is not substantially different from diets containing meat and other flesh foods. The evidence used to reach this conclusion included a randomized controlled trial in 21 women, aged 20–42 years, in which the effect of consuming a lacto-ovo-vegetarian or omnivorous diet for eight weeks on serum ferritin concentrations was determined. There was no difference in iron status between the groups fed a Western-style vegetarian diet or a diet containing meat, indicating that the iron bioavailability of the two diets was similar (Hunt and Roughead, 1999). One possible weakness of this study is the short time duration, which may not have been long enough to elicit a change in serum ferritin. The UK DRVs which were published in 1991 (Department of Health, 1991) used the FAO/WHO value of 15% bioavailability (Food Agriculture Organization of the United Nations, & World Health Organization, 1988) to convert iron requirements to dietary reference values. However, they cautioned that iron in diets containing little or no meat is less well absorbed and that people habitually consuming such diets may need a higher iron intake, although they noted that “data do not exist to quantify this precisely”.

It is possible that the current, and anticipated, reduction in meat consumption may have an impact on iron status. Dietary patterns are constantly evolving in response to food security, changes in lifestyle, and the types and availability of different foods. Meat has a long-established role in the UK diet in relation to its contribution towards well-absorbed dietary iron. It is possible that results of

older surveys evaluating the adequacy of dietary iron intake to meet physiological requirements may no longer be pertinent if dietary iron bioavailability falls. Careful monitoring of the iron status of vulnerable groups (particularly teenage girls and women of child-bearing age) is warranted to confirm that they have the capacity to upregulate the efficiency of iron absorption from diets of lower bioavailability.

## Author contributions

The author confirms being the sole contributor of this work and has approved it for publication.

## Funding

The author is funded by the University of East Anglia.

## Conflict of interest

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

## Publisher's note

All claims expressed in this article are solely those of the author and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

## References

- Anderson, G. J., and Frazer, D. M. (2017). Current understanding of iron homeostasis. *Am. J. Clin. Nutr.* 106 (Suppl 6), 1559S–1566S. doi: 10.3945/ajcn.117.155804
- Armah, C. N., Sharp, P., Mellon, F. A., Pariagh, S., Lund, E. K., Dainty, J. R., et al. (2008). L-alpha-glycerophosphocholine contributes to meat's enhancement of nonheme iron absorption. *J. Nutr.* 138, 873–877. doi: 10.1093/jn/138.5.873
- Bakaloudi, D. R., Halloran, A., Rippin, H. L., Oikonomidou, A. C., Dardavesis, T. I., Williams, J., et al. (2021). Intake and adequacy of the vegan diet. *A systematic Rev. evidence. Clin. Nutr.* 40, 3503–3521. doi: 10.1016/j.clnu.2020.11.035
- Bezodwa, W. R., Bothwell, T. H., Charlton, R. W., Torrance, J. D., MacPhail, A. P., Derman, D. P., et al. (1983). The relative dietary importance of haem and non-haem iron. *S. Afr. Med. J.* 64, 552–556.
- Björn-Rasmussen, E., Hallberg, L., Isaksson, B., and Arvidsson, B. (1974). Food iron absorption in man. applications of the two-pool extrinsic tag method to measure heme and nonheme iron absorption from the whole diet. *J. Clin. Invest.* 53, 247–255. doi: 10.1172/JCI107545
- Bryngelsson, S., Moshaghian, H., Bianchi, M., and Hallström, E. (2022). Nutritional assessment of plant-based meat analogues on the Swedish market. *Int. J. Food Sci. Nutr.* 73, 889–901. doi: 10.1080/09637486.2022.2078286
- Clement, N., Torrance, J. D., Bothwell, T. H., and Charlton, R. W. (1972). Iron compounds in muscle. *S. Afr. J. Med. Sci.* 37, 7–14.
- Conrad, M. E., Cortell, S., Williams, H. L., and Foy, A. L. (1966). Polymerization and intraluminal factors in the absorption of hemoglobin-iron. *J. Lab. Clin. Med.* 68, 659–668.
- Consalez, F., Ahern, M., Andersen, P., and Kjellekvold, M. (2022). The effect of the meat factor in animal-source foods on micronutrient absorption: a scoping review. *Adv. Nutr.* 2, nmac089. doi: 10.1093/advances/nmac089
- Cook, J. D. (1990). Adaptation in iron metabolism. *Am. J. Clin. Nutr.* 51, 301–308. doi: 10.1093/ajcn/51.2.301
- Cook, J. D., Dassenko, S. A., and Lynch, S. R. (1991). Assessment of the role of nonheme-iron availability in iron balance. *Am. J. Clin. Nutr.* 54, 717–722. doi: 10.1093/ajcn/54.4.717
- Cook, J. D., and Monsen, E. R. (1976). Food iron absorption in human subjects. III. comparison of the effect of animal proteins on nonheme iron absorption. *Am. J. Clin. Nutr.* 29, 859–867. doi: 10.1093/ajcn/29.8.859
- Craig, W. J., Mangels, A. R., Fresán, U., Marsh, K., Miles, F. L., Saunders, A. V., et al. (2021). The safe and effective use of plant-based diets with guidelines for health professionals. *Nutrients* 13, 4144. doi: 10.3390/nu13114144
- Cross, A. J., Harnly, J. M., Ferrucci, L. M., Risch, A., Mayne, S. T., and Sinha, R. (2012). Developing a heme iron database for meats according to meat type, cooking method and doneness level. *Food Nutr. Sci.* 3, 905–913. doi: 10.4236/fns.2012.37120
- D'Amato, R., Regni, L., Falcinelli, B., Mattioli, S., Benincasa, P., Dal Bosco, A., et al. (2020). Current knowledge on selenium biofortification to improve the nutraceutical profile of food: a comprehensive review. *J. Agric. Food Chem.* 68 (14), 4075–4097. doi: 10.1021/acs.jafc.0c00172
- Department of Health (1991). “Dietary reference values for food energy and nutrients for the united kingdom,” in *Report on health and social subjects no 41* (London: HMSO).

- EFSA NDA and Panel (2015). Scientific opinion on dietary reference values for iron. *EFSA J.* 13:4254, 115 pp. doi: 10.2903/j.efsa.2015.4254
- Etcheverry, P., Hawthorne, K. M., Liang, L. K., Abrams, S. A., and Griffin, I. J. (2006). Effect of beef and soy proteins on the absorption of non-heme iron and inorganic zinc in children. *J. Am. Coll. Nutr.* 25, 34–40. doi: 10.1080/07315724.2006.10719512
- Fabricius, F. A., Thomsen, S. T., Fagt, S., and Nauta, M. (2021). The health impact of substituting unprocessed red meat by pulses in the Danish diet. *Eur. J. Nutr.* 60, 3107–3118. doi: 10.1007/s00394-021-02495-2
- Fairweather-Tait, S., and Sharp, P. (2021). Iron. *Adv. Food Nutr. Res.* 96, 219–250. doi: 10.1016/bs.afnr.2021.01.002
- Food Agriculture Organization of the United Nations, & World Health Organization (1988). *Requirements of vitamin a, iron, folate and vitamin B12: report of a joint FAO/WHO expert consultation* (Rome: Food and Agriculture Organization of the United Nations).
- Gaitán, D., Flor, S., Saavedra, P., Miranda, C., Olivares, M., Arredondo, M., et al. (2011). Calcium does not inhibit the absorption of 5 milligrams of nonheme or heme iron at doses less than 800 milligrams in nonpregnant women. *J. Nutr.* 141, 1652–1656. doi: 10.3945/jn.111.138651
- Gaitán, D., Olivares, M., Lönnerdal, B., Brito, A., and Pizarro, F. (2012). . non-heme iron as ferrous sulfate does not interact with heme iron absorption in humans. *Biol. Trace Elem. Res.* 150, 68–73. doi: 10.1007/s12011-012-9496-4
- Gandemer, G., Scisłowski, V., Portanguen, S., and Kondjoyan, A. (2020). The impact of cooking of beef on the supply of heme and non-heme iron for humans. *Food Nutr. Sc.* 11, 629–648. doi: 10.4236/fns.2020.117045
- Godfray, H. C. J., Aveyard, P., Garnett, T., Hall, J. W., Key, T. J., Lorimer, J., et al. (2018). Meat consumption, health, and the environment. *Science* 361 (6399), eam5324. doi: 10.1126/science.2018.05324
- Haider, L. M., Schwingshackl, L., Hoffmann, G., and Ekmekcioglu, C. (2018). The effect of vegetarian diets on iron status in adults: a systematic review and meta-analysis. *Crit. Rev. Food Sci. Nutr.* 58, 1359–1374. doi: 10.1080/10408398.2016.1259210
- Hallberg, L., Hultén, L., and Gramatkovski, E. (1997). Iron absorption from the whole diet in men: how effective is the regulation of iron absorption? *Am. J. Clin. Nutr.* 66, 347–356. doi: 10.1093/ajcn/66.2.347
- Hallberg, L., Rossander-Hulthén, L., Brune, M., and Gleerup, A. (1993). Inhibition of haem-iron absorption in man by calcium. *Br. J. Nutr.* 69, 533–540. doi: 10.1079/BJN19930053
- Han, D. K. W., McMillan, K. W., Godber, J. S., Bidner, T. D., Younathan, M. T., Marshall, D. L., et al. (1993). Iron distribution in heated beef and chicken muscles. *J. Food Sci.* 58, 697–700. doi: 10.1111/j.1365-2621.1993.tb09337.x
- Hilaj, N., Zimmermann, M. B., Galetti, V., Zeder, C., Murad Lima, R., Hammer, L., et al. (2022). The effect of dechitinization on iron absorption from mealworm larvae (*Tenebrio molitor*) flour added to maize meals: stable-isotope studies in young females with low iron stores. *Am. J. Clin. Nutr.* 116, 1135–1145. doi: 10.1093/ajcn/nqac210
- Hornsey, I. I. C. (1956). The colour of cooked cured pork. estimation of the nitric oxide-haem pigments. *J. Food Agric. Sci.* 7, 534–540. doi: 10.1002/jfsa.2740070804
- Huh, E. C., Hotchkiss, A., Brouillette, J., and Glahn, R. P. (2004). Carbohydrate fractions from cooked fish promote iron uptake by caco-2 cells. *J. Nutr.* 134, 1681–1689. doi: 10.1093/jn/134.7.1681
- Hunt, J. R., and Roughead, Z. K. (1999). Nonheme-iron absorption, fecal ferritin excretion, and blood indexes of iron status in women consuming controlled lactoovo-vegetarian diets for 8 wk. *Am. J. Clin. Nutr.* 69, 944–952. doi: 10.1093/ajcn/69.5.944
- Hurrell, R. F. (2022). Ensuring the efficacious iron fortification of foods: a tale of two barriers. *Nutrients* 14, 1609. doi: 10.3390/nu14081609
- Hurrell, R. F., Reddy, M. B., Juillerat, M., and Cook, J. D. (2006). Meat protein fractions enhance nonheme iron absorption in humans. *J. Nutr.* 136, 2808–2812. doi: 10.1093/jn/136.11.2808
- Institute of Medicine (2003). *Dietary reference intakes for vitamin a, vitamin K, arsenic, boron, chromium, copper, iodine, iron, manganese, molybdenum, nickel, silicon, vanadium, and zinc* (Washington, DC: National Academies Press).
- Ismail, I., Hwang, Y. H., and Joo, S. T. (2020). Meat analog as future food: a review. *J. Anim. Sci. Technol.* 62, 111–120. doi: 10.5187/jast.2020.62.111
- Johnston, B. C., Zeraatkar, D., Han, M. A., Vernooij, R. W. M., Valli, C., Dib, R. E., et al. (2019). Unprocessed red meat and processed meat consumption: dietary guideline recommendations. *Ann. Internal Med* 171, 756–764. doi: 10.7326/M19-1621
- Jongstra, R., Mwangi, M. N., Burgos, G., Zeder, C., Low, J. W., Mzembe, G., et al. (2020). Iron absorption from iron-biofortified sweetpotato is higher than regular sweetpotato in Malawian women while iron absorption from regular and iron-biofortified potatoes is high in Peruvian women. *J. Nutr.* 150, 3094–3102. doi: 10.1093/jn/nxaa267
- La Frano, M. R., de Moura, F. F., Boy, E., Lönnerdal, B., and Burri, B. J. (2014). Bioavailability of iron, zinc, and provitamin a carotenoids in biofortified staple crops. *Nutr. Rev.* 72, 289–307. doi: 10.1111/nure.12108
- Latunde-Dada, G. O., and Neale, R. J. (1986). Pigeon (*Columba l.*) meat iron solubility and availability for absorption in rats. *Br. J. Nutr.* 55, 409–418. doi: 10.1079/bjn19860047
- Layrisse, M., Martínez-Torres, C., Cook, J. D., Walker, R., and Finch, C. A. (1973). Iron fortification of food: its measurement by the extrinsic tag method. *Blood* 41, 333–352. doi: 10.1182/blood.V41.3.333.333
- Layrisse, M., Martínez-Torres, C., Renzy, M., and Leets, I. (1975). Ferritin iron absorption in man. *Blood* 45, 689–698. doi: 10.1182/blood.V45.5.689.689
- Li, Y., Jiang, H., and Huang, G. (2017). Protein hydrolysates as promoters of non-haem iron absorption. *Nutrients* 9, 609. doi: 10.3390/nu9060609
- Lombardi-Boccia, G., Domingues, B. M., and Aguzzi, A. (2002). Total heme and non-heme iron in raw and cooked meats. *J. Food Sc.* 67, 1–4. doi: 10.1111/j.1365-2621.2002.tb08715.x
- Lynch, S. R., Skikne, B. S., and Cook, J. D. (1989). Food iron absorption in idiopathic hemochromatosis. *Blood* 74, 2187–2193. doi: 10.1182/blood.V74.6.2187.bloodjournal7462187
- Martínez-Torres, C., and Layrisse, M. (1970). Effect of amino acids on iron absorption from a staple vegetable food. *Blood* 35, 669–682. doi: 10.1182/blood.V35.5.669.669
- Martínez-Torres, C., Leets, I., Taylor, P., Ramírez, J., del Valle Camacho, M., and Layrisse, M. (1986). Heme, ferritin and vegetable iron absorption in humans from meals denatured of heme iron during the cooking of beef. *J. Nutr.* 116, 1720–1725. doi: 10.1093/jn/116.9.1720
- Martínez-Torres, C., Renzi, M., and Layrisse, M. (1976). Iron absorption by humans from hemisiderin and ferritin, further studies. *J. Nutr.* 106, 128–135. doi: 10.1093/jn/106.1.128
- McArthur, K. E., Walsh, J. H., and Richardson, C. T. (1988). Soy protein meals stimulate less gastric acid secretion and gastrin release than beef meals. *Gastroenterology* 95, 920–926. doi: 10.1016/0016-5085(88)90164-3
- Milman, N. T. (2020). A review of nutrients and compounds, which promote or inhibit intestinal iron absorption: making a platform for dietary measures that can reduce iron uptake in patients with genetic haemochromatosis. *J. Nutr. Metab. Sep* 14, 7373498. doi: 10.1155/2020/7373498
- Monsen, E. R. (1988). Iron nutrition and absorption: dietary factors which impact iron bioavailability. *J. Am. Diet. Assoc.* 88, 786–790. doi: 10.1016/S0002-8223(21)07902-5
- Monsen, E. R., and Balintfy, J. L. (1982). Calculating dietary iron bioavailability: refinement and computerization. *J. Am. Diet. Assoc.* 80, 307–311. doi: 10.1016/S0002-8223(21)08469-8
- Monsen, E. R., Hallberg, L., Layrisse, M., Hegsted, D. M., Cook, J. D., Mertz, W., et al. (1978). Estimation of available dietary iron. *Am. J. Clin. Nutr.* 31, 134–141. doi: 10.1093/ajcn/31.1.134
- Mwangi, M. N., Oonincx, D. G. A. B., Hummel, M., Utami, D. A., Gunawan, L., Veenbos, M., et al. (2022). Absorption of iron from edible house crickets: a randomized crossover stable-isotope study in humans. *Am. J. Clin. Nutr.* 116, 1146–1156. doi: 10.1093/ajcn/nqac223
- Mwangi, M. N., Oonincx, D. G. A. B., Stouten, T., Veenbos, M., Melse-Boonstra, A., Dicke, M., et al. (2018). Insects as sources of iron and zinc in human nutrition. *Nutr. Res. Rev.* 31, 248–255. doi: 10.1017/S0954422418000094
- Neill, H. R., Gill, C. I. R., McDonald, E. J., McRoberts, W. C., and Pourshahidi, L. K. (2021). Vitamin d biofortification of pork may offer a food-based strategy to increase vitamin d intakes in the UK population. *Front. Nutr.* 8, doi: 10.3389/fnut.2021.777364
- Neufingerl, N., and Eilander, A. (2021). Nutrient intake and status in adults consuming plant-based diets compared to meat-eaters: a systematic review. *Nutrients* 14, 29. doi: 10.3390/nu14010029
- Petry, N., Boy, E., Wirth, J. P., and Hurrell, R. F. (2015). Review: the potential of the common bean (*Phaseolus vulgaris*) as a vehicle for iron biofortification. *Nutrients* 7 (2), 1144–1173. doi: 10.3390/nu7021144
- Petry, N., Egli, I., Gahutu, J. B., Tugirimana, P. L., Boy, E., and Hurrell, R. (2014). Phytic acid concentration influences iron bioavailability from biofortified beans in Rwandese women with low iron status. *J. Nutr.* 144, 1681–1687. doi: 10.3945/jn.114.192989
- Pizarro, F., Olivares, M., Hertrampf, E., Mazariegos, D. I., and Arredondo, M. (2003). Heme-iron absorption is saturable by heme-iron dose women. *J. Nutr.* 133, 2214–2217. doi: 10.1093/jn/133.7.2214
- Pourkhalili, A., Mirolohi, M., and Rahimi, E. (2013). Heme iron content in lamb meat is differentially altered upon boiling, grilling, or frying as assessed by four distinct analytical methods. *Sc. Wld. J.*, 374030. doi: 10.1155/2013/374030
- Pretorius, B., Schönfeldt, H. C., and Hall, N. (2016). Total and haem iron content in lean meat cuts and the contribution to the diet. *Food Chem.* 193, 97–101. doi: 10.1016/j.foodchem.2015.02.109
- Public Health England (2020). Available at: <https://www.gov.uk/government/statistics/ndns-results-from-years-9-to-11-2016-to-2017-and-2018-to-2019>.
- Roughead, Z. K., and Hunt, J. R. (2000). Adaptation in iron absorption: iron supplementation reduces nonheme-iron but not heme-iron absorption from food. *Am. J. Clin. Nutr.* 72, 982–989. doi: 10.1093/ajcn/72.4.982
- Roughead, Z. K., Zito, C. A., and Hunt, J. R. (2005). Inhibitory effects of dietary calcium on the initial uptake and subsequent retention of heme and nonheme iron in humans: comparisons using an intestinal lavage method. *Am. J. Clin. Nutr.* 82, 589–597. doi: 10.1093/ajcn.82.3.589

- Schricker, B. R., Miller, D. D., and Stouffer, J. R. (1982). Measurement and content of nonheme and total iron in muscle. *J. Fd. Sc.* 47, 740–743. doi: 10.1111/j.1365-2621.1982.tb12704.x
- Scientific Advisory Committee on Nutrition (2010). *Iron and health* (London: TSO).
- Szymlek-Gay, E. A., Ferguson, E. L., Heath, A. L., Gray, A. R., and Gibson, R. S. (2009). Food-based strategies improve iron status in toddlers: a randomized controlled trial. *Am. J. Clin. Nutr.* 90, 1541–1551. doi: 10.3945/ajcn.2009.27588
- Taylor, P. G., Martínez-Torres, C., Romano, E., and Layrisse, M. (1986). The effect of cysteine-containing peptides released during meat digestion on iron absorption in humans. *Am. J. Clin. Nutr.* 43, 68–71. doi: 10.1093/ajcn/43.1.68
- Thavamani, A., Sferra, T. J., and Sankararaman, S. (2020). Meet the meat alternatives: the value of alternative protein sources. *Curr. Nutr. Rep.* 9, 346–355. doi: 10.1007/s13668-020-00341-1
- Troesch, B., Egli, I., Zeder, C., Hurrell, R. F., de Pe, S., and Zimmermann, M. B. (2009). Optimization of a phytase-containing micronutrient powder with low amounts of highly bioavailable iron for in-home fortification of complementary foods. *Am. J. Clin. Nutr.* 89, 539–544. doi: 10.3945/ajcn.2008.27026
- Tso, R., and Forde, C. G. (2021). Unintended consequences: nutritional impact and potential pitfalls of switching from animal- to plant-based foods. *Nutrients*. 13, 2527. doi: 10.3390/nu13082527
- Turnbull, A., Cleton, F., and Finch, C. A. (1962). Iron absorption. IV. the absorption of hemoglobin iron. *J. Clin. Inv.* 41 *Nutr. Rev.* 47, 51–53. doi: 10.1111/j.1753-4887.1989.tb02786.x
- Wells, A. M., Haub, M. D., Fluckey, J., Williams, D. K., Chernoff, R., and Campbell, W. W. (2003). Comparisons of vegetarian and beef-containing diets on hematological indexes and iron stores during a period of resistive training in older men. *J. Am. Diet. Assoc.* 103, 594–601. doi: 10.1053/jada.2003.50112
- Yaskolka Meir, A., Tsaban, G., Zelicha, H., Rinott, E., Kapla, A., Youngster, I., et al. (2019). A green-Mediterranean diet, supplemented with mankai duckweed, preserves iron-homeostasis in humans and is efficient in reversal of anemia in rats. *J. Nutr.* 149, 1004–1011. doi: 10.1093/jn/nxy321
- Young, M. F., Griffin, I., Pressman, E., McIntyre, A. W., Cooper, E., McNanley, T., et al. (2010). Utilization of iron from an animal-based iron source is greater than that of ferrous sulfate in pregnant and nonpregnant women. *J. Nutr.* 140, 2162–2166. doi: 10.3945/jn.110.127209



## OPEN ACCESS

## EDITED BY

Ian Givens,  
University of Reading, United Kingdom

## REVIEWED BY

Begoña Panea,  
Aragon Agrifood Research and Technology  
Center (CITA), Spain  
Maria Aspri,  
Cyprus University of Technology, Cyprus

## \*CORRESPONDENCE

Maeve Henchion  
✉ [maeve.henchion@teagasc.ie](mailto:maeve.henchion@teagasc.ie)

## †PRESENT ADDRESS

Georgia Lavranou,  
Department of Psychology, Maynooth  
University, Kildare, Ireland

RECEIVED 21 December 2022

ACCEPTED 09 May 2023

PUBLISHED 07 June 2023

## CITATION

Lavranou G, Henchion M, McCarthy MB  
and O'Reilly SJ (2023) Valorizing  
meat by-products for human  
consumption: understanding  
consumer attitude  
formation processes.  
*Front. Anim. Sci.* 4:1129241.  
doi: 10.3389/fanim.2023.1129241

## COPYRIGHT

© 2023 Lavranou, Henchion, McCarthy and  
O'Reilly. This is an open-access article  
distributed under the terms of the [Creative  
Commons Attribution License \(CC BY\)](#). The  
use, distribution or reproduction in other  
forums is permitted, provided the original  
author(s) and the copyright owner(s) are  
credited and that the original publication in  
this journal is cited, in accordance with  
accepted academic practice. No use,  
distribution or reproduction is permitted  
which does not comply with these terms.

# Valorizing meat by-products for human consumption: understanding consumer attitude formation processes

Georgia Lavranou<sup>1†</sup>, Maeve Henchion<sup>1\*</sup>, Mary B. McCarthy<sup>2</sup>  
and Seamus J. O'Reilly<sup>3</sup>

<sup>1</sup>Department of Agrifood Business and Spatial Analysis, Rural Economy Development Programme, Teagasc Food Research Centre, Dublin, Ireland, <sup>2</sup>Department of Management & Marketing, Cork University Business School, University College Cork, Cork, Ireland, <sup>3</sup>Department of Food Business & Development, Cork University Business School, University College Cork, Cork, Ireland

**Introduction:** A considerable body of research has identified that meat by-products contain significant amounts of high-quality protein, which when properly extracted can lead to valuable opportunities for the food industry. However, the market success of food products containing protein extracted from meat byproducts is subject to consumer acceptance. This study explores Irish consumers' attitudes toward hypothetical food products containing protein derived from beef offal sources.

**Methods:** A nationally representative survey (n = 953) was undertaken to investigate what attitude processes, that is intuitive and/or deliberative, dominate attitude formation toward food products containing beef offal-derived protein, while accounting for the effects of product familiarity and information provision. Using a 2 x 3 between-subject design, study participants were randomly assigned to one of the 6 study conditions. Participants were exposed to Affect Misattribution Procedure (AMP) tasks which measured their intuitive evaluations, followed by a number of questions that measured deliberative evaluation, attitude ambivalence, attitudes and acceptability toward the food products containing protein extracted from beef offal.

**Results:** The study reveals that consumers' intuitive and deliberative evaluations worked in the same direction, predicting overall attitudes toward these products; however, deliberative evaluation was found to be a better predictor of consumers' attitudes than intuitive evaluation. Moreover, intuitive evaluations do not influence deliberative evaluations, suggesting that information provision that prompts deliberative evaluations could lead to the formation of more considered and stable attitudes. Familiarity influences acceptance: these findings suggest that the potential impact of a lack of familiarity with the ingredient is offset by familiarity with the carrier products. Consumers who received benefit information about the health and environmental consequences of consuming food products containing protein extracted from beef offal expressed a more positive deliberative attitude toward these products. However, interestingly, the provision of benefit- and risk-orientated information



at the same time at the same time also had a positive effect on deliberative evaluations.

**Discussion:** The findings have implications for new product development, and more generally for strategies that seek to promote sustainable food production and consumption.

#### KEYWORDS

meat by-products, protein, information, consumer behavior, attitude formation, consumer, valorization, AMP

## 1 Introduction

The global population is predicted to grow to 9.7 billion by 2050, reflecting a growth of about one-third compared with the figure in 2015 (FAO, 2018). Alongside this are several factors that will influence the nature of the demand for food in the coming decades. These include global concerns regarding climate change and the availability of finite resources, particularly fossil fuel-based resources; the loss of natural ecosystems and declining biodiversity resulting from an expansion of land and fresh water used to produce food for a growing population (IPCC, 2019); health inequalities, such as obesity and malnutrition, which co-exist in many countries (FAO, 2018); and socioeconomic changes, such as urbanization and rapid income growth in some regions. Thus, the quantity of food required is expected to increase significantly, and the nature of food needed will change significantly too. This will place significant demands on the food production system, as evidenced by a recognition that the current means of food production and patterns of consumption are not sustainable (Steenson and Buttriss, 2020) and that fundamental changes to the food production system are required (FAO, 2018; Willett et al., 2019).

In this context, protein has attracted particular attention, with more sustainable and alternative protein sources being demanded by consumers, pursued by industry and researchers, and driven by policymakers at all levels (Clark and Lenaghan, 2020). Their approaches have targeted both existing and novel sources of protein. A review by Henchion et al. (2017) concluded that different factors influence the potential of these sources to sustainably satisfy protein demand. They found that the sustainability of existing protein sources, particularly animal-derived foods, is primarily limited by their negative environmental impacts and some concerns around health. However, high levels of consumer acceptance and social and economic benefits support their ongoing production. In contrast, proponents of novel proteins have to pay close attention to consumer acceptance, and related issues such as production costs and safety.

The global demand for animal-derived protein is expected to double by 2050 (Westhoek, 2011), thus necessitating particular attention. Novel protein production opportunities are available in this industry, with a focus on increasing the valorization of co-products in several sectors. There are several arguments in favor of

this. First, raw materials are available in significant quantities—cattle slaughtering and processing generates by-products that account for 40%–50% of the total weight of the animal slaughtered (Cavaleiro et al., 2013). Second, they represent undervalored sources of high-quality protein, and many other nutrients including essential amino acids, vitamins, minerals, antioxidants, and bioactive peptides (Florek et al., 2012; Jayathilakan et al., 2012; Mullen et al., 2017; Álvarez et al., 2018). Overall, there is growing scientific awareness that animal by-products contain significant amounts of nutritious and functional components when treated and processed correctly. Indeed, the development of techniques for the recovery and the utilization of protein from such sources has attracted considerable interest in recent years (Darine et al., 2010; Toldrá et al., 2012; Baiano, 2014; Lynch et al., 2017; Mullen et al., 2017). Last, their current use in many countries means that they are treated as waste, incurring costs for meat processors and representing a potential threat to the environment. Thus, from a sustainability perspective, making better use of by-products can help to reduce the environmental impact of meat production, and address the need to use animal proteins in a more responsible manner than is currently the case (Van Der Spiegel et al., 2013).

However, using animal by-products as a significant source of protein on a global basis is likely to elicit challenges relating to the fact that they are co-products and are animal derived. Martins et al. (1997) suggest that consumers tended to exhibit stronger neophobic responses in relation to animal products than to non-animal products, possibly as a result of the greater potential pathogenic threat posed by animal products. Thus, they are likely to be more wary of novel proteins from animal by-products than other sources. Moreover, if consumers are not familiar with potential innovations in this area, they may consider by-products as unhealthy and possibly not edible. Frewer and Gremmen (2007) argue that “unless consumers can agree that the benefits of by-products management are equivalent to sustainable, desirable, and acceptable food production practices, consumers are unlikely to recognize and realize many of the potential benefits of by-products management” (p. 32). This paper aims to explore Irish consumers’ attitudes toward incorporating protein extracted from beef offal into food products. It builds on the methodology used in the study by De Beukelaar et al. (2019), adding theoretical concepts and applying it in a new context.

## 2 Theoretical framework

Consumers' food choices and behaviors are influenced by numerous sociocultural and sociopsychological factors, with most of these factors being internalized by individuals through the formation of attitudes. Attitudes are defined as "a psychological tendency that is expressed by evaluating a particular entity with some degree of favor or disfavor" (Eagly and Chaiken, 1993, p. 1). Within food research, the important influence of the attitude construct on consumers' behavior is evident through its omnipresence in numerous analytical theories, models, and frameworks that examine food choices (e.g., Randall, 1981; Ajzen, 1991; Shepherd, 1999; Rozin, 2006).

### 2.1 Attitude formation processes

In some cases, people form attitudes effortlessly, without much conscious awareness of their formation, while in other cases, attitudes are consciously controlled and arise from the intentional and thoughtful consideration of attitude-relevant information (Marquardt and Hoeger, 2009; Kruglanski and Gigerenzer, 2011; Olson and Kendrick, 2011; Pachur and Spaar, 2015). The first process, referred to as "intuitive" within this paper, has been described as unintentional, immediate, stimulus based, and can involve emotion-based judgments based on quick intuitions such as "gut" feelings (Haidt, 2001; Duckworth et al., 2002; Pachur and Spaar, 2015). The second process described, referred to as "deliberative" within this paper, is an analytic mode that requires individuals to think at complex levels and critically make evaluative judgments (Epstein, 2010). People can engage in both processes simultaneously, with each process exerting either independent or interdependent effects on evaluations (Moskowitz et al., 1995; Marquardt and Hoeger, 2009; Bohnet et al., 2011).

Both processes may jointly influence people's evaluations in an additive, competitive, or sequential manner (Evans, 2008; Gawronski and Creighton, 2013). For example, when deliberative processing is incongruent with the judgment implied from intuition, deliberative evaluation can entirely set aside the intuitive process (Gawronski and Creighton, 2013). This might occur because the outcome implied by deliberate processing is likely to be seen as more reliable, and, therefore, the influence of intuition is reduced (Zuckerman and Chaiken, 1998). People use a common set of core values in their food choices, such as taste, cost, health, and convenience, and attach meanings to these values (Furst et al., 1996; Sobal and Bisogni, 2009). If all these values cannot be met at the same time, people develop ways of negotiating and balancing them (Sobal and Bisogni, 2009). Deliberative evaluation of a food product's health value may override an initial intuitive evaluation of disgust or a "gut" feeling for this product if consumers are health conscious. Thus, consumers' attitudes toward a food product can be the result of both intuitive and deliberate evaluations, with intuitive evaluations being formed first.

With the findings in the above literature and the study by De Beukelaar et al. (2019) in mind, it can be hypothesized that:

Hypothesis 1: the more positive consumers' intuitive and deliberative evaluations toward the food product containing offal-derived protein are, the more positive their overall attitude toward this product will be.

Hypothesis 2: the more positive consumers' intuitive evaluation toward the food product containing offal-derived protein is, the more positive their deliberate evaluation toward this product will be.

### 2.2 Ambivalence

Consumers' food choices and related behavior has been associated with ambivalence (Sparks et al., 2001). Ambivalence can be conceptualized as a state in which an individual "is inclined to give it [an attitude object] equivalently strong positive or negative evaluations" (Thompson et al., 1995, p. 367). For instance, a person may hold an ambivalent attitude toward meat consumption, deriving from strongly held positive and negative attitudes toward the associated benefits and risks. Attitudinal research has shown that individuals are motivated to reduce ambivalence and its associated negative feelings (Stone and Cooper, 2001; Zembrain and Johar, 2007; Sawicki et al., 2013). Empirical studies have shown that ambivalence is related to more effort and deliberation, as ambivalent attitude-holders experience an internal evaluative inconsistency, and, therefore, invest cognitive resources to come to a more unequivocal attitude (Van Harreveld and Van Der Pligt, 2004; Van Harreveld et al., 2004). Therefore, it is reasonable to assume that:

Hypothesis 3: the more ambivalent consumers' attitudes toward the food product concept containing protein extracted from beef offal, the greater the effect of deliberate evaluation on overall attitudes toward this product.

### 2.3 Familiarity with food product concept

Previous empirical research (e.g., Wansink, 2002; Fischer and Frewer, 2009; Gmuer et al., 2016) has shown that product familiarity plays an important role in introducing new foods to the market. Research on insects as food has repeatedly shown that insects are likely to be more acceptable when they are incorporated into familiar foods (Schösler et al., 2012; Tan et al., 2015; Gmuer et al., 2016; Tan et al., 2016). Some researchers have also suggested that incorporating insects and offal into convenience foods, such as burger patties and sausages, might be one of the most effective ways of encouraging consumer acceptance (Wansink, 2002; Schösler et al., 2012; Verbeke, 2015). Consumers' familiarity with a product concept they are required to evaluate might also affect the evaluation process that they use. In cases where individuals have limited knowledge and experience with the attitude object, it is more likely that they will access affective associations than construct cognitive associations (Van Giesen et al., 2015). Research on attitudes toward relatively unfamiliar food developments, such as genetically modified foods and nanotechnology applications, has indicated that affective/intuitive input is the main driver of attitude

formation (Lee et al., 2005; Van Giesen et al., 2015). Given the above literature it can be hypothesized that:

Hypothesis 4: consumers who are exposed to an image of a familiar product concept are more likely to have more positive intuitive evaluation toward the food product containing offal-derived protein than consumers who are exposed to unfamiliar product concepts.

## 2.4 Attitude formation and information processing

Attitude formation is highly related to information provision and processing (Crano and Prislin, 2006; Eagly and Chaiken, 2007), as attitudes can be formed (or altered) as a result of received information (McCarthy et al., 2003). Health-related information is increasingly used in the marketing of food products, and research has shown that it affects consumers' responses to foods in general, and to unfamiliar or novel foods in particular (Leathwood et al., 2007; Lampila et al., 2009; Lähteenmäki, 2013). Research on functional foods, for example, has shown that consumers are more willing to accept them if information on health benefits is provided (Siegrist et al., 2008; Lalor et al., 2011). In a study on consumer acceptance of unfamiliar acai berry-based fruit juices, Sabbe et al. (2009) demonstrated that health information leads to an increase in overall liking for these unfamiliar fruit juices. In addition or alongside the effect of health benefit information on consumer acceptance of new or unfamiliar foods, the effect of information on environmental benefits has also been studied. In a recent study, Barsics et al. (2017) showed that information on insect-based foods encompassing ecological, health, and gastronomic aspects could change consumers' attitudes and acceptance of novel insect-based food samples. In a similar vein, Verneau et al. (2016) investigated the effect of benefit communication on insect consumption and showed that providing information about the individual (i.e., health benefits) and social (i.e., environmental benefits) benefits of eating insects increased peoples' intention to eat insect-based food. Gorissen and Weijters (2016) investigated how consumers process information on the environmental impact of food products and how this information can be subject to biased processing. In one of their experiments, the authors found that people rated a hamburger together with an organic apple as having a lower environmental impact compared with the hamburger alone. The authors attributed this result to the biased effect of the "green product".

Consumers are often confronted with contradicting information regarding products' attributes and/or benefits. Insufficient or contradictory information leads to the ambivalence that characterizes public reactions to new foods (Grunert et al., 2001; Bäckström et al., 2003). According to the heuristic-systematic model (HSM) (Chaiken, 1980), in conditions where information is ambiguous, information can be interpreted in line with a heuristic cue and bias the results of deliberate processing (Gawronski and Creighton, 2013).

Hypothesis 5: individuals who are provided with either benefit or ambiguous information are more likely to have a more positive deliberate evaluation of product concepts containing protein

extracted from beef offal than people who are provided with no information.

Hypothesis 6: for individuals who are exposed to ambiguous information, it is more likely that their deliberate evaluation will be determined by intuitive evaluation.

## 3 Materials and methods

### 3.1 Participants

Data were collected in January 2019 using an online survey. Participants were recruited by a field market research agency, from their consumer panel. Quota controls were applied in terms of age, gender, education, social class, and geographical area to ensure a representative sample of the Irish adult population. All responders had been living continuously in Ireland for the past 3 years and were consumers of burgers and sausages. A total of 1,027 consumers took part in the survey. From those, 74 respondents were excluded due to their not meeting the qualifying criteria<sup>1</sup>, resulting in a final sample of 953 respondents.

### 3.2 Manipulations

#### 3.2.1 Carrier product

Previous research on consumer attitudes toward new and novel foods, such as functional foods and insects, has stressed the important role of perceived fit of carrier-ingredient combination on acceptability (e.g., Bech-Larsen and Grunert, 2003; Van Kleef et al., 2005; Lyly et al., 2007; Verbeke et al., 2009; Krutulyte et al., 2011; Lu, 2015; Tan et al., 2015; Tan et al., 2017). In this study, the carrier effect was removed by choosing carrier products that conceptually represent an appropriate carrier-ingredient combination. In accordance with the study by De Beukelaar et al. (2019), we decided to include two different food product concepts to control for individual differences in liking for the specific food products and to serve as internal replications for the study. Sausages and burgers were chosen to fulfil these criteria. Given that these products are commonly produced with minced meat and/or red offal in a patty format, it was expected that it would be ideationally congruent to add ingredients extracted from offal to these products, as opposed to a product characterized by totally different properties (e.g., orange juice). This choice was also reinforced by a review of the meat science literature undertaken by the research team, which indicated that most recommendations concerning the applications of offal-extracted protein for the food industry were focused on processed meat products.

<sup>1</sup> A total of 47 participants were excluded during the analysis due to self-reported missing observations for one or more of the explanatory variables of the analysis. Possible causes for failure to complete the section(s) could be limitations associated with the devices on which the survey was undertaken (e.g., small screen) in combination with the short duration for which some images were presented.

### 3.2.2 Familiarity

Familiarity with the product concepts was manipulated in terms of product concepts containing protein extracted from familiar compared with unfamiliar beef offal sources. Selection was based on the results of a pretest conducted with 26 Irish consumers, who reported their familiarity with burgers and sausages containing protein extracted from six different beef offal sources: heart, blood, liver, lung, bone, and skin. Familiarity with these product concepts was measured using a five-point scale according to Tuorila et al. (2001). Based on the reported differences in familiarity in this pretest, the following choices were made:

- familiar products consisted of “burger containing protein extracted from beef liver” and “sausages containing protein extracted from beef liver”
- unfamiliar products consisted of “burger containing protein extracted from beef lung” and “sausages containing protein extracted from beef lung”.

### 3.2.3 Information provision

Manipulations in information provision within the survey consist of three levels: no information, benefit information, and ambiguous information. Participants in all conditions were informed that the presented food products contained protein extracted from beef liver or lung. In the “benefit information” condition, information was given to participants about the health and environmental benefits of protein extracted from beef liver or lung for human consumption. In the “ambiguous information” condition, a more extensive text was given to participants containing ambiguous arguments regarding the health and environmental benefits of protein extracted from beef liver or lung for human consumption. A pretest with 29 Irish third-level students confirmed that the two fictitious information texts differed significantly in terms of the strength and valence of their arguments.

Literature suggests that the impact of information provision on consumers’ attitudes is strongly affected by the perceived credibility and trustworthiness of the information source (e.g., Frewer et al., 2003; Gray et al., 2005; Costa-Font et al., 2008; Cash et al., 2015; Henchion et al., 2016), and this is the case especially in situations where attitudes have not yet crystallized (Frewer et al., 1998). In this study, the source of the information was intentionally unspecified to minimize the potential effect of information source credibility on participants’ expressed attitudes.

## 3.3 Experimental design

In line with De Beukelaar et al.’s (2019) study design, of a  $2 \times 3$  between-subject design, participants were randomly assigned to one of six possible study conditions (see Table 1). The conditions differed according to the two factors: product concept familiarity (two levels: familiar or unfamiliar) and provision of information (three levels: no information provided, benefit information provided, or ambiguous information provided).

## 3.4 Measures

### 3.4.1 Intuitive evaluations

Intuitive evaluations of the product concepts containing protein extracted from beef offal were measured with an affect misattribution procedure (AMP), which was developed by Payne et al. (2005). The AMP has been used in food studies (e.g., Hofmann et al., 2009; Richard et al., 2017; Woodward et al., 2017) exhibiting relatively high levels of reliability (Lebel and Paunonen, 2011). Payne and Lundberg (2014) reported Cronbach’s alpha coefficients ranging from 0.47 to 0.95 from 45 studies.

According to Payne et al. (2005), the AMP is an implicit measure, in the sense that participants do not directly report their attitudes, but their attitudes are inferred from the responses. This priming-based procedure measures automatically activated responses based on the principle that exposure to a visual positive or negative stimulus causes an affective state, which then automatically biases the evaluation of a subsequent neutral object (Payne and Lundberg, 2014). According to the AMP process, participants have to view pairs of pictures “flashed” rapidly one after the other; the visual prime, followed by a neutral Chinese character<sup>2</sup> (Payne et al., 2005, p. 280). Subsequently, they are asked to make evaluative judgments about the neutral target stimulus (i.e., the Chinese character) and are explicitly asked to ignore the photo prime. The stimulus (i.e., the Chinese character) tends to be judged more positively (vs. negatively) when it is preceded by a positive (vs. negative) prime (Payne et al., 2005).

During the survey, each participant was exposed to two AMP tasks containing images from one of the six conditions. Every AMP task began with briefly showing (1,200 ms) a photograph of the product (burger/sausages) containing protein extracted from beef offal (visual prime). After the prime, a Chinese character (see Figure 1) was shown for 1200 ms. Participants were asked to rate the Chinese character on a seven-point scale, ranging from “not very pleasant” to “very pleasant”, plus the option to report “unable to see the image” (Figure 2). Before starting this part of the study, participants were explicitly instructed to ignore the photos prior to the Chinese characters. However, in accordance with AMP principles, it is expected that despite the given instruction, participants are more inclined to perceive the Chinese characters as (un)pleasant if they have formed a (un)favorable intuitive evaluation toward the visual primes, that is the food product concepts containing protein extracted from beef liver or lung.













### 3.4.2 Deliberative evaluation

Deliberate evaluation of the product concepts containing protein extracted from beef offal was assessed using three deliberate attitude items on a seven-point semantic differential scale from Bruner (2017).

<sup>2</sup> The research team decided that it was appropriate to exclude individuals who speak Chinese, as their knowledge of the meanings of the Chinese characters could alter the results from the AMP tests.



TABLE 1 The two stimuli in each of the six study conditions.

Factor: product familiarity		Familiar (protein extracted from beef liver)	Unfamiliar (protein extracted from beef lung)
Factor: information provision	Not provided	 <p><i>This burger contains protein extracted from beef liver</i></p>  <p><i>These sausages contain protein extracted from beef liver</i></p>	 <p><i>This burger contains protein extracted from beef lung</i></p>  <p><i>These sausages contain protein extracted from beef lung</i></p>
	Benefit information provided	 <p><i>This burger contains protein extracted from beef liver. Protein extracted from beef liver has a high health value and is environmentally friendly</i></p>  <p><i>These sausages contain protein extracted from beef liver. Protein extracted from beef liver has a high health value and is environmentally friendly</i></p>	 <p><i>This burger contains protein extracted from beef lung. Protein extracted from beef lung has a high health value and is environmentally friendly</i></p>  <p><i>These sausages contain protein extracted from beef lung. Protein extracted from beef lung has a high health value and is environmentally friendly</i></p>
	Ambiguous information provided	 <p><i>This burger contains protein extracted from beef liver. Protein extracted from beef liver has a high health value and is environmentally friendly. However, when improperly treated, protein extracted from beef liver does not supply any health value and can have a negative environmental impact</i></p>  <p><i>These sausages contain protein extracted from beef liver. Protein extracted from beef liver has a high health value and is environmentally friendly. However, when improperly treated, protein extracted from beef liver does not supply any health value and can have a negative environmental impact</i></p>	 <p><i>This burger contains protein extracted from beef lung. Protein extracted from beef lung has a high health value and is environmentally friendly. However, when improperly treated, protein extracted from the lung does not supply any health value and can have a negative environmental impact</i></p>  <p><i>These sausages contain protein extracted from beef lung. Protein extracted from beef lung has a high health value and is environmentally friendly. However, when improperly treated, protein extracted from beef lung does not supply any health value and can have a negative environmental impact</i></p>

3.4.3 Attitude ambivalence

Participants’ “attitude ambivalence” toward the product concepts was measured using three items on a seven-point scale in accordance with [Priester and Petty \(1996\)](#). This scale has been used in numerous research papers (e.g., [Nowlis et al., 2002](#); [Nordgren et al., 2006](#); [Clark et al., 2008](#)). The scale is composed of three items that assess the extent to which a person reports having mixed feelings when making an evaluation.

3.4.4 Overall attitude

*Overall attitude* toward the food products containing protein extracted from beef offal was measured using three items on a seven-point bipolar continuum, in accordance with [Pham and Avnet \(2004\)](#) and [Kempf and Laczniaik \(2001\)](#) (with reported Cronbach’s alpha coefficients of 0.97 and 9.4, respectively).

3.4.5 Acceptability

In addition to the attitudinal measurements toward the food products containing protein extracted from beef offal, it was

deemed useful to measure individuals’ acceptance of these products. No specific hypotheses were made around acceptability; however, an explanatory analysis of the relationships between attitudinal constructs and acceptance will provide some additional insight. Acceptability was measured using three items on a seven-point scale based on that in the study by [Tan et al. \(2016\)](#).

3.5 Survey procedure

Participants were invited *via* email by the market research agency to take part in the survey. To avoid self-selection bias, specific project details were not included in the email invitation. Instead, individuals were invited to complete a survey and given the general survey details, that is, the survey theme and the length of survey. On clicking the survey link, participants were informed about the purpose of the study, that the information provided would be protected and anonymous, and asked to provide their consent to proceed with the survey.



The online survey consisted of four parts, which altogether took around 15 min to complete. In part 1, demographic and product consumption questions, and the exclusion criteria questions, were asked. If participants met the requirements to participate in the survey, they were randomly assigned to one of the six study conditions. In part 2, participants completed the AMP task. In part 3, participants rated their overall attitude, attitude ambivalence, and deliberate evaluation and acceptance of the food products containing protein extracted from beef offal. Finally, in part 4, participants rated their general attitudes toward eating burgers and sausages and their attitudes toward the Chinese characters. Piloting

was undertaken with 56 participants to ensure the suitability and validity of the data collection instrument and of study manipulations. Age categories were defined *a priori* and were based on common age bands for adults. Social class categories were defined using a common market research classification, as follows: A—upper middle class; B—middle class; C1—lower middle class, C2—skilled working class; D—working class; E—non-working; and F—farmers.

### 3.6 Data analysis

Data analysis was performed using IBM SPSS 24. A critical *p*-value of 0.05 was selected. Prior to analysis, items denoted with (R) were reversed, so that higher-scale scores denote positive valence. For testing the hypotheses and the two scores for the individual products (burgers and sausages) were averaged to obtain a single aggregated score for each variable. Analyses consisted of reliability analysis of scales used (all scales had a Cronbach's alpha value > 0.70), descriptive statistics, Pearson's chi-squared correlations, and, finally, a regression analysis and analysis of variance (ANOVA) to test the hypotheses.

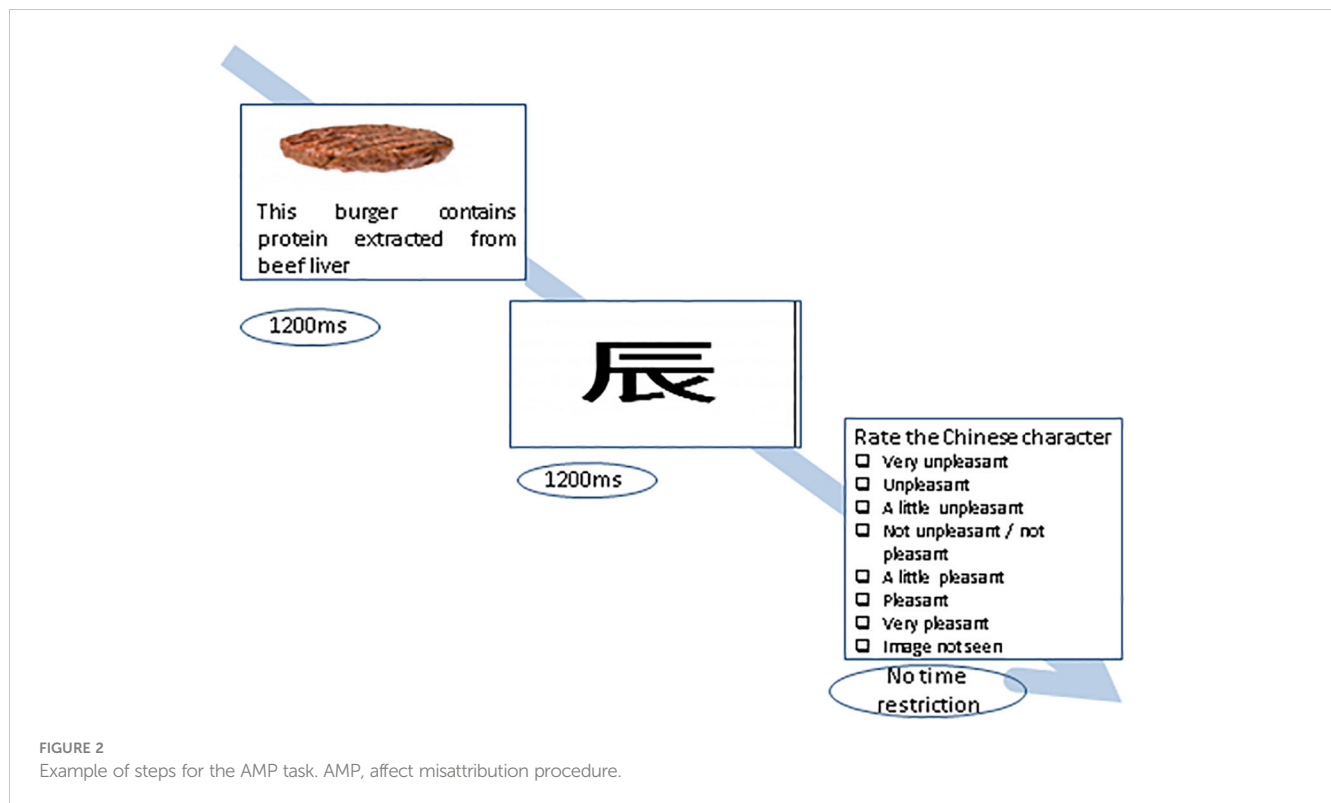
## 4 Results

The study sample is representative of the Irish adult population in terms of gender, age, education, and social class [according to the most recent census survey, conducted by the Central Statistics Office (CSO) in 2016]. Participants' general attitudes toward the two product carriers indicate that participants were equally positive about consuming burgers and sausages. In terms of consumption frequency, more than two-thirds of the participants (almost 73%) reported eating burgers "less than once per month" or "1–3 times per month", whereas almost two-thirds of the sample (64%) reported eating sausages "once a week" or "1–3 times per month". These reported frequencies indicate that more people consume sausages more frequently than burgers<sup>3</sup> (see Table 2 for further details).

Pearson's chi-squared coefficients show that participants were equally assigned across the six experimental conditions, with respect to sociodemographic characteristics. In addition, participants' general attitudes toward the two Chinese signs, which were used as the stimuli items in the "intuitive evaluation" section of the survey, in accordance with the AMP method, showed similar results (sign 1: mean = 3.65 SD = 1.12; sign 2: M = 3.70, SD = 1.07). A within-subjects repeated measures ANOVA showed that there were no significant differences between participants' attitudes toward the two Chinese signs [(F(1,952) = 3.83, *p* = 0.05, partial  $\eta^2$  = 0.004], which suggests that the two Chinese signs were perceived as being equally attractive by participants. This

<sup>3</sup> This sample represents burger and sausage consumers, as the consumption of these products was a qualifying criterion for participating in the survey.





indicates that any possible statistical difference in participants' intuitive evaluations was not due to differences in the perceived attractiveness of the Chinese signs.

## 4.1 Descriptive analysis

### 4.1.1 Main measured variables across conditions and products

An overview of the means and standard deviations for the main measured variables is provided in Table 3. For almost all variables, the highest values were noted when benefit information was provided and when protein was extracted from the liver (rather than the lung). In comparison, the lowest values were noted when no information was provided and when protein was extracted from the lung. Moreover, when comparing the variable scores acquired for the two product carriers, that is, burgers and sausages, there were no differences in the scores. This confirms that it is reasonable to average the measures coming for the two products to obtain an aggregated score for each variable.

## 4.2 Hypothesis testing

### 4.2.1 Predicting attitude formation

*Intuitive evaluation* had a significant effect on participants' *deliberate evaluation* of food products containing offal-derived protein, regardless of the experimental condition [ $F(1,951) = 117.30, p < 0.001$ ]. The direction of this effect was found to be positive ( $\beta = 0.33$ ), meaning that participants with a more positive

intuitive evaluation subsequently expressed a more positive deliberative evaluation.

The *overall attitudes* toward food products containing offal-derived protein were well predicted by data for the *deliberate* and the *intuitive* evaluations [ $F(1,951) = 1429.99, p < 0.001, R^2 = 0.87$ ], with *deliberate evaluation* ( $\beta = 0.85$ ) having a greater positive influence on *overall attitudes* than *intuitive evaluation* ( $\beta = 0.03$ ). Therefore, results confirm hypothesis 1 and hypothesis 2.

The interaction effect of *deliberate evaluation* and *attitude ambivalence* was found to be insignificant [ $F(1,951) = 719.75, p = 0.11$ ], indicating that participants' *deliberate evaluation* affected their overall attitude toward these products containing offal-derived protein regardless of experienced ambivalence. Thus, hypothesis 3 is not supported by the data.

### 4.2.2 Effect of familiarity and information manipulations on the main variables

We found that *familiarity* had no significant main effect on the *intuitive evaluation* of product concepts containing protein extracted from beef offal [ $F(1,951) = 1.46, p = 0.23$ ]. Thus, hypothesis 4 is not supported by the data. Although not hypothesized, a significant main effect of *familiarity* on *deliberate evaluation* was detected [ $F(1,951) = 9.52, p < 0.001$ ]. Specifically, participants' *deliberate evaluation* for familiar product concepts was significantly more positive than that for unfamiliar product concepts.

We found that *information provision* had a significant main effect on *deliberative evaluation* [ $F(1,951) = 19.49, p < 0.01$ ] in the direction that providing information, either of benefit or ambiguous, led to a significantly more positive *deliberate*

TABLE 2 Participant demographics ( $n = 953$ ) and Pearson's chi-squared test to ensure no sampling bias across the six study conditions.

	CSO <sup>1</sup> ,%	<i>n</i> (%) or M (SD)		Distribution across survey conditions
Gender				
Male	48.9	492	(51.6%)	$\chi^2(5) = 3.99, p = 0.55$
Female	51.1	461	(48.4%)	
Age category				
18–24 years	11.2	85	(8.9%)	$\chi^2(25) = 18.86, p = 0.84$
25–34 years	18.5	166	(17.4%)	
35–44 years	20.6	214	(22.5%)	
45–54 years	17.6	191	(20.0%)	
55–64 years	14.2	159	(16.7%)	
65+ years	17.9	138	(14.5%)	
Highest level of education completed				
Primary school	11.7	7	(0.7%)	$\chi^2(15) = 17.96, p = 0.26$
Secondary school	45.5	272	(28.5%)	
Third level (non-degree, i.e., diploma, certificate)	11.7	327	(34.3%)	
Third level (degree or higher, i.e., undergraduate, postgraduate, PhD, etc.)	30.9	347	(36.4%)	
Social Class				
AB	24.3	203	(21.3%)	$\chi^2(20) = 21.98, p = 0.34$
C1	17.1	304	(31.9%)	
C2	37.3	142	(14.9%)	
DE	14.8	292	(30.6%)	
F	6.6	12	(1.3%)	
Provnieco f resiedenc				
Dublin	22.8	280	(29.4%)	$\chi^2(20) = 23.49, p = 0.27$
Rest of Leinster	21.4	252	(26.4%)	
Munster	33.7	274	(28.8%)	
Connacht	14.5	100	(10.5%)	
Ulster (part of ROI)	7.6	47	(4.9%)	
Survey condition				
Familiar + no information		161	(16.9%)	
Familiar + benefit information		155	(16.3%)	
Familiar + ambiguous information		164	(17.2%)	
Unfamiliar + no information		158	(16.6%)	
Unfamiliar + benefit information		159	(16.7%)	
Unfamiliar + ambiguous information		156	(16.4%)	
Attitudes toward consuming product carriers <sup>a</sup>				
Burgers		4.65	(1.49)	
Sausages		4.85	(1.43)	
Frequency of burger consumption				
Less than once per month		341	(35.8%)	
1–3 times a month		351	(36.8%)	
Once a week		208	(21.8%)	
2–4 times per week		48	(5%)	
5–6 times per week		3	(0.3%)	
Daily		2	(0.2%)	
Frequency of sausage consumption				
Less than once per month		187	(19.6%)	
1–3 times a month		278	(29.2%)	
Once a week		334	(35%)	
2–4 times per week		124	(13%)	
5–6 times per week		22	(2.3%)	
Daily		8	(0.9%)	

<sup>a</sup>Evaluated by one item: “I am positive about eating...” on a seven-point scale (1 = strongly disagree, 7 = strongly agree).<sup>1</sup>CSO, Central Statistics Office; M, mean; SD, standard deviation.

TABLE 3 Means (SDs) for intuitive evaluation, deliberate evaluation, overall attitude, and acceptance toward burgers tabulated by study conditions (measured on a seven-point scale) ( $n = 953$ ).

		Protein extraction source	Intuitive evaluation	Deliberate evaluation	Overall attitude	Acceptance
Sausages	No information	Liver	3.84 (1.28)	3.70 (1.48)	3.57 (1.82)	3.81 (1.65)
		Lung	3.72 (1.31)	3.40 (1.56)	3.12 (1.87)	3.20 (1.76)
	Benefit information	Liver	3.82 (1.33)	4.25 (1.54)	4.30 (1.71)	4.26 (1.53)
		Lung	3.77 (1.09)	4.15 (1.62)	4.25 (1.83)	4.17 (1.73)
	Ambiguous information	Liver	4.00 (1.04)	4.12 (1.38)	4.17 (1.63)	4.17 (1.53)
		Lung	3.81 (1.29)	3.75 (1.58)	3.78 (1.87)	3.68 (1.74)
Burgers	No information	Liver	3.57 (1.18)	3.74 (1.34)	3.92 (1.70)	3.92 (1.59)
		Lung	3.58 (1.31)	3.33 (1.48)	3.19 (1.74)	3.14 (1.68)
	Benefit information	Liver	3.75 (1.36)	4.39 (1.50)	4.50 (1.78)	4.37 (1.52)
		Lung	3.66 (1.10)	4.16 (1.62)	4.15 (1.67)	4.19 (1.62)
	Ambiguous information	Liver	3.70 (1.14)	4.16 (1.30)	4.24 (1.62)	4.20 (1.47)
		Lung	3.63 (1.17)	4.03 (1.56)	3.89 (1.90)	3.80 (1.68)

Red font denotes the highest value; blue font denotes the lowest value. SD, standard deviation.

evaluation than when no information was provided [ $t(950) = 6.03$ ,  $p < 0.05$  (one-tailed)]. These results provide support for hypothesis 5, that is, receiving any kind of information significantly positively increased deliberate evaluation compared with not receiving any information.

The interaction effect for *intuitive evaluation* and *ambiguous information* on *deliberate evaluation* was not significant [ $F(1,951) = 39.72$ ,  $p = 0.38$ ]. These results do not confirm hypothesis 6 and indicate that participants' intuitive evaluation of products containing protein extracted from beef offal affected their deliberate evaluation of these products similarly, whether or not ambiguous information was provided to them.

## 5 Discussion

Although we found that attitude ambivalence did not impact on overall attitude, the nature of this attitude needs to be considered. It has been noted that attitude ambivalence is associated with weaker attitudes (Britt et al., 2011; Simons et al., 2019), more susceptibility to change (Bassili, 1996; Armitage and Conner, 2000), and less attitude-behavior consistency (Armitage and Conner, 2004). These three factors need consideration and indeed ambivalence, as it exists in our study, could lead to a significant attitude behavior gap. Furthermore, the behaviors of two individuals displaying the same overall attitudes could vary dramatically. Attitude instability because of ambivalence may result in an openness to new information, resulting in a shift toward either a more positive or negative attitude valence. The credibility, transparency, and relevance of the information provided (to addressing sources of

ambivalence) is key to ensuring the emergence of more stable overall attitudes.

Using familiar carrier foods has been shown to increase the acceptance of novel foods (Wansink, 2002; Hartmann et al., 2015); however, exceptions occur when the combination of ingredients is perceived to be inappropriate (Stallberg-White and Pliner, 1999). To counter this risk, in the current study, we used two familiar carrier products. These were mince-based meats, to which the offal ingredient was added. Through this mechanism we were able to test the impact of familiarity of the ingredient on overall attitude. Our findings suggest that the potential impact of lack of familiarity with the ingredient is offset by familiarity with the carrier products. Building on the evidence base that incorporating novel ingredients into familiar foods impacts on the acceptance of the former, importantly, this study suggests that the impact is equal across novel ingredients, irrespective of their level of novelty. The study findings also corroborate the conclusion put forward by Henchion et al. (2016), namely that “familiarity with the form of the carrier was significant in overcoming ideational influences”. This is important because ideation could lead to a disgust response, which could manifest in intuitive evaluations. A disgust response results in foods being rejected “because of what they are, where they came from, or their social history” (Martins and Pliner, 2005 p. 215). The evidence here suggests that a disgust response is not dominating the evaluation of these novel foods but creating a “good gut feeling” about their consumption, which could in turn improve intuitive evaluations and indeed attenuate the effect of attitude ambivalence (Groenendyk, 2019).

With respect to attitude formation, this study found that consumers' intuitive and deliberate evaluations toward the

products with novel ingredients worked in the same direction, and predicted their overall attitudes toward these products. However, deliberate evaluation was found to be a better predictor of consumers' overall attitudes. This result can be related to the differential roles of intuitive and deliberate evaluation. Research has suggested a dissociation pattern, with intuitive evaluation influencing spontaneous choices and behaviors, and deliberate evaluations influencing conscious evaluations (Perugini, 2005; Richetin et al., 2007; König et al., 2016).

In addition, this analysis found that intuitive evaluations do not influence deliberate evaluations, suggesting that information provision that prompts deliberate evaluations could lead to the formation of more considered and stable attitudes. Although this study concurs with the argument of information studies in general and in related areas of application [e.g., Pelchat and Pliner, 1995, Verneau et al. (2016) in relation to insect-based products and Bekker et al. (2017) in relation to cultured meat] that providing information on product benefits results in more positive evaluations, it also found that the provision of information, be it benefit or benefit–risk orientated, has a positive effect on deliberate evaluations. This finding adds to the suggestion that explicitly referencing uncertainty, in this case the risk, can increase persuasion. Karmarkar and Tormala (2010) found that, in certain conditions, when an expert source expresses some level of uncertainty, deeper message processing can occur with a positive impact.

## 6 Practical implications

The current study demonstrates that consumers expressed relatively positive attitudes toward the food products containing protein extracted from beef offal, indicating that protein extracted from beef offal has a realistic potential of being incorporated into food products as an alternative protein source, and being accepted by consumers in Ireland. Specifically, familiar product concepts containing protein extracted from beef offal were more (deliberately) positively evaluated, than unfamiliar product concepts. Therefore, product developers should focus on incorporating protein extracted from familiar beef offal sources, such as the liver or heart rather than those that are more unfamiliar, such as lungs. Beyond the results of this study which was conducted with Irish consumers, it should be noted that familiarity and exposure to beef offal is culture dependent, and the social influence on individuals' choices to eat the meat of some animals and avoid that of others may vary among collectivistic and individualistic cultural contexts (Ruby and Heine, 2012).

Consumers' attitudes and acceptance of food products containing protein extracted from beef offal should be also considered at a societal level. Achieving acceptance on both personal and societal levels might support the emergence of stable attitudes, and, therefore, of decisions to consume these food products. Public acceptance of many new foods (e.g., sushi and avocado, in the European context) and associated technologies (e.g., GM) appears to be an evolutionary rather than a revolutionary process. Studies on foods that were initially perceived as novel and

that gained widespread acceptance over time show that new foods initially gain popularity in one small social segment before diffusing further (House, 2016). Technologies that are more established also tend to be viewed more positively by some consumer segments (Food Standard Agency, 2020). Following on from work on the establishment of other new foods, it is recommended that early adopters, rather than general populations, receive greater attention, and familiar food technologies might positively contribute to public acceptance. In this way, the overall market acceptance of food products containing protein extracted from beef offal could be increased over time.

In addition to carefully designing products containing protein extracted from beef offal and ensuring the availability of these products, other elements of the marketing mix, particularly promotion, should be considered as a precondition for their success. Promotion of these products through social media, which allows businesses to be in direct contact with consumers, could be a promising channel of communication. Social networks and platforms enable people to communicate with each other, share information and content, and, in many cases, are used as a way to spread awareness and influence others. Communication of new things is often cognitive in nature, with a focus on explaining (Dudo, 2013). Indeed, the current study shows that providing information about the health and environmental benefits of consuming food products containing protein extracted from beef offal was (deliberately) positively evaluated. Therefore, any action that would favor deliberation is likely to increase the possibility that deliberate attitudes would drive consumers' attitudes and potentially their decisions in the marketplace. However, the present research also indicates that it is important to address affect when presenting these food products, as consumers' intuitive evaluations are also important. Therefore, communication campaigns for products containing protein extracted from beef offal should be carefully designed and incorporate both affective and cognitive elements.

Finally, it should be noted that in order to achieve successful inclusion of protein extracted from beef offal into humans' diet, collective action of a variety of stakeholders (e.g., nutrition experts, the food industry, policymakers, and food quality agencies) is necessary. Although marketing strategies at the product level (i.e., around the food product containing protein extracted from beef offal) are essential, broader communication which targets the consumer acceptance of products containing ingredients that have been extracted from co-processing streams more generally is also very important. This communication could be embedded in the context of drive toward a circular economy and the aim of transitioning toward a more sustainable food system. Moreover, this transdisciplinary approach facilitating engagement between different stakeholders supports learning and knowledge exchange across organizations and sectors. In this way, industry awareness will also be achieved, with manufacturers—across food and non-food sectors—having access to information regarding the opportunities to develop products containing ingredients from co-processing streams. Socializing the idea of valorizing meat by-products for human consumption, through different channels and with the use of consistently delivered, transparent, reliable, and

informative content could be an effective strategy to include beef offal extracted protein in diets. In essence, the end goal would be that food products containing protein extracted from beef offal could turn into habitual purchases for some consumer segments. In this process, consumers need to have the tools available to accommodate deliberative evaluation, and, when attitudes are positive, choices can turn into habits.

## 7 Limitations

As with any research, the scope of the present study is necessarily restricted. One limitation concerns the conceptualization of familiar and unfamiliar product concepts. Although the carrier products, that is, burgers and sausages, are well-established food products, familiarity with the product concepts was addressed through the incorporation of one more familiar (i.e., beef liver) and one more unfamiliar (i.e., beef lung) protein source into the product carriers. Future research should further identify what other product carrier–ingredient combinations are truly familiar or unfamiliar. Comparing attitudes toward unfamiliar food products from other cultures to familiar food products from one's own culture could be an interesting research direction.

A further limitation has to do with the experimental setup used in this study to investigate consumers' attitudes. Although a questionnaire-based survey is the most commonly used method, thanks to its relatively low cost and ease of administration, this method suffers from some limitations. The most salient of these are self-representation biases (e.g., responding in a way that reflects social desirability) and an inability to report actual cognitive contents and behaviors (Greenwald and Banaji, 2010; Glöckner and Herbold, 2011). The possible impact of the survey methodology on consumer responses also needs to be considered, as it is unlikely that consumers go through substantial elaboration in the process of attitude expression for most of their daily food decisions.

Finally, limitations arise for the measures used to depict intuitive evaluations such as the AMP used in this study. No intuitive measurement is process pure, as they are all based on a behavioral task that involves a controlled process (e.g., press a button, make a choice) besides the automatic evaluation (Conrey et al., 2005). Physiological measurements such as galvanic skin response, heart rate variability, fMRI (a technique that measures brain activity by detecting changes associated with blood flow), and eye tracking provide insights into underlying psychological processes, without constraining any of the involved processes (Glöckner and Witteman, 2010). Although it is practically impossible to apply these tools to a large study sample, it would be interesting to combine these experimental studies with large representative sample surveys to acquire a deeper understanding of the underlying processes in attitude formation toward the specific food products under investigation.

## Data availability statement

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

## Ethics statement

Ethics approval was not provided for this study on human participants because ethics approval was not required according to local legislation or lead research (Teagasc) institutional requirements. However, ethics and data protection guidelines as set down in the EC Ethics and data protection (2018) document were followed. Participants provided informed consent and were afforded the opportunity to withdraw from the study. In addition, all data were anonymized, and the data protection standards applied in all institutions were adhered to. The patients/participants provided their written informed consent to participate in this study.

## Author contributions

GL: conceptualization, methodology, analysis, data curation, and writing—original draft. MH: conceptualization, methodology, supervision, writing—review and editing, and funding acquisition. MM: conceptualization, methodology, supervision, writing—review and editing, and funding acquisition. SO'R: conceptualization, methodology supervision, and writing—review and editing. All authors contributed to the article and approved the submitted version.

## Funding

This research was funded through the Teagasc Walsh Fellowship Programme and forms part of the ReValueProtein Research Programme, which was supported by the Department of Agriculture, Food, and the Marine (DAFM) through the Food Institutional Research Measure (FIRM) (11/F/043).

## 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.

## Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.



## References

- Ajzen, I. (1991). The theory of planned behavior. *Organ. Behav. Hum. Decis. Processes* 50, 179–211. doi: 10.1016/0749-5978(91)90020-T
- Álvarez, C., Drummond, L., and Mullen, A. M. (2018). Expanding the industrial applications of a meat co-product: generation of low-haemoglobin content plasma by means of red cells crenation. *J. Clean. Prod.* 185, 805–813. doi: 10.1016/j.jclepro.2018.03.077
- Armitage, C. J., and Conner, M. (2000). Attitudinal ambivalence: a test of three key hypotheses. *Pers. Soc. Psychol. Bull.* 26 (11), 1421–1432. doi: 10.1177/0146167200263009
- Armitage, C. J., and Conner, M. (2004). “The effects of attitudinal ambivalence on attitude-intention-behavior relations,” in *Contemporary perspectives on the psychology of attitudes*. Eds. G. Haddock and G. R. Maio (New York, NY: Psychology Press), 121–143.
- Bäckström, A., Pirttilä-Backman, A. M., and Tuorila, H. (2003). Dimensions of novelty: a social representation approach to new foods. *Appetite* 40, 299–307. doi: 10.1016/S0195-6663(03)00005-9
- Baiano, A. (2014). Recovery of biomolecules from food wastes - a review. *Molecules* 19, 14821–14842. doi: 10.3390/molecules190914821
- Barsics, F., Caparros Megido, R., Brostaux, Y., Barsics, C., Blecker, C., Haubruge, E., et al. (2017). Could new information influence attitudes to foods supplemented with edible insects? *Br. Food J.* 119, 2027–2039. doi: 10.1108/BFJ-11-2016-0541
- Bassili, J. N. (1996). Meta-judgmental versus operative indexes of psychological attributes: the case of measures of attitude strength. *J. Pers. Soc. Psychol.* 71 (4), 637–653. doi: 10.1037/0022-3514.71.4.637
- Bech-Larsen, T., and Grunert, K. G. (2003). The perceived healthiness of functional foods: a conjoint study of Danish, Finnish and American consumers' perception of functional foods. *Appetite* 40, 9–14. doi: 10.1016/S0195-6663(02)00171-x
- Bekker, G. A., Fischer, A. R. H., Tobi, H., and Van Trijp, H. C. M. (2017). Explicit and implicit attitude toward an emerging food technology: the case of cultured meat. *Appetite* 108, 245–254. doi: 10.1016/j.appet.2016.10.002
- Bohner, G., Erb, H. P., and Siebler, F. (2011). Information processing approaches to persuasion: integrating assumptions from the dual- and single-processing perspectives. *Attitudes Attitude Change*. New York: Psychology Press. doi: 10.4324/9780203838068
- Britt, T. W., Pusilo, C. L., McKibben, E. S., Kelley, C., Baker, A. N., and Nielson, K. A. (2011). Personality and strength related attitude dimensions: between and within-person relationships. *J. Res. Pers.* 45, 586–596. doi: 10.1016/j.jrp.2011.07.006
- Bruner, G. (2017). *Marketing scales handbook: multi-item measures for consumer insight research*. Vol. Volume 9 (Texas, USA: CreateSpace Independent Publishing Platform).
- Cash, T., Desbrow, B., Leveritt, M., and Ball, L. (2015). Utilization and preference of nutrition information sources in Australia. *Health Expect.* 18, 2288–2295. doi: 10.1111/hex.12198
- Cavaleiro, A. J., Ferreira, T., Pereira, F., Tommaso, G., and Alves, M. M. (2013). Biochemical methane potential of raw and pre-treated meat-processing wastes. *Bioresour. Technol.* 129, 519–525. doi: 10.1016/j.biortech.2012.11.083
- Chaiken, S. (1980). Heuristic versus systematic information processing and the use of source versus message cues in persuasion. *J. Pers. Soc. Psychol.* 39, 752–766. doi: 10.1037/0022-3514.39.5.752
- Clark, W., and Lenaghan, M. (2020). *The future of food: sustainable protein strategies around the world* (Stirling, Scotland, UK: Zero Waste Scotland).
- Clark, J. K., Wegener, D. T., and Fabrigar, L. R. (2008). Attitudinal ambivalence and message-based persuasion: motivated processing of pro-attitudinal information and avoidance of counter attitudinal information. *Pers. Soc. Psychol. Bull.* 34, 565–577. doi: 10.1177/014616720731
- Conrey, F. R., Gawronski, B., Sherman, J. W., Hugenberg, K., and Groom, C. J. (2005). Separating multiple processes in implicit social cognition: the quad model of implicit task performance. *J. Pers. Soc. Psychol.* 89, 469–487. doi: 10.1037/0022-3514.89.4.469
- Costa-Font, M., Gil, J. M., and Traill, W. B. (2008). Consumer acceptance, valuation of and attitudes towards genetically modified food: review and implications for food policy. *Food Policy* 33, 99–111. doi: 10.1016/j.foodpol.2007.07.002
- Crano, W. D., and Prislin, R. (2006). Attitudes and persuasion. *Annu. Rev. Psychol.* 57, 345–374. doi: 10.1146/annurev.psych.57.102904.190034
- Darine, S., Christophe, V., and Gholamreza, D. (2010). Production and functional properties of beef lung protein concentrates. *Meat Sci.* 84, 315–322. doi: 10.1016/j.meatsci.2009.03.007
- De Beukelaar, M. F. A., Zeinstra, G. G., Mes, J. J., and Fischer, A. R. H. (2019). Duckweed as human food. the influence of meal context and information on duckweed acceptability of Dutch consumers. *Food Qual. Prefer.* 71, 76–86. doi: 10.1016/j.foodqual.2018.06.005
- Duckworth, K. L., Bargh, J. A., Garcia, M., and Chaiken, S. (2002). The automatic evaluation of novel stimuli. *psychol. Sci.* 13, 513–519. doi: 10.1111/1467-9280.00490
- Dudo, A. (2013). Toward a model of scientists' public communication activity: the case of biomedical researchers. *Sci. Commun.* 35, 476–501. doi: 10.1177/10755470124608
- Eagly, A. H., and Chaiken, S. (1993). *The psychology of attitudes* (Fort Worth, TX: Harcourt Brace Jovanovich College Publishers).
- Eagly, A. H., and Chaiken, S. (2007). The advantages of an inclusive definition of attitude. *Soc. Cogn.* 25, 582–602. doi: 10.1521/soco.2007.25.5.582
- Epstein, S. (2010). Demystifying intuition: what it is, what it does, and how it does it. *psychol. Inq.* 21, 295–312. doi: 10.1080/1047840X.2010.523875
- Evans, J. S. B. T. (2008). Dual-processing accounts of reasoning, judgment, and social cognition. *Annu. Rev. Psychol.* doi: 10.1146/annurev.psych.59.103006.093629
- FAO (2018). *The future of food and agriculture—alternative pathways to 2050* (Rome, Italy: Food and Agriculture Organization of the United Nations).
- Fischer, A. R. H., and Frewer, L. J. (2009). Consumer familiarity with foods and the perception of risks and benefits. *Food Qual. Prefer.* 20, 576–585. doi: 10.1016/j.foodqual.2009.06.008
- Flórek, M., Litwińczuk, Z., Skalecki, P., Ke, dzierska-Matysek, M., and Grodzicki, T. (2012). Chemical composition and inherent properties of offal from calves maintained under two production systems. *Meat Sci.* 90, 402–409. doi: 10.1016/j.meatsci.2011.08.007
- Food Standard Agency (2020) *Consumer attitudes towards emerging food technologies*. Available at: [https://www.food.gov.uk/sites/default/files/media/document/consumer-attitudes-emerging-food-technologies\\_0.pdf](https://www.food.gov.uk/sites/default/files/media/document/consumer-attitudes-emerging-food-technologies_0.pdf).
- Frewer, L. J., and Gremmen, B. (2007). “Consumer's interests in food processing waste management and co-product recovery,” in *Handbook of waste management and Co-product recovery in food processing*, vol. Vol. 1. Ed. K. Waldron (Cambridge, UK: Woodhead Publishing), 21–33.
- Frewer, L. J., Howard, C., and Shepherd, R. (1998). The influence of initial attitudes on responses to communication about genetic engineering in food production. *Agric. Hum. Values* 15, 15–30. doi: 10.1023/A:1007465730039
- Frewer, L. J., Scholderer, J., and Bredahl, L. (2003). Communicating about the risks and benefits of genetically modified foods: the mediating role of trust. *Risk Anal.* 23, 1117–1133. doi: 10.1111/j.0272-4332.2003.00385.x
- Furst, T., Connors, M., Bisogni, C. A., Sobal, J., and Falk, L. W. (1996). Food choice: a conceptual model of the process. *Appetite* 26, 247–265. doi: 10.1006/appe.1996.0019
- Gawronski, B., and Creighton, L. A. (2013). “Dual process theories,” in *The Oxford handbook of social cognition*. Ed. D. E. Carlston (Oxford University Press), 282–312.
- Glöckner, A., and Herbold, A. K. (2011). An eye-tracking study on information processing in risky decisions: evidence for compensatory strategies based on automatic processes. *J. Behav. Decis. Mak.* 24, 71–98. doi: 10.1002/bdm.684
- Glöckner, A., and Witteman, C. (2010). Beyond dual-process models: a categorisation of processes underlying intuitive judgement and decision making. *Think. Reason.* 16, 1–25. doi: 10.1080/13546780903395748
- Gmuer, A., Nuessli Guth, J., Hartmann, C., and Siegrist, M. (2016). Effects of the degree of processing of insect ingredients in snacks on expected emotional experiences and willingness to eat. *Food Qual. Prefer.* 54, 117–127. doi: 10.1016/j.foodqual.2016.07.003
- Gorissen, K., and Weijters, B. (2016). The negative footprint illusion: perceptual bias in sustainable food consumption. *J. Environ. Psychol.* 45, 50–65. doi: 10.1016/j.jenvp.2015.11.009
- Gray, N. J., Klein, J. D., Noyce, P. R., Sesselberg, T. S., and Cantrill, J. A. (2005). Health information-seeking behavior in adolescence: the place of the internet. *Soc. Sci. Med.* 60, 1467–1478. doi: 10.1016/j.socscimed.2004.08.010
- Greenwald, A. G., and Banaji, M. R. (2010). Implicit social cognition: attitudes, self-esteem, and stereotypes. *Psychol. Market.* 27, 921–927. doi: 10.1037/0033-295x.102.1.4
- Groenendyk, E. (2019). Of two minds, but one heart: a good “Gut” feeling moderates the effect of ambivalence on attitude formation and turnout. *Am. J. Pol. Sci.* 63 (2), 368–384. doi: 10.1111/ajps.12419
- Grunert, K. G., Lahteenmaki, L., Nielsen, N. A., Poulsen, J. B., Ueland, O., and Astrom, A. (2001). Consumer perceptions of food products involving genetic modification - results from a qualitative study in four Nordic countries. *Food Qual. Prefer.* 12, 527–542. doi: 10.1016/S0950-3293(01)00049-0
- Haidt, J. (2001). The emotional dog and its rational tail: a social intuitionist approach to moral judgment. *psychol. Rev.* 108, 814–834. doi: 10.1037/0033-295X.108.4.814
- Hartmann, C., Shi, J., Giusto, A., and Siegrist, M. (2015). The psychology of eating insects: a cross-cultural comparison between Germany and China. *Food Qual. Prefer.* 44, 148–156. doi: 10.1016/j.foodqual.2015.04.013
- Henchion, M., Hayes, M., Mullen, A. M., Fenelon, M., and Tiwari, B. (2017). Future protein supply and demand: strategies and factors influencing a sustainable equilibrium. *Foods* 6 (7), 53. doi: 10.3390/foods6070053
- Henchion, M., McCarthy, M., and O'Callaghan, J. (2016). Transforming beef by-products into valuable ingredients: which spell/recipe to use? *Front. Nutr.* 3. doi: 10.3389/fnut.2016.00053



- Hofmann, W., Friese, M., and Roefs, A. (2009). Three ways to resist temptation: the independent contributions of executive attention, inhibitory control, and affect regulation to the impulse control of eating behavior. *J. Exp. Soc. Psychol.* 45, 431–435. doi: 10.1016/j.jesp.2008.09.013
- House, J. (2016). Consumer acceptance of insect-based foods in the Netherlands: academic and commercial implications. *Appetite* 107, 47–58. doi: 10.1016/j.appet.2016.07.023
- Intergovernmental Panel on Climate Change (2019). “Summary for policymakers,” in *Climate change and land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems*. Eds. P. R. Shukla, J. Skea, E. Calvo Buendia, V. Masson-Delmotte, H.-O. Pörtner, D. C. Roberts and P. Zhai In press.
- Jayatilakan, K., Sultana, K., Radhakrishna, K., and Bawa, A. S. (2012). Utilization of byproducts and waste materials from meat, poultry and fish processing industries: a review. *J. Food Sci. Technol.* 49, 278–293. doi: 10.1007/s13197-011-0290-7
- Karmarkar, U. R., and Tormala, Z. L. (2010). Believe me, I have no idea what I’m talking about: the effects of source certainty on consumer involvement and persuasion. *J. Consum. Res.* 36, 1033–1049. doi: 10.1086/648381
- Kempf, D. S., and Laczniak, R. N. (2001). Advertising’s influence on subsequent product trial processing. *J. Advert.* 30, 37–38. doi: 10.1080/00913367.2001.10673643
- König, L. M., Giese, H., Schupp, H. T., and Renner, B. (2016). The environment makes a difference: the impact of explicit and implicit attitudes as precursors in different food choice tasks. *Front. Psychol.* 7. doi: 10.3389/fpsyg.2016.01301
- Kruglanski, A. W., and Gigerenzer, G. (2011). Intuitive and deliberate judgments are based on common principles. *psychol. Rev.* 118, 97–109. doi: 10.1037/a0020762
- Krutulyte, R., Grunert, K. G., Scholderer, J., Lähteenmäki, L., Hagemann, K. S., Elgaard, P., et al. (2011). Perceived fit of different combinations of carriers and functional ingredients and its effect on purchase intention. *Food Qual. Prefer.* 22, 11–16. doi: 10.1016/j.foodqual.2010.06.001
- Lähteenmäki, L. (2013). Claiming health in food products. *Food Qual. Prefer.* 27, 196–201. doi: 10.1016/j.foodqual.2012.03.006
- Lalor, F., Madden, C., McKenzie, K., and Wall, P. G. (2011). Health claims on foodstuffs: a focus group study of consumer attitudes. *J. Funct. Foods* 3, 56–59. doi: 10.1016/j.jff.2011.02.001
- Lampila, P., van Lieshout, M., Gremmen, B., and Lähteenmäki, L. (2009). Consumer attitudes towards enhanced flavonoid content in fruit. *Food Res. Int.* 42, 122–129. doi: 10.1016/j.foodres.2008.09.002
- Leathwood, P. D., Richardson, D. P., Sträter, P., Todd, P. M., and Van Trijp, H. C. M. (2007). Consumer understanding of nutrition and health claims: sources of evidence. *Br. J. Nutr.* 98, 474–484. doi: 10.1017/S000711450778697X
- Lebel, E. P., and Paunonen, S. V. (2011). Sexy but often unreliable: the impact of unreliability on the replicability of experimental findings with implicit measures. *Pers. Soc. Psychol. Bull.* 37, 570–583. doi: 10.1177/0146167211400619
- Lee, C. J., Scheufele, D. A., and Lewenstein, B. V. (2005). Public attitudes toward emerging technologies: examining the interactive effects of cognitions and affect on public attitudes toward nanotechnology. *Sci. Commun.* 27, 240–267. doi: 10.1177/1075547005281
- Lu, J. (2015). The effect of perceived carrier-ingredient fit on purchase intention of functional food moderated by nutrition knowledge and health claim. *Br. Food J.* 117, 1872–1885. doi: 10.1108/BFJ-11-2014-0372
- Lyly, M., Roininen, K., Honkapää, K., Poutanen, K., and Lähteenmäki, L. (2007). Factors influencing consumers’ willingness to use beverages and ready-to-eat frozen soups containing oat  $\beta$ -glucan in Finland, France and Sweden. *Food Qual. Prefer.* 18, 242–255. doi: 10.1016/j.foodqual.2005.12.001
- Lynch, S. A., Mullen, A. M., O’Neill, E. E., and García, C. Á. (2017). Harnessing the potential of blood proteins as functional ingredients: a review of the state of the art in blood processing. *Compr. Rev. Food Sci. Food Saf.* 16, 330–344. doi: 10.1111/1541-4337.12254
- Marquardt, N., and Hoeger, R. (2009). The effect of implicit moral attitudes on managerial decision-making: an implicit social cognition approach. *J. Bus. Ethics* 85, 157–171. doi: 10.1007/s10551-008-9754-8
- Martins, Y., Pelchat, M. L., and Pliner, P. (1997). “Try it; it’s good and it’s good for you”: effects of taste and nutrition information on willingness to try novel foods. *Appetite* 28 (2), 89–102. doi: 10.1006/appe.1996.0064
- Martins, Y., and Pliner, P. (2005). Human food choices: an examination of the factors underlying acceptance/rejection of novel and familiar animal and non-animal foods. *Appetite* 45, 212–214. doi: 10.1016/j.appet.2005.08.002
- McCarthy, M., De Boer, M., O’Reilly, S., and Cotter, L. (2003). Factors influencing intention to purchase beef in the Irish market. *Meat Sci.* 65, 1071–1083. doi: 10.1016/S0309-1740(02)00325-X
- Moskowitz, G. B., Chaiken, S., and Böhner, G. (1995). The interplay of heuristic and systematic processing of social information. *Eur. Rev. Soc. Psychol.* 6, 33–68. doi: 10.1080/14792779443000003
- Mullen, A. M., Álvarez, C., Zeugolis, D. I., Henchion, M., O’Neill, E., and Drummond, L. (2017). Alternative uses for co-products: harnessing the potential of valuable compounds from meat processing chains. *Meat Sci.* 132, 90–98. doi: 10.1016/j.meatsci.2017.04.243
- Nordgren, L. F., Van Harreveld, F., and van der Pligt, J. (2006). Ambivalence, discomfort, and motivated information processing. *J. Exp. Soc. Psychol.* 42, 252–258. doi: 10.1016/j.jesp.2005.04.004
- Nowlis, S. M., Kahn, B. E., and Dhar, R. (2002). Coping with ambivalence: the effect of removing a neutral option on consumer attitude and preference judgments. *J. Consum. Res.* 29, 319–334. doi: 10.1086/344431
- Olson, M. A., and Kendrick, R. V. (2011). *Origins of attitudes. Attitudes Attitude Change*. New York: Psychology Press. doi: 10.4324/9780203838068
- Pachur, T., and Spaar, M. (2015). Domain-specific preferences for intuition and deliberation in decision making. *J. Appl. Res. Memory Cogn.* 4, 303–311. doi: 10.1016/j.jarmac.2015.07.006
- Payne, B. K., Cheng, C. M., Govorun, O., and Stewart, B. D. (2005). An inkblot for attitudes: affect misattribution as implicit measurement. *J. Pers. Soc. Psychol.* 89, 277–293. doi: 10.1037/0022-3514.89.3.277
- Payne, K., and Lundberg, K. (2014). The affect misattribution procedure: ten years of evidence on reliability, validity, and mechanisms. *Soc. Pers. Psychol. Compass* 8, 672–686. doi: 10.1111/spc3.12148
- Pelchat, M. L., and Pliner, P. (1995). “Try it, you’ll like it”: effects of information on willingness to try novel foods. *Appetite* 24, 153–165. doi: 10.1016/S0195-6663(95)99373-8
- Perugini, M. (2005). Predictive models of implicit and explicit attitudes. *Br. J. Soc. Psychol.* 44, 29–45. doi: 10.1348/014466604X23491
- Pham, M. T., and Avnet, T. (2004). Ideals and oughts and the reliance on affect versus substance in persuasion. *J. Consum. Res.* 30, 503–518. doi: 10.1086/380285
- Priester, J. R., and Petty, R. E. (1996). The gradual threshold model of ambivalence: relating the positive and negative bases of attitudes to subjective ambivalence. *J. Pers. Soc. Psychol.* 71, 431–449. doi: 10.1037/0022-3514.71.3.431
- Randall, E. (1981). Food preferences—their conceptualization and relationship to consumption. *Ecol. Food Nutr.* 11, 151–161. doi: 10.1080/03670244.1981.9990671
- Richard, A., Meule, A., Friese, M., and Blechert, J. (2017). Effects of chocolate deprivation on implicit and explicit evaluation of chocolate in high and low trait chocolate cravers. *Front. Psychol.* 8. doi: 10.3389/fpsyg.2017.01591
- Richetin, J., Perugini, M., Adjali, I., and Hurling, R. (2007). The moderator role of intuitive versus deliberative decision making for the predictive validity of implicit and explicit measures. *Eur. J. Pers.* 21, 529–546. doi: 10.1002/per.625
- Rozin, P. (2006). *The Integration of Biological, Social, Cultural and Psychological Influences on Food Choice*. Eds. R. Shepherd and M. Raats. Oxfordshire: The Psychology of Food Choice, CAB. doi: 10.1079/9780851990323.0019
- Ruby, M. B., and Heine, S. J. (2012). Too close to home: factors predicting meat avoidance. *Appetite* 59 (1), 47–52. doi: 10.1016/j.appet.2012.03.020
- Sabbe, S., Verbeke, W., Deliza, R., Matta, V., and Van Damme, P. (2009). Effect of a health claim and personal characteristics on consumer acceptance of fruit juices with different concentrations of açai (*Euterpe oleracea* mart.). *Appetite* 53, 84–92. doi: 10.1016/j.appet.2009.05.014
- Sawicki, V., Wegener, D. T., Clark, J. K., Fabrigar, L. R., Smith, S. M., and Durso, G. R. O. (2013). Feeling conflicted and seeking information: when ambivalence enhances and diminishes selective exposure to attitude-consistent information. *Pers. Soc. Psychol. Bull.* 39, 735–747. doi: 10.1177/0146167213481388
- Schösler, J., Boer, J. D., and Boersema, J. J. (2012). Can we cut out the meat of the dish? constructing consumer-oriented pathways towards meat substitution. *Appetite* 58, 39–47. doi: 10.1016/j.appet.2011.09.009
- Shepherd, R. (1999). Social determinants of food choice. *Proc. Nutr. Soc.* 58 (4), 807–812. doi: 10.1017/S0029665199001093
- Siegrist, M., Stampfli, N., and Kastenholz, H. (2008). Consumers’ willingness to buy functional foods: the influence of carrier, benefit and trust. *Appetite* 51, 526–529. doi: 10.1016/j.appet.2008.04.003
- Simons, J. J. P., Schneider, I. K., and Sanchez-Burks, J. (2019). *Ambivalence, the person and the attitude object: individual differences in the experience of ambivalence* (PsyArXiv). doi: 10.31234/osf.io/t7tvd
- Sobal, J., and Bisogni, C. A. (2009). Constructing food choice decisions. *Ann. Behav. Med.* 38, S37–S46. doi: 10.1007/s12160-009-9124-5
- Sparks, P., Conner, M., James, R., Shepherd, R., and Povey, R. (2001). Ambivalence about health-related behaviors: an exploration in the domain of food choice. *Br. J. Health Psychol.* 6, 53–68. doi: 10.1348/135910701169052
- Stallberg-White, C., and Pliner, P. (1999). The effect of flavor principles on willingness to taste novel foods. *Appetite* 33 (2), 209–221. doi: 10.1006/appe.1999.0263
- Steenson, S., and Buttriss, J. (2020). The challenges of defining a healthy and ‘sustainable’ diet. *Nutr. Bull.* 45, 206–222. doi: 10.1111/mbu.12439
- Stone, J., and Cooper, J. (2001). A self-standards model of cognitive dissonance. *J. Exp. Soc. Psychol.* 37, 228–243. doi: 10.1006/jesp.2000.1446
- Tan, H. S. G., Fischer, A. R. H., Tinchin, P., Stieger, M., Steenbekkers, L. P. A., and Van Trijp, H. C. M. (2015). Insects as food: exploring cultural exposure and individual experience as determinants of acceptance. *Food Qual. Prefer.* 42, 78–89. doi: 10.1016/j.foodqual.2015.01.013
- Tan, H. S. G., Tibboel, C. J., and Stieger, M. (2017). Why do unusual novel foods like insects lack sensory appeal? investigating the underlying sensory perceptions. *Food Qual. Prefer.* 60, 48–58. doi: 10.1016/j.foodqual.2017.03.012
- Tan, H. S. G., Van Den Berg, E., and Stieger, M. (2016). The influence of product preparation, familiarity and individual traits on the consumer acceptance of insects as food. *Food Qual. Prefer.* 52, 222–231. doi: 10.1016/j.foodqual.2016.05.003

- Thompson, M. M., Zanna, M. P., and Griffin, D. W. (1995). "Let's not be indifferent about (attitudinal) ambivalence," in *Attitude strength: antecedents and consequences*. Eds. R. E. Petty and J. A. Krosnick (Lawrence Erlbaum Associates, Inc), 361–386.
- Toldrá, F., Aristoy, M. C., Mora, L., and Reig, M. (2012). Innovations in value-addition of edible meat by-products. *Meat Sci.* 92, 290–296. doi: 10.1016/j.meatsci.2012.04.004
- Tuorila, H., Lähteenmäki, L., Pohjalainen, L., and Lotti, L. (2001). Food neophobia among the fins and related responses to familiar and unfamiliar foods. *Food Qual. Prefer.* 12, 29–37. doi: 10.1016/S0950-3293(00)00025-2
- Van Der Spiegel, M., Noordam, M., and van der Fels-Klerx, H. J. (2013). Safety of novel protein sources (Insects, microalgae, seaweed, duckweed, and rapeseed) and legislative aspects for their application in food and feed production. *Compr. Rev. Food Sci. Food Saf.* 12 (6), 662–678. doi: 10.1111/1541-4337.12032
- Van Giesen, R. I., Fischer, A. R. H., Van Dijk, H., and Van Trijp, H. C. M. (2015). Affect and cognition in attitude formation toward familiar and unfamiliar attitude objects. *PLoS One* 10. doi: 10.1371/journal.pone.0141790
- Van Harreveld, F., and Van Der Pligt, J. (2004). Attitudes as stable and transparent constructions. *J. Exp. Soc. Psychol.* 40, 666–674. doi: 10.1016/j.jesp.2003.12.004
- Van Harreveld, F., van der Pligt, J., De Vries, N. K., Wenneker, C., and Verhue, D. (2004). Ambivalence and information integration in attitudinal judgment. *Br. J. Soc. Psychol.* 43, 431–447. doi: 10.1348/0144666042037971
- Van Kleef, E., Van Trijp, H. C. M., and Luning, P. (2005). Functional foods: health claim-food product compatibility and the impact of health claim framing on consumer evaluation. *Appetite* 44, 299–308. doi: 10.1016/j.appet.2005.01.009
- Verbeke, W. (2015). Profiling consumers who are ready to adopt insects as a meat substitute in a Western society. *Food Qual. Prefer.* 39, 147–155. doi: 10.1016/j.foodqual.2014.07.008
- Verbeke, W., Scholderer, J., and Lähteenmäki, L. (2009). Consumer appeal of nutrition and health claims in three existing product concepts. *Appetite* 52, 684–692. doi: 10.1016/j.appet.2009.03.007
- Verneau, F., La Barbera, F., Kolle, S., Amato, M., Del Giudice, T., and Grunert, K. (2016). The effect of communication and implicit associations on consuming insects: an experiment in Denmark and Italy. *Appetite* 106, 30–36. doi: 10.1016/j.appet.2016.02.006
- Wansink, B. (2002). Changing eating habits on the home front: lost lessons from world war II research. *J. Public Policy Market.* 21, 90–99. doi: 10.1509/jppm.21.1.90.17614
- Westhoek, H. (2011). *The protein puzzle: the consumption and production of meat, dairy and fish in the European union* (The Hague: Netherlands Environmental Assessment Agency (PBL). Available at: [http://www.pbl.nl/sites/default/files/cms/publicaties/Protein\\_Puzzle\\_web.pdf](http://www.pbl.nl/sites/default/files/cms/publicaties/Protein_Puzzle_web.pdf).
- Willett, W., Rockström, J., Loken, B., Springmann, M., Lang, T., Vermeulen, S., et al. (2019). Food in the anthropocene: the EAT-lancet commission on healthy diets from sustainable food systems. *Lancet* 393 (10170), 447–492. doi: 10.1016/S0140-6736(18)31788-4
- Woodward, H. E., Treat, T. A., Cameron, C. D., and Yegorova, V. (2017). Valence and arousal-based affective evaluations of foods. *Eat. Behav.* 24, 26–33. doi: 10.1016/j.eatbeh.2016.11.004
- Zemboirain, M. R., and Johar, G. V. (2007). Attitudinal ambivalence and openness to persuasion: a framework for interpersonal influence. *J. Consum. Res.* 33, 506–514. doi: 10.1086/510224
- Zuckerman, A., and Chaiken, S. (1998). A heuristic-systematic processing analysis of the effectiveness of product warning labels. *Psychol. Market.* 15, 621–642. doi: 10.1002/(SICI)1520-6793(199810)15:7<621::AID-MAR2>3.0.CO;2-H



## OPEN ACCESS

## EDITED BY

Jeff Wood,  
University of Bristol, United Kingdom

## REVIEWED BY

Mara Miele,  
Cardiff University, United Kingdom  
Luciano Pinotti,  
University of Milan, Italy

## \*CORRESPONDENCE

Stephen L. Woodgate  
✉ [stephenwoodgate@gmail.com](mailto:stephenwoodgate@gmail.com)

RECEIVED 15 July 2023

ACCEPTED 28 August 2023

PUBLISHED 11 September 2023

## CITATION

Woodgate SL (2023) Meat industry by-products: a bio-refinery approach to the production of safe, value added products for sustainable agriculture applications. *Front. Anim. Sci.* 4:1259200. doi: 10.3389/fanim.2023.1259200

## COPYRIGHT

© 2023 Woodgate. This is an open-access article distributed under the terms of the [Creative Commons Attribution License \(CC BY\)](https://creativecommons.org/licenses/by/4.0/). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.

# Meat industry by-products: a bio-refinery approach to the production of safe, value added products for sustainable agriculture applications

Stephen L. Woodgate\*

Beacon Research, Market Harborough, United Kingdom

This mini-review review examines the role of animal by-products (ABP), produced by the process known as rendering. It explains how the use of rendered products has evolved and changed over the last 50 years and how the bovine spongiform encephalopathy (BSE) epidemic in the UK and the rest of Europe challenged the survival of the industry. The subsequent changes to the rendering industry resulting from BSE are described by way of key research and regulatory changes. As a result of the developments in the modern rendering industry, it has evolved into an important component of the current human food chain. The role of the rendering industry in producing a wide range of safe, high quality, sustainable products from ABP materials is explored.

## KEYWORDS

meat, by-products, ABP, BSE, rendering, PAP, sustainability

## 1 Introduction

Animal by-products (ABPs) are produced as a direct consequence of livestock farming for production of meat, milk and eggs but they are often ignored by many in the livestock industry. It is therefore necessary to emphasise the importance and relevance of ABPs to the livestock industry. [Table 1](#) illustrates the typical proportions of food (meat) and ABP contributed by each of the four main species or types of land animal farmed for the production of human food in Europe. The evolution and rationale for the risk-based categorisation of ABP by the European Union (EU) is described in full in Section 2. ABPs play a very significant role in the economics and dynamics of the European meat industry, as the portion of the animal not utilised as food (meat) can range from 25-50% of its liveweight. This significant ABP portion of the liveweight requires prompt processing by the rendering industry to ensure that the raw material does not degrade due to microbiological activity. This processing thus ensures the continued operation of the meat industry.

The rendering process is described in full by [Woodgate & Wilkinson \(2021\)](#). In essence the following steps involve using steam at high pressure to indirectly heat ABPs (following

**TABLE 1** Typical composition of meat, meat products and Animal By-Products (ABP) from livestock farmed for food and the categorisation of ABP in Europe.

	Cattle*	Sheep**	Pigs***	Poultry****
Description	Meat and meat products intended for human consumption			
% animal liveweight	60	55	70	68
Description	Animal By-Products <b>NOT</b> intended for Human Consumption			
% animal liveweight	40	45	30	32
% ABP Category 1 <sup>Ω</sup>	3	5		
% ABP Category 2 <sup>Ω</sup>	17	12	11	3
% ABP Category 3 <sup>Ω</sup>	20	28	19	29

References: \*AHDB Beef yield guide (2020) \*\*AHDB lamb yield guide (2020) \*\*\*AHDB Pig yield guide (2020) \*\*\*\* Foxcroft and Woodgate; Foxcroft and Woodgate (2004). <sup>Ω</sup> Regulation (2002).

size reduction) to; i) evaporate the water present (typically 55–80% moisture), ii) to break open the cellular structure to allow the fat to be separated (rendered) from the protein meal iii) to microbiologically sterilise the final products of rendering, i.e. protein meal (meat and bone meal [MBM] and rendered fat [Tallow]). The former and latter were traditionally used as ingredients in the manufacture of compound feeds for animals, and the latter in the soap and the preparation of industrial fatty acids (oleochemicals) industry. The resulting products, a high protein meal and a rendered fat are therefore dehydrated, stable and microbiologically sterile such that the MBM was safe to be used by the animal feed industry. In the early development of the rendering industry, the rendering process was operated as a batch process, but during the 1960's and into the 1970's the majority of batch processes were replaced by continuous systems (Burnham, 1978). Until 1980, ABPs were generally processed as a mixture of all types of raw material from all species in local rendering plants servicing abattoirs and farms within a relatively compact local area. However, while rendering is, in principle, a simple process, there were many different commercial processes on the market. In practice, the dynamic aspects of rendering, such as particle size, retention time and temperature ranges throughout the process were poorly characterised prior to 1985. Nonetheless at the time, the criterion for approval of rendering plants relied upon the protein meal being free from any salmonella bacteria. (PAPO, 1981).

Following confirmation of the link between feeding MBM and bovine spongiform encephalopathy (BSE), (Wilesmith et al., 1988), a radical overhaul of the rendering industry resulted in the complete re-evaluation of ABPs, rendering processes and utilisation of rendered products. As the economic value of ABPs declined, disposal of ABPs became an additional cost to the animal production and meat sectors, and the economic viability of the rendering industry declined.

## 2 Bovine spongiform encephalopathy and rendering

BSE is a fatal neurological disease in cattle identified in 1986 (Wells et al., 1987) which resulted in over 175,000 infected animal cases in the UK by 2000 (BSE Inquiry, 2000). However, it was not

considered to be a zoonotic disease until 1996 when research concluded that there was a strong causal link between BSE in cattle and new variant Creutzfeldt-Jacob disease (v CJD) in young humans (Dorrell, 1996). An indirect consequence of this finding in the UK, was the establishment of the European Food Safety Authority (EFSA) (EFSA, 2001) with the acknowledgement that the rendering industry was considered to be key link in the human food chain. A comprehensive narrative review of the Bovine Spongiform Encephalopathy (BSE) epidemic, from the perspective of the European rendering industry was given by Woodgate and Wilkinson (2021). This paper describes the research background concerning the design and trials conducted to determine if any rendering process was able to inactivate the BSE and/or scrapie agents (both members of the Transmissible Spongiform Encephalopathy (TSE) family of prion diseases). Full details of the research into the inactivation of BSE and sheep scrapie are given in Taylor et al. (1995) and Taylor et al. (1997) respectively. In summary, the results indicated that one of the rendering systems was unable to inactivate TSE agents, and others showed only limited ability to inactivate TSE agents. One system, a high-pressure steam process, provided the greatest level of TSE inactivation. Subsequently, the results of these inactivation trials were used to inform the European Commission and new EU legislation was enacted immediately, as described by Woodgate and van der Veen (2004).

One of the key features resulting from the BSE epidemic was an animal feed ban, introduced in stages, from the UK in 1989 to the entire EU in 2001 (Regulation, 2001). This ban prohibited all rendered animal proteins for use in animal feeds for monogastric, ruminant and aquatic animals farmed for food production. The only practical exemption allowed use of rendered animal proteins in pet foods, as companion and pet animals are not considered to be part of the food chain. This regulation was, in principle, temporary therefore no time limit was set. As such, the rendering industry was in a dilemma about how it could continue even though it was considered to be an essential component of the slaughter and meat production industry. Although the EU regulations in place by 2002 indicated that the rendering industry appeared to have a future, albeit a different future to that expected in the last 25 years, many were uncertain that it would survive. Consequently, the options for rendering and alternative processes for the future were explored by



Woodgate (2006) who considered potential replacements for the methods of processing ABPs but without the products being used in animal feeds. One of the areas explored in depth was combustion of the organic content of MBM (75–80 g/100g) by developmental or commercial incinerators to assess if they could both destroy any potential prion contamination and yield enough energy, such as steam or electricity, to be commercially viable. As will be described later, development of technologies of this type became invaluable for the future direction of the rendering industry.

A vital aspect of the key EU regulation (Regulation, 2002) was the introduction of categories of ABP according to risk to animal and human health, since in 2002, BSE was considered the most important risk to be managed. All of the requirements introduced by this regulation are currently active in the EU and the UK, although the original 2002 regulation was amended (Regulation, 2009 and Commission Regulation, 2011). It is important to note that the 2002 regulation marked a significant change between rendered animal proteins produced before 2002 (termed MBM) and those produced after (termed PAP or MBM according to category of ABP). Regulation (2002) defined three categories of ABP as follows; Category 1: BSE risk materials and deadstock containing BSE risk materials; Category 2: Deadstock and ABP condemned at a slaughterhouse; Category 3: ABP from animals fit for human consumption, slaughtered in an approved abattoir. Importantly, processing standards that could be validated and the potential applications for the products of each category of ABP (now termed derived products) were set down in the EU regulation (Regulation, 2002). Category 1 products are required to be disposed of by incineration (directly or indirectly after rendering) or by rendering followed by combustion of the products to avoid the possibility of contamination of the food chain, via animal feed. Category 2 products may be disposed of by the same route as Category 1 products or if the high-pressure steam process is applied, the MBM produced could be used as a component in organic fertiliser and the rendered fat used as an ingredient in biodiesel. Importantly, proteins and fats derived from Category 1 and 2 ABP are not approved for use within animal feeds and hence do not enter the food chain. Only Category 3 derived products (processed animal protein (PAP) and rendered fat) produced from approved and validated processes may be used in animal feeds, subject to the TSE regulations, i.e., no ruminant proteins in feed for any animal, compliance with the intra-species feed ban for monogastric animals (aquafeed, pigs, poultry), (Regulation, 2001).

## 3 Rendering: opportunities in a post-BSE world

### 3.1 Alternative uses for rendered products

The requirement to incinerate Category 1 ABP led to the development of new technologies to combust the products of rendered Categories 1 and 2 ABP, i.e. the protein meal (MBM) and the rendered fat to ensure that they posed no further TSE risk. Accordingly, rendered fat was developed as a bio-fuel replacement for fossil fuel in steam raising boilers and MBM was used as fuel in

fluid bed combustors to raise steam that powered turbines to produce electricity. A consequence of this process was the production of significant amounts of bone ash (225,000 tonnes per annum in the UK), as the ash content of MBM ranges between 20–25g/100g. The ash material was initially designated as waste for disposal in landfill sites incurring additional cost to the livestock industry. Research was therefore initiated to determine how the chemical structure of bone was affected by combustion of the organic component and to determine if there were any potential use options available (Etok et al., 2007; Dybowska et al., 2009). In summary, the research highlighted important phosphorus-related properties of the bone ash such that the research focus altered to consider if the bone ash could be used as a renewable source of phosphorus fertiliser. Following farm studies to evaluate the benefit to crops, bone ash is now widely used as source of renewable phosphorus in UK agriculture.

The evolution of biofuels in the form of MBM and rendered fat led to consideration that they could partly replace fossil fuels used for steam generation required by the rendering process and this in turn, could reduce the environmental impact of rendering. Accordingly, research was initiated to study the impact of rendering and rendered products resulting from these changes with the focus on assessment of the energy consumption by the UK rendering industry and the quantification of greenhouse gases (GHG) produced using Life Cycle Assessment (LCA). System boundaries were described in accordance with the current ABP categorisation, i.e. Category 1 (and Category 2) ABP rendered products used as a carbon neutral fuel to provide the steam required to process Category 3 ABP into PAP for use in animal feeds (Ramirez et al., 2012). The results of this study illustrated the potential for the rendering industry to provide fats and protein sources with a lower global warming potential than traditional vegetable-based alternatives such as palm oil and soyabean meal. Data from the research above and LCA studies of rendered products in the EU (EFPPRA, 2020) are currently being used in LCA projects that are considering the environmental impact of all types of feed ingredients used in livestock production. The recently operational Global Feed LCA Institute (GFLI) is the product of an international consortium that was formed to establish a global standard for calculating the carbon impact of feed ingredients (including rendered products) for animal feeds, (GFLI, 2022).

### 3.2 Rendering: new opportunities for animal feeds

The EU regulations of 2001 (Regulation, 2001) and their successors set out the conditions under which certain PAPs may be used in animal feeds. Accordingly, research was conducted to determine the species identity of PAPs, a pre-requisite for their approval in animal feeds. The specific conditions laid down in EU animal feed regulations stipulated that a) no ruminant protein should be present in any animal feed and b) that there is no *intra-species* recycling of proteins (no porcine to porcine, no poultry to poultry and no fish to fish-although fish caught in the open sea were exempted from this constraint). The first research

challenge was the preparation of standardised species-specific PAP products by rendering. Thereafter a series of experimental methods were assessed to determine the most appropriate method to detect a target species protein within a mixture. The criteria included the accuracy, sensitivity, and reproducibility. The results of the research published by Woodgate et al. (2009) resulted in a focus being placed on Polymerase Chain Reaction (PCR) techniques which appeared to be more suitable for the detection of low levels of potentially heat denatured proteins in PAPs. Subsequent research at the EU Research Laboratory for PAP (EURL-PAP) (Fumiere et al., 2012) resulted in the EU regulatory approval of PCR methods for the detection of ruminant protein in mixtures of PAPs and animal feeds, (Commission Regulation, 2013a). The situation regarding the potential for safe use of PAPs in animal feeds at the time was reviewed by Woodgate (2012). This paper updated the progress of applying HACCP principles to rendering (Woodgate, 2010), to ensure that rendering processes producing PAPs were compliant with the approved regulatory standard.

It is important to recognise that PAPs are essentially a new potential feed ingredient from 2002 onwards, with no prior history of nutritional evaluation in farmed animals. Even then, PAPs were not approved for use in animal feeds until species identity tests were validated and feed legislation updated. This fact explains the limited number of nutritional studies until post 2013 (in aqua feeds) and post 2021 (for pigs and poultry). Nonetheless, the utilisation of processed animal proteins (PAPs) in several marine fish species was studied in a university setting by Davies et al. (2009). The PAPs evaluated were produced under characterised, validated process conditions which enabled the nutritional data to be more meaningfully interpreted. The investigation produced valuable data for the digestibility coefficients of essential amino acids such that these can be used in feed formulations that include specification limits for digestible amino acids in the diets of three temperate marine species, namely European sea bass, gilthead sea bream and turbot. In addition to the nutritional data yielded, this paper was used as evidence by the European Commission to show the efficacy of PAPs in aquafeed. Subsequently, the use of non-ruminant PAP in feeds for aquatic species was approved, (Commission Regulation, 2013b), and the use of animal proteins in aquatic species was reviewed and updated by Woodgate et al. (2021). Details of the analytical and nutritional profiles of modern PAPs, are described by Woodgate and Wilkinson (2021). More recently, the use of pig or poultry PAP in diets for poultry and pigs respectively was approved (Commission Regulation, 2021). Recent research on the use of poultry PAP in the diet of weaned and growing pigs indicated that it may be used as a sustainable protein ingredient in pig diets (Davin and Bikker, 2021; Davin et al., 2021). It is expected that future nutritional studies will focus on comparison of terrestrial PAPs with PAPs produced from fish by-products (Fishmeal or fish PAP) or Insect PAP which may compete for the same space in feed formulations. However, it is important to note that Insect PAP for use in animal feed can only be produced from feedstock free from ABP. In effect, insects manufactured into insect PAP, must have been feed on a vegetarian feedstock which might affect its production costs and therefore its commercial potential.

Importantly for the rendering industry and the economy of the meat processing chain, the use of PAPs in pet foods has continued since 2002 and has matured to be able to utilise the ruminant and mixed species PAPs that are not able to be used in feeds for food producing animals. The use of PAPs in petfood are regulated by EU and UK rendering and feed regulations and their use in the petfood market is both encouraged and significant (75% of all EU PAPs are currently used in petfood products). Furthermore, PAPs are accepted as important and declared ingredients for omnivore and carnivore pets (dogs and cats) by nutritionists and pet food manufacturers.

However, it is clear to many that meeting safety standards per se is not necessarily the only factor in any assessment that consumers might consider when considering the use of PAP in animal feeds. Consumers (essentially represented by supermarkets) appear to resist the concept of using PAPs even if their use is in full compliance with the intra-species feeding ban. It seems that consumers expect not only that rendered products should meet maximum health safety standards for both animals and humans, but also have a low environmental impact and make a positive contribution to the nutrition, health and welfare of animals farmed for food.

### 3.3 Rendering: an integrated environmentally responsible process?

The amounts of ABP produced by the EU livestock industry are considerable, amounting to 18.5 mega tonnes per annum (Mtpa). Following rendering, the derived products (of all categories of ABP) amount to approximately 4 Mtpa of protein meals and 3 Mtpa of rendered fats per year (Alm, 2021). Table 2 describes the options for the processing of the different EU categories of ABPs taking the one or two process steps necessary to produce the final derived products. The potential utilisation of the products, in one or more applications, is shown by way of coloured circles. Table 2 also includes data showing the major use by each application in Europe, in 2021.

Interestingly, not all the possible application opportunities described are realised simultaneously due to changing global circumstances, such as supply and demand for proteins, fat and energy. Economics play a crucial role in directing the utilisation of rendered products and this feature is illustrated in practice when considering the role of renewable (or short carbon cycle) rendered products, several of which are confirmed as having excellent sustainability credentials (EFPRA, 2020). Should these renewable products, such as rendered fat, be encouraged as replacement for fossil derived fuels, by given a carbon saving credit? Unless this occurs, rendered fat will be utilised by industries, such as biodiesel and oleochemical processors that are willing to pay for the commodity based on supply and demand. If this occurs, the potential for reducing the environmental impact LCA of ABPs and of the primary product, meat, may be lost. Nonetheless, Table 2 illustrates the wide range of possible uses for the products derived from the essential processing of ABPs from the animal production.



TABLE 2 Potential applications and amounts of derived products from the rendering of ABPs in the EU.

ABP Category	EU Category 3 ABP					
Amount (Mtpa)	13.5					
ABP Input	Poultry		Porcine		Ruminant	
Energy Input	Fossil Fuel or Bio Energy <div><div></div></div> from rendering					
1 <sup>st</sup> Process	Render		Render		Render	
1 <sup>st</sup> Products	PAP	RF	PAP	RF	PAP	RF
2 <sup>nd</sup> Process						
2 <sup>nd</sup> Products						
Application Options and amounts (2021)						
Aquafeed	<div><div></div></div>		<div><div></div></div>			
Poultry feed			<div><div></div></div>			
Pig feed	<div><div></div></div>					
Pet foods	<div><div></div></div>	<div><div></div></div>	<div><div></div></div>	<div><div></div></div>	<div><div></div></div>	<div><div></div></div>
Agronomy	<div><div></div></div>		<div><div></div></div>		<div><div></div></div>	
Transport fuel		<div><div></div></div>		<div><div></div></div>		<div><div></div></div>
Process Energy		<div><div></div></div>		<div><div></div></div>		<div><div></div></div>
Tonnes (,000) pa	Aq-F	AF	PF	Fert	TF	Oleo
Protein	240	150	2150	310		
Rendered Fat		560	375		810	505
Mineral Ash						

EU Category 2 ABP		EU Category 1 ABP		
5.0				
Poultry/Porcine		Poultry/Porcine/Ruminant		
Fossil Fuel or Bio Energy <div><div></div></div> from rendering				
C2 Render		C1 Render		
MBM	RF	MBM		RF
Fertilizer Production	Biodiesel Production	Combustion		Biodiesel Production
Fertilizer	Biodiesel	Ash	Energy	Biodiesel
Application Options and amounts (2021)				
<div><div></div></div>		<div><div></div></div>		
	<div><div></div></div>			<div><div></div></div>
	<div><div></div></div>		<div><div></div></div>	<div><div></div></div>
C2 Fert	TF	Fert	PE	TF
205			985	
	120		25	420
		220		

Colour key: Animal feed, Pet Foods, Fertiliser, Transport fuel (Biodiesel), Process Fuel for rendering.  
Key: ABP (animal by-product); MBM (meat and bone meal); PAP (processed animal protein); RF (rendered fat); Aq-F (Aqua feed) AF; Animal (pig/poultry) feed; PF (Pet food); Fert (fertiliser); TF (transport fuel); PE (process energy); Oleo (Oleochemical/soap).

## 4 Conclusions

This review has been written from an EU perspective that includes the UK. Interestingly, the advent of Brexit may in the future offer opportunities for the UK to develop innovative technologies and products for non-EU markets that are not constrained by the EU regulations described in the review. Nonetheless, the processing of ABPs by rendering has undergone reformatory changes over the last 50 years. The catalyst for change was the BSE epidemic in UK and rest of Europe such that even though the basic process remains unchanged, the way the industry operates has been transformed. Rendering is now considered to be an essential component in an integrated livestock system that prioritises human and animal health. The modern rendering process may be considered to be a bio-refinery that produces a wide range of safe, environmentally sustainable and economically valuable products that are able to contribute to society as a whole.

## Author contributions

SLW: Writing – original draft, Conceptualization.

## References

- AHDB beef yield guide (2020). Available at: <https://ahdb.org.uk/beef-yield-guide> (Accessed February 12, 2023).
- AHDB lamb yield guide (2020). Available at: <https://ahdb.org.uk/lamb-yield-guide> (Accessed February 12, 2023).
- AHDB pig yield guide (2020). Available at: <https://ahdb.org.uk/pork-yield-guide> (Accessed February 12, 2023).
- Alm, M. (2021). *Overview of the animal by-products industry in europe in 2021 in webinar 'Circular bio economy'* Schothorst, NL (Schothorst, NL).
- Burnham, F. A. (1978). *Rendering: The invisible industry*. Fallbrook (CA, USA: Aero Publishers).
- Commission Regulation (2011). Commission Regulation (EU) of 25 February 2011 on implementing Regulation (EC) No. 1069/2009 of the European Parliament and of the Council laying down health rules as regards animal by-products and derived products not intended for human consumption (142/2011). *Off. J. Eur. Communities* L54, 1.
- Commission Regulation (2013a). Commission Regulation (EC) of 16 January 2013 on amending Regulation (EC) No. 152/2009 as regards the methods of analysis for the determination of constituents of animal origin for the official control of feed (51/2013). *Off. J. Eur. Communities* L184, 43.
- Commission Regulation (2013b). Commission Regulation (EC) of 16 January 2013 on amending Annexes 1 and IV to Regulation (EC) No. 999/2001 of the European Parliament and of the Council laying down rules for the prevention, control and eradication of certain transmissible spongiform encephalopathies (56/2013). *Off. J. Eur. Communities* L21, 3.
- Commission Regulation (2021). Commission Regulation (EU) 2021/1372 of 17 August 2021 amending Annex IV to Regulation (EC) No 999/2001 of the European Parliament and of the Council as regards the prohibition to feed non-ruminant farmed animals, other than fur animals, with protein derived from animals. *Off. J. Eur. Communities* L295, 1.
- Davies, S. J., Gouveia, A., Laporte, J., Woodgate, S. L., and Nates, S. (2009). Nutrient digestibility profile of premium animal protein by-products for temperate marine fish species (European sea bass, gilthead sea bream and turbot). *Aquaculture Res.* 06/2009; 40 (15), 1759–11769.
- Davin, R. J., and Bikker, P. (2021). *Abstracts of the 72<sup>nd</sup> Annual Meeting of the European Federation of Animal Science Replacement of soybean meal with poultry based processed animal proteins in growing pigs*. p325. doi: 10.3920/978-90-8686-918-3
- Davin, R. J., Van Baal, J., and Bikker, P. (2021). *Abstracts of the 72<sup>nd</sup> Annual Meeting of the European Federation of Animal Science Replacement of soybean meal with poultry-based processed animal proteins in weaned pigs*. p324.
- Dorrell, S. (1996). Available at: <https://api.parliament.uk/historic-hansard/commons/1996/mar/20/bse-health>.
- Dybowska, A., Manning, D. A. C., Collins, M. J., Wess, T., Woodgate, S. L., and Valsami-Jones, E. (2009). An evaluation of the reactivity of synthetic and natural apatites in the presence of aqueous metals. *Sci. Total Environ.* 02/2009; 407 (8), 2953–2965. doi: 10.1016/j.scitotenv.2008.12.053
- EFPPA (2020). *LCA data of EFPPA rendered products for the GLFI database* (EFPPA: Blonk Consultants).
- EFSA (2001). Regulation (EC) of the European Parliament and of the Council laying down the general principles and requirements of food, establishing the European Food Safety Authority and laying down procedures in matters of food safety (No. 178). *Off. J. Eur. Communities* L31, 1–24.
- Etok, S. E., Valsami-Jones, E., Wess, T. J., Hiller, J. C., Maxwell, C. A., Rogers, K. D., et al. (2007). Structural and chemical changes of thermally treated bone apatite. *J. Material Sci.* 42, 9807–9816. doi: 10.1007/s10853-007-1993-z
- Foxcroft, P. D., and Woodgate, S. L. (2004). *Temperton fellowship: full utilisation of the poultry carcass* (UK: Harper Adams University College).
- Fumiere, O., Marien, A., and Berben, G. (2012). *EURL-AP implementation test*. Gembloux, Belgium: Walloon Agricultural Research Centre. Available at: [http://eurl.craw.eu/img/page/interlaboratory/EURL\\_AP\\_PCR\\_ILS\\_2012\\_final\\_version.pdf](http://eurl.craw.eu/img/page/interlaboratory/EURL_AP_PCR_ILS_2012_final_version.pdf)
- GLFI (2022). Available at: <https://globalfeedlca.org> (Accessed November 15, 2022).
- Inquiry, B. S. E. (2000). *The report, evidence and supporting papers* (House of Commons Papers) (London, England: Stationery Office Books).
- PAP0 (1981). "The diseases of animals (protein processing) order 1981," in *Statutory instruments 1981* (London, England: Her Majesty's Stationery Office).
- Ramirez, A. D., Humphries, A. C., Woodgate, S. L., and Wilkinson, R. G. (2012). Greenhouse gas life cycle assessment of products arising from the rendering of mammalian animal by-products in the UK. *Environ. Sci. Technol.* 46, 447–453. doi: 10.1021/es201983t
- Regulation (2001). Regulation (EC) 22 May 2001 of the European Parliament and of the Council of laying down rules for the prevention, control and eradication of certain transmissible spongiform encephalopathies (999/2001). *Off. J. Eur. Communities* L147, 1.
- Regulation (2002). Regulation (EC) of the European Parliament and of the Council of 3 October on laying down health rules concerning animal by-products not intended for human consumption. *Off. J. Eur. Communities* L273, 1
- Regulation (2009). Regulation (EC) 21 October 2009 of the European Parliament and of the Council of on laying down health rules as regards animal by-products and derived products not intended for human consumption and repealing Regulation (EC) No. 1774/2002 (animal by-products regulation) (No. 1069/2009). *Off. J. Eur. Communities* L300, 1.
- Taylor, D. M., Woodgate, S. L., and Atkinson, M. J. (1995). Inactivation of the bovine spongiform encephalopathy agent by rendering procedures. *Veterinary Rec.* 137, p605–p610.
- Taylor, D. M., Woodgate, S. L., Fleetwood, A. J., and Cawthorne, R. J. G. (1997). Effect of rendering procedures on the scrapie agent. *Veterinary Rec.* 141, p643–p664.

## Funding

The author declare that no financial support was received for the research, authorship, and/or publication of this article.

## Conflict of interest

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

## Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

- Wells, G. A. H., Scott, A. C., Johnson, C. T., Gunning, R. F., Hancock, R. D., Jeffrey, M., et al. (1987). A novel progressive spongiform encephalopathy in cattle. *Veterinary Rec.* 121, 419–420. doi: 10.1136/vr.121.18.419
- Wilesmith, J. W., Wells, G. A. H., Cranwell, M. P., and Ryan, J. B. M. (1988). Bovine spongiform encephalopathy: epidemiological studies. *Veterinary Rec.* 123, 638–644.
- Woodgate, S. L. (2006). “What would a world without rendering look like?,” in *Essential Rendering: All about the animal by-products industries*. Ed. D. Meeker, 277.
- Woodgate, S. L. (2010) *Process validation: an essential step in establishing a rendering HACCP system*. Available at: [www.rendermagazine.com](http://www.rendermagazine.com).
- Woodgate, S. L. (2012). “Ensuring the safe supply of animal-derived ingredients for animal feed,” in *Animal feed contamination: Effects on Livestock and Food Safety*. Ed. J. Fink-Gremmels, 589.
- Woodgate, S. L., van den Hoven, S., Vaessen, J., and Margry, R. (2009). Control tools to detect processed animal proteins in feed and in animal by-products: specificity and challenges. *Biotechnology, Agronomy, Society and Environment* 13, 9–13.
- Woodgate, S. L., and van der Veen, J. T. (2004). The use of fat processing and rendering in the European Union animal production industry. *Biotechnology Agronomy Soc. Environ.* 8, 283–294.
- Woodgate, S. L., Wan, A. H. L., Hartnett, F., Wilkinson, R. G., and Davies, S. J. (2021). The utilisation of European processed animal proteins as safe, sustainable and circular ingredients for global aquafeeds. *Rev. Aquac.* 00, 1–25.
- Woodgate, S. L., and Wilkinson, R. G. (2021). The role of rendering in relation to the BSE epidemic, the development of EU animal by-product legislation and the reintroduction of rendered products into animal feeds. *Ann. Appl. Biol.* 178, 430–441A. doi: 10.1111/aab.12676.



## OPEN ACCESS

## EDITED BY

Virginia C. Resconi,  
University of Zaragoza, Spain

## REVIEWED BY

Paolo Silacci,  
Agroscope, Switzerland  
Margherita Caccamo,  
Consorzio Ricerca Filiera Lattiero-Caseari  
Ragusa (CoRFiLaC), Italy

## \*CORRESPONDENCE

Aila Vanhatalo  
✉ aila.vanhatalo@helsinki.fi

RECEIVED 16 August 2023

ACCEPTED 16 October 2023

PUBLISHED 02 November 2023

## CITATION

Halmemies-Beauchet-Filleau A,  
Jaakkola S, Kokkonen T, Turpeinen AM,  
Givens DJ and Vanhatalo A (2023)  
Milled rapeseeds and oats decrease  
milk saturated fatty acids and  
ruminal methane emissions in  
dairy cows without changes in  
product sensory quality.  
*Front. Anim. Sci.* 4:1278495.  
doi: 10.3389/fanim.2023.1278495

## COPYRIGHT

© 2023 Halmemies-Beauchet-Filleau,  
Jaakkola, Kokkonen, Turpeinen, Givens and  
Vanhatalo. This is an open-access article  
distributed under the terms of the [Creative  
Commons Attribution License \(CC BY\)](#). The  
use, distribution or reproduction in other  
forums is permitted, provided the original  
author(s) and the copyright owner(s) are  
credited and that the original publication in  
this journal is cited, in accordance with  
accepted academic practice. No use,  
distribution or reproduction is permitted  
which does not comply with these terms.

# Milled rapeseeds and oats decrease milk saturated fatty acids and ruminal methane emissions in dairy cows without changes in product sensory quality

Anni Halmemies-Beauchet-Filleau<sup>1</sup>, Seija Jaakkola<sup>1</sup>,  
Tuomo Kokkonen<sup>1</sup>, Anu M. Turpeinen<sup>2</sup>, D. Ian Givens<sup>3</sup>  
and Aila Vanhatalo<sup>1\*</sup>

<sup>1</sup>Department of Agricultural Sciences, University of Helsinki, Helsinki, Finland, <sup>2</sup>R&D, Valio Ltd., Helsinki, Finland, <sup>3</sup>Institute of Food, Nutrition and Health, University of Reading, Reading, United Kingdom

Plant lipids in the diet are known to modify milk fatty acid (FA) composition and mitigate ruminal methane emissions. The objective of the present work was to examine the potential of milled rapeseeds and oats to decrease both milk saturated FAs and ruminal methane emissions in practical farm settings. In the pilot study, six Finnish Ayrshire cows were fed a control diet for 3 weeks, which was then followed by a lipid-rich test diet for 3 weeks. The experimental diets were based on grass silage supplemented with barley and rapeseed meals in the control diet and with oats and milled rapeseeds in the test diet. The lipid inclusion rate was 55 g/kg dry matter (DM). In the main study, the whole Finnish Ayrshire research herd in milk ( $n = 49$ – $59$ ) was used in a switch-back-designed study. The cows were fed a control diet for 3 weeks, then a test diet for 4 weeks, and, finally, a control diet for 3 weeks. The diets were the same as in the pilot study except for a lower lipid inclusion level of 50 g/kg DM. The test diet decreased DM intake by 15% and energy-corrected milk (ECM) yield by 13% in the pilot study. The adjustment of supplemental lipids from 55 g/kg to 50 g/kg DM was successful, as the DM intake decreased only by 4% relative to the control diet in the main study. Furthermore, the yields of milk, lactose, protein, and fat were also unaffected by dietary lipids in the main study. The milk fat composition was significantly altered in both studies. The milk fat saturated FAs were decreased by 16%–20% in the test diet, mainly due to the *de novo* FAs of 6- to 16-carbons (a reduction of 22%–48%). Milk fat *cis*-9 18:1 was increased by 63%–78% in the test diet relative to the control. Dairy products' (milk, butter, and cheese) organoleptic quality was not compromised by the modified lipid profile. Ruminal methane and hydrogen intensities ( $n = 23$ ; g or mg/kg ECM) were 20% and 39% lower, respectively, in the test diet than in the control diet. This reduction can be attributed to a lower amount of organic matter fermented in the rumen, as indicated by the lower DM intake and nutrient digestibility.

## KEYWORDS

plant lipid, grass silage, milk fat, saturated fatty acid, trans fatty acid, organoleptic quality, methane, hydrogen

# 1 Introduction

Ruminants are dependent on the anaerobic microbial ecosystem in the rumen to ferment and transform human-indigestible forages into dairy and meat products of high quality. However, due to the microbial metabolism of carbohydrates, ruminants are also significant producers of enteric methane (CH<sub>4</sub>). In addition, CH<sub>4</sub> formation represents an unproductive loss of dietary energy to the ruminant animal (Min et al., 2022). Adding plant lipids that are not fermentable in the rumen to dairy cow diets suppresses CH<sub>4</sub> emission intensity [g CH<sub>4</sub>/kg energy-corrected milk (ECM)], on average, by 12% (Hristov et al., 2022). Oilseeds have a CH<sub>4</sub> mitigation potential similar to that of pure oils, with the advantage that the lipid may be released at a slower rate in the rumen. Therefore, oilseeds may have a less harmful effect on the rumen function (Hristov et al., 2022) and, in turn, allow further lactational performance at high levels of lipid inclusion. However, practical evidence on the feasibility and effectiveness of feeding milled full-fat oilseeds at the whole-herd level to mitigate ruminant methane emissions is lacking.

Cardiovascular disease (CVD) is the leading cause of morbidity and mortality for humans worldwide (Perna and Hewlings, 2023). Compiled evidence suggests that the replacement of saturated fatty acids (SFAs) with unsaturated ones in dairy products may alleviate human CVD risk (Livingstone et al., 2012; Clifton and Keogh, 2017; Vasilopoulou et al., 2020). The research on the effects of individual SFAs is inconclusive, but most studies indicate that SFAs of 12- to 18-carbons may increase the risk for CVD, whereas shorter-chain SFAs may be beneficial or neutral (Perna and Hewlings, 2023). However, some studies suggest that 18:0 stearic acid (SA) does not increase CVD risk (Briggs et al., 2017). Dietary unsaturated fatty acids (FAs) have great potential to modify the FA composition of ruminant milk by decreasing the proportion of SFAs and increasing that of unsaturated FAs inherent to lipid supplements, such as *cis*-9 18:1 oleic acid (OA) rich in the lipids of rapeseed (*Brassica napus*) and oats (*Avena sativa*) (Collomb et al., 2004; Fant et al., 2023). Furthermore, the ability to increase milk fat monounsaturated FAs through dietary inclusion is much greater in magnitude than with polyunsaturated ones (Kliem and Shingfield, 2016). Beyond a certain threshold of dietary lipid supply, both feed intake and milk yield decline significantly (Drackley et al., 2007; Huhtanen et al., 2008; Vanhatalo and Halmemies-Beauchet-Filleau, 2020). Consequently, this threshold, influenced by various factors, especially the basal diet and the characteristics of the lipid supplement (Benchaa et al., 2015; Halmemies-Beauchet-Filleau et al., 2017), should not be exceeded when adjusting milk fat composition in practical farm settings. Moreover, the form in which lipids are included in the ruminant diet significantly affects their bioavailability and the ultimate composition of the final product. Furthermore, rupture of rapeseed seedcoats is necessary to enhance the availability of lipids within the seeds for absorption (Kairenius et al., 2009).

The milk FA composition affects the texture, flavor, and shelf life of dairy products (Kennelly, 1996; Hillbrink and Augustin, 2002). However, monounsaturated FAs are less prone to oxidation than polyunsaturated ones (Kennelly, 1996), which

reduces the risk for off-flavors and shorter shelf lives. Furthermore, dairy products with lipids rich in OA have resulted in products with softer textures, but with similar flavors to standard products (Chen et al., 2004; Ryhänen et al., 2005).

The objective of this study was to examine the potential of the lipid in milled rapeseeds and oats to replace a part of the SFAs in milk fat with monounsaturated ones inherent to these lipid supplements and to mitigate ruminal methane emissions in practical farm settings. We hypothesized that replacing rapeseed meal and barley with milled rapeseed and oats in a dairy cow diet will not impair the lactation performance or sensory quality of the dairy products but will soften the milk fat and mitigate rumen methanogenesis.

# 2 Materials and methods

The experiments were conducted at the University of Helsinki Viikki research farm (60°13'N, 24°02'E) in Finland. The pilot dairy cow study was conducted in the spring of 2018 and the main dairy cow study in the autumn of 2018. Similar dietary ingredients and the same analytical methods were used in both experiments.

## 2.1 Pilot dairy cow study

The effects of a tailored test diet elevated in lipids were first studied with a limited number of dairy cows. This pilot study was carried out to ensure maximal changes in milk fat composition, without compromising animal health and performance, when later implementing the test diet for a large number of animals. The pilot study was conducted with six multiparous Finnish Ayrshire cows that weighed (mean ± SD) 711 kg ± 35.3 kg, were of parity 3.0 ± 0.63, were 181 ± 32.5 days in milk, and were producing 36.0 kg/d ± 4.77 kg/d of milk pre-trial. All cows were fed a control diet for 3 weeks (period 1), followed by a lipid-rich test diet for another 3 weeks (period 2). The dietary shift was made gradually over 5 days. The dairy cow partial mixed rations (PMRs) were based on grass silage (Table 1). The prewilted grass silage was prepared from a first cut of mixed timothy (*Phleum pratense*) and meadow fescue (*Festuca pratensis*) sward, which was ensiled with a formic acid-based additive (4–6 L/t feed; AIV® 2 Plus Na; Taminco Finland Ltd, Eastman Chemical Company, Oulu, Finland) in big bales. The concentrates in the PMRs comprised home-grown cereals, rapeseed feeds as a protein supplement, molassed sugar-beet pulp (Opti Leike mure; Lantmännen Feed Ltd, Turku, Finland), and vitamins and minerals (Seleeni-E-Melli TMR; Lantmännen Feed Ltd). The rapeseed protein was isonitrogenously supplied either as a lipid-extracted meal (control diet; Farmarin Rypsi Mixer; Hankkija Ltd, Hyvinkää Suomi) or as domestic full-fat seeds (Hauhon Myllärit Ltd, Hauho, Finland), and was milled using a sieve pore size of 6–8 mm (test diet). The cereal in the control diet was barley (*Hordeum vulgare*), and in the test diet, oats (Table 1). The amount of additional plant lipids in the test diet from rapeseeds and oats was adjusted to ca. 55 g/kg diet dry matter (DM). The PMRs were distributed three times per day at 09:00, 15:00, and 20:00, fed freely,



TABLE 1 The ingredients of the partially mixed rations.

Ingredient (g/kg dry matter)	Pilot study		Main study	
	Control diet	Test diet	Control diet	Test diet
Grass silage	600	600	600	600
Barley	194	–	189	–
Oats	–	138	–	136
Rapeseed meal	122	18	120	34
Milled rapeseeds	–	160	–	139
Molassed sugar-beet pulp	69	69	70	70
Minerals and vitamins	15	15	17	17
Propylene glycol	–	–	4	4

and supplemented with 3 kg/d of commercial concentrate (Maituri 10 000; Lantmännen Feed Ltd) at milking times. The main ingredients of the commercial concentrate were rapeseed meal, wheat, barley, molassed sugar-beet pulp, sugar-beet molasses, faba beans, and protected fat. The cows had free access to drinking water.

The cows were kept in tie-stalls equipped with PMR feeding troughs (Insentec RIC, Marknesse, the Netherlands) that registered intakes. They were milked twice a day (Delpro; DeLaval, Tumba, Sweden) starting at 06:00 and 17:00. The samples of feed and feces were collected during the last week of both periods. The fecal spot (1-L) sample was taken from the rectum during five consecutive milkings, starting on the morning milking of day 17. Furthermore, all milk from the cows was collected over these milkings to produce around 350 L of control and modified milk. This milk was analyzed for major constituents (using a 15- to 20-ml sample preserved with Bronopol; lactose, crude fat, crude protein, urea), as well as FAs (using an unpreserved milk sample of 100 ml). In addition, ultra-high temperature (UHT) processed milk, cheese, and butter were prepared from raw milk for sensory analyses. After adjusting the milk fat content to 1.5%, UHT milk was produced at Valio R&D (Helsinki, Finland) by heating the milk to 150°C for 3 s. The butter and semi-hard Dutch-type cheese were produced at Häme University of Applied Sciences' pilot dairy plant (Hämeenlinna, Finland). To produce butter, the cream was pasteurized and churned in two phases at 10°C. Salt was added to achieve a salt content of 1.4%. The test diet butter required a longer churning time than the control diet butter (120 min vs. 240 min). To produce semi-hard Dutch-type cheese, raw milk was standardized to a fat-to-protein ratio of 0.8 and pasteurized (for a minimum of 72°C for 15 s). The DVS CHN-019 starter culture (Chr. Hansen, Hørsholm, Denmark) and the CHY-MAX E (Chr. Hansen) rennet were added. The cheese loaves were ripened for 7 weeks at 11°C. The dry matter and fat contents for the control diet cheese were 53.6% and 19.0%, respectively, and for the test diet cheese 54.0% and 20.0%, respectively. In addition, the samples of milk from individual cows were taken every third day at the morning and evening milking starting from the dietary change. The samples were composited according to milk yield by cow and by day and

analyzed in a similar way to the tank milk for the major constituents and FAs.

## 2.2 Main dairy cow study

The whole Finnish Ayrshire research herd in milk ( $n = 49$ –59) was used in a switch-back-designed study. The cows were fed a control diet for 3 weeks (period 1) followed by the lipid-rich test diet for 4 weeks (period 2). After this, all cows were switched back to the control diet (3 weeks; period 3). The dietary shifts were made gradually over 5 days. The last week of all periods was the sampling week. The cows were housed in an insulated free-stall barn equipped with a milking robot (Lely Astronaut A3; Lely, Maassluis, the Netherlands). The dairy herd was predominantly autumn calving and the number of cows in milk was 49, 52, 50, and 59 at the beginning of the experiment and during the sampling weeks of periods 1, 2, and 3, respectively. The number of days in milk was, on average, 176, 153, 141, and 117 at the beginning of the experiment and in the sampling weeks of periods 1, 2, and 3, respectively.

The dietary ingredients were the same as in the pilot study. However, based on the observations of the pilot study, the amount of supplemental lipids in the test diet was adjusted from 55 to 50 g/kg DM in order to promote feed intake, and, in turn, higher milk production while on the test diet. The adjustment was carried out by reducing the proportion of milled rapeseed and, correspondingly, increasing that of rapeseed meal in the test diet PMR (Table 1). In addition, propylene glycol was added to the PMR concentrate mixture to prevent concentrate dusting. The chemical composition of the PMR concentrate ingredients is presented in Table 2. The animals had free access to PMRs that were distributed four times per day at 08:00, 12:00, 18:00, and 22:00. When visiting the milking robot, the cows producing less than 30 kg of milk per day, between 30 kg of milk per day and 40 kg of milk per day and over 40 kg of milk per day at the beginning of the trial received 3 kg/d, 4 kg/d or 5 kg/d of commercial concentrate (Maituri 10000, Lantmännen Feed Ltd), respectively, throughout the experiment.

TABLE 2 The chemical composition of the partial mixed rations (PMRs) concentrate ingredients in the main study.

	Barley	Oats	Rapeseed meal	Milled rapeseeds	Molassed sugar-beet pulp
Dry matter (g/kg)	880	874	880	909	880
<b>In dry matter (g/kg)</b>					
Ash	25.3	39.7	77.0	45.2	39.8
Crude protein	117	158	389	242	106
Starch	607	351	4.60	6.10	229
Neutral detergent fiber	173	317	248	149	338
Total fat	25.2	43.4	43.2	434	38.3
ME (MJ/kg dry matter <sup>1</sup> )	13.2	11.5	11.4	19.0	12.2
<b>Fatty acids (FA) (g/100 g FA)</b>					
16:0	22.0	17.9	8.27	4.76	13.4
18:0	1.70	2.09	2.14	1.85	1.50
<i>cis</i> -9 18:1	11.8	34.0	46.1	52.6	38.2
<i>cis</i> -9, <i>cis</i> -12 18:2	53.9	39.7	24.6	21.6	35.9
<i>cis</i> -9, <i>cis</i> -12, <i>cis</i> -15 18:3	6.98	2.50	6.82	12.0	6.22
<i>cis</i> -13 22:1	0.16	0.24	0.30	0.02	0.12
Saturated FAs	25.0	21.3	12.7	8.07	16.1
Monounsaturated FAs	14.0	36.5	55.9	58.2	41.7
Polyunsaturated FAs	61.0	42.3	31.5	33.7	42.2
Total FAs (g/kg dry matter)	10.2	27.5	24.3	373	28.5

<sup>1</sup>Metabolizable energy (ME) calculated according to Luke (2023).

The main ingredients of the commercial concentrate were rapeseed meal, maize, barley, sugar-beet molasses, molassed sugar-beet pulp, and protected fat.

The PMR feeding troughs (Insentec RIC) registered intakes automatically and individually. The milk yield, body weight, and commercial concentrate distribution were individually registered by the milking robot throughout the experiment. The experimental feeds were sampled once a day during the sampling week ( $n = 7$ ), composited by periods, and stored frozen at  $-20^{\circ}\text{C}$  until analysis.

The milk and feces were sampled from 13 multiparous dairy cows that weighed (mean  $\pm$  SD)  $678 \text{ kg} \pm 62.4 \text{ kg}$ , were of parity  $2.9 \pm 1.75$ , and were producing  $32.1 \text{ kg/d} \pm 7.5 \text{ kg/d}$  of milk pre-trial. Of these cows, 10 were in late lactation (number of days in milk ranging from 153 to 308 at the beginning of the experiment) and three were in early lactation (number of days in milk ranging from 13 to 27 at the beginning of the experiment). The milk was individually sampled on day 15 of period 1 onwards, via the Lely Shuttle, from the first milking every third day at 09:00 onwards. The milk preserved with Bronopol (15 ml–20 ml) was analyzed for lactose, crude fat, crude protein, and urea, and unpreserved milk (10 ml) for FAs. The milk FA samples were stored frozen at  $-20^{\circ}\text{C}$  prior to analysis. In addition, the tank milk was sampled every second day at 09:00 and analyzed for lactose, crude fat, crude

protein, and urea throughout the study. The spot fecal samples (1 L) from the rectum were taken every day during the sampling week ( $n = 7$ ) at 09:00 onwards, composited by cow and period, and frozen at  $-20^{\circ}\text{C}$  before the analysis.

All cows freely visited the milking robot equipped with the GreenFeed system (C-Lock Inc., Rapid City, SD, USA) that measures gas exchange (Huhtanen et al., 2015). Automatic gas calibrations using a mixture of nitrogen ( $\text{N}_2$ ) and oxygen ( $\text{O}_2$ ), and a mixture of  $\text{CH}_4$ ,  $\text{O}_2$ , hydrogen ( $\text{H}_2$ ), and carbon dioxide ( $\text{CO}_2$ ) were performed daily. The  $\text{CO}_2$  recovery tests were conducted at the beginning of the experiment and every sampling week. Only the records of cows ( $n = 23$ ) that were in milk during all three experimental periods and, on average, had 10 or more accepted readings from the GreenFeed system (more than 2 min of uninterrupted gas recordings during a visit) in the last week of each experimental period were used in the statistical analysis. These cows weighed  $646 \text{ kg} \pm 72.8 \text{ kg}$ , were of parity  $2.3 \pm 1.70$ , and produced  $30.5 \text{ kg} \pm 7.74 \text{ kg}$  of milk per day pre-trial. Eight cows were in late lactation (number of days in milk ranging from 155 to 332 at the beginning of the experiment) and 15 were in early lactation (number of days in milk ranging from 0 to 36 at the beginning of the experiment). The energy-corrected milk for the gas intensity data was calculated from the tank milk composition of the sampling week and individual milk yields.

## 2.3 Sample analysis

The primary DM content of feeds and feces was determined by oven drying at 103°C for 20–24 h. The silage DM content was corrected for volatile losses by [Huida et al. \(1986\)](#). The chemical composition of feeds and feces was analyzed by standard procedures. Prior to the analysis, the dried feed (50°C for 48 h) and fecal (70°C for 48 h) samples were ground to pass through a 1-mm sieve. The ash was determined by ashing at 600°C for 20–24 h (Heraeus Thermicon T; Heraeus, Hanau, Germany). The neutral detergent fiber (NDF) was determined using sodium sulfite ([Van Soest et al., 1991](#)) and  $\alpha$ -amylase (only concentrates) with an automatic FiberTherm FT12 analyzer (Gerhardt, Königswinter, Germany). The NDF content is reported on an ash-free basis. The crude protein was analyzed, as described by [Pitkänen et al. \(2023\)](#), using undried material for feces. For the analysis of total fat, the samples were hydrolyzed with 800 mL of HCl (4 mol/L) (SoxCap 2047 hydrolysis unit; FOSS Analytical, Hillerød, Denmark) following an extraction with 90 mL of petroleum ether (FOSS Soxtec 8000 extraction unit; FOSS Analytical, Hillerød, Denmark). The starch content was measured by using the amyloglucosidase and  $\alpha$ -amylase method with a K-TSTA kit (Megazyme Co., Wicklow, Ireland) and a spectrophotometer (Shimadzu UV-VIS mini1240; Shimadzu Europa GmbH, Duisburg, Germany), according to the manufacturer's instructions ([Pitkänen et al., 2023](#)). The silage fermentation quality was determined from undried samples, as described by [Pitkänen et al. \(2023\)](#). The FA analysis of feeds and milk is described in detail by [Lamminen et al. \(2019\)](#). In brief, the lipids in feeds were extracted with a mixture of hexane and isopropanol (3: 2, vol: vol), and the lipids in milk with a mixture of ammonia, ethanol, diethyl ether, and hexane (0.2: 1.0: 2.5: 2.5, vol: vol). The fatty acid methyl esters were prepared and analyzed using a gas chromatograph (GC2010 Plus; Shimadzu, Kyoto, Japan) equipped with a 100-m fused silica capillary column (CP-SIL 88, Agilent J&W, Santa Clara, CA, USA). The milk lactose, crude fat, crude protein, and urea contents were determined by mid-infrared analysis in a commercial laboratory (MilkoScan FT+, Foss Electric A/S, Hillerød, Denmark; Valio Ltd, Seinäjoki, Finland). A trained sensory panel ( $n = 10$ ) was used to evaluate the test and control UHT milks. Overall liking was rated, and the sensory profile of the milks was studied using the Check-All-That-Apply (CATA) method. Regarding the test and control butter and cheese, both the concept and sensory properties were evaluated by the respondents ( $n = 151$ ), who were at least monthly users of butter and at least weekly users of cheese. Interest toward the concept, overall liking, product attributes (CATA), preference (which butter/cheese would you prefer), and reasons for preference were studied.

## 2.4 Calculations and statistical analysis

Energy-corrected milk yield was corrected to an energy content of 3.14 MJ/kg ([Luke, 2023](#)). The metabolizable energy (ME), metabolizable protein (MP), and protein balance in the rumen

(PBV) were calculated according to the Finnish feed evaluation system ([Luke, 2023](#)). The apparent digestibility of nutrients was calculated using acid-insoluble ash as an internal marker in feeds and feces ([Van Keulen and Young, 1977](#)).

The data were analyzed using PROC MIXED of the Statistical Analysis System (SAS version 9.4, 2012). In the pilot dairy cow study, the data on nutrient intake and digestibility were analyzed with pairwise  $t$ -tests (PDIF option), with a statistical model containing diet as a fixed effect and cow as a random effect. The time series data on lactational performance and milk composition were analyzed by ANOVA for repeated measures using polynomial contrast (linear, quadratic, cubic), and a model that had the sampling day as the fixed effect with a Satterthwaite correction. The AR(1) covariance structure was applied with a cow as the subject for repeated measures. In the main dairy cow study, only data obtained during sampling weeks were analyzed by ANOVA for linear and quadratic responses. The statistical model contained period as a fixed and cow as a random effect. The RedJade Sensory Software (RedJade Sensory Solutions LLC, Pleasant Hill, CA, USA) was used for the collection and analysis of the sensory data of the UHT milks evaluated by an expert panel. The Z test was used to analyze differences between the milks in overall liking and sensory profile. Data on the sensory evaluation of cheese and butter by a consumer panel was analyzed using Microsoft Excel® (version 2016; Microsoft Corporation, Redmond, WA, USA). The differences in overall liking and product preference were analyzed using the  $t$ -test, and the frequencies of the different product attributes and product preferences were calculated. The reasons to prefer a cheese/butter were asked with an open question. In all analyses, the results were considered statistically significant when the  $p$ -value was  $\leq 0.05$ . The differences at a  $p$ -value  $> 0.05$  to 0.10 were considered as a trend toward significance. The normality of the residuals was tested using a univariate procedure and the Shapiro–Wilk test. If the residuals were not normally distributed, the variables were transformed (log, square, inverse) to obtain a normal distribution of the residuals.

## 3 Results

### 3.1 Feed and diet composition

The chemical composition of the experimental feeds is presented in [Table 3](#). The grass silages were of high (main study) or moderate (pilot study) nutritive value in terms of their digestible organic matter contents, which is typical of the early to normal growth stage for silage making. In the main study, the grass silage was restrictively fermented, as indicated by the low levels of fermentation acids and high levels of residual sugars. In the pilot study, the grass silage was more extensively fermented. The forage-to-concentrate ratio of the diets consumed averaged 54: 46 and 51:49 on a DM basis for the pilot and the main dairy cow studies, respectively. The experimental PMR concentrates were isonitrogenous for rapeseed protein, but in the control diet, the concentrate contained more starch and less total fat than that of the test diet. Furthermore, milled rapeseeds contained 10 times more

TABLE 3 The chemical composition of the experimental feeds in the pilot study and in the main study.

	Pilot study				Main study			
	Grass silage <sup>1</sup>	Control diet PMR concentrate	Test diet PMR concentrate	Concentrate at milkings	Grass silage <sup>2</sup>	Control diet PMR concentrate	Test diet PMR concentrate	Concentrate at milking robot
Dry matter (g/kg)	253	863	892	862	411	875	889	878
<b>In dry matter (g/kg)</b>								
Ash	78.7	52.3	76.4	66.9	73.9	93.1	83.0	73.7
Crude protein	146	206	175	191	136	201	195	203
Metabolizable protein <sup>3</sup>	81.2	116	104	119	82.2	93.0	89.3	119
Protein balance in the rumen <sup>3</sup>	24.8	28.2	26.5	38.0	12.9	64.1	63.3	38.0
Starch	–	293	151	283	2.50	328	162	298
Neutral detergent fiber	552	236	248	236	508	219	258	203
Total fat	28.1	35.7	186	42.2	24.9	25.4	170	31.3
Digestible organic matter	675				696			
Metabolizable energy (MJ/kg dry matter <sup>3</sup> )	10.8	11.8	14.5	12.8	11.1	12.0	13.8	12.8
<b>Fatty acid (FA) composition (g/100 g FA)</b>								
16:0	17.4	12.3	5.61	33.6	17.9	14.7	5.90	42.3
18:0	1.25	1.68	1.80	2.43	1.60	2.09	1.87	2.36
<i>cis</i> -9 18:1	3.26	37.5	53.6	32.4	3.22	34.5	51.0	23.4
<i>cis</i> -9, <i>cis</i> -12 18:2	18.2	33.4	21.9	23.7	29.5	35.6	23.1	24.2
<i>cis</i> -9, <i>cis</i> -12, <i>cis</i> -15 18:3	54.5	7.18	10.5	3.27	55.0	5.72	11.2	2.91
<i>cis</i> -13 22:1	0.01	0.15	0.03	0.05	–	0.16	0.04	0.07
Saturated FAs	21.2	15.3	8.69	37.4	22.4	18.4	9.23	46.0
Monounsaturated FAs	5.93	44.1	58.9	35.6	6.12	39.3	56.5	26.9
Polyunsaturated FAs	72.8	40.6	32.5	27.0	71.4	41.4	34.3	27.1
Total FAs (g/kg dry matter)	16.5	15.0	179	36.8	14.4	17.4	167	27.8

<sup>1</sup>Fermentation characteristics: pH 4.32; in dry matter (g/kg) water-soluble carbohydrates 83.5, lactic acid 80.5, acetic acid 7.49, propionic acid < 0.01, and butyric acid < 0.01; and ammonium-N of total N (g/kg N) 74.9.

<sup>2</sup>Fermentation characteristics: pH 4.70; in dry matter (g/kg) water-soluble carbohydrates 165, lactic acid 2.48, acetic acid 1.49, propionic acid 1.88, butyric acid 0.09, and ethanol 9.99; and ammonium-N of total N (g/kg N) 31.0.

<sup>3</sup>Calculated according to Luke (2023).

total fat than rapeseed meal (Table 2). The predominant FA in grass silage was *cis*-9,*cis*-12,*cis*-15 18:3  $\alpha$ -linolenic acid (ALA), whereas for the PMR concentrates *cis*-9,*cis*-12 18:2 linoleic acid (LA) and OA were the most abundant (Table 3). The FA composition of the PMR concentrate ingredients used in the main dairy cow study is presented in Table 2. Of the total FA in the milled rapeseeds, OA formed 53 g/100 g FA followed by 22 g/100 g FA of LA, and 12 g/100 g FA of ALA. The lipids in all the experimental rapeseed feeds were low in *cis*-13 22:1 erucic acid. The oats contained 1.7 times more total fat than barley. Compared with barley lipids, oat lipids contained more OA (12 g/100 g FA vs 34 g/100 g FA) and less LA (54 g/100 g FA vs 40 g/100 g FA).

## 3.2 Nutrient intake and digestibility

In the pilot dairy cow study, milled rapeseeds together with the oats tended to decrease DM intake by 3.3 kg/d ( $p = 0.072$ ; Table 4) relative to the control diet, but on ME intake the decrease was only numerical ( $p > 0.10$ ). The test diet increased the intake of total fat by 0.78 kg/d ( $p < 0.001$ ). The intake of all FA, OA, LA, and ALA, in particular, was increased by the test diet ( $p < 0.001$ ; Supplemental Table 1). Furthermore, the apparent total tract digestibility of all nutrients was lower for

the test than the control diet ( $p \leq 0.003$ ; Table 4; Supplemental Table 1).

In the main dairy cow study, milled rapeseeds together with oats decreased the DM intake by 0.9 kg/d ( $p = 0.027$  for quadratic response; Table 5) relative to the control diet; the decrease originating mainly from the lower silage intake ( $p = 0.009$ ). Furthermore, the test diet decreased crude protein and starch intake ( $p \leq 0.003$ ), but increased that of energy-rich total fat by 0.98 kg/d ( $p < 0.001$ ). Of the individual FAs, the consumption of OA, LA, and ALA in particular was increased by the test diet relative to the control ( $p < 0.001$ ). Lipid supplementation had no effect on ME intake ( $p > 0.10$ ). For both diets, the PBV was positive and was, on average, 34 g/kg diet DM. The apparent total tract digestibility of all nutrients was lower for the test than for the control diet ( $p < 0.001$ ).

## 3.3 Milk production and composition

In the pilot dairy cow study, the milk yield tended to decrease cubically from 26.6 kg/d to 23.3 kg/d ( $p = 0.053$ ) and the ECM yield decreased linearly from 27.6 kg/d to 23.9 kg/d ( $p = 0.041$ ) after switching from the control to the test diet (Supplemental Table 2). However, dietary plant lipids had no effect on milk fat, lactose, protein, and urea concentrations ( $p > 0.10$ ).

TABLE 4 Nutrient intake, apparent total tract digestibility coefficients, and the composition of tank milk used for processing dairy products, and the dairy product sensory quality in the pilot study.

	Control diet	Test diet	SEM	Significance
<b>Intake<sup>1</sup> (kg/d)</b>				
Dry matter	21.9	18.6	1.18	0.072
Starch	2.70	1.93	0.109	< 0.001
Neutral detergent fiber	9.00	7.43	0.539	0.068
Total fat	0.73	1.51	0.073	< 0.001
ME-corrected intake <sup>2</sup> (MJ/d)	233	219	11.7	0.411
<b>Digestibility coefficients<sup>1</sup></b>				
Organic matter	0.744	0.647	0.0040	< 0.001
Neutral detergent fiber	0.613	0.478	0.0065	< 0.001
Total fat	0.763	0.612	0.0275	0.003
<b>Tank milk composition</b>				
Lactose (g/kg)	41.6	42.3		
Protein (g/kg)	35.7	35.6		
Fat (g/kg)	42.9	43.1		
Fatty acid (FA) <sup>1</sup> (g/100 g FA)				
4- to 14-carbon FAs	29.1	18.7		
16:0	31.4	19.4		
18:0	8.95	17.4		
<i>cis</i> -9 18:1	18.1	31.2		

(Continued)



TABLE 4 Continued

	Control diet	Test diet	SEM	Significance
Saturated FAs	71.8	57.8		
Monounsaturated FAs	24.6	38.9		
Polyunsaturated FAs	2.81	2.43		
<i>Trans</i> FAs	3.55	5.33		
<b>Ultra-high temperature-processed milk</b>				
Overall rating, average <sup>3</sup>	2.9	2.6	0.11	0.081
Attributes	Neutral, musty, old	Old, grainy flavor, pea flavor		
<b>Butter</b>				
Overall rating, average <sup>4</sup>	4.9	5.1	0.19	0.219
Attributes	Difficult to spread, natural taste, hard	Natural taste, low salt, yellow color		
Preference <sup>5</sup>	47%	53%		
Reasons to prefer the product	Better taste, natural taste, optimal saltiness	Better taste, natural taste, better spreadability		
<b>Cheese</b>				
Overall rating, average <sup>4</sup>	4.7	4.7	0.21	0.826
Attributes	Soft, aromatic, full taste	Soft, tasty, optimal saltiness		
Preference <sup>5</sup>	51%	49%		
Reasons to prefer the product	Better taste, stronger taste, better structure	Better taste, better structure, softer		

<sup>1</sup>Nutrient intake, digestibility coefficients, and milk fatty acids are presented in more detail in [Supplemental Table 1](#).

<sup>2</sup>Metabolizable energy intake corrected for the associative effects according to [Luke \(2023\)](#).

<sup>3</sup>Scale 1–4 (1—I do not like it at all; 4—I like it very much).

<sup>4</sup>Scale 1–7 (1—I do not like it at all; 7—I like it very much).

<sup>5</sup>Percentage of respondents who preferred the product.

In the main dairy cow study, milled rapeseeds together with oats did not affect the yields of milk, ECM, lactose, fat, or protein ( $p > 0.10$  for quadratic response; [Table 6](#)). However, the yields of milk, ECM, lactose, and protein decreased linearly ( $p \leq 0.025$ ) during the experiment. Dietary plant lipids had no effect on milk fat or lactose concentration ( $p > 0.10$ ), but there was a subtle quadratic increase ( $p = 0.010$ ) in the milk protein concentration, with a concomitant linear decrease ( $p = 0.028$ ) in the milk urea concentration as the experiment progressed.

The milk FA composition was similarly modified by the test diet in both experiments ([Table 6](#); [Supplemental Table 2](#)), with the large changes reaching a plateau within 10 days after the dietary changes ([Figures 1, 2](#); [Supplemental Table 2](#)). The milled rapeseeds together with oats decreased the total SFA in milk fat by 11.7% to 14.2%-units ( $p < 0.001$  for quadratic response; [Table 6](#); [Supplemental Table 2](#)) relative to the control diet. The milk fat concentration of all SFAs of 6- to 16-carbon, 16:0 palmitic acid (PA), in particular, was decreased ( $p \leq 0.005$ ) by the test diet. By contrast, it almost doubled the milk fat OA and SA concentrations ( $p < 0.001$ ) relative to the control diet. Furthermore, it resulted in minor decreases in milk fat LA and ALA ( $p < 0.001$ ) concentrations. The test diet increased milk fat concentration of total *trans* FAs ( $p < 0.001$ ), of which *trans*-11 18:1 predominated. However, the increases in milk fat *trans* FAs were rather limited in magnitude.

### 3.4 Sensory quality of dairy products

No significant differences in sensory characteristics were seen in the UHT milk, butter, and cheese produced from the test milk and the control milk ( $p > 0.05$ ; [Table 4](#)). In overall ratings, the new products with less saturated fat got very similar ratings to the control products. There was also no major difference in which products, the test or the control, were preferred. The test butter was considered softer and easier to spread, and more than 40% of respondents found nothing to improve in the butter. The saltiness of the test cheese was better and the taste milder than in the control cheese. Both cheeses were soft, and a slightly harder construction had been hoped for. Regarding the concept of reduced saturated fat dairy products, over half of the respondents considered a good FA composition important. Based on the product description, 70% of respondents would probably buy milk products with a modified FA composition.

### 3.5 Gas exchange

The dairy cow gas exchange is presented in [Table 7](#). The milled rapeseeds together with the oats decreased ruminal CH<sub>4</sub> and H<sub>2</sub> total emissions (g/d and mg/d, respectively), yields (g/kg DM intake

TABLE 5 Nutrient intake and apparent total tract digestibility coefficients in the main study.

	Diet			Mean response to the test diet <sup>1</sup>	SEM	Significance	
	Control Period 1	Test Period 2	Control Period 3			Linear	Quadratic
Intake, (kg/d)							
Dry matter	21.9	21.2	22.2	−0.9	0.70	0.582	0.027
Silage	11.1	10.6	11.4	−0.7	0.36	0.468	0.009
Organic matter	20.2	19.5	20.4	−0.80	0.64	0.671	0.045
Crude protein	3.80	3.50	3.65	−0.23	0.119	0.034	0.003
MP <sup>2</sup>	2.00	1.92	2.03	−0.10	0.064	0.674	0.008
PBV <sup>2</sup>	0.75	0.72	0.76	−0.04	0.024	0.622	0.013
Starch	3.47	2.21	3.50	−1.28	0.108	0.205	< 0.001
Neutral detergent fiber	8.02	7.81	8.15	−0.28	0.256	0.576	0.073
Total fat	0.56	1.56	0.60	0.98	0.031	< 0.001	< 0.001
ME-corrected intake <sup>3</sup> (MJ/d)	239	240	242	−1	7.2	0.569	0.863
Fatty acid intake (g/d)	380	1,280	409	885.5	24.5	< 0.001	< 0.001
16:0	72.0	125	115	31.5	4.06	< 0.001	< 0.001
18:0	5.05	5.22	4.87	0.26	0.186	0.104	0.003
<i>cis</i> -9 18:1 <sup>4</sup>	69.4	558	70.0	488.3			
	(1.84)	(2.74)	(1.84)		0.015	< 0.001	< 0.001
<i>cis</i> -9, <i>cis</i> -12 18:2	98.7	290	94.0	193.7	5.60	0.015	< 0.001
<i>cis</i> -9, <i>cis</i> -12, <i>cis</i> -15 18:3	105	197	99.1	95.0	4.37	0.419	< 0.001
<i>cis</i> -13 22:1	0.23	0.49	0.32	0.22	0.011	< 0.001	< 0.001
Saturated FAs	88.7	153	130	43.7	4.65	< 0.001	< 0.001
Monounsaturated FAs <sup>4</sup>	89.2	641	87.4	552.7			
	(1.95)	(2.80)	(1.94)		0.015	< 0.001	< 0.001
Polyunsaturated FAs	204	488	193	290	9.9	0.063	<0.001
Digestibility coefficients							
Dry matter	0.709	0.608	0.675	−0.084	0.0063	< 0.001	< 0.001
Organic matter	0.721	0.623	0.688	−0.081	0.0065	< 0.001	< 0.001
Crude protein	0.700	0.633	0.655	−0.045	0.0080	< 0.001	< 0.001
Neutral detergent fiber	0.523	0.387	0.463	−0.106	0.0134	< 0.001	< 0.001
Total fat <sup>5</sup>	0.590	0.484	0.631	−0.127			
	(0.348)	(0.247)	(0.399)		0.0180	0.121	< 0.001

<sup>1</sup>Calculated as: test diet; period 2−(control diet; period 1 + control diet; period 3)/2.  
<sup>2</sup>Metabolizable protein (MP) and protein balance in the rumen (PBV) were calculated according to Luke (2023).  
<sup>3</sup>Metabolizable energy intake corrected for associative effects according to Luke (2023).  
<sup>4</sup>Log<sub>10</sub> conversion is given in parentheses below to obtain normality.  
<sup>5</sup>Square conversion is given in parentheses below to obtain normality.

or mg/kg DM intake), and intensities (g/kg ECM or mg/kg ECM;  $p < 0.001$  for the quadratic response). Depending on the emission unit, the decrease was 16%–20% for CH<sub>4</sub> and 36%–39% for H<sub>2</sub>. However, the effect of plant lipids on CO<sub>2</sub> emissions (decrease of 3%–5%;  $p \leq 0.084$ ) was limited in magnitude. The plant lipids had no major effect on the O<sub>2</sub> consumption of dairy cows ( $p > 0.10$ ).

## 4 Discussion

The novel feature of this experiment was in assessing the feasibility of simultaneously decreasing both bovine milk fat SFAs and ruminal methane emissions when milled rapeseeds and oats instead of rapeseed meal and barley are fed to animals in practical

TABLE 6 Milk yield and milk composition in the main study.

	Diet			Mean response to the test diet <sup>1</sup>	Significance		
	Control Period 1	Test Period 2	Control Period 3		SEM	Linear	Quadratic
Yield (kg/d)							
Milk	31.4	29.7	27.6	0.2	2.66	< 0.001	0.638
Energy-corrected milk	32.4	30.8	29.0	0.1	2.61	0.025	0.796
Lactose	1.41	1.34	1.23	0.02	0.133	< 0.001	0.418
Fat	1.32	1.27	1.18	0.02	0.113	0.123	0.727
Protein	1.13	1.05	1.03	−0.03	0.083	0.007	0.488
Concentration in milk							
Lactose (g/kg)	44.5	44.7	44.1	0.4	0.60	0.216	0.156
Fat (g/kg)	42.8	43.3	43.6	0.1	2.27	0.726	0.996
Protein (g/kg)	36.4	36.3	38.1	−1.0	1.03	0.002	0.010
Urea (mg/dL)	27.3	27.0	24.9	0.9	1.37	0.028	0.254
Concentration in milk fat [g/100 g fatty acids (FAs)]							
4:0	3.32	3.06	3.12	−0.16	0.085	0.002	0.030
6:0	2.15	1.64	2.03	−0.45	0.047	< 0.001	< 0.001
8:0	1.36	0.91	1.26	−0.40	0.035	< 0.001	< 0.001
10:0	3.25	1.88	2.95	−1.22	0.101	< 0.001	< 0.001
12:0	3.95	2.19	3.63	−1.60	0.131	< 0.001	< 0.001
14:0	12.5	8.91	12.0	−3.34	0.250	0.004	< 0.001
16:0	32.3	21.5	33.1	−11.2	0.48	0.609	< 0.001
18:0	8.55	16.2	8.26	7.80	0.379	0.364	< 0.001
<i>cis</i> -9 18:1	18.0	29.6	18.4	11.4	0.60	0.013	< 0.001
<i>trans</i> -10 18:1 <sup>2</sup>	0.14	0.32	0.15	0.18			
	(7.19)	(3.29)	(6.91)		0.209	0.004	< 0.001
<i>trans</i> -11 18:1 <sup>2</sup>	0.88	0.92	0.89	0.04			
	(1.18)	(1.11)	(1.78)		0.062	0.950	0.330
<i>cis</i> -9, <i>cis</i> -12 18:2	1.29	1.05	1.26	−0.23	0.044	0.187	< 0.001
<i>cis</i> -9, <i>trans</i> -11 18:2	0.47	0.50	0.49	0.02	0.035	0.503	0.561
<i>cis</i> -9, <i>cis</i> -12, <i>cis</i> -15 18:3	0.41	0.35	0.37	−0.04	0.015	0.006	< 0.001
<i>cis</i> -13 22:1	0.007	0.006	0.008	-0.002	0.0005	0.017	< 0.001
Saturated FAs	72.3	60.1	71.2	−11.7	0.69	0.002	< 0.001
Monounsaturated FAs	24.4	36.9	25.4	12.0	0.64	< 0.001	< 0.001
Polyunsaturated FAs	2.69	2.26	2.66	−0.42	0.077	0.351	< 0.001
<i>Trans</i> FAs <sup>2</sup>	3.51	4.53	3.61	1.15			
	(0.32)	(0.23)	(0.28)		0.010	0.004	< 0.001

<sup>1</sup>Calculated as: test diet; period 2−(control diet; period 1 + control diet; period 3)/2.<sup>2</sup>Inverse conversion is given in parentheses below to obtain normality.

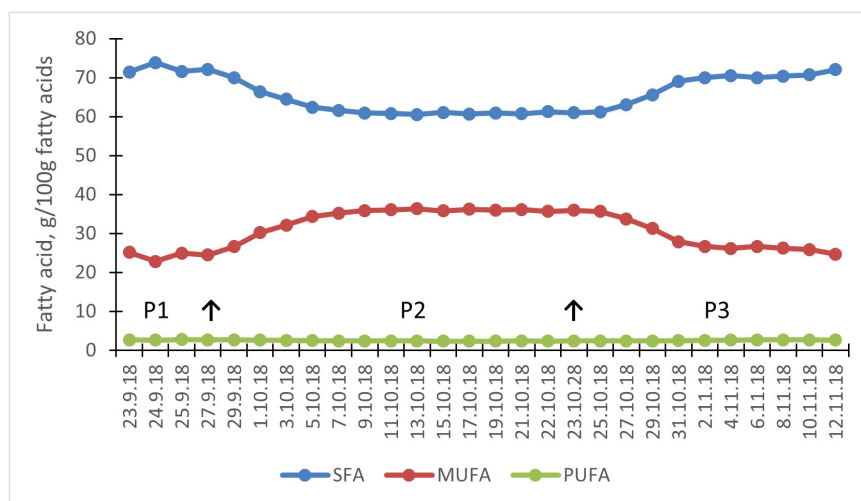


FIGURE 1

Effect of milled rapeseeds and oats on tank milk saturated fatty acid (SFA), monounsaturated fatty acid (MUFA), and polyunsaturated fatty acid (PUFA) concentrations in the main dairy cow study. Arrows represent the dietary change of the whole herd from control diet in period 1 (P1) to lipid supplemented diet in period 2 (P2), and back to control diet for period 3 (P3).

whole-herd conditions. In addition, the milk was processed into several dairy products (e.g., UHT milk, butter, and cheese), of which the sensory quality was evaluated to confirm the applicability up to the final products.

Given the limited number of animals, the results on feed intake and milk yields obtained in the pilot study should be interpreted with some caution. However, it is noteworthy that the results were highly consistent between the pilot and the main dairy cow studies, except for variations in animal performance. Nevertheless, at high lipid inclusion rates, a significant decrease in feed intake and milk yield, as observed in the pilot study, is expected when a situation-specific threshold in lipid supply is

surpassed (Drackley et al., 2007; Benchaar et al., 2015; Halmemies-Beauchet-Filleau et al., 2017). This is discussed in more detail later below.

#### 4.1 Feed and diet composition

The main forage component of the diet affects bovine milk FAs (Glasser et al., 2008) and CH<sub>4</sub> response to plant lipids (Vanhatalo and Halmemies-Beauchet-Filleau, 2020). Our experimental diets were based on digestible grass silage that is typical in northern latitudes. The grass silage-rich diets together with using oats instead

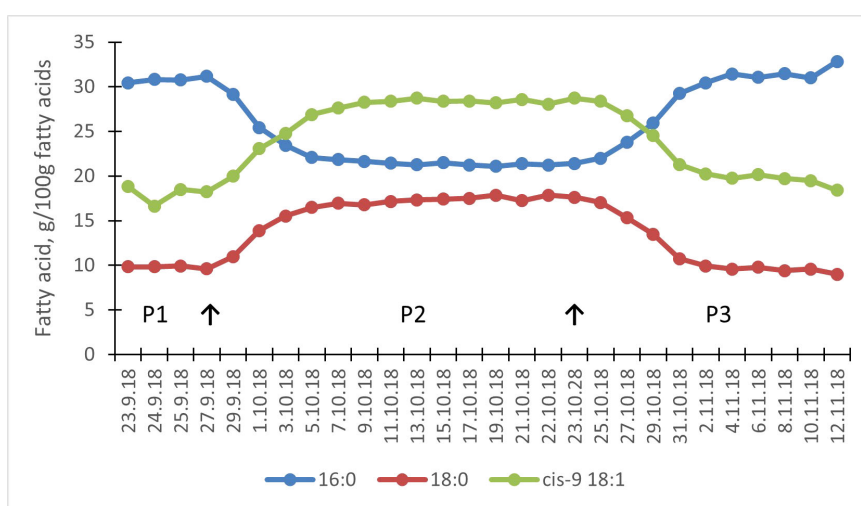


FIGURE 2

Effect of milled rapeseeds and oats on tank milk palmitic acid (PA, 16:0), stearic acid (SA, 18:0), and oleic acid (OA, cis-9 18:1) concentrations in the main dairy cow study. Arrows represent the dietary change of the whole herd from control diet in period 1 (P1) to lipid supplemented diet in period 2 (P2), and back to control diet for period 3 (P3).

TABLE 7 Gas production or consumption (mass per day), gas yield (mass per dry matter intake), and gas intensity (mass per energy-corrected milk production) in the main study.

	Diet			Mean response to the test diet <sup>1</sup>	SEM	Significance	
	Control Period 1	Test Period 2	Control Period 3			Linear	Quadratic
Methane							
g/d	456	378	468	−84	16.9	0.783	< 0.001
g/kg DMI <sup>2</sup>	22.2	18.0	20.7	−3.5	0.66	0.007	< 0.001
g/kg ECM <sup>3</sup>	14.1	12.1	16.0	−3.0	1.09	0.050	< 0.001
Carbon dioxide							
g/d	12,447	11,870	12,575	−641	352.8	0.735	< 0.001
g/kg DMI <sup>2</sup>	605	564	560	−19	13.7	< 0.001	0.084
g/kg ECM <sup>3,4</sup>	376	377	418	−20			
	(2.56)	(2.56)	(2.60)		0.027	0.005	0.035
Hydrogen							
mg/d	653	399	598	−227	49.6	0.157	< 0.001
mg/kg DMI <sup>2</sup>	31.7	18.6	26.7	−10.6	2.23	0.018	< 0.001
mg/kg ECM <sup>3,4</sup>	19.4	12.1	20.3	−7.8			
	(1.25)	(1.05)	(1.23)		0.044	0.318	< 0.001
Oxygen							
g/d	10,592	10,271	10,141	−96	270.0	0.003	0.606
g/kg DMI <sup>2</sup>	516	488	452	4	10.7	< 0.001	0.268
g/kg ECM <sup>3,5</sup>	320	325	337	−4			
	(0.003)	(0.003)	(0.003)		0.0002	0.324	0.778

<sup>1</sup>Calculated as: test diet; period 2−(control diet; period 1 + control diet; period 3)/2.

<sup>2</sup>Dry matter intake.

<sup>3</sup>Energy-corrected milk (ECM) calculated using tank milk composition determined every second day.

<sup>4</sup>Log<sub>10</sub> conversion is given in parentheses below to obtain normality.

<sup>5</sup>Inverse conversion is given in parentheses below to obtain normality.

of barley as the cereal for the test diet PMR led to moderate starch contents for the control (123–158 g/kg DM) and test diets (104 g/kg DM). The lipid content and the FA composition of milled rapeseeds, oats, and barley were similar to previous reports (Welch, 1975; Brask et al., 2013b), with OA forming a major part of the lipid for both milled rapeseeds (53 g/100 g FA) and oats (34 g/100 g FA) in the present work.

## 4.2 Nutrient intake and digestibility

The milled rapeseeds together with oats decreased DM intake by 15% relative to the control diet in the pilot study. The fluctuation in the daily feed intake indicated a slight excess in lipid supplementation for efficient rumen function. This was reflected also in the standard error of the mean (SEM), which was moderately high for feed intake. To maintain a higher and more regular feed intake, the lipid

supplementation rate was decreased from 55 g/kg to 50 g/kg test diet DM for the main study. The lower rate was successful as DM intake was only decreased by 4% relative to the control diet in the main study. At high inclusion rates (i.e., at 40 g/kg or more in DM), lipid supplementation has often suppressed feed intake (Huhtanen et al., 2008; Bayat et al., 2018; Ramin et al., 2021a), with the decrease being generally more pronounced on starch-rich diets (Benchaar et al., 2015; Vanhatalo and Halmemies-Beauchet-Filleau, 2020). The rather low dietary starch content together with the non-excessive lipid inclusion rate probably explains the limited reduction in the feed intake in the main study. In addition to the decreased DM intake, using oats that contain less starch than barley in the test diet relative to the control diet contributed to 0.77 kg and 1.28 kg lower daily starch intake by the test diet cows in the pilot and main dairy cow studies, respectively. However, the lower starch intake on the test diet was compensated by energy-rich lipids leading to similar ME intakes between diets in both studies.



The milled rapeseeds together with oats substantially increased OA, LA, and ALA intakes relative to the control diet, thus reflecting the FA content and composition of the dietary feed ingredients. The vast majority of the supplemental OA was derived from milled rapeseeds and to a lesser extent from oats. The increase in OA intake was of similar magnitude to the previous studies using high rapeseed oil supplementation (Ferlay et al., 1993; Bayat et al., 2018). It is noteworthy that on the control diet ALA, inherent to the chloroplasts in forage leaves (Glasser et al., 2013), represented the major FA consumed by cows; therefore, highlighting the importance of the basal forage to FA intake. Though forages have rather low lipid concentrations, lipid intake from forage can be substantial because forage intake is typically high in ruminant diets (Glasser et al., 2013).

In the present study, supplying a 50–55 g/kg diet DM of lipids from milled rapeseeds and oats significantly suppressed organic matter and the fiber total tract digestibility. This may also explain, at least in part, the decrease in DM intake of the test diet relative to the control diet. Jenkins (1993) proposed various explanatory mechanisms for this, including the direct adverse effects of unsaturated FAs on ruminal microbial communities, cellulolytic microbes in particular, and free FAs forming a protective lipid layer over feed particles in the rumen. However, several reports have subsequently challenged these theories on fiber-rich diets based on grass or legume silage that indicate little if any effect of plant oils on fiber digestibility, even at rather high inclusion rates (Benchaa et al., 2015; Halmemies-Beauchet-Filleau et al., 2017; Bayat et al., 2018). In addition to lipid supplementation, switching cereal fiber quality from barley in the control diet to oats in the test diet may have contributed to a lowered fiber digestion of the test diet. Furthermore, replacing barley with oats has previously decreased NDF digestibility (Vanhatalo et al., 2006; Ramin et al., 2021b). This can be attributed to the significantly higher indigestible NDF content of oats relative to barley (Ramin et al., 2021b).

Once the seedcoat is ruptured, the lipid digestibility of whole rapeseeds is similar to pure oil (Brask et al., 2013b). The digestibility of lipids is often increased (Benchaa et al., 2015; Halmemies-Beauchet-Filleau et al., 2017) or unaffected (Ferlay et al., 1993; Brask et al., 2013a; Brask et al., 2013b) by plant lipid supplementation. In the present studies, however, the apparent digestibility of total fat was unexpectedly lower for the lipid-supplemented test diet than for the control diet. In part, this may be attributable to the reduced intestinal absorption of SA at high post-ruminal flows (Glasser et al., 2008). Indeed, the intake of 18-carbon dietary unsaturated FAs was many times higher on the test diet relative to the control diet, with SA being the end-product of their ruminal biohydrogenation (Shingfield et al., 2010). Though the milling of rapeseeds was assessed as being visually successful, it can also be speculated that some seeds may have escaped the milling through the 6- to 8-mm sieves intact.

### 4.3 Milk production and composition

The linear decrease in the ECM yield in the pilot study after dietary change from the control to the test diet is in line with the

concomitant large reduction in feed intake, and a numerical 6% decrease in the ME intake. However, due to the experimental design, the effect of time and diet cannot be separated in the pilot study. Therefore, a part of the linear decline in animal performance can be attributed to the natural and gradual decline in the milk yield of late-lactation cows. However, in the main dairy cow study, the ECM yield was unaffected by dietary plant lipids, which is consistent with similar ME intakes across treatments due to a much more limited decrease in feed intake. Previously milled rapeseeds have neither affected the ECM yields when supplementing diets based on grass silage (Kairenius et al., 2009; Mierlita et al., 2023) nor a mixture of grass and maize silages (Brask et al., 2013b). In addition, replacing barley with oats has not affected the ECM (Ramin et al., 2021b) or slightly increased it (Vanhatalo et al., 2006). Similar to the pilot study, the linear decrease in the ECM, and protein and lactose yields during the main study can be attributed to the advances in the lactation stage of animals, as 10 out of 13 were in late lactation at the beginning of the experiment and thus on a descending lactation curve. It is worth noting, however, that the decline in milk yield was almost twice less rapid in the main study than in the pilot study between the periods. This confirms that the advance in the lactation stage was not the only cause of the decline in the milk yield in the pilot study. Overall, milled rapeseeds together with oats had negligible effects on the production of milk and the major constituents of milk in the main dairy cow study.

The milled rapeseeds together with oats significantly modified milk FA composition. Relative to the control diet, the total SFA content of milk fat on the test diet was 14.2%-units lower in the pilot study and 11.7%-units lower in the main study. Plant lipids decreased total SFA by, on average, 0.013%- to 0.015%-units per g of supplemental FA. This decrease was similar in extent to previous reports for milled rapeseeds (0.013%-units per g of supplemental FA; Collomb et al., 2004), and for pure rapeseed oil supplementation (0.015%- to 0.019%-units per g of supplemental FA; Bayat et al., 2018; Razzaghi et al., 2022) the decrease in SFA being generally lower on diets high in fiber and low in starch (Razzaghi et al., 2022; Mierlita et al., 2023). Moreover, the 6- to 16-carbon SFAs, derived entirely or in the case of PA 50%–80% from mammary *de novo* synthesis (Halmemies-Beauchet-Filleau et al., 2013), were consistently 22% to 48% lower in milk fat from the test diet than from the control diet. This is in good agreement with the increased supply of long-chain FAs known to inhibit mammary *de novo* synthesis of short- and medium-chain SFAs (Shingfield et al., 2010).

The total monounsaturated FA was 48%–59% higher in milk fat from the test diet than the control diet. This increase principally originated from OA (0.013%- to 0.015%-units per g of supplemental FA) which was the predominant FA in the dietary lipid sources rapeseeds and oats. The increase in milk fat OA was similar to previous studies with rapeseed oil (0.010%- to 0.016%-units per g of supplemental FA; Bayat et al., 2018; Razzaghi et al., 2022) or when replacing barley with oats (0.015%-units per g of supplemental FA; Fant et al., 2023). Milk fat OA has a dual origin. Part of it originates from direct mammary uptake, with circulating OA being derived predominantly from the diet (Shingfield et al., 2010) or during a negative energy balance also from adipose tissue mobilization

(Gross et al., 2011; Jorjong et al., 2014). Another part of milk fat OA originates from mammary desaturation of SA, which is the end-product of ruminal biohydrogenation of dietary 18-carbon unsaturated FA (Shingfield et al., 2010). Therefore, the significant increase in OA, LA, and ALA intakes for the test diet is directly, and, via SA, also indirectly reflected in the milk OA in the present study. The increase in milk fat SA on the test diet is a typical response to plant lipid supplementation (Bayat et al., 2018; Razzaghi et al., 2022; Fant et al., 2023).

The present increases in milk *trans* FAs were limited for lipid in milled rapeseeds and oats (0.0011%– to 0.0014%–units per g of supplemental FA) compared with previous studies with pure rapeseed oil (0.0046%– to 0.0062%–units per g of supplemental FA; Bayat et al., 2018; Razzaghi et al., 2022). In addition, the major *trans* isomers increased in milk fat by the test diet were *trans*-11 18:1 vaccenic acid and *cis*-9,*trans*-11 18:2 rumenic acid, with potentially beneficial effects on human health (Field et al., 2009; Koba and Yanagita, 2014). The moderate increase in milk fat *trans* FAs was in line with a previous report indicating higher ruminal OA and lower *trans*-FA outflow when milled rapeseeds were used instead of pure rapeseed oil supplementation (Kairenius et al., 2009). This suggests partial protection from the ruptured rapeseed seedcoat against ruminal lipid metabolism.

Despite the higher LA and ALA intakes, their milk fat concentrations were slightly lower on the test diet relative to the control diet. This is consistent with more extensive biohydrogenation of LA and ALA relative to OA in the rumen (Shingfield et al., 2010) and the limited effects on milk LA and ALA, when these polyunsaturated FAs have been supplemented in the form of plant oils (Rego et al., 2009; Halmemies-Beauchet-Filleau et al., 2017). The increase in ALA intake through forage generally results in a higher transfer efficiency from the diet into milk (Kalač and Samková, 2010; Halmemies-Beauchet-Filleau et al., 2013), probably due to the fact that more microbial digestion of surrounding material is needed before forage lipids are exposed to ruminal metabolism. This is supported by the concomitant decrease in milk fat ALA content and grass silage consumption despite higher general ALA intake on the test diet in the present study.

#### 4.4 Dairy products with modified FA composition

The sensory characteristics of the UHT milk, butter, and cheese containing less SFAs were similar to those of the control products and were preferred by an equal percentage of consumers as the control products. In general, the test diet butter and cheese were perceived to be of softer texture relative to the control products. Rapeseed lipid inclusion in the diet resulted in softer textures of dairy products, with acceptable organoleptic quality also previously (Ryhänen et al., 2005; Halmemies-Beauchet-Filleau et al., 2011). Furthermore, no change in the milk sensory quality was observed when oats replaced barley as a cereal in the dairy cow diet (Vanhatalo et al., 2006). The concept of reduced-saturated-fat dairy products was received positively by

Finnish consumers, and respondents had a positive view of it. Most consumers considered the products suitable for themselves, and they would be ready to buy them if the product quality is the same as with current products. Some consumers did not entirely understand how the change in FA composition was achieved. This should be taken into account when communicating about these types of products. The consumers' level of acceptance and attitudes toward test butter with low levels of SFAs and a low carbon emission footprint has been reported in a separate paper (Asioli et al., 2023). This complementary study indicated that about one-third of Finnish consumers was willing to pay a premium price for the new type of butter, the consumer attitudes being most promising with young and highly educated consumers.

For a considerable time, many human dietary guidelines recommend that SFA intake should be restricted to reduce the risk of CVD. As dairy foods are often the single greatest dietary source of SFAs, there has been a considerable number of studies examining how dairy cow diets can be modified to reduce the SFA content of milk fat, mainly by replacing them with *cis*-monounsaturated FAs or ALA. There are, however, few detailed human randomized controlled trials (RCTs) examining the chronic impact of such changes on milk FAs on markers of CVD risk. The review of 10 published RCTs, by Livingstone et al. (2012), indicated a tendency toward a believed beneficial lowering effect on fasting serum total and low-density lipoprotein cholesterol (LDL-C) following chronic consumption of modified milk and dairy foods. The recent detailed RESET RCT (Vasilopoulou et al., 2020) used diets containing milk, cheese, and butter with normal (control) or modified FA composition (Kliem et al., 2019), which was similar to the test diet milk in the current dairy cow studies. The study found that in adults at a moderate CVD risk, the consumption of FA-modified dairy foods for 12 weeks significantly moderated the increase in the levels of serum LDL-C seen on the conventional dairy food diet and improved vascular endothelial function. This provides more confidence that milk FA modification, as in the current studies, can provide health benefits. There is, however, increasing uncertainty that the heavy reliance on serum LDL-C as the key risk factor for CVD is too simplistic, in part because it takes no account of the variation in risk linked to the LDL particle size profile (Givens, 2023).

#### 4.5 Gas exchange

The effects of plant lipids on ruminal methanogenesis are dependent on the level of supplementation, the FA profile of the supplements, and the composition of the basal diet (Vanhatalo and Halmemies-Beauchet-Filleau, 2020). Lipids in milled rapeseeds and oats significantly decreased ruminal H<sub>2</sub> load in the main dairy cow study. In addition, CH<sub>4</sub> and H<sub>2</sub> intensities (g or mg gas/kg ECM) were 20% and 39% lower, respectively, on the test diet than on the control diet. For each 1% plant lipid added to the diet, CH<sub>4</sub> intensity was reduced by 4.6%. This agrees well with previous plant lipid data for rapeseed oil (a reduction of 4.5%–5.2% in CH<sub>4</sub> intensity for each

additional 1% in plant lipid; Bayat et al., 2018; Razzaghi et al., 2022) and replacing barley with oats (a reduction of 6.0% in CH<sub>4</sub> intensity for each additional 1% in plant lipid; Fant et al., 2021; Ramin et al., 2021b) on high-grass silage diets. However, it was less effective compared with milled rapeseeds in a diet based on a mixture of grass and maize silage (a reduction of 8.2% in CH<sub>4</sub> intensity for each additional 1% in plant lipid; Brask et al., 2013b).

The reduction of ruminal CH<sub>4</sub> and H<sub>2</sub> production in the present study can be attributed to the lower amount of organic matter fermented in the rumen, as indicated by the lower DM intake and nutrient whole-tract digestibility. Having more organic matter in the feces could be expected to increase CH<sub>4</sub> emissions from manure. However, Ramin et al. (2021a) reported similar total fecal CH<sub>4</sub> emissions *in vitro* (L/d) from feces of cows fed rapeseed lipids compared with unsupplemented ones, despite higher amounts of organic matter being left in the feces. This was due to a significantly lower CH<sub>4</sub> yield (L/kg fecal organic matter) from the feces of cows fed rapeseed lipids. Furthermore, it is possible that the ruminal biohydrogenation of dietary unsaturated FAs served as a minor alternative sink for metabolic H<sub>2</sub> to mitigate CH<sub>4</sub> formation (Beauchemin et al., 2022). Dietary lipid supplementation may also shift rumen fermentation patterns from acetate to propionate (Vanhatalo and Halmemies-Beauchet-Filleau, 2020). However, decreases in methane production due to rapeseed lipids have not been associated with shifts in ruminal fermentation patterns on grass silage-based diets (Brask et al., 2013a; Bayat et al., 2018).

About 155.2 million tons of bovine milk is produced in EU-27 (Eurostat, 2021). If all the dairy cows in EU-27 consumed a diet mitigating CH<sub>4</sub> emissions by 3 g of each kg of milk produced, which is comparable to the decrease observed in the present study, then annual CH<sub>4</sub> emissions would decrease by 465,600 t in the EU-27 area. This decrease would represent about 8.4% of the annual bovine CH<sub>4</sub> emission, 5.6% of the annual agricultural CH<sub>4</sub> emission, and 3.2% of the annual total CH<sub>4</sub> emission in EU-27 (Eurostat, 2021).

## 5 Conclusion

Replacing rapeseed meal and barley with full-fat milled rapeseed and oats in a whole-dairy-herd diet had no adverse effects on ME intake and milk production at a 50 g/kg lipid supplementation rate in the diet DM, but modified milk fat composition as OA inherent to lipid supplements replaced a substantial proportion of the SFAs in the milk fat. This decrease in milk fat SFAs can be attributed to the lower level of mammary *de novo* synthesis due to the increased supply of OA and its biohydrogenation end-product SA for milk fat synthesis. The dairy products (UHT milk, butter, cheese) with a modified lipid profile were of a similar organoleptic quality to the control products. Further research is needed to assess whether or not the changed milk FA profile has long-lasting health benefits when consumed by humans. The lipids in the milled rapeseeds and oats significantly decreased ruminal H<sub>2</sub> load and further CH<sub>4</sub> emissions, which is consistent with lower DM intake and nutrient digestibility. Therefore, milled rapeseeds and oats as regular dietary ingredients

are an efficient means to soften milk fat and mitigate methane emissions at the whole-herd level.

## Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

## Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because no prior authorization is required for projects that are likely to cause a level of harm lower than that caused by the introduction of a needle. Therefore, milk and fecal sampling carried out in this project did not require ethical approval according to national regulations (<https://avi.fi/en/services/individuals/licences-notices-and-applications/animals/laboratory-animals>).

## Author contributions

AH-B-F: Conceptualization, Supervision, Writing – review & editing, Writing – original draft. SJ: Conceptualization, Writing – review & editing, Supervision. TK: Conceptualization, Supervision, Writing – review & editing. AT: Writing – original draft, Writing – review & editing. DG: Conceptualization, Funding acquisition, Project administration, Writing – review & editing. AV: Conceptualization, Funding acquisition, Project administration, Writing – review & editing.

## Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. This study was financed in part by EIT Food Project: Dairy products with reduced saturated fatty acids (grant number 18095).

## Acknowledgments

The authors thank the contribution of the staff at the University of Helsinki Viikki research farm and the laboratory of Animal Science. The valued contributions of MSc students Milja Korjus, Kasper Ojala, Vappu Tauriainen, and Tuire Tapola for practical experimental work at the dairy barn are much appreciated.

## Conflict of interest

Author AT was employed by the company Valio Ltd.

The remaining 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.

## Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the

reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fanim.2023.1278495/full#supplementary-material>

## References

- Asioli, D., Zhou, X., Halmemies-Beauchet-Filleau, A., Vanhatalo, A., Givens, D. I., Rondoni, A., et al. (2023). Consumers' valuation for low-carbon emission and low-saturated fat butter. *Food Qual. Pref.* 108, 104859. doi: 10.1016/j.foodqual.2023.104859
- Bayat, A. R., Tapio, I., Vilkki, J., Shingfield, K. J., and Leskinen, H. (2018). Plant oil supplements reduce methane emissions and improve milk fatty acid composition in dairy cows fed grass silage-based diets without affecting milk yield. *J. Dairy Sci.* 101, 1136–1151. doi: 10.3168/jds.2017-13545
- Beauchemin, K. A., Ungerfeld, E. M., Abdalla, A. L., Alvarez, C., Arndt, C., Becquet, P., et al. (2022). Invited review: Current enteric methane mitigation options. *J. Dairy Sci.* 105, 9297–9326. doi: 10.3168/jds.2022-22091
- Benchaa, C., Hassanat, F., Martineau, R., and Gervais, R. (2015). Linseed oil supplementation to dairy cows fed diets based on red clover silage or corn silage: Effects on methane production, rumen fermentation, nutrient digestibility, N balance, and milk production. *J. Dairy Sci.* 98, 7993–8008. doi: 10.3168/jds.2015-9398
- Brask, M., Lund, P., Hellwing, A. L. F., Poulsen, M., and Weisbjerg, M. R. (2013a). Enteric methane production, digestibility and rumen fermentation in dairy cows fed different forages with and without rapeseed fat supplementation. *Anim. Feed Sci. Technol.* 184, 67–79. doi: 10.1016/j.anifeeds.2013.06.006
- Brask, M., Lund, P., Weisbjerg, M. R., Hellwing, A. L. F., Poulsen, M., Larsen, M. K., et al. (2013b). Methane production and digestion of different physical forms of rapeseed fat supplements in dairy cows. *J. Dairy Sci.* 96, 2356–2365. doi: 10.3168/jds.2011-5239
- Briggs, M. A., Petersen, K. S., and Kris-Etherton, P. M. (2017). Saturated fatty acids and cardiovascular disease: Replacements for saturated fat to reduce cardiovascular risk. *Healthc. (Basel)* 5, 29. doi: 10.3390/healthcare5020029
- Chen, S., Bobe, G., Zimmerman, S., Hammond, E. G., Luhman, C. M., Boylston, T. D., et al. (2004). Physical and sensory properties of dairy products from cows with various milk fatty acid compositions. *J. Agric. Food Chem.* 52, 3422–3428. doi: 10.1021/jf035193z
- Clifton, P. M., and Keogh, J. B. (2017). A systematic review of the effect of dietary saturated and polyunsaturated fat on heart disease. *Nutr. Metab. Cardiovasc. Dis.* 27, 1060–1080. doi: 10.1016/j.numecd.2017.10.010
- Collomb, M., Sollberger, H., Bütikofer, U., Sieber, R., Stoll, W., and Schaeren, W. (2004). Impact of a basal diet of hay and fodder beet supplemented with rapeseed, linseed and sunflowerseed on the fatty acid composition of milk fat. *Int. Dairy J.* 14, 549–559. doi: 10.1016/j.idairyj.2003.11.004
- Drackley, J. K., Overton, T. R., Ortiz-Gonzalez, G., Beaulieu, A. D., Barbano, D. M., Lynch, J. M., et al. (2007). Responses to increasing amounts of high-oleic sunflower fatty acids infused into the abomasum of lactating dairy cows. *J. Dairy Sci.* 90, 5165–5175. doi: 10.3168/jds.2007-0122
- Eurostat (2021). Available at: <https://ec.europa.eu/eurostat> (Accessed June 27, 2023).
- Fant, P., Leskinen, H., Ramin, M., and Huhtanen, P. (2023). Effects of replacement of barley with oats on milk fatty acid composition in dairy cows fed grass silage-based diets. *J. Dairy Sci.* 106, 2347–2360. doi: 10.3168/jds.2022-22327
- Fant, P., Ramin, M., and Huhtanen, P. (2021). Replacement of barley with oats and dehulled oats: Effects on milk production, enteric methane emissions, and energy utilization in dairy cows fed a grass silage-based diet. *J. Dairy Sci.* 104, 12540–12552. doi: 10.3168/jds.2021-20409
- Ferlay, A., Chabrot, J., Elmeddah, Y., and Doreau, M. (1993). Ruminant lipid balance and intestinal digestion by dairy cows fed calcium salts of rapeseed oil fatty acids or rapeseed oil. *J. Anim. Sci.* 71, 2237–2245. doi: 10.2527/1993.7182237x
- Field, C. J., Blewett, H. H., Proctor, S., and Vine, D. (2009). Human health benefits of vaccenic acid. *Appl. Physiol. Nutr. Metab.* 34, 979–991. doi: 10.1139/H09-079
- Givens, D. I. (2023). Dairy foods and cardiometabolic diseases: an update and a reassessment of the impact of saturated fatty acids. *Proc. Nutr. Soc.* 82, 320–345. doi: 10.1017/S0029665123000083
- Glasser, F., Doreau, M., Maxin, G., and Baumont, R. (2013). Fat and fatty acid content and composition of forages: A meta-analysis. *Anim. Feed Sci. Technol.* 185, 19–34. doi: 10.1016/j.anifeeds.2013.06.010
- Glasser, F., Ferlay, A., and Chilliard, Y. (2008). Oilseed lipid supplements and fatty acid composition of cow milk: a meta-analysis. *J. Dairy Sci.* 91, 4687–4703. doi: 10.3168/jds.2008-0987
- Gross, J., van Dorland, H. A., Bruckmaier, R. M., and Schwarz, F. J. (2011). Milk fatty acid profile related to energy balance in dairy cows. *J. Dairy Res.* 78, 479–488. doi: 10.1017/S0022029911000550
- Halmemies-Beauchet-Filleau, A., Kairenius, P., Ahvenjärvi, S., Toivonen, V., Huhtanen, P., Vanhatalo, A., et al. (2013). Effect of forage conservation method on plasma lipids, mammary lipogenesis, and milk fatty acid composition in lactating cows fed diets containing a 60:40 forage-to-concentrate ratio. *J. Dairy Sci.* 96, 5267–5289. doi: 10.3168/jds.2013-6571
- Halmemies-Beauchet-Filleau, A., Kokkonen, T., Lampi, A. M., Toivonen, V., Shingfield, K. J., and Vanhatalo, A. (2011). Effect of plant oils and camelina expeller on milk fatty acid composition in lactating cows fed diets based on red clover silage. *J. Dairy Sci.* 94, 4413–4430. doi: 10.3168/jds.2010-3885
- Halmemies-Beauchet-Filleau, A., Shingfield, K. J., Simpura, I., Kokkonen, T., Jaakkola, S., Toivonen, V., et al. (2017). Effect of incremental amounts of camelina oil on milk fatty acid composition in lactating cows fed diets based on a mixture of grass and red clover silage and concentrates containing camelina expeller. *J. Dairy Sci.* 100, 305–324. doi: 10.3168/jds.2016-11438
- Hillbrick, G., and Augustin, M. A. (2002). Milkfat characteristics and functionality: opportunities for improvement. *Aust. J. Dairy Tech.* 57, 45–51.
- Hristov, A. N., Melgar, A., Wasson, D., and Arndt, C. (2022). Symposium review: Effective nutritional strategies to mitigate enteric methane in dairy cattle. *J. Dairy Sci.* 105, 8543–8557. doi: 10.3168/jds.2021-21398
- Huhtanen, P., Cabezas-Garcia, E. H., Utsumi, S., and Zimmerman, S. (2015). Comparison of methods to determine methane emissions from dairy cows in farm conditions. *J. Dairy Sci.* 98, 3394–3409. doi: 10.3168/jds.2014-9118
- Huhtanen, P., Rinne, M., and Nousiainen, J. (2008). Evaluation of concentrate factors affecting silage intake of dairy cows: a development of the relative total diet intake index. *Animal* 2, 942–953. doi: 10.1017/S1751731108001924
- Huida, L., Väättäin, H., and Lampila, M. (1986). Comparison of dry matter contents in grass silages as determined by oven drying and gas chromatographic water analysis. *Ann. Agric. Fenn.* 25, 215–230. <http://urn.fi/URN:NBN:fi-fe2014102145444>.
- Jenkins, T. C. (1993). Lipid metabolism in the rumen. *J. Dairy Sci.* 76, 3851–3863. doi: 10.3168/jds.S0022-0302(93)77727-9
- Jorjong, S., Van Kneegsel, A. T. M., Verwaeren, J., Lahoz, M. V., Bruckmaier, R. M., De Baets, B., et al. (2014). Milk fatty acids as possible biomarkers to early diagnose elevated concentrations of blood plasma nonesterified fatty acids in dairy cows. *J. Dairy Sci.* 97, 7054–7064. doi: 10.3168/jds.2014-8039
- Kairenius, P., Toivonen, V., Ahvenjärvi, S., Vanhatalo, A., Givens, D. I., and Shingfield, K. J. (2009). "Effects of rapeseed lipids in the diet on ruminal lipid metabolism and milk fatty acid composition in cows fed grass silage-based diets. Abstract," in *Ruminant Physiology: Digestion, Metabolism and Effects of Nutrition on Reproduction and Welfare. Proc. XI Int. Symp. Rum. Phys.* (Wageningen, The Netherlands: Wageningen Academic Publishers).
- Kalač, P., and Samková, E. (2010). The effects of feeding various forages on fatty acid composition of bovine milk fat: A review. *Czech J. Anim. Sci.* 55, 521–537. doi: 10.17221/2485-CJAS
- Kennelly, J. J. (1996). The fatty acid composition of milk fat as influenced by feeding oilseeds. *Anim. Feed Sci. Technol.* 60, 137–152. doi: 10.1016/0377-8401(96)00973-X
- Kliem, K., Humphries, D., Markey, O., Vasilepoulou, D., Fagan, C., Grandison, A., et al. (2019). Food chain approach to lowering the saturated fat of milk and dairy products. *Int. J. Dairy Technol.* 72, 100–109. doi: 10.1111/1471-0307.12564
- Kliem, K. E., and Shingfield, K. J. (2016). Manipulation of milk fatty acid composition in lactating cows: Opportunities and challenges. *Eur. J. Lipid Sci. Technol.* 118, 1661–1683. doi: 10.1002/ejlt.201400543



- Koba, K., and Yanagita, T. (2014). Health benefits of conjugated linoleic acid (CLA). *Obes. Res. Clin. Pract.* 8, e525–e532. doi: 10.1016/j.orcp.2013.10.001
- Lamminen, M., Halmemies-Beauchet-Filleau, A., Kokkonen, T., Jaakkola, S., and Vanhatalo, A. (2019). Different microalgae species as a substitutive protein feed for soya bean meal in grass silage based dairy cow diets. *Anim. Feed Sci. Technol.* 247, 112–126. doi: 10.1016/j.anifeedsci.2018.11.005
- Livingstone, K. M., Lovegrove, J. A., and Givens, D. I. (2012). The impact of substituting SFA in dairy products with MUFA or PUFA on CVD risk: evidence from human intervention studies. *Nutr. Res. Rev.* 25, 193–206. doi: 10.1017/S095442241200011X
- Luke (2023) *Finnish feed tables and nutrient requirements of farm animals*. Available at: <https://www.luke.fi/en/luonnonvaratieta/science-and-information/feed-tables-and-nutrient-requirements> (Accessed June 27, 2023).
- Mierlita, D., Santa, A., Mierlita, S., Daraban, S. V., Suteu, M., Pop, I. M., et al. (2023). The effects of feeding milled rapeseed seeds with different forage: concentrate ratios in Jersey dairy cows on milk production, milk fatty acid composition, and milk antioxidant capacity. *Life* 13, 46. doi: 10.3390/life13010046
- Min, B. R., Lee, S., Jung, H., Miller, D. N., and Chen, R. (2022). Enteric methane emissions and animal performance in dairy and beef cattle production: Strategies, opportunities, and impact of reducing emissions. *Animals* 12, 948. doi: 10.3390/ani12080948
- Perna, M., and Hewlings, S. (2023). Saturated fatty acid chain length and risk of cardiovascular disease: A systematic review. *Nutrients* 15, 30. doi: 10.3390/nu15010030
- Pitkänen, O., Halmemies-Beauchet-Filleau, A., Räisänen, S. E., Jaakkola, S., Kokkonen, T., and Vanhatalo, A. (2023). Processed fava bean as a substitute for rapeseed meal with or without rumen-protected methionine supplement in grass silage-based dairy cow diets. *J. Dairy Sci.* 106, 3217–3232. doi: 10.3168/jds.2022-22897
- Ramin, M., Chagas, J. C., Smidt, H., Exposito, R. G., and Krizsan, S. J. (2021a). Enteric and fecal methane emissions from dairy cows fed grass or corn silage diets supplemented with rapeseed oil. *Animals* 11, 1322. doi: 10.3390/ani11051322
- Ramin, M., Fant, P., and Huhtanen, P. (2021b). The effects of gradual replacement of barley with oats on enteric methane emissions, rumen fermentation, milk production, and energy utilization in dairy cows. *J. Dairy Sci.* 104, 5617–5630. doi: 10.3168/jds.2020-19644
- Razzaghi, A., Leskinen, H., Ahvenjärvi, S., Aro, H., and Bayat, A. R. (2022). Energy utilization and milk fat responses to rapeseed oil when fed to lactating dairy cows receiving different dietary forage to concentrate ratio. *Anim. Feed Sci. Technol.* 293, 115454. doi: 10.1016/j.anifeedsci.2022.115454
- Rego, O. A., Alves, S. P., Antunes, L. M. S., Rosa, H. J. D., Alfaia, C. F. M., Prates, J. A. M., et al. (2009). Rumen biohydrogenation-derived fatty acids in milk fat from grazing dairy cows supplemented with rapeseed, sunflower, or linseed oils. *J. Dairy Sci.* 92, 4530–4540. doi: 10.3168/jds.2009-2060
- Ryhänen, E. L., Tallavaara, K., Griinari, J. M., Jaakkola, S., Mantere-Alhonen, S., and Shingfield, K. J. (2005). Production of conjugated linoleic acid enriched milk and dairy products from cows receiving grass silage supplemented with a cereal-based concentrate containing rapeseed oil. *Int. Dairy J.* 15, 207–217. doi: 10.1016/j.idairyj.2004.07.003
- Shingfield, K. J., Bernard, L., Leroux, C., and Chilliard, Y. (2010). Role of trans fatty acids in the nutritional regulation of mammary lipogenesis in ruminants. *Animal* 4, 1140–1166. doi: 10.1017/S1751731110000510
- Vanhatalo, A., and Halmemies-Beauchet-Filleau, A. (2020). “Optimising ruminal function: the role of silage and concentrate in dairy cow nutrition to improve feed efficiency and reduce methane and nitrogen emissions,” in *Improving rumen function*. Eds. C. S. McSweeney and R. I. Mackie (Cambridge, United Kingdom: Burleigh Dodds Science Publishing), 651–692.
- Vanhatalo, A., Gäddnäs, T., and Heikkilä, T. (2006). Microbial protein synthesis, digestion and lactation responses of cows to grass or grass-red clover silage diet supplemented with barley or oats. *Agric. Food Sci.* 15, 252–267. doi: 10.2137/145960606779216236
- Van Keulen, J., and Young, B. A. (1977). Evaluation of insoluble ash as a natural marker in ruminant digestibility studies. *J. Anim. Sci.* 44, 282–287. doi: 10.2527/jas1977.442282x
- Van Soest, P. V., Robertson, J. B., and Lewis, B. A. (1991). Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. *J. Dairy Sci.* 74, 3583–3597. doi: 10.3168/jds.S0022-0302(91)78551-2
- Vasilopoulou, D., Markey, O., Kliem, K. E., Fagan, C. C., Grandison, A. S., Humphries, D. J., et al. (2020). Reformulation initiative for partial replacement of saturated with unsaturated fats in dairy foods attenuates the increase in low-density lipoprotein cholesterol and improves flow-mediated dilatation compared with conventional dairy: the randomized, controlled RESET study. *Am. J. Clin. Nutr.* 111, 739–748. doi: 10.1093/ajcn/nqz344
- Welch, R. W. (1975). Fatty acid composition of grain from winter and spring sown oats, barley and wheat. *J. Sci. Food Agric.* 26, 429–435. doi: 10.1002/jsfa.2740260408





## OPEN ACCESS

## EDITED BY

Jeff Wood,  
University of Bristol, United Kingdom

## REVIEWED BY

Valerie Berthelot,  
AgroParisTech Institut des Sciences et  
Industries du Vivant et de L'environnement,  
France  
HongGu Lee,  
Konkuk University, Republic of Korea

## \*CORRESPONDENCE

Payam Vahmani  
✉ pvahmani@ucdavis.edu

RECEIVED 17 August 2023

ACCEPTED 20 October 2023

PUBLISHED 06 November 2023

## CITATION

Xu Y, Dugan MER, Mapiye C and  
Vahmani P (2023) Health effects of  
ruminant trans fatty acids with  
emphasis on type 2 diabetes.  
*Front. Anim. Sci.* 4:1278966.  
doi: 10.3389/fanim.2023.1278966

## COPYRIGHT

© 2023 Xu, Dugan, Mapiye and Vahmani.  
This is an open-access article distributed  
under the terms of the [Creative Commons  
Attribution License \(CC BY\)](#). The use,  
distribution or reproduction in other  
forums is permitted, provided the original  
author(s) and the copyright owner(s) are  
credited and that the original publication in  
this journal is cited, in accordance with  
accepted academic practice. No use,  
distribution or reproduction is permitted  
which does not comply with these terms.

# Health effects of ruminant trans fatty acids with emphasis on type 2 diabetes

Yanqing Xu<sup>1</sup>, Michael E. R. Dugan<sup>2</sup>, Cletos Mapiye<sup>3</sup>  
and Payam Vahmani<sup>1\*</sup>

<sup>1</sup>Department of Animal Science, University of California, Davis, Davis, CA, United States, <sup>2</sup>Agriculture and Agri-Food Canada, Lacombe Research and Development Centre, Lacombe, AB, Canada,

<sup>3</sup>Department of Animal Sciences, Stellenbosch University, Cape Town, South Africa

Recent government bans on industrial trans fatty acids (TFA) in developed countries has left naturally occurring TFA from ruminant products (e.g., dairy, beef, and lamb) as the sole source of TFA in the food supply. In contrast to industrial TFA, which have undisputed adverse health effects, ruminant TFA such as trans vaccenic acid (TVA; trans11-18:1), rumenic acid (RA; cis9, trans11-18:2) and trans palmitoleic acid (TPA; trans9-16:1) have been associated with reduced risk for some diseases such as type 2 diabetes. The present review summarizes the findings from observational, animal and human studies investigating the effects of ruminant TFA on metabolic parameters related to type 2 diabetes, and provides an update on the current knowledge of their biosynthesis, intake and factors affecting their concentrations in ruminant derived foods. Overall, observational studies and a small number of animal studies suggest that ruminant TFA may be protective against type 2 diabetes, whereas the same benefits have not been observed in other animal studies or in human clinical trials. Additional clinical and mechanistic studies are needed to better understand the isomer-specific effects of ruminant TFA. Until then, production practices resulting in increased levels of this group of fatty acids in ruminant milk and meat should be carefully reconsidered.

## KEYWORDS

conjugated linoleic acid, trans vaccenic acid, trans palmitoleic acid, type 2 diabetes, ruminant fats

## Introduction

Trans fatty acids (TFA) are unsaturated fatty acids that contain at least one double bond in the trans configuration (i.e. the two hydrogen atoms are on opposite sides of the carbon to carbon double bond), resulting in a straighter shape more similar to saturated fatty acids. Consequently, TFA are less fluid and have a higher melting point than unsaturated fatty acids with cis double bonds, which are the major monounsaturated fatty acids (MUFA) and polyunsaturated fatty acids (PUFA) in plants and animals (Bhardwaj et al., 2011).

TFA in foods mainly come from two sources, including partially hydrogenated vegetable oils (i.e. industrial TFA) and ruminant-derived foods such as dairy and beef (i.e. ruminant TFA). Industrial TFA are found in partially hydrogenated vegetable oils generated using hydrogen in the presence of a catalyst (Bhardwaj et al., 2011), while ruminant TFA are made by rumen bacteria using a process called biohydrogenation (Lichtenstein, 2000; Dhaka et al., 2011).

Until recently, industrial TFA were extensively used by the food industry as a replacement for saturated fats. However, in recent years, many countries have banned industrial TFA from the food supply due to their detrimental effects on cardiovascular health (Lichtenstein, 2000; Mozaffarian et al., 2006). Recent government bans on industrial TFA in developed countries including the U.S, Canada and the E.U has left ruminant-derived fats (e.g. dairy, beef, lamb and goat) as the sole source of TFA in the food supply. As such, there is heightened interest in the composition, content, and health effects of ruminant TFA particularly conjugated linoleic acid (CLA) and trans 18:1 isomers (Brouwer et al., 2010; Prada et al., 2022). The aim of this review is to provide an update of the current state of knowledge on the biosynthesis, concentration range and factors affecting the concentration of TFA in ruminant fats, current intake of ruminant TFA, and to evaluate evidence on their health effects with an emphasis on type 2 diabetes.

## Biosynthesis of ruminant TFA

Ruminant TFA are formed via biohydrogenation of unsaturated fatty acids in the rumen. The process of biohydrogenation is performed by rumen bacteria, during which dietary unsaturated fatty acids are converted to saturated fatty acids (Lichtenstein, 2000; Dhaka et al., 2011; Dugan et al., 2018). Dietary unsaturated

fatty acids are toxic to rumen microbes, hence they biohydrogenate them to saturated fatty acids which are neutral or less toxic (Jenkins et al., 2008). The biohydrogenation process includes several isomerization and hydrogenation steps which result in the formation of many intermediates including conjugated and non-conjugated trienoic, dienoic and monoenoic trans fatty acids (Jenkins et al., 2008; Vahmani et al., 2015). A small portion of these intermediates passes the rumen and subsequently find their way into tissues and milk after post-ruminal absorption (Lichtenstein, 2000; Dugan et al., 2018).

The predominant fatty acids in ruminant diets include 18:2n-6 (linoleic acid; LNA) and 18:3n-3 (alpha-linolenic acid; ALA) and thus are considered the main substrates for ruminal biohydrogenation. It is estimated that on average, about 80% and 92% of dietary LNA and ALA are biohydrogenated in the rumen (Conte et al., 2017). Several different biohydrogenation pathways have been proposed for LNA and ALA. Several factors including forage-to-concentrate ratio and ruminal passage rate/residence time can determine the pathway and extent of the biohydrogenation of LNA and ALA (Chilliard et al., 2014; Dugan et al., 2018; Dewanckele et al., 2020).

The main pathways for the biohydrogenation of LNA and ALA have been described by Harfoot and Hazlewood (1997). Pathways for both LNA and ALA are characterized by initial isomerization of the cis double bond at carbon 12 to a trans double bond at carbon 11 resulting in the production of cis9, trans11-18:2, an isomer of CLA (also known as rumenic acid; RA), and cis9, trans11, cis15-18:3, respectively (Figure 1). This is followed by rounds of hydrogenation and isomerization leading to a trans 18:1 isomer (e.g., trans11-18:1) and eventually complete hydrogenation to 18:0 (stearic acid) as the end product (Dewanckele et al., 2020).

It is noteworthy that the abovementioned pathways were elucidated when greater forage-to-grain ratios (forage-based diets)

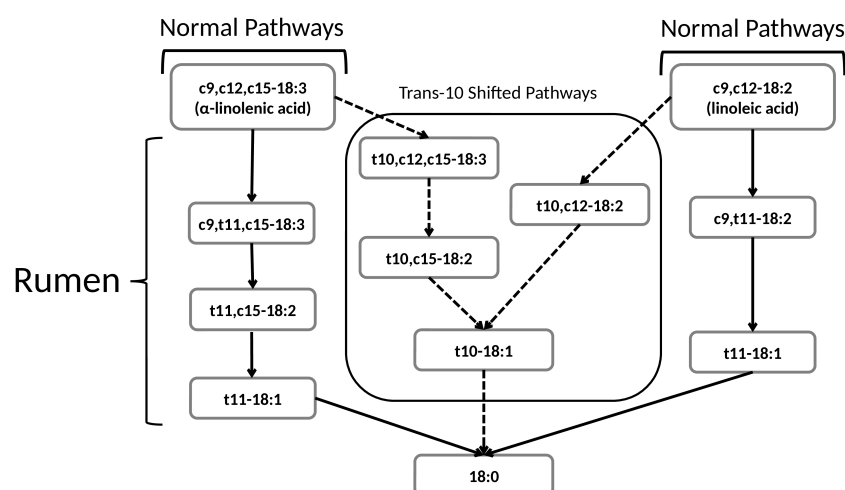


FIGURE 1

Normal and trans-10 shifted biohydrogenation pathways of linoleic acid (cis9,cis12-18:2) and alpha-linolenic acid (cis9,cis12,cis15-18:3). Arrow with solid lines show the main pathways in ruminants fed forage-based diets, and arrows with dashed lines show pathways in ruminants fed grain-based diets (Adopted from Alves et al., 2021).

were fed. When feeding grain-based diets (e.g., feedlot diets), isomerization of the *cis* 9 double bonds for LA shifts towards a *trans* double bond at carbon 10, with the same happening for ALA shifts, resulting in the production of *trans*10, *cis*12-18:2 and *trans*10, *cis*12, *cis*15-18:3, respectively (Alves and Bessa, 2014). These have been referred to as the “*trans*-10 shifted” biohydrogenation pathways (Figure 1) which result in the accumulation of *trans*10-18:1 as the main TFA in ruminant products such as beef from feedlot (grain-finished) cattle (Alves and Bessa, 2014; Alves et al., 2021). Whereas *trans*11-18:1 (*trans* vaccenic acid; TVA) is typically the main TFA found in milk and meat from ruminants fed forage-based diets (e.g., grass-fed beef) (Jaakamo et al., 2019). Findings from animal model studies suggest that *trans*10-18:1 may harm health in a similar fashion to industrial TFA (Alves et al., 2021). On the other hand, TVA can be converted to RA (*cis*9, *trans* 11-CLA), both of which have been associated with several health benefits such as prevention of cancer, cardiovascular disease, and inflammation as well as improved immune function (Derakhshande-Rishehri et al., 2014; Kim et al., 2016). Consequently, TVA and RA are sometimes referred to as “good” TFA (Diane et al., 2016; Vahmani et al., 2020).

In addition to the main biohydrogenation pathways mentioned above, there are numerous minor pathways active in the rumen resulting in a plethora of biohydrogenation intermediates including conjugated and non-conjugated trienoic (18:3), dienoic (18:2) and monoenoic (18:1 and 16:1) TFA isomers (Vahmani et al., 2020). In fact, milk and meat fats from ruminants (e.g. cattle, sheep and goats) have the most complex fatty acid composition (> 100 different fatty acids) among all edible fats, in part due to the presence of numerous biohydrogenation intermediates. However, the human health effects of many of these intermediates are for the most part unknown.

## Types and concentrations of TFA in ruminant fats

The biohydrogenation process results in about 50 different types of TFA including *trans*-16:1 (*trans*6- to *trans*12-16:1), *trans*-18:1 (*trans*4- to *trans*16-18:1), conjugated 18:2 known as CLA ( $\geq 12$  different CLA isomers with *cis/trans* or *trans/cis* configurations), non-conjugated non-methylene interrupted 18:2 known as atypical dienes ( $\geq 10$  different isomers with *cis/trans* or *trans/cis* configurations) and conjugated 18:3 ( $\geq 3$  different isomers with *cis/trans/trans* or *cis/trans/cis* configurations). *Trans*-18:1s are the predominant TFA (70-80% of total TFA), followed by CLA (10-25% of total TFA), atypical dienes (5-15% of total TFA), *trans*-16:1 (5-10% of total TFA) and conjugated linolenic acid (CLnA, <5% of total TFA) (Table 1). Among individual TFA isomers, TVA, RA and *trans*9-16:1 (*trans* palmitoleic acid; TPA) have been the most studied isomers in terms of health effects and bioactivity, due to their high prevalence in ruminant foods and commercial availability (i.e. pure fatty acid isomers).

## Current intake of ruminant TFA

There have been numerous studies done on the health effects of industrial TFA during the past 4 decades. These studies have consistently found that industrial TFA have been associated with an increased risk of cardiovascular disease, mainly by lowering HDL and raising LDL levels (Stender et al., 2008; Brouwer et al., 2010; Radtke et al., 2017; Oteng et al., 2019). In the mid-1990s, many developed countries including the EU made recommendations to limit the intake of industrial TFA to 1% of the daily energy intake (Wanders et al., 2017). According to a study in 2010, the average daily TFA intake for adults was around 2.5 to 3.49% of daily energy intake in the U.S. (Micha et al., 2014), which was much higher than the 1% recommended limit. About 10 years later in 2015, the U.S. Food and Drug Administration (FDA) ruled that industrial TFA are not safe in food and set a June 2018 deadline for their removal from the food system (USDA, 2020). The official ban on industrial TFA has left ruminant-derived fats as the sole dietary source of TFA in the U.S., as well as in Canada and most European countries.

The estimated dietary intake of ruminant TFA varies between 0.8% to 1.7% of total energy intake depending on the country, with the average intake of ruminant TFA in the U.S. estimated to be about 1.2% of energy intake (Gebauer et al., 2011). In a more recent study, however, ruminant TFA intake in Europe and the U.S. was estimated to be around 0.5% of energy intake (Brouwer et al., 2013). Given recent bans on industrial TFA, there is need for new studies to determine the current intake of TFA from ruminant derived foods.

## Factors affecting concentrations of TFA in ruminant-derived foods

The TFA composition of ruminant derived foods is largely influenced by dietary, management and animal factors. Among these factors, diet composition is the main determinant of biohydrogenation pathways, and consequently of the content and composition of TFA in ruminant fats. Adding sources of PUFA to the diet (e.g. plant oil and oilseeds) significantly increases the contents of TFA in ruminant milk and meat including RA, TVA and TPA (Scollan et al., 2017; Guillocheau et al., 2020; Guo et al., 2023). The source of PUFA has the largest impact, with LNA-rich oils, yielding the greatest RA, TVA and TPA contents (Bessa et al., 2015; Kliem and Shingfield, 2016). Feeding ALA-rich sources also enhances CLnA content in ruminant fats (Kliem and Shingfield, 2016; Chikwanha et al., 2018). Seemingly effective novel alternative oil sources for increasing TFA, such as insect oils, warrant further investigation (Hervás et al., 2022). Furthermore, the amount of PUFA increases TFA content, reaching a peak when feeding between 50 and 80 g/kg DM intake (Scollan et al., 2017; Chikwanha et al., 2018). Besides PUFA, feeding forage-based diets, as opposed to grain-based diets, effectively increases TFA with *trans*-11 double bonds (TVA and RA) in ruminant fats

TABLE 1 The TFA composition of common ruminant fats.

	Bovine milk fat <sup>1</sup>		Grass-fed beef fat <sup>2</sup>		Grain-fed beef fat <sup>2</sup>	
Fatty acid	% of total FA	% of TFA	% of total FA	% of TFA	% of total FA	% of TFA
t6-8-16:1	0.24	3.41	0.51	6.35	0.28	5.78
t9-16:1	0.05	0.77	0.09	1.10	0.02	0.37
t10-16:1	0.01	0.19	0.01	0.15	0.01	0.11
t11-12-16:1	0.04	0.59	0.05	0.68	0.03	0.70
t14-16:1	0.02	0.33	0.04	0.47	NR	NR
<b>Σtrans16:1</b>	0.37	5.29	0.70	8.74	0.34	6.96
t4-18:1	0.04	0.59	0.02	0.27	0.02	0.39
t5-18:1	0.04	0.62	0.02	0.23	0.02	0.44
t6-8-18:1	0.43	6.14	0.17	2.09	0.40	8.22
t9-18:1	0.39	5.52	0.21	2.65	0.37	7.62
t10-18:1	0.73	10.32	0.19	2.36	2.05	42.30
t11-18:1	1.18	16.70	3.37	42.25	0.52	10.81
t12-18:1	0.58	8.17	0.12	1.57	0.10	2.14
t13-14-18:1	1.09	15.48	0.32	4.07	0.15	3.03
t15-18:1	0.75	10.65	0.15	1.88	NR	NR
t16-18:1	0.41	5.74	0.34	4.32	0.09	1.87
<b>Σtrans18:1</b>	5.64	79.93	4.92	61.67	3.57	73.79
t11,t15-18:2	0.01	0.08	0.09	1.18	0.01	0.16
t9,t12-18:2	0.01	0.18	0.02	0.25	0.01	0.26
c9,t13-/t8,c12-18:2	0.23	3.30	0.25	3.14	0.15	3.18
t8,c13-18:2	0.09	1.32	0.12	1.52	0.07	1.35
c9,t12-18:2	NR	NR	NR	NR	0.06	1.21
t9,c12-18:2	0.03	0.43	NR	NR	0.01	0.29
t11,c15-18:2	0.04	0.53	0.57	7.18	0.04	0.92
<b>ΣAD</b>	0.41	5.83	1.06	13.27	0.36	7.37
t7,c9-18:2	0.06	0.79	NR	NR	NR	NR
c9,t11-18:2/t8,c10-18:2	0.44	6.18	0.90	11.34	0.39	8.07
t10,c12-18:2	0.03	0.41	0.01	0.12	0.04	0.87
t11,c13-18:2	0.01	0.15	0.12	0.22	0.02	0.34
t12,t14-/t13,t15-18:2	0.01	0.15	0.03	0.34	0.02	0.37
t11,t13-18:2	0.03	0.40	0.05	0.67	0.02	0.44
t7,t9-t10,t12-18:2	0.04	0.50	0.02	0.31	0.02	0.49
<b>ΣCLA</b>	0.61	8.57	1.15	14.46	0.55	11.31
c9,t11,t15-18:3	0.01	0.10	0.06	0.77	0.01	0.29
c9,t11,c15-18:3	0.02	0.27	0.09	1.09	0.01	0.29
<b>ΣCLnA</b>	0.03	0.37	0.15	1.86	0.03	0.57

NR, not reported; TFA, total trans fatty acids; c, cis; t, trans; ΣCLA, sum of conjugated linoleic acid isomers; ΣAD, sum of atypical dienes (non-conjugated non-methylene interrupted 18:2; ΣCLnA, sum of conjugated linolenic acid (18:3) isomers.

<sup>1</sup>(Rosemond, 2021).

<sup>2</sup>(Klopatek et al., 2022).

(Chikwanha et al., 2018; Cabiddu et al., 2022). However, the effectiveness of forage-based diets at increasing TFA is determined by several factors relating to the source of forage including species diversity, cultivars, phenological stage, maturity, conservation method, particle length, presence of bioactive compounds and seasonality (Frutos et al., 2020; Cabiddu et al., 2022). Noteworthy, feeding a combination of forages and PUFA for an extend period substantially enhances presence of TFA in ruminant fats (Kliem and Shingfield, 2016; Vahmani et al., 2020; Alves et al., 2021), particularly when forage and PUFA sources are feed separately (Vahmani et al., 2017).

High-grain diets supplemented with LNA substantially increases the content of trans10-18:1 and trans10,cis12-CLA (i.e., trans10-shift) in ruminant meat and milk (Mapiye et al., 2015; Kliem and Shingfield, 2016). The t10-shift is exacerbated by feeding small grains (i.e. barley and wheat versus corn), pelleting, and increasing feeding duration (Mapiye et al., 2012; Mutsvangwa et al., 2012). A multitude of strategies to avoid the trans10-shift such as the addition of forages, non-starch fibers, strong buffers, antibiotics, antioxidants, yeast, chitosan, and agro-industrial by-products to high-grain diets, have been attempted with varying success (Alves et al., 2021; Amin and Mao, 2021; Hervás et al., 2022). Additionally, PUFA protective treatments and adsorbents inhibit the trans10-shift to a limited extent (Guo et al., 2023).

Notably, contents of TFA are more effectively increased in milk versus meat and in small versus large ruminants (Chilliard et al., 2007; Dugan et al., 2011; Chikwanha et al., 2018). The TFA contents in milk are somewhat influenced by animal individuality, breed, stage of lactation and parity (Samková et al., 2012). In meat animals, breed, sex, slaughter age and weight, anatomical location of fat depot and muscle type have marginal effects on TFA contents (Mapiye et al., 2015).

## Metabolism of ruminant TFA in the human body

Most published data on TFA metabolism comes from studies on trans 18:1, which are the predominant fatty acid type in both ruminant and industrial TFA. Trans 18:1 isomers are intestinally absorbed to the same extent as cis 18:1 isomers and the double-bond position has little or no effect on their absorption (Baer et al., 2003). After absorption, trans 18:1 isomers can be incorporated into cell membrane phospholipids, or stored in the triacylglycerols of adipose tissues. Trans 18:1 isomers can be metabolized by oxidation, elongation, and desaturation processes, which result in isomer-specific metabolites with different biochemical properties (Vahmani et al., 2020). For TVA, two main metabolic fates have been characterized which include chain shortening to TPA and delta-9 desaturation to RA (Figure 2). It has been estimated that ~19% of TVA, the main t-18:1 isomer in milk and meat from forage-fed ruminants consumed by humans, can be converted to RA by tissue-level  $\Delta$ -9 desaturation which is catalyzed by the stearoyl-CoA desaturase 1 (SCD1) enzyme (Turpeinen et al., 2002; Miller et al., 2003).

In addition to  $\Delta$ -9 desaturation, chain shortening of TVA by  $\beta$ -oxidation (peroxisomal  $\beta$ -oxidation of TVA) can lead to elevated levels of TPA in the plasma or tissues after consuming foods containing TVA, particularly grass-fed beef and dairy products. The conversion rate of TVA to TPA has been estimated to be 10% in cultured rat hepatocytes incubated with TVA (Jaudszus et al., 2014), however, the whole body (*in vivo*) conversion rate of TVA to TPA is not known. Given the very low concentration of TPA in the food supply including ruminant-derived foods (<0.05% of total fatty acids), the major origin of circulating TPA in humans is assumed to be from TVA intake from consumption of ruminant derived foods (Jaudszus et al., 2014).

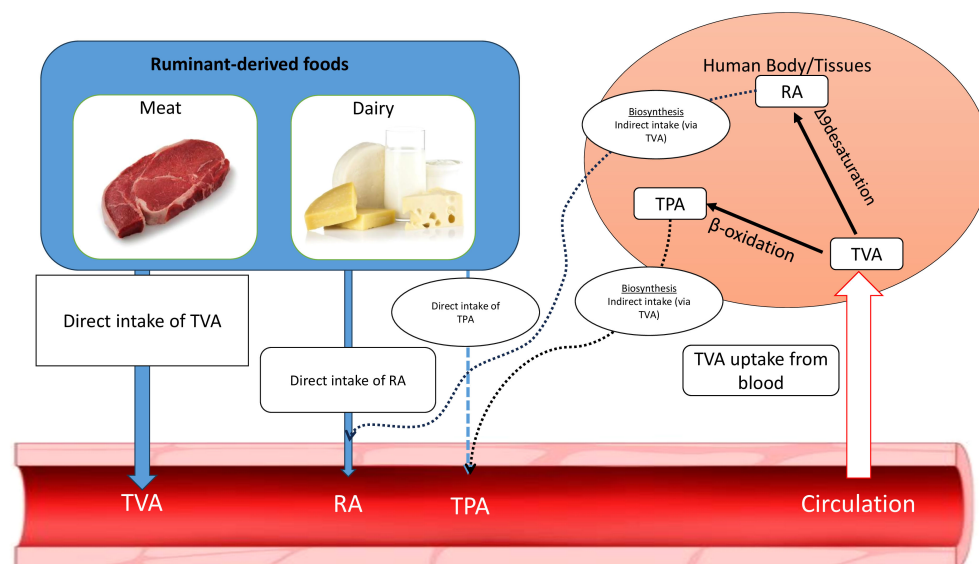


FIGURE 2

Origin of ruminant trans fatty acids in human blood. TPA, trans-palmitoleic acid (trans9-16:1); TVA, trans vaccenic acid (trans11-18:1); RA, rumenic acid (cis9,trans11-18:2); Arrows with thick solid lines describes the major origins, arrow with narrow lines indicates minor origins, arrows with dashed lines shows the very minor origins (Turpeinen et al., 2002; Miller et al., 2003; Jaudszus et al., 2014).



## Health effects of ruminant TFA

The effects of ruminant- versus industrial- TFA on human health have been controversial and a subject of debate for many years. The recent removal of industrial TFA from the food supply in developed countries has renewed interest in understanding the human health effects of ruminant TFA. Several epidemiological studies have shown that, in contrast to industrial TFA, ruminant TFA do not appear to increase cardiovascular disease (CVD) risk and mortality (Ascherio et al., 1994; Pietinen et al., 1997; Jakobsen et al., 2008; Bendsen et al., 2011; Sacks et al., 2017). This has been attributed to the different isomeric profile of trans18:1 between ruminant and industrial TFA, as well as the low concentrations of total TFA in ruminant fats (2–6% of total fatty acids) compared to partially hydrogenated vegetable oils (60–65% of total fatty acids) (Stender et al., 2008). Conversely, based on recent human clinical trials, both industrial- and ruminant- TFA adversely affect cholesterol homeostasis (i.e. increased blood LDL-cholesterol and reduced HDL cholesterol) when consumed at comparable levels (Motard-Bélanger et al., 2008; Brouwer et al., 2013; Gebauer et al., 2015; Stender, 2015; Verneque et al., 2022). However, there is limited information available on the effect of ruminant TFA on other cardiovascular disease risk markers and the development of other chronic diseases such as type 2 diabetes. In the following section, we summarize published data from observational studies, clinical trials and animal studies on the effects of ruminant TFA on metabolic parameters related to type 2 diabetes.

## Observational studies

Since 2010, several prospective epidemiological studies have consistently shown that increased blood levels of TPA, the chain shortening product of TVA (the most abundant TFA in ruminant fats) was associated with lower risk and incidence of type 2 diabetes (Mozaffarian et al., 2010). Similarly, two meta-analyses reported circulating TPA was inversely associated with type 2 diabetes (Imamura et al., 2018). In a more recent epidemiological study, circulating TVA but not TPA was inversely associated with diabetes risk (Prada et al., 2022). This discrepancy could be in part due to the limitations in the analytical methods used to determine TFA isomeric profile in human blood samples (Guillocheau et al., 2020). Although available data from observational studies point towards potential antidiabetic properties of ruminant TFA, a cause-and-effect relationship has not yet been proven in humans.

## Clinical trials

There is very limited clinical data on the human health effects of ruminant TFA. Gebauer et al. (2015) compared the effects of isocaloric diets containing different TFA isomers in a randomized, crossover feeding trial in 106 healthy subjects who were each provided the diets for 24 days. Diets were designed to have stearic acid replaced with the following TFA isomers (percentage of energy): ~3% pure TVA, ~3% mixed isomers of industrial TFA from partially

hydrogenated vegetable oil, or 1% pure RA. In this study, there was no difference among treatments in terms of metabolic parameters related to type 2 diabetes including blood glucose, insulin, or insulin resistance index (HOMA-IR). Another study using a hyperinsulinemic-euglycemic clamp in abdominally obese male subjects reported that supplementation with pure RA (~1% of energy intake for 12 weeks) reduced insulin sensitivity compared with an olive oil placebo (Risérus et al., 2004). To our knowledge, there has been no clinical study investigating the health effect of TPA supplementation in humans, likely due to the lack of pure TPA (Guillocheau et al., 2020). In fact, the above two studies are the only two human clinical studies examining health effects of pure ruminant TFA isomers. However, there are four published clinical studies in which ruminant TFA-enriched dairy fats were fed. In these studies, TVA+RA-enriched butter (1–1.5% of energy intake from TVA+RA) did not alter blood glucose and insulin, HOMA-IR or glucose tolerance in healthy subjects compared with standard butters (Tholstrup et al., 2006; Tricon et al., 2006; Brown et al., 2011; Penedo et al., 2013; Werner et al., 2013). Although observational studies showed that higher circulating levels of ruminant TFA may be protective against type 2 diabetes, available data from clinical trials do not support a beneficial effect of ruminant TFA on glucose homeostasis in humans. It is noteworthy, however, almost all of these clinical trials were done in healthy subjects and not in people with prediabetes or type 2 diabetes.

## Animal studies

Most available data regarding the promising health effects of ruminant TFA including their postulated antidiabetic properties come from animal model studies. Feeding a diet enriched with 1% pure TVA (~4.5% of energy intake) to obese insulin resistant JCR-LA:cp rats resulted in significant reductions in fasting and postprandial insulin levels and an increase in insulin sensitivity (lower HOMA-IR) (Jacome-Sosa et al., 2014). The authors attributed these insulin-sensitizing effects of TVA to activation of peroxisome proliferator-activated receptor- $\gamma$ . In fact, both TVA and its delta-9 desaturation product, RA, have been shown to act as ligands for PPAR $\gamma$  and PPAR $\alpha$ , which are transcription factors for several genes involved in lipid and glucose metabolism (Moya-Camarena et al., 1999; Wang et al., 2012). Feeding beef fat enriched with TVA and RA to obese/insulin-resistant JCR : LA-cp rats reduced fasting insulin and HOMA-IR, and lowered insulin secretion following a meal tolerance test, which were accompanied by higher protein expression of PPAR $\gamma$  and PPAR $\alpha$  in the liver (Diane et al., 2016). Similarly, feeding Wistar rats a high-fat diet containing TVA+RA-enriched butter reduced fasting serum insulin and increased hepatic PPAR $\gamma$  protein expression compared to rats fed a control high-fat diet containing standard butter (De Almeida et al., 2014). The apparent insulin-sensitizing effects of TVA and RA in the above rodent studies were attributed to their potential to bind and activate PPAR $\gamma$ -regulated pathways in the liver and adipose tissues. Moreover, it has been suggested that TVA can also restore glucose homeostasis by promoting insulin secretion from pancreatic islets. In diabetic Sprague–Dawley rats (induced by

high-fat diet/streptozotocin), 8 weeks supplementation with pure TVA (1.2% of diet mass) reduced both fed and fasting blood glucose, and increased  $\beta$ -cell area (Wang et al., 2016). In addition, in this study, hyperglycemic clamp showed that TVA increased glucose turnover in diabetic rats, accompanied by an elevated plasma C-peptide concentration, suggesting improved insulin secretion. Moreover, isolated islets from TVA fed diabetic rats had higher glucose-stimulated insulin secretion (GSIS) than the control diabetic rats (Wang et al., 2016). Thus, the authors concluded that TVA may improve glucose homeostasis in diabetic rats in part by promoting insulin secretion (Wang et al., 2016). Consistent with these findings, Wang et al. recently reported that feeding pure TVA to diabetic rats could promote insulin secretion through stimulating G-protein coupled receptor 40 (GPR40) expression and signaling in islets (Wang et al., 2019).

The above studies should be weighed against other studies that have not found ruminant TFA to improve glucose homeostasis in animal models of insulin resistance and type 2 diabetes. In obese/insulin resistant JCR-LA:cp rats, feeding a diet enriched with pure TVA (1.5% of diet as TVA) did not alter fasting levels of insulin or glucose, nor insulin and glucose responses to a meal tolerance test (Wang et al., 2008). Another study using Wistar rats showed that 8 weeks of feeding diets enriched (4% of energy intake) with either TVA, mixed industrial TFA mixed isomers or oleic acid did not alter insulin and glucose responses to an intraperitoneal glucose tolerance test (Tardy et al., 2008). Similarly, dietary supplementation with pure TPA (0.7% of energy intake) did not modify glucose homeostasis in high fat diet-induced obese (DIO) mice as measured by glucose/insulin tolerance tests and insulin-mediated Akt activation (Chávaro-Ortiz et al., 2022). Another recent study using DIO mice showed that feeding a high-fat diet containing beef fat naturally enriched with TVA and RA (beef fat from flaxseed-fed cattle) for 19 weeks worsened glucose tolerance and liver steatosis compared to mice fed a control high fat diet (Xu et al., 2022). The authors partly attributed the adverse effects on glucose tolerance and liver health to other TFA present in TVA+RA enriched beef fat. It is noteworthy that no study to date has tested the effects of pure TVA or RA in DIO mouse model which is one of the most clinically translatable animal models to test the efficacy of natural compounds and/or drugs against prediabetes and type 2 diabetes.

The discrepancy in findings may be attributed to methodological differences among studies, such as animal model, diet composition, study duration, as well as specific techniques used to assess glucose homeostasis and parameters related to type 2 diabetes. It is noteworthy that no study to date has tested the effects of pure TVA or RA in DIO mouse model which is one of the most clinically translatable animal models to test the efficacy of natural compounds and/or drugs against prediabetes and type 2 diabetes.

## References

Alves, S. P., and Bessa, R. J. B. (2014). The trans-10,cis-15 18:2: A missing intermediate of trans-10 shifted rumen biohydrogenation pathway? *Lipids* 49, 527–541. doi: 10.1007/s11745-014-3897-4

## Conclusion

Taken together, although TVA and its metabolites (TPA and RA) have been touted as having antidiabetic properties based on data from observational studies and a small number of animal studies, while the same effects have not been observed in other animal studies or in human clinical trials. Additional clinical and mechanistic studies are needed to better understand the isomer-specific effects of ruminant TFA. Nevertheless, based on the current knowledge regarding potential adverse effects of ruminant TFA on blood lipoprotein profiles, practices resulting in increased levels of this group of fatty acids in ruminant milk and meat should be carefully reconsidered.

## Author contributions

PV: Conceptualization, Writing – original draft, Writing – review & editing. YX: Writing – original draft. MD: Writing – review & editing. CM: Writing – original draft, Writing – review & editing.

## Funding

The author(s) declare that no financial support was received for the research, authorship, and/or publication of this article.

## 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.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

## Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Alves, S. P., Vahmani, P., Mapiye, C., McAllister, T. A., Bessa, R. J. B., and Dugan, M. E. R. (2021). Trans-10 18:1 in ruminant meats: A review. *Lipids* 56, 539–562. doi: 10.1002/lipid.12324

- Amin, A. B., and Mao, S. (2021). Influence of yeast on rumen fermentation, growth performance and quality of products in ruminants: A review. *Anim. Nutr.* 7, 31–41. doi: 10.1016/j.aninu.2020.10.005
- Ascherio, A., Hennekens, C. H., Buring, J. E., Master, C., Stampfer, M. J., and Willett, W. C. (1994). Trans-fatty acids intake and risk of myocardial infarction. *Circulation* 89, 94–101. doi: 10.1161/01.CIR.89.1.94
- Baer, D. J., Judd, J. T., Kris-Etherton, P. M., Zhao, G., and Emken, E. A. (2003). Stearic acid absorption and its metabolizable energy value are minimally lower than those of other fatty acids in healthy men fed mixed diets. *J. Nutr.* 133, 4129–4134. doi: 10.1093/jn/133.12.4129
- Bendsen, N. T., Christensen, R., Bartels, E. M., and Astrup, A. (2011). Consumption of industrial and ruminant trans fatty acids and risk of coronary heart disease: A systematic review and meta-analysis of cohort studies. *Eur. J. Clin. Nutr.* 65, 773–783. doi: 10.1038/ejcn.2011.34
- Bessa, R. J. B., Alves, S. P., and Santos-Silva, J. (2015). Constraints and potentials for the nutritional modulation of the fatty acid composition of ruminant meat. *Eur. J. Lipid Sci. Technol.* 117, 1325–1344. doi: 10.1002/ejlt.201400468
- Bhardwaj, S., Passi, S. J., and Misra, A. (2011). Overview of trans fatty acids: Biochemistry and health effects. *Diabetes Metab. Syndr. Clin. Res. Rev.* 5, 161–164. doi: 10.1016/j.dsx.2012.03.002
- Brouwer, I. A., Wanders, A. J., and Katan, M. B. (2010). Effect of animal and industrial Trans fatty acids on HDL and LDL cholesterol levels in humans - A quantitative review. *PLoS One* 5. doi: 10.1371/journal.pone.0009434
- Brouwer, I. A., Wanders, A. J., and Katan, M. B. (2013). Trans fatty acids and cardiovascular health: Research completed? *Eur. J. Clin. Nutr.* 67, 541–547. doi: 10.1038/ejcn.2013.43
- Brown, A. W., Trenkle, A. H., and Beitz, D. C. (2011). Diets high in conjugated linoleic acid from pasture-fed cattle did not alter markers of health in young women. *Nutr. Res.* 31, 33–41. doi: 10.1016/j.nutres.2010.12.003
- Cabiddu, A., Peratoner, G., Valenti, B., Monteils, V., Martin, B., and Coppa, M. (2022). A quantitative review of on-farm feeding practices to enhance the quality of grassland-based ruminant dairy and meat products. *Animal* 16, 100375. doi: 10.1016/j.animal.2021.100375
- Chávaro-Ortiz, L. I., Tapia, B. D., Navarrete-Fuentes, M., Gutiérrez-Aguilar, R., and Frigolet, M. E. (2022). Trans-palmitoleic acid prevents weight gain, but does not modify glucose homeostasis in a rodent model of diet-induced obesity. *Clin. Nutr. Open Sci.* 44, 42–48. doi: 10.1016/j.nutres.2022.06.003
- Chikwanha, O. C., Vahmani, P., Muchenje, V., Dugan, M. E. R., and Mapiye, C. (2018). Nutritional enhancement of sheep meat fatty acid profile for human health and wellbeing. *Food Res. Int.* 104, 25–38. doi: 10.1016/j.foodres.2017.05.005
- Chilliard, Y., Glasser, F., Ferlay, A., Bernard, L., Rouel, J., and Doreau, M. (2007). Diet, rumen biohydrogenation and nutritional quality of cow and goat milk fat. *Eur. J. Lipid Sci. Technol.* 109, 828–855. doi: 10.1002/ejlt.200700080
- Chilliard, Y., Toral, P. G., Shingfield, K. J., Rouel, J., Leroux, C., and Bernard, L. (2014). Effects of diet and physiological factors on milk fat synthesis, milk fat composition and lipolysis in the goat: A short review. *Small Rumin. Res.* 122, 31–37. doi: 10.1016/j.smallrumres.2014.07.014
- Conte, G., Serra, A., and Mele, M. (2017). “Dairy cow breeding and feeding on the milk fatty acid pattern,” in *Nutrients in dairy and their implications for health and disease* (London, United Kingdom: Academic Press, Elsevier). doi: 10.1016/B978-0-12-809762-5.00002-4
- De Almeida, M. M., Luquetti, S. C. P. D., Sabarense, C. M., Corrêa, J. O. D. A., Dos Reis, L. G., Da Conceição, E. P. S., et al. (2014). Butter naturally enriched in cis-9, trans-11 CLA prevents hyperinsulinemia and increases both serum HDL cholesterol and triacylglycerol levels in rats. *Lipids Health Dis.* 13. doi: 10.1186/1476-511X-13-200
- Derakhshande-Rishehri, S. M., Mansourian, M., Kelishadi, R., and Heidari-Beni, M. (2014). Association of foods enriched in conjugated linoleic acid (CLA) and CLA supplements with lipid profile in human studies: A systematic review and meta-analysis. *Public Health Nutr.* 18, 2041–2054. doi: 10.1017/S1368980014002262
- Dewanckele, L., Toral, P. G., Vlaeminck, B., and Fievez, V. (2020). Invited review: Role of rumen biohydrogenation intermediates and rumen microbes in diet-induced milk fat depression: An update. *J. Dairy Sci.* 103, 7655–7681. doi: 10.3168/jds.2019-17662
- Dhaka, V., Gulia, N., Ahlawat, K. S., and Khatkar, B. S. (2011). Trans fats-sources, health risks and alternative approach - A review. *J. Food Sci. Technol.* 48, 534–541. doi: 10.1007/s13197-010-0225-8
- Diane, A., Borthwick, F., Mapiye, C., Vahmani, P., David, R. C., Vine, D. F., et al. (2016). Beef fat enriched with polyunsaturated fatty acid biohydrogenation products improves insulin sensitivity without altering dyslipidemia in insulin resistant JCR:LA-cp rats. *Lipids* 51, 821–831. doi: 10.1007/s11745-016-4148-7
- Dugan, M., Aldai, N., Aalhus, J., Rolland, D., and Kramer, J. (2011). Review: Transforming beef to provide healthier fatty acid profiles. *Can. J. Anim. Sci.* 91, 545–556. doi: 10.4141/cjas2011-044
- Dugan, M. E. R., Mapiye, C., and Vahmani, P. (2018). “Polyunsaturated fatty acid biosynthesis and metabolism in agriculturally important species,” in *Polyunsaturated Fatty Acid Metab.*, 61–86. doi: 10.1016/B978-0-12-811230-4.00004-1
- Frutos, P., Hervás, G., Natalello, A., Luciano, G., Fondevila, M., Priolo, A., et al. (2020). Ability of tannins to modulate ruminal lipid metabolism and milk and meat fatty acid profiles. *Anim. Feed Sci. Technol.* 269, 114623. doi: 10.1016/j.anifeedsci.2020.114623
- Gebauer, S. K., Chardigny, J. M., Jakobsen, M. U., Lamarche, B., Lock, A. L., Proctor, S. D., et al. (2011). Effects of ruminant trans fatty acids on cardiovascular disease and cancer: A comprehensive review of epidemiological, clinical, and mechanistic studies. *Adv. Nutr.* 2, 332–354. doi: 10.3945/an.111.000521
- Gebauer, S. K., Destailats, F., Dionisi, F., Krauss, R. M., and Baer, D. J. (2015). Vaccenic acid and trans fatty acid isomers from partially hydrogenated oil both adversely affect LDL cholesterol: A double-blind, randomized controlled trial. *Am. J. Clin. Nutr.* 102, 1339–1346. doi: 10.3945/ajcn.115.116129
- Guillocheau, E., Legrand, P., and Rioux, V. (2020). Trans-palmitoleic acid (trans-9-C16:1, or trans-C16:1 n-7): Nutritional impacts, metabolism, origin, compositional data, analytical methods and chemical synthesis. A review. *Biochimie* 169, 144–160. doi: 10.1016/j.biochi.2019.12.004
- Guo, Q., Li, T., Qu, Y., Liang, M., Ha, Y., Zhang, Y., et al. (2023). New research development on trans fatty acids in food: Biological effects, analytical methods, formation mechanism, and mitigating measures. *Prog. Lipid Res.* 89, 101199. doi: 10.1016/j.plipres.2022.101199
- Harfoot, C., and Hazlewood, G. P. (1997). “Lipid metabolism in the rumen,” in *The rumen microbial ecosystem*. Eds. P. N. Hobson and C. S. Stewart. (Amsterdam, The Netherlands: Elsevier Science Publishers). 382–426. doi: 10.1007/978-94-009-1453-7\_9
- Hervás, G., Boussalía, Y., Labbouz, Y., Della Badia, A., Toral, P. G., and Frutos, P. (2022). Insect oils and chitosan in sheep feeding: Effects on *in vitro* ruminal biohydrogenation and fermentation. *Anim. Feed Sci. Technol.* 285, 115222. doi: 10.1016/j.anifeedsci.2022.115222
- Imamura, F., Fretts, A., Marklund, M., Ardisson Korat, A. V., Yang, W. S., Lankinen, M., et al. (2018). Fatty acid biomarkers of dairy fat consumption and incidence of type 2 diabetes: A pooled analysis of prospective cohort studies. *PLoS Med.* 15. doi: 10.1371/journal.pmed.1002670
- Jaakamo, M. J., Luukkainen, T. J., Kairenius, P. K., Bayat, A. R., Ahvenjärvi, S. A., Tupasela, T. M., et al. (2019). The effect of dietary forage to concentrate ratio and forage type on milk fatty acid composition and milk fat globule size of lactating cows. *J. Dairy Sci.* 102, 8825–8838. doi: 10.3168/jds.2018-15833
- Jacome-Sosa, M. M., Borthwick, F., Mangat, R., Uwiera, R., Reaney, M. J., Shen, J., et al. (2014). Diets enriched in trans-11 vaccenic acid alleviate ectopic lipid accumulation in a rat model of NAFLD and metabolic syndrome. *J. Nutr. Biochem.* 25, 692–701. doi: 10.1016/j.jnutbio.2014.02.011
- Jakobsen, M. U., Overvad, K., Dyerberg, J., and Heitmann, B. L. (2008). Intake of ruminant trans fatty acids and risk of coronary heart disease. *Int. J. Epidemiol.* 37, 173–182. doi: 10.1093/ije/dym243
- Jaudszus, A., Kramer, R., Pfeuffer, M., Roth, A., Jahreis, G., and Kuhnt, K. (2014). Trans Palmitoleic acid arises endogenously from dietary vaccenic acid. *Am. J. Clin. Nutr.* 99, 431–435. doi: 10.3945/ajcn.113.076117
- Jenkins, T. C., Wallace, R. J., Moate, P. J., and Mosley, E. E. (2008). BOARD-INVITED REVIEW: Recent advances in biohydrogenation of unsaturated fatty acids within the rumen microbial ecosystem 1. *J. Anim. Sci.* 86, 397–412. doi: 10.2527/jas.2007-0588
- Kim, J. H., Kim, Y., Kim, Y. J., and Park, Y. (2016). Conjugated linoleic acid: potential health benefits as a functional food ingredient. *Annu. Rev. Food Sci. Technol.* 7, 221–265. doi: 10.1146/annurev-food-041715-033028
- Kliem, K. E., and Shingfield, K. J. (2016). Manipulation of milk fatty acid composition in lactating cows: Opportunities and challenges. *Eur. J. Lipid Sci. Technol.* 118, 1661–1683. doi: 10.1002/ejlt.201400543
- Klopatek, S. C., Xu, Y., Yang, X., Oltjen, J. W., and Vahmani, P. (2022). Effects of multiple grass- and grain-fed production systems on beef fatty acid contents and their consumer health implications. *ACS Food Sci. Technol.* 2, 712–721. doi: 10.1021/acsfodscitech.2c00021
- Lichtenstein, A. H. (2000). “Dietary trans fatty acid,” in *J. Cardiopulm. Rehabil.* (Amsterdam, The Netherlands: B.V.) 20, 143–146. Available at: <http://www.embase.com/search/results?subaction=viewrecord&from=export&id=L30368506>.
- Mapiye, C., Aldai, N., Turner, T. D., Aalhus, J. L., Rolland, D. C., Kramer, J. K. G., et al. (2012). The labile lipid fraction of meat: From perceived disease and waste to health and opportunity. *Meat Sci.* 92, 210–220. doi: 10.1016/j.meatsci.2012.03.016
- Mapiye, C., Vahmani, P., Mlambo, V., Muchenje, V., Dzama, K., Hoffman, L. C., et al. (2015). The trans-octadecenoic fatty acid profile of beef: Implications for global food and nutrition security. *Food Res. Int.* 76, 992–1000. doi: 10.1016/j.foodres.2015.05.001
- Micha, R., Khatibzadeh, S., Shi, P., Fahimi, S., Lim, S., Andrews, K. G., et al. (2014). Global, regional, and national consumption levels of dietary fats and oils in 1990 and 2010: A systematic analysis including 266 country-specific nutrition surveys. *BMJ* 348. doi: 10.1136/bmj.g2272
- Miller, A., McGrath, E., Stanton, C., and Devery, R. (2003). Vaccenic acid (t11-18:1) is converted to c9,t11-CLA in MCF-7 and SW480 cancer cells. *Lipids* 38, 623–632. doi: 10.1007/s11745-003-1107-8
- Motard-Bélanger, A., Charest, A., Grenier, G., Paquin, P., Chouinard, Y., Lemieux, S., et al. (2008). Study of the effect of trans fatty acids from ruminants on blood lipids and other risk factors for cardiovascular disease. *Am. J. Clin. Nutr.* 87, 593–599. doi: 10.1093/ajcn/87.3.593



- Moya-Camarena, S. Y., Vanden Heuvel, J. P., Blanchard, S. G., Leesnitzer, L. A., and Belury, M. A. (1999). Conjugated linoleic acid is a potent naturally occurring ligand and activator of PPAR $\alpha$ . *J. Lipid Res.* 40, 1426–1433. doi: 10.1016/s0022-2275(20)33384-8
- Mozaffarian, D., Cao, H., King, I. B., Lemaitre, R. N., Song, X., Siscovick, D. S., et al. (2010). Trans-palmitoleic acid, metabolic risk factors, and new-onset diabetes in U.S. Adults. *Ann. Intern. Med.* 153, 790–799. doi: 10.1059/0003-4819-153-12-201012210-00005
- Mozaffarian, D., Katan, M. B., Ascherio, A., Stampfer, M. J., and Willett, W. C. (2006). Trans fatty acids and cardiovascular disease. *Obstet. Gynecol. Surv.* 61, 525–526. doi: 10.1097/01.ogx.0000228706.09374.e7
- Mutsavangwa, T., Hobin, M. R., and Gozho, G. N. (2012). Effects of method of barley grain processing and source of supplemental dietary fat on duodenal nutrient flows, milk fatty acid profiles, and microbial protein synthesis in dairy cows. *J. Dairy Sci.* 95, 5961–5977. doi: 10.3168/jds.2012-5491
- Oteng, A. B., Loregger, A., van Weeghel, M., Zelcer, N., and Kersten, S. (2019). Industrial trans fatty acids stimulate SREBP2-mediated cholesterol synthesis and promote non-alcoholic fatty liver disease. *Mol. Nutr. Food Res.* 63. doi: 10.1002/mnfr.201900385
- Penedo, L. A., Nunes, J. C., Gama, M. A. O. S., Leite, P. E. C., Quirico-Santos, T. F., and Torres, A. G. (2013). Intake of butter naturally enriched with cis-9,trans-11 conjugated linoleic acid reduces systemic inflammatory mediators in healthy young adults. *J. Nutr. Biochem.* 24, 2144–2151. doi: 10.1016/j.jnutbio.2013.08.006
- Pietinen, P., Ascherio, A., Korhonen, P., Hartman, A. M., Willett, W. C., Albanes, D., et al. (1997). Intake of fatty acids and risk of coronary heart disease in a cohort of Finnish men. The Alpha-Tocopherol, Beta-Carotene Cancer Prevention Study. *Am. J. Epidemiol.* 145, 876–887. doi: 10.1093/oxfordjournals.aje.a009047
- Prada, M., Wittenbecher, C., Eichmann, F., Wernitz, A., Kuxhaus, O., Kroger, J., et al. (2022). Plasma industrial and ruminant trans fatty acids and incident type 2 diabetes in the EPIC-potsdam cohort. *Diabetes Care* 45, 845–853. doi: 10.2337/dc21-1897
- Radtke, T., Schmid, A., Trepp, A., Dähler, F., Coslovsky, M., Eser, P., et al. (2017). Short-term effects of trans fatty acids and risk of coronary heart disease in a cohort of surrogate markers of cardiovascular risk in healthy men and women: A randomized, controlled, double-blind trial. *Eur. J. Prev. Cardiol.* 24, 534–543. doi: 10.1177/2047487316680691
- Riserus, U., Vessby, B., Ärnlov, J., and Basu, S. (2004). Effects of cis-9, trans-11 conjugated linoleic acid supplementation on insulin sensitivity, lipid peroxidation, and proinflammatory markers in obese men. *Am. J. Clin. Nutr.* 80, 279–283. doi: 10.1093/ajcn/80.2.279
- Rosemond, R. (2021). Impacts of Feeding Monensin to High Producing Dairy Cattle fed a Contemporary California Diet. *UC Davis. ProQuest ID: Rosemond\_ucdavis\_0029M\_20367.*
- Sacks, F. M., Lichtenstein, A. H., Wu, J. H. Y., Appel, L. J., Creager, M. A., Kris-Etherton, P. M., et al. (2017). Dietary fats and cardiovascular disease: A presidential advisory from the American Heart Association. *Circulation* 136, e1–e23. doi: 10.1161/CIR.0000000000000510
- Samková, E., Špička, J., Pešek, M., Pelikánová, T., and Hanuš, O. (2012). Animal factors affecting fatty acid composition of cow milk fat: A review. *S. Afr. J. Anim. Sci.* 42, 83–100. doi: 10.4314/sajas.v42i2.1
- Scollan, N. D., Price, E. M., Morgan, S. A., Huws, S. A., and Shingfield, K. J. (2017). Can we improve the nutritional quality of meat? *Proc. Nutr. Soc.* 76, 603–618. doi: 10.1017/S0029665117001112
- Stender, S. (2015). In equal amounts, the major ruminant trans fatty acid is as bad for LDL cholesterol as industrially produced trans fatty acids, but the latter are easier to remove from foods. *Am. J. Clin. Nutr.* 102, 1301–1302. doi: 10.3945/ajcn.115.123646
- Stender, S., Astrup, A., and Dyerberg, J. (2008). Ruminant and industrially produced trans fatty acids: Health aspects. *Food Nutr. Res.* 52. doi: 10.3402/fnr.v52i0.1651
- Tardy, A. L., Giraudet, C., Rousset, P., Rigaudière, J. P., Laillet, B., Chalancon, S., et al. (2008). Effects of trans MUFA from dairy and industrial sources on muscle mitochondrial function and insulin sensitivity. *J. Lipid Res.* 49, 1445–1455. doi: 10.1194/jlr.M700561-JLR200
- Tholstrup, T., Raff, M., Basu, S., Nonboe, P., Sejrnsen, K., and Straarup, E. M. (2006). Effects of butter high in ruminant trans and monounsaturated fatty acids on lipoproteins, incorporation of fatty acids into lipid classes, plasma C-reactive protein, oxidative stress, hemostatic variables, and insulin in healthy young men. *Am. J. Clin. Nutr.* 83, 237–243. doi: 10.1093/ajcn/83.2.237
- Tricon, S., Burdge, G. C., Jones, E. L., Russell, J. J., El-Khazen, S., Moretti, E., et al. (2006). Effects of dairy products naturally enriched with cis-9,trans-11 conjugated linoleic acid on the blood lipid profile in healthy middle-aged men. *Am. J. Clin. Nutr.* 83, 744–753. doi: 10.1093/ajcn/83.4.744
- Turpeinen, A. M., Mutanen, M., Aro, A., Salminen, I., Basu, S., Palmquist, D. L., et al. (2002). Bioconversion of vaccenic acid to conjugated linoleic acid in humans. *Am. J. Clin. Nutr.* 76, 504–510. doi: 10.1093/ajcn/76.3.504
- USDA (2020). *Dietary guidelines for american—2025.* (Washington, D.C., U.S.: U.S. Department of Health and Human Services). doi: 10.1177/21650799211026980
- Vahmani, P., Mapiye, C., Prieto, N., C.Rolland, D., A.McAllister, T., L.Aalhus, J., et al. (2015). The scope for manipulating the polyunsaturated fatty acid content of beef: a review. *J. Anim. Sci. Biotechnol.* 6. doi: 10.1186/s40104-015-0026-z
- Vahmani, P., Ponnampalam, E. N., Kraft, J., Mapiye, C., Bermingham, E. N., Watkins, P. J., et al. (2020). Bioactivity and health effects of ruminant meat lipids. Invited Review. *Meat Sci.* 165, 108114. doi: 10.1016/j.meatsci.2020.108114
- Vahmani, P., Rolland, D. C., Mapiye, C., Dunne, P. G., Aalhus, J. L., Juarez, M., et al. (2017). Increasing desirable polyunsaturated fatty acid concentrations in fresh beef intramuscular fat. *CAB Rev. Perspect. Agric. Vet. Sci. Nutr. Nat. Resour.* 12. doi: 10.1079/PAVSNNR201712020
- Verneque, B. J. F., MaChado, A. M., de Abreu Silva, L., Lopes, A. C. S., and Duarte, C. K. (2022). Ruminant and industrial trans-fatty acids consumption and cardiometabolic risk markers: A systematic review. *Crit. Rev. Food Sci. Nutr.* 62, 2050–2060. doi: 10.1080/10408398.2020.1836471
- Wanders, J. A., Zock, L. P., and Brouwer, A. I. (2017). Trans fat intake and its dietary sources in general populations worldwide: A systematic review. *Nutrients* 9. doi: 10.3390/nu9080840
- Wang, X., England, A., Sinclair, C., Merkosky, F., and Chan, C. B. (2019). Trans-11 vaccenic acid improves glucose homeostasis in a model of type 2 diabetes by promoting insulin secretion via GPR40. *J. Funct. Foods* 60. doi: 10.1016/j.jff.2019.06.012
- Wang, X., Gupta, J., Kerslake, M., Rayat, G., Proctor, S. D., and Chan, C. B. (2016). Trans-11 vaccenic acid improves insulin secretion in models of type 2 diabetes in vivo and in vitro. *Mol. Nutr. Food Res.* 60, 846–857. doi: 10.1002/mnfr.201500783
- Wang, Y., Jacome-Sosa, M. M., Ruth, M. R., Lu, Y., Shen, J., Reaney, M. J., et al. (2012). The intestinal bioavailability of vaccenic acid and activation of peroxisome proliferator-activated receptor- $\alpha$  and - $\gamma$  in a rodent model of dyslipidemia and the metabolic syndrome. *Mol. Nutr. Food Res.* 56, 1234–1246. doi: 10.1002/mnfr.201100517
- Wang, Y., Lu, J., Ruth, M. R., Goruk, S. D., Reaney, M. J., Glimm, D. R., et al. (2008). Trans-11 vaccenic acid dietary supplementation induces hypolipidemic effects in JCR: LA-cp rats. *J. Nutr.* 138, 2117–2122. doi: 10.3945/jn.108.091009
- Werner, L. B., Hellgren, L. I., Raff, M., Jensen, S. K., Petersen, R. A., Drachmann, T., et al. (2013). Effects of butter from mountain-pasture grazing cows on risk markers of the metabolic syndrome compared with conventional Danish butter: A randomized controlled study. *Lipids Health Dis.* 12. doi: 10.1186/1476-511X-12-99
- Xu, Y., Haj, F., Koike, S., and Vahmani, P. (2022). PSI-4 Beef fat Enriched with Vaccenic Acid and cis-9, Trans-11-Conjugated Linoleic Acid Promotes Hepatic Steatosis and Glucose Intolerance in High-fat-fed C57BL/6 Mice. *J. Anim. Sci.* 100, 232–233. doi: 10.1093/jas/skac247.421



## OPEN ACCESS

## EDITED BY

Jeff Wood,  
University of Bristol, United Kingdom

## REVIEWED BY

Zachary Clayton,  
University of Colorado Boulder,  
United States  
Małgorzata Karwowska,  
University of Life Sciences of Lublin, Poland

## \*CORRESPONDENCE

Adesbola T. Adesogan  
✉ adesogan@ufl.edu

RECEIVED 01 August 2023

ACCEPTED 10 November 2023

PUBLISHED 27 November 2023

## CITATION

Tiwari C, Balehegn M, Adesogan AT  
and McKune SL (2023) Benefits,  
perceived and actual risks and barriers  
to egg consumption in low- and middle-  
income countries.  
*Front. Anim. Sci.* 4:1270588.  
doi: 10.3389/fanim.2023.1270588

## COPYRIGHT

© 2023 Tiwari, Balehegn, Adesogan and  
McKune. This is an open-access article  
distributed under the terms of the [Creative  
Commons Attribution License \(CC BY\)](#). The  
use, distribution or reproduction in other  
forums is permitted, provided the original  
author(s) and the copyright owner(s) are  
credited and that the original publication in  
this journal is cited, in accordance with  
accepted academic practice. No use,  
distribution or reproduction is permitted  
which does not comply with these terms.

# Benefits, perceived and actual risks and barriers to egg consumption in low- and middle-income countries

Chhavi Tiwari<sup>1</sup>, Mulubrhan Balehegn<sup>2</sup>, Adegbola T. Adesogan<sup>2\*</sup>  
and Sarah L. McKune<sup>1,3</sup>

<sup>1</sup>Department of Environmental and Global Health, College of Public Health and Health Professions, University of Florida, Gainesville, FL, United States, <sup>2</sup>Feed the Future Innovation Lab for Livestock Systems, Department of Animal Sciences, Global Food Systems Institute, IFAS, University of Florida, Gainesville, FL, United States, <sup>3</sup>The Center for African Studies, University of Florida, Gainesville, FL, United States

Eggs like other animal-source foods (ASFs), contain an array of macro and micronutrients that promote physical and cognitive growth, nutrition, and health outcomes. Hence, they can be used to reduce rampant undernutrition in low- and middle-income countries (LMICs). Yet consumption of eggs remains low in such countries for various reasons. Given their potential as a tool for reducing malnutrition, this paper reviews the literature on the benefits, risks, and barriers to egg consumption in LMICs. Research indicates that egg consumption is associated with several nutritional and health benefits in newborns, young children, and pregnant and lactating women, but few studies on other groups exist. Effects of egg consumption on diet-related chronic diseases seem to be inconclusive, and early introduction of eggs to infants has reduced allergy risk of eggs later in life in several studies. Some main barriers to egg consumption in LMIC include unaffordability and unavailability, partly due to low poultry productivity, high poultry feed prices, cultural beliefs, and social taboos, many of which disproportionately restrict egg consumption among children and pregnant women. The evidence supports egg intake as a mechanism for meeting nutrient recommendations and a healthy diet in LMIC.

## KEYWORDS

animal source foods (ASF), eggs, health, nutrition, health risks, low- and middle-income countries (LMICs)

## 1 Introduction

Consumption of animal-source foods (ASF) such as meat, fish, dairy, and eggs are linked to improvements in nutrition and health status due to their rich profile of nutrients, including as protein, essential fatty acids, minerals, and vitamins (Asare et al., 2022; Fite et al., 2022). ASF has been described as the best nutrient-dense source of food for children



under 2 years of age (WHO, 2014). They are also the best source of catalytic proteins that are important for cellular growth and differentiation but cannot be synthesized within the human body. Thus, they must be obtained via the diet (Headey et al., 2018). Adding small quantities of ASF to plant-based diets can augment nutritional and health outcomes in consumers (Neumann et al., 2007; Eaton et al., 2019).

Despite the significant potential contribution of ASF to nutritional security, ASF consumption is very low in low- and middle-income countries (LMICs), where diets are often highly comprised of starchy foods, relative to levels in high-income countries (HICs) (Adesogan et al., 2020). The low ASF consumption in LMICs is attributed to several factors, including low animal productivity, unaffordability, cultural norms, and religious beliefs. Usually, ASF are costlier per calorie in LMICs compared to grains and staple foods, which creates a significant economic barrier to ASF consumption (Headey, 2018), a problem disproportionately affecting the poorest populations (Rawlins et al., 2014; Hoddinott et al., 2015). Taboos on consumption of ASF also hinder their intake in several societies, unfortunately during important periods of development, such as pregnancy and infancy. For example, seafood and eggs are taboos for pregnant women and young children in Southeastern Nigeria (Ekwochi et al., 2016). In Ethiopia, which has one of the largest livestock populations on the planet, meat and fish consumption during pregnancy is low (Nguyen et al., 2013; Zerfu et al., 2016), and avoidance of ASF during fasting seasons is the custom in the Orthodox Christian faith. Many other major world religions also forbid the consumption of certain ASF. In India, most religious and ethnic groups, including Jains, Sikhs, and upper caste Hindus, prohibit the consumption of beef (Dasgupta et al., 2023), yet beef is a good source of iron and India has the highest global prevalence of anemia (Stevens et al., 2013).

Like many ASF, eggs are a rich source of micro and macronutrients (Lutter et al., 2018). Eggs have been considered among the best sources of protein because of the similarity of the amino acid profile to that of reference proteins (Rao et al., 1964; FAO, 2023). Eggs contain relatively high concentrations of vitamins A, D, E, K, B1, B2, B5, B6, B9, and B12 (Réhault-Godbert et al., 2019), as well as choline (Patterson et al., 2007). Eggs also contain phosphorus, calcium, potassium, iron, iodine, zinc, and essential fatty acids (EFAs) (Lutter et al., 2018).

Eggs are unique in their support for early growth and development (Iannotti et al., 2014). The essential omega-3 and 6 fatty acids in eggs, especially docosahexanoic acid (DHA) are important for vision and the early stages of brain development (Iannotti et al., 2014). Hence, such fatty acids from eggs are essential during pregnancy and infant development (Miranda et al., 2015). Adding eggs more frequently in diet can also help older people to maintain their muscle strength and function, thereby preserving their functional capacity (Smith and Gray, 2016).

In many HIC, but not most LMIC, eggs are nutrient-dense whole food, relatively low cost sources of protein (Drewnowski, 2010; Alexander et al., 2016) and have the lowest planetary impact amongst ASF (Myers and Ruxton, 2023). They are a renewable source of protein (Lesniewski and Stangierski, 2018) that can

contribute to household food security whether they are produced at home or purchased. Eggs, kept with intact shells under appropriate conditions, are sterile and easy to cook (Board et al., 1994), which are significant advantages over other ASF, for which food safety is a concern (Bukachi et al., 2021). Chickens or other egg-laying poultry, such as guinea fowl, are often ubiquitous in rural, smallholder farming communities of LMICs. Yet, the productivity of poultry and egg consumption is often low in such areas (Wong et al., 2017; Stark et al., 2021). This is partly because food taboos exist in many of such places limiting egg consumption (Onuorah and Ayo, 2003; Iradukunda, 2020), but may also be because of culturally derived norms and understandings of the chicken-egg lifecycle (Stark et al., 2021). Figure 1 shows that egg consumption has remained low in LMICs as compared to HICs over time.

Against this background, we present a review of the literature on benefits and risks of chicken egg (hereafter, egg) consumption (Figure 2), particularly in LMICs, and outline the rationale for further investigation of benefits of egg consumption and the attendant policy implications. First, the paper examines the literature on nutritional benefits of egg consumption and then it examines actual and perceived health risks of egg consumption. Finally, it explores the barriers to increasing egg consumption, particularly among LMICs. The conclusion provides a brief synopsis of key deductions and potential solutions for increasing egg consumption in LMICs.

## 2 Egg consumption and health benefits

The nutritional benefits of eggs to human health likely cover the lifespan, including infants, young children, adolescents, adults, childbearing, pregnant and lactating women, adult men, and the elderly (McKune et al., 2022). However, there is little published information on the benefits of egg consumption except in infants, young children and pregnant and lactating women. In the US, egg consumption is associated with greater energy intake, protein, total choline, lutein + zeaxanthin, fat and other micronutrients (Papanikolaou and Fulgoni, 2018). These authors reported that relative to non-egg consumers, egg consumers had lower prevalence of people with calcium, iron, magnesium, and vitamins A, C, and E levels below the respective estimated average requirements, and greater prevalence of people with potassium and choline levels above the average requirements. A recent review by Myers and Ruxton (2023) found increased muscle protein synthesis and reduced fat mass due to increased egg consumption.

### 2.1 Infants and young children

During infancy and early childhood, a nutritious, diverse diet is vital for optimal physical and cognitive growth (McKune et al., 2022). This stage demands more than double the energy requirement per kilogram compared to that for adults (Bégin and Aguayo, 2017). Eggs can contribute substantially to children's development because they provide approximately half of the daily

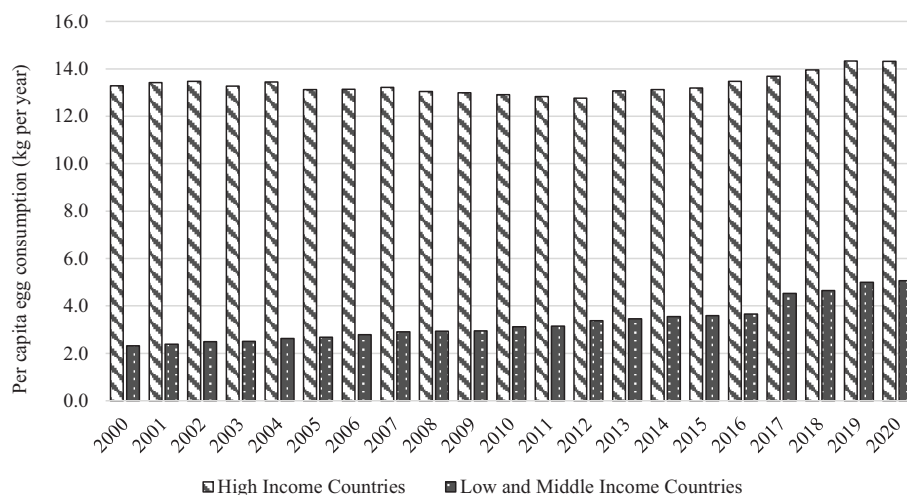


FIGURE 1

Pattern of per capita egg consumption in High Income Countries (HICs) and Low- and middle-income countries (LMICs) during 2000 to 2020. Data source: FAOSTAT, Food and Agriculture Organization of the United Nations. Retrieved from <http://www.fao.org/faostat/en/#data/FBS> on October 23, 2023.

nutritional requirements of children (Waters et al., 2018). In support, a 49-country study of children aged 6–23 months (Headey et al., 2018) found that egg consumption was associated with a lower (1.3%) prevalence of stunting.

A Randomized Controlled Trial (RCT) by Iannotti et al. (2017) compared nutritional outcomes among 6–9-month-old children in a treatment that supplemented one egg per day for 6 months versus those in a Control group with a usual unsupplemented diet in Ecuador. They found that length for age z-score (LAZ) increased by 0.63 Standard Deviation (SD), that stunting prevalence decreased by 47% in the treatment group compared to the Control group, and they attributed the difference at least partly to an increase in choline

levels in the treatment group by 0.35. Other early growth outcomes, such as weight, length, and head circumference, were unaffected. However, the same research team (Stewart et al., 2019) conducted a similar RCT in Malawi with 660 children of the same age (6–9 months), but did not find any increase in LAZ, weight-for-age (WAZ), or weight-for-length z-scores (WLZ) due to egg consumption. The latter study attributed the lack of effect of egg consumption on nutritional measures to a fish-rich background diet and low prevalence of stunting at baseline. Nevertheless, authors reported that egg consumption increased head circumference for age, sometimes used to measure cognitive development (Veena et al., 2010; Wright and Emond, 2015).

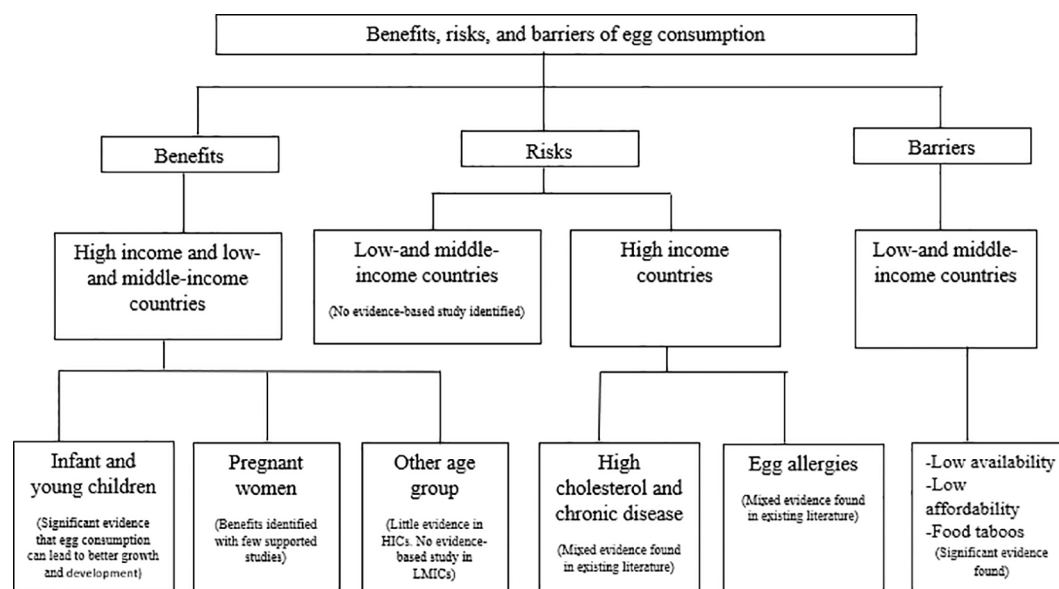


FIGURE 2

Overview of the study.

In Uganda, Baum et al. (2017) evaluated the provision of one versus two versus no eggs five days per week to children aged 6–9 months in a school feeding program. Compared to those receiving no eggs, children receiving two eggs had significantly higher growth and weight gain at 6 months as well as lower tricep skinfold thickness (−0.64 cm) and greater mid-upper arm circumference (MUAC) (+0.52 cm).

In a three-arm trial in Burkina Faso, McKune et al. (2020) examined effects of providing chickens and nutritional training (full intervention), only nutritional training (partial intervention) and no intervention (Control) to 270 mother-child dyads on egg consumption and anthropometry. The study reported increases in egg consumption among children in full and partial intervention groups. Wasting (increase in WLZ by 0.58) and underweight (increase in WAZ by 0.47) were reduced among children in the full intervention group versus the Control group. In a similar study in Ethiopia, Omer et al. (2022) compared an intervention of nutritional training (to mothers) combined with child-owned egg-laying hens to a Control group with only nutrition education. The intervention significantly increased egg intake and WAZ and WLZ by 0.38 and 0.43, respectively, among 6–18 months-old children. The study also noted that in the intervention group, children were 54% and 42% less likely to be underweight and stunted than in the Control group. Asare et al. (2022) examined the effects of ASF consumption in LMICs among 6–24-month-old children. They concluded that egg consumption non-statistically increased LAZ and WAZ with clinically relevant high effect sizes of 0.31 and 0.2, respectively. However, among 3–8-year-old children in Haiti, Stewart (2018) did not find any improvement in child growth outcomes with an intervention of two eggs per day (10 per week) in the diet for 6 months. The study attributed the null results to limited food access and non-compliance with the study design. In Malaysia, Ihab et al. (2014) conducted a trial examining the effect of milk and egg as supplements for malnourished children aged 2–10 years. No significant difference in height and weight gains was reported, but supplementation with milk and eggs almost doubled MUAC values relative to those in the Control group.

The improvements in nutritional status and anthropometry measures in the studies above are at least partly attributable to the macro and micronutrient supply from eggs. By increasing concentrations of DHA and other micronutrients like vitamin B12, zinc and iron, increased consumption of eggs by young children potentially impacts cognitive development. DHA is vital for neurodevelopment, but is often low in diets of young children in resource-poor settings (Forsyth et al., 2017). One 50g egg contains approximately 30 mg DHA, which translates to 30% of the recommended amount for children under 24 months of age by the European Food Safety Authority (100 mg DHA/day) (Papanikolaou and Fulgoni, 2018). A DHA supplement intervention study in Ghana (Van Der Merwe et al., 2013) among 3–9 month-olds resulted in greater concentrations of plasma n–3 fatty acid and MUAC at 9 months. The previously described Ecuador study (Iannotti et al., 2017) found that egg consumption increased the effect size of DHA concentration by 0.43. In another study in Ecuador, Sibbald et al. (2021) found egg consumption to be a significant factor for cerebellar diameter. They observed trends for

positive effects of maternal consumption of eggs on fetal brain dimensions. Omer et al. (2022) found that children in the intervention (with child-owned poultry and nutritional training for mothers) achieved higher scores in motor skills (running, kicking a ball, and throwing a ball) at a younger age than those in the Control group (with nutritional training for mothers alone). These children had 1.43, 1.39, and 1.37 times greater chances of attaining the milestones mentioned above than the Control group children. From the discussion above, it is evident that eggs can contribute often missing essential nutrients for optimal growth and development in the diets of young children in LMIC.

## 2.2 Pregnant and lactating women

Eggs can contribute to nutritional needs during adolescence—“a period of rapid growth, hormonal changes, and brain restructuring” (Bundy et al., 2017), as well as during pregnancy and lactation (Lutter et al., 2018). For several vital nutrients, eggs can contribute a large portion of the Recommended Daily Allowance (RDA) or adequate intake (AI) for pregnant and lactating women; for instance, two 50-g eggs provide between 20% and 35% of the AI/RDA for vitamin A, riboflavin, pantothenic acid, vitamin B12 and phosphorus for pregnant and lactating women, and more than 18% of the RDA for protein and 50% of the AI/RDA for choline and selenium (Lutter et al., 2018). Studies in the US and South Africa show that pregnant mothers had choline intakes below the AI, and this was associated with lower egg and dairy intake (Wallace and Fulgoni, 2017; Robb et al., 2021). Wallace and Fulgoni (2017) reported that meeting the AI for choline without egg consumption or a dietary supplement is challenging, even in the US. Choline supports various cellular membrane reactions and is a precursor of acetylcholine, an important neurotransmitter and non-neuronal signalling molecule essential for memory, muscle control, mood, and other brain and nervous systems functions (Wallace and Fulgoni, 2017). Yet published studies on the effect of egg consumption on nutritional and health outcomes in pregnant or lactating women are few. Such studies have shown that compared to pregnant non-egg consumers, pregnant egg consumers had higher intakes of protein, fat, vitamin K, vitamin E, selenium, beta carotene, lutein and zeaxanthin, cholesterol, total polyunsaturated fatty acids, and DHA among predominantly Puerto Rican Latinas (Bermúdez-Millán et al., 2009), lower gestational diabetes and blood pressure in Iran (Milajerdi et al., 2018), and lower prevalence of anemia in Ghana (Tibambuya et al., 2019). These beneficial responses highlight the need for more studies on the nutritional and health benefits of egg consumption in pregnant and lactating women in LMICs and in other adolescents and adults.

## 3 Risks associated with egg consumption

Despite the nutritional benefits mentioned above, egg consumption has been associated with adverse effects on human health (Miranda et al., 2015). Associated health risks of egg

consumption such as cancer, diabetes, cardiovascular diseases (CVD) are studied in several meta-analyses. But the evidence was often conflicting, complicating the making of dietary recommendations. (Zhang et al., 2020) Further, most of the studies investigating the risks of egg consumption are conducted in middle and high-income countries. Below we summarize the risks of egg consumption that might be relevant for LMICs.

### 3.1 High cholesterol content and its association with diet related chronic diseases

Health risks attributed to egg consumption have usually been associated with the high cholesterol content in eggs. Egg cholesterol accounts for 26–32% of total dietary cholesterol intake in the USA and 48% of total dietary cholesterol intake in Japan (Nakamura et al., 2006). However, the effects of egg consumption on plasma cholesterol levels is not straightforward. While some studies suggest that increased consumption of eggs increases plasma total cholesterol, others do not. One study noticed that daily consumption of 3 eggs for four weeks did not affect plasma cholesterol in people with metabolic syndrome (DiBella et al., 2020). Another study concluded that more than 70% of human subjects experience only little or no increase in plasma cholesterol concentration when they consumed high levels of dietary cholesterol, as could occur from consumption of eggs (Asare et al., 2022). A third study suggested that eggs do not increase plasma cholesterol concentration because the cholesterol they supply appears to regulate the endogenous synthesis of cholesterol so that the LDL-C/HDL-C ratio is maintained (Lemos et al., 2018). In another study, a 100 mg daily increase in dietary cholesterol from eggs, equivalent to 3–4 eggs a week, increased LDL cholesterol by approximately only 0.05 mmol/L (Natoli et al., 2007).

Further, there is some evidence that daily egg intake may favorably shift HDL lipid composition and function beyond increasing plasma HDL-C in individuals with metabolic syndrome (Andersen et al., 2013). However, it is also important to note that other studies have reported increased plasma cholesterol due to egg consumption. For instance, in a meta-analysis of 17 randomized controlled trials Li et al. (2020) concluded that egg consumption increased LDL-C/HDL-C ratio and LDL-C levels, especially with a longer intervention period. Another meta-analysis by Rouhani et al. (2018) concluded that egg consumption increased total cholesterol, LDL-C, and HDL-C, but not LDL-C:HDL-C, TC : HDL-C, and Triglycerides compared with low egg Control diets. Clayton et al. (2015) found a significant decrease in triglycerides levels among participants who consumed egg-based (2 eggs per day) versus bagel-based breakfasts for 12 weeks but reported no effect on total cholesterol.

Existing evidence, therefore, indicates a complex relationship between egg consumption and cholesterol levels due to factors such as preparation methods, other dietary components, and individual variations that might affect cholesterol metabolism (Miranda et al., 2015). Others have also attributed the inconsistent plasma

cholesterol response to egg consumption in different studies to individual variation (Herron et al., 2006; Sanlier and Üstün, 2021).

Higher egg consumption has been linked to both positive and negative effects on specific health conditions. For example, higher egg consumption was associated with increased blood glucose levels among individuals with type 2 diabetes and/or impaired glucose tolerance (Guo et al., 2018). However, improved blood glucose levels associated with egg consumption were reported in people with pre-diabetes and type 2 diabetes (Pearce et al., 2011; DiBella et al., 2020). Meta analyses studies have also yielded conflicting results (Shin et al., 2013; Tamez et al., 2016; Wallin et al., 2016).

Another risk sometimes linked to egg consumption is CVD, but the literature findings are inconclusive. Some studies found no positive relationship between egg consumption and CVD, such as myocardial infarction or stroke (Rong et al., 2013; Zhong et al., 2019). In contrast, moderate egg consumption has been associated with a reduced risk of metabolic syndrome, lower risk of cardiovascular disease, and lower risk of developing hemorrhagic stroke (Myers & Ruxton, 2023; Qin et al., 2018; Woo et al., 2016). A meta-analysis by Alexander et al. (2016) indicated that daily intake of 1 egg was associated with reduced risk of stroke but no clear association for coronary heart disease. Further, some studies report no correlation between egg intake and CVD risk (Fernandez and Calle, 2010). Godos et al. (2021) in their meta-analysis found no conclusive evidence on the role of egg in CVD risk. Similarly, meta-analysis conducted by Krittanawong et al. (2021) also suggested no association between higher egg consumption and increased CVD risk, but they found that higher egg consumption was associated with a significant reduction in coronary artery disease. Consequently, it has been suggested, that where evident, the harmful effects of eggs on CVD may be attributed to negative dietary patterns associated with high levels of food intake rather than egg consumption (Fardet and Boirie, 2014).

From the evidence above, it is inferred that the effects of egg consumption on health outcomes are multifaceted and vary among individuals. Consequently, more research is needed on this subject. In the absence of definitive studies, therefore, dietary recommendations aiming to restrict egg consumption should not be generalized for all, as there seems to be considerable evidence that healthy populations experience no increased risk of developing diet-related chronic disease by increasing egg consumption (Fernandez, 2006).

### 3.2 Egg allergies

Allergies are another important risk often associated with consumption of eggs. Egg allergies are immune responses triggered by proteins found in eggs, mainly ovalbumin, ovomucoid, lysosome, ovomucin and ovotransferrin (Heine et al., 2006). Egg allergies are common in children, with various reported prevalence rates: 1.3–2.5% among children under 5 years of age in Japan (Nishino et al., 2022), 8.9% among one-year-olds in Australia (Loh and Tang, 2018), 0.07% to 2.18% among two-year-olds in Europe (Xepapadaki et al., 2016), and 3 to 4% among 0 to 2 year



olds in China (Lee et al., 2013). In the US, egg allergies are the second most common food allergy in children after cow's milk, with a prevalence of 0.9% among all children and 1.3% among children under the age of five (Samady et al., 2020). These allergies can manifest as immediate-type reactions, such as hives, swelling, and anaphylaxis, or delayed-type reactions, including gastrointestinal symptoms and atopic dermatitis (Loh and Tang, 2018; Lunhui et al., 2021). Allergic reactions to eggs can cause physical discomfort, anxiety, and social limitations (Morou et al., 2021). Individuals with egg allergies may have an increased risk of developing allergies to other foods, such as milk, peanuts, and tree nuts (Jo et al., 2019). Sensitization to egg proteins can also occur through exposure to other allergenic sources such as chicken serum albumin (De Silva et al., 2018).

Various published studies, predominantly from MHICs, show that introducing eggs to infants does not increase the risk of allergy incidence or egg sensitization and, in fact, may reduce the risk of egg allergies later in life. Bellach et al. (2017) did not find any evidence that egg introduction to 4–6-month-olds prevented egg allergy in Germany. However, Natsume et al. (2017) conducted a RCT in Japan among infants 4–5 months of age, assigning them to 50 mg of egg powder per day from 6–9 months and 250 mg per day thereafter until 12 months of age, concluding that early egg treatment is a safe and effective way to prevent egg allergy in high-risk infants. Likewise, in their systematic reviews and meta analyses, Burgess et al. (2019) and Al-Saud and Sigurdardóttir (2018) concluded that introducing eggs to 4 month olds and 3–6 month olds was associated with reduced risk of egg allergies. Wei-Liang Tan et al. (2017) found that introducing egg whites to the diets of infants reduced sensitization to egg whites by 9.8% in Australia.

## 4 Barriers to egg consumption and solutions

Despite their nutritional advantages and relative availability and affordability compared to other ASF, the per capita consumption of eggs is still low in many countries, especially in LMICs. For instance, the per capita egg consumption in the United States in 2020 was 286 eggs a year (Snibbe, 2021). In contrast, the average long term per capita egg consumption in Sub-Saharan Africa is estimated to be 44 eggs (Vincent, 2023). In Africa, based on 24 hour recall prior to the survey, only 12.6% of children reported egg consumption, and in India, the corresponding number was just 14.7% of children, a level much lower than other South Asian countries (25.0%) (Morris et al., 2018). Only 9 out of the 43 countries in the Sub-Saharan Africa consume a yearly average of 2 kg of eggs per person, equivalent to 30 to 40 eggs, and in many countries, including Burundi and Rwanda) consumption is much lower (Júlia Pié Orpí, 2020). A study in Ethiopia found out that only 20% of households consumed eggs one to two times per week (Daba et al., 2021). Another study in Burkina Faso found out that eggs were amongst the least consumed foods in 618 children studied and only 6.6% women gave eggs to their breastfed children (Bougma et al., 2023).

### 4.1 Low availability

Numerous factors contribute to the low consumption of eggs in LMICs. Generally, the productivity of poultry in LMIC is low, particularly among indigenous breeds, which are hardier and disease resistant, thus often favored. The low productivity of local breeds, limited supply of quality feed, low adoption of best management practices, underdeveloped veterinary services, and generally high and increasing cost of production are the main reasons for the low levels and efficiency of egg production in these countries (Bachewe et al., 2017; Birhanu et al., 2023), which both contribute to low availability.

### 4.2 Low affordability and increasing production cost

Low-income households consume lower amounts of eggs compared to higher income countries. A study in Ethiopia found low egg consumption in infants and young children was associated with low economic status, indicated by wealth and occupation (Kase et al., 2022). Similarly, in India, per capita income is a determinant of egg purchase probability and consumption (Umanath et al., 2016).

Generally egg consumption is found to be highly correlated with affordability and nationwide availability, both of which are related to the price of eggs (Morris et al., 2018). Studies report that eggs are more expensive sources of calories than staple cereal crops and that this difference is higher in LMICs. For instance, while in MHICs, egg are 2.3 times as expensive source of calories as the cheapest cereal, reflecting the increased poultry productivity overtime and large economies of scale (Narrod et al., 2007), in Latin America, Eastern Europe and Central Asia, the relative prices are three to five times higher; and in sub-Saharan Africa, eggs are 9.5 times as expensive as cereals (Morris et al., 2018).

The low affordability of eggs is primarily attributable to the high and increasing production costs. The cost of poultry feed has been continuously increasing in several African countries, thus increasing the cost of poultry products (Conway, 2019; Wongnaa et al., 2023). In Nigeria the price of feed ingredients has risen by over 168% in the last 3 years (2019–2022) threatening many poultry farms (Poultry World, 2022). Notable increases in price of poultry feed have been reported in other African countries, including 350% in the past year in Ethiopia, forcing the closure of 15 large commercial poultry farms (Business Info Ethiopia, 2022).

Global factors such as COVID-19, the Russo-Ukrainian war, and other local conflicts have also compounded the problem of high prices of livestock feed and, hence, egg prices. For instance, in Bangladesh, broiler chicken and egg prices increased by 40% and 30%, respectively, following the COVID-19 pandemic (Amin et al., 2023). Severe outbreaks of bird flu in the United States and France, together with breakdown of global market networks due to the Ukraine war, tightened global egg supplies and raised prices, especially in LMICs that depend on imported eggs (Polansek and



de la Hamaide, 2022). Table 1 shows recent increases in prices of poultry feed and eggs in LMIC.

### 4.3 Food taboos, restrictions, and allocation biases

Communities all over the world have various taboos or restrictions against consumption of various types of foods. Some cultures have restrictions on egg consumption for some members of the household or community (Madzimure et al., 2011); such taboos on egg (and poultry) consumption that target pregnant women are common in many cultures (Washington, 2015; Schnefke et al., 2019). For example, women are discouraged from eating eggs when pregnant because they are thought to increase fetal growth and cause labor pain and difficult birth in many countries (Meyer-Rochow, 2009; Arzoaquoi et al., 2015; Chakona and Shackleton, 2019; Tsegaye et al., 2021). Other reasons for taboos against egg consumption by pregnant women include perceptions that they have adverse effects on mental health and cognitive development of newborns in Kenya (Kariuki et al., 2017), cause early deaths among infants in Ethiopia (Zerfu et al., 2016), and cause development of bad habits among children in Ghana (Gadegbeku et al., 2002). In many cultures, the avoidance or restrictions usually target a certain

age, gender, or reproductive status, often pregnant women. However, in some countries, the restriction applies to members of the whole community. For example, in India, consumption of non-dairy ASF (including eggs) is forbidden because of religious beliefs and the idea of non-violence among Jains and upper caste Hindus, respectively. Such taboos restricting or regulating consumption of nutritious foods such as eggs based on gender or age have been described as traditional mechanisms by which members of households with the highest decision power, mostly men, control the allocation of nutritious foods (Blum et al., 2023). Hence most of the egg taboos tend to favor men over more vulnerable groups such as women, particularly pregnant women and children (McNamara and Wood, 2019).

### 4.4 Limited knowledge of nutrition

Limited knowledge of nutrition among parents and caregivers can contribute to inadequate feeding practices, including the lack of diversity in complementary diets for children (Waswa et al., 2015). In Ethiopia, 53.4% of children did not consume eggs in a seven-day study period and the probability of a child consuming eggs during the study period was 4.33 times higher when caregivers had some college education compared with no education (Kase et al., 2022). In Ghana a very low per capita consumption of eggs (about 12 eggs per year) was attributed in some communities to lack of education and misconceptions about the health benefits of eggs (Abive-Bortsi et al., 2022).

High cholesterol intake concerns are common reasons for limited consumption of eggs among communities and households who have adequate access to eggs (Kralik et al., 2020; Sanlier and Üstün, 2021), and even among educated consumers in developing countries (Abive-Bortsi et al., 2022).

### 4.5 Tackling barriers to egg consumption

Both demand and supply side policies can serve as strategic solutions to removing barriers to egg consumption in LMICs (Headey, 2018). Supply-side policies, including those targeting agriculture, trade, value chain policies, and investment, can help drive down the relative price of feed, poultry production, and ultimately eggs, thereby increasing egg affordability. Further enabling policies that provide incentives, the requisite training, and affordable resources to farmers and value chain agents for increasing poultry production can increase egg availability. In addition, demand-side policies through nutritional counselling and media campaigns, including behavior-change campaigns, social protection programs, inclusion of eggs in school meals, etc. can remove the cultural barriers and taboos and significantly foster and facilitate egg consumption in LMICs (Lutter et al., 2018; McKune et al., 2020). Such social marketing and behavior change messaging strategies can be particularly successful when they account for cultural norms and involve individuals respected by the community. For instance, McKune et al. (2020) successfully increased egg consumption among 6- to 12-month-olds in Burkina

TABLE 1 Recent increases in poultry feed and egg prices in selected countries.

Country	Increase in price of poultry feed and time frame	Increase in price of eggs and time frame	References
Nigeria	168% between 2019-2022	37.40% between 2019-2022	(Poultry World, 2022)
Ethiopia	45-55*% between 2020-21	46% between 2020-21	(Business Info Ethiopia, 2022; Negash, 2022)
China	4.3-6.6% between 2021-22	N/A	(Doris, 2022)
US	N/A	60% between 2021-22	(Swann, 2023)
Bangladesh	70% between 2021-22	17% in a month Feb-March 2023	(Financial Express, 2023; TBS News, 2023)
Kenya	31% between mid-2022 to early 2023	26% between mid-2022 to early 2023	(Capital FM, 2023)
India	25-30% in 6 months in early 2022	20.7% between 2021-22	(CNBC TV-18, 2022; Nahata, 2022)
Pakistan	32% between 2018-2020	5.2% between 2018-2020	(Tribune, 2021)
United Kingdom	N/A	20-27% between 2020-23	(Davey, 2022; Julia, 2023)
Ghana	N/A	25-35% between 202-21	(Kinsley, 2021)

\*Increase is for all animal-source foods. N/A, not cited.

Faso who rarely ate eggs (from 0 to 6 eggs per week) by involving village chiefs in a culturally tailored behavior-change campaign.

## 5 Conclusion

This paper presents a review of evidence-based literature on health benefits, risks and barriers to egg consumption in LMICs. While the health benefits of egg consumption in infants and young children are better documented, few studies from LMICs exist on benefits in pregnant and lactating women and adolescence or adulthood, emphasizing the need for more studies that focus on life stages outside of infancy and childhood. Studies on the risks of egg consumption in LMICs are also limited, and those available from MHICs are largely inconclusive for health risks including cholesterol, cardiovascular disease, and allergies. Early introduction (3 to 6 month) of eggs to infants is associated with reduced egg allergies. Barriers hindering the consumption of eggs in LMICs include high feed costs, unavailability, unaffordability, cultural beliefs, and social norms. These barriers vary across communities and primarily limit consumption of eggs among women and children. Given the health benefits of eggs, it is imperative that governments enact and or implement policies that 1, make egg consumption more affordable in LMICs, 2, provide enabling environments, which increase poultry production and egg availability, and 3, enhance understanding about the nutritional importance of eggs in the diet while countering sociocultural norms that restrict egg consumption by children and pregnant women who need them most. In addition, tailored behavior-change campaigns may be needed to break the cultural barriers, norms, or taboos that limit egg consumption.

## Author contributions

AA: Conceptualization, Formal Analysis, Methodology, Supervision, Validation, Writing – review & editing. SM:

Conceptualization, Formal Analysis, Methodology, Supervision, Validation, Writing – review & editing. CT: Conceptualization, Data curation, Investigation, Methodology, Writing – original draft. MB: Conceptualization, Data curation, Investigation, Methodology, Writing – original draft.

## Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. This work was funded in whole or part by the United States Agency for International Development (USAID) Bureau for Food Security under Agreement # AID-OAA-L-15-00003 as part of Feed the Future Innovation Lab for Livestock Systems. Any opinions, findings, conclusions, or recommendations expressed here are those of the authors alone.

## Conflict of interest

AA serves on the Advisory Committee of Protein Pact.

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

## Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

## References

- Abive-Bortsi, M., Baidoo, S. T., and Amiteye, S. (2022). Assessment of consumers' Perception of chicken eggs consumption and associated health implications in the Volta region of Ghana. *Nutr. Metab. Insights* 15, 11786388221118872. doi: 10.1177/11786388221118872
- Adesogan, A. T., Havelaar, A. H., McKune, S. L., Eilittä, M., and Dahl, G. E. (2020). Animal source foods: Sustainability problem or malnutrition and sustainability solution? Perspective matters. *Global Food Secur.* 25, 100325. doi: 10.1016/j.gfs.2019.100325
- Alexander, D. D., Miller, P. E., Vargas, A. J., Weed, D. L., and Cohen, S. S. (2016). Meta-analysis of egg consumption and risk of coronary heart disease and stroke. *J. Am. Coll. Nutr.* 35, 704–716. doi: 10.1080/07315724.2016.1152928
- Al-Saud, B., and Sigurdardóttir, S. T. (2018). Early introduction of egg and the development of egg allergy in children: A systematic review and meta-analysis. *Int. Arch. Allergy Immunol.* 177, 350–359. doi: 10.1159/000492131
- Amin, M. R., Alam, G. M. M., Parvin, M. T., and Acharjee, D. C. (2023). Impact of COVID-19 on poultry market in Bangladesh. *Heliyon* 9, e13443. doi: 10.1016/j.heliyon.2023.e13443
- Andersen, C. J., Blesso, C. N., Lee, J., Barona, J., Shah, D., Thomas, M. J., et al. (2013). Egg consumption modulates HDL lipid composition and increases the cholesterol-accepting capacity of serum in metabolic syndrome. *Lipids* 48, 557–567. doi: 10.1007/s11745-013-3780-8
- Arzoaquoi, S. K., Essuman, E. E., Gbagbo, F. Y., Tenkorang, E. Y., Soyiri, I., and Laar, A. K. (2015). Motivations for food prohibitions during pregnancy and their enforcement mechanisms in a rural Ghanaian district. *J. Ethnobiol. Ethnomed.* 11, 59. doi: 10.1186/s13002-015-0044-0
- Asare, H., Rosi, A., Faber, M., Smuts, C. M., and Ricci, C. (2022). Animal-source foods as a suitable complementary food for improved physical growth in 6 to 24-month-old children in low- and middle-income countries: a systematic review and meta-analysis of randomised controlled trials. *Br. J. Nutr.* 128, 2453–2463. doi: 10.1017/S0007114522000290
- Bachewe, F. N., Minten, B., and Yimer, F. (2017). The rising costs of animal-source foods in Ethiopia: Evidence and implications. *Intl. Food Policy Res. Inst.* 108.
- Baum, J. L., Miller, J. D., and Gaines, B. L. (2017). The effect of egg supplementation on growth parameters in children participating in a school feeding program in rural Uganda: a pilot study. *Food Nutr. Res.* 61, 1330097. doi: 10.1080/16546628.2017.1330097
- Bégin, F., and Aguayo, V. M. (2017). First foods: Why improving young children's diets matter. *Matern. Child Nutr.* 13, e12528. doi: 10.1111/mcn.12528
- Bellach, J., Schwarz, V., Ahrens, B., Trendelenburg, V., Aksünger, Ö., Kalb, B., et al. (2017). Randomized placebo-controlled trial of hen's egg consumption for primary prevention in infants. *J. Allergy Clin. Immunol.* 139, 1591–1599.e2. doi: 10.1016/j.jaci.2016.06.045

- Bermúdez-Millán, Á., Hromi-Fiedler, A., Damio, G., Segura-Pérez, S., and Pérez-Escamilla, R. (2009). Egg contribution towards the diet of pregnant Latinas. *Ecol. Food Nutr.* 48, 383–403. doi: 10.1080/03670240903170517
- Birhanu, M. Y., Osei-Amponsah, R., Yeboah Obese, F., and Dessie, T. (2023). Smallholder poultry production in the context of increasing global food prices: roles in poverty reduction and food security. *Anim. Front.* 13, 17–25. doi: 10.1093/af/vfac069
- Blum, L. S., Swartz, H., Olisenekwu, G., Erhabor, I., and Gonzalez, W. (2023). Social and economic factors influencing intrahousehold food allocation and egg consumption of children in Kaduna State, Nigeria. *Maternal Child Nutr.* 19, e13442. doi: 10.1111/mcn.13442
- Board, R. G., Clay, C., Lock, J., and Dolman, J. (1994). “The egg: a compartmentalized, aseptically packaged food,” in *Microbiology of the Avian Egg*. Eds. R. G. Board and R. Fuller (Boston, MA: Springer US), 43–61. doi: 10.1007/978-1-4615-3060-2\_3
- Bougma, S., Tapsoba, F., Semporé, J. N., Bougma, S., Sibiri, Dounia, P., et al. (2023). Socio-cultural influences on children’s feeding habits and feeding frequencies in Ouagadougou, Burkina Faso: a retrospective survey. *BMC Nutr.* 9, 45. doi: 10.1186/s40795-023-00698-w
- Bukachi, S. A., Ngutu, M., Muthiru, A. W., Lépine, A., Kadiyala, S., and Domínguez-Salas, P. (2021). Consumer perceptions of food safety in animal source foods choice and consumption in Nairobi’s informal settlements. *BMC Nutr.* 7, 35. doi: 10.1186/s40795-021-00441-3
- Bundy, D. A. P., De Silva, N., Horton, S., Jamison, D. T., and Patton, G. C. (2017). *Disease Control Priorities, Third Edition (Volume 8): Child and Adolescent Health and Development* (Washington, DC: World Bank). doi: 10.1596/978-1-4648-0423-6
- Burgess, J. A., Dharmage, S. C., Allen, K., Koplin, J., Garcia-Larsen, V., Boyle, R., et al. (2019). Age at introduction to complementary solid food and food allergy and sensitization: A systematic review and meta-analysis. *Clin. Exp. Allergy* 49, 754–769. doi: 10.1111/cea.13383
- Business Info Ethiopia (2022). *Poultry Farms are Halting Operations Due to a Rise in the Price of Poultry Feed*.
- Capital, F. M. (2023) *Kenya: Egg Prices Spiral Up Amid Scarcity As Feed Costs Surge 30pc in 6 Months - allAfrica.com* [WWW Document]. Available at: <https://allafrica.com/stories/202301100262.html>.
- Chakona, G., and Shackleton, C. (2019). Food taboos and cultural beliefs influence food choice and dietary preferences among pregnant women in the Eastern Cape, South Africa. *Nutrients* 11, 2668. doi: 10.3390/nu11112668
- Clayton, Z. S., Scholar, K. R., Shelechi, M., Hernandez, L. M., Barber, A. M., Petrisko, Y. J., et al. (2015). Influence of resistance training combined with daily consumption of an egg-based or bagel-based breakfast on risk factors for chronic diseases in healthy untrained individuals. *J. Am. Coll. Nutr.* 34, 113–119. doi: 10.1080/07315724.2014.946622
- CNBC TV-18 (2022) *Egg and chicken prices might come down - but here's how it impacts the poultry farmer* [WWW Document]. Moneycontrol. Available at: <https://www.moneycontrol.com/news/business/economy/egg-and-chicken-prices-might-come-down-but-heres-how-it-impacts-the-poultry-farmer-9065931.html>.
- Conway, A. (2019). *Developing countries demand 88 million tons of poultry in 2028* (WATTAgNet | WATT poultry.com). Available at: <https://www.wattagnet.com/egg/egg-production/article/15530102/developing-countries-demand-88-million-tons-of-poultry-in-2028-wattagnet>.
- Daba, A. K., Murimi, M., Abegaz, K., and Hailu, D. (2021). Determinants and constraints to household-level animal source food consumption in rural communities of Ethiopia. *J. Nutr. Sci.* 10, e58. doi: 10.1017/jns.2021.52
- Dasgupta, A., Majid, F., and Orman, W. H. (2023). The nutritional cost of beef bans in India. *J. Dev. Econ.* 163, 103104. doi: 10.1016/j.jdeveco.2023.103104
- Davey, J. (2022). Britain’s broken egg industry shows the price of food inflation. Available at: <https://www.reuters.com/markets/commodities/britains-broken-egg-industry-shows-price-food-inflation-2022-12-19/> (Accessed 6.29.23).
- De Silva, C., Dhanapala, P., King, S., Doran, T., Tang, M., and Suphioglu, C. (2018). Immunological Comparison of Native and Recombinant Hen’s Egg Yolk Allergen, Chicken Serum Albumin (Gal d 5), Produced in *Kluyveromyces lactis*. *Nutrients* 10, 757. doi: 10.3390/nu10060757
- DiBella, M., Thomas, M. S., Alyousef, H., Millar, C., Blesso, C., Malysheva, O., et al. (2020). Choline intake as supplement or as a component of eggs increases plasma choline and reduces interleukin-6 without modifying plasma cholesterol in participants with metabolic syndrome. *Nutrients* 12, 3120. doi: 10.3390/nu12103120
- Doris, Z. (2022) *Analysis of China’s Feed Production in Q1 of 2022*. Available at: <https://www.linkedin.com/pulse/analysis-Chinas-feed-production-q1-2022-doris-zhang>.
- Drewnowski, A. (2010). The Nutrient Rich Foods Index helps to identify healthy, affordable foods. *Am. J. Clin. Nutr.* 91, 1095S–1101S. doi: 10.3945/ajcn.2010.28450D
- Eaton, J. C., Rothpletz-Puglia, P., Dreker, M. R., Iannotti, L., Lutter, C., Kaganda, J., et al. (2019). Effectiveness of provision of animal-source foods for supporting optimal growth and development in children 6 to 59 months of age. *Cochrane Database System. Rev.* 2019. doi: 10.1002/14651858.CD012818.pub2
- Ekwochi, U., Osuorah, C. D. I., Ndu, I. K., Ifediora, C., Asinobi, I. N., and Eke, C. B. (2016). Food taboos and myths in South Eastern Nigeria: The belief and practice of mothers in the region. *J. Ethnobiol. Ethnomed.* 12, 7. doi: 10.1186/s13002-016-0079-x
- FAO. (2023). *Contribution of terrestrial animal source food to healthy diets for improved nutrition and health outcomes – An evidence and policy overview on the state of knowledge and gaps*. (Rome: FAO). doi: 10.4060/cc3912en
- Fardet, A., and Boirie, Y. (2014). Associations between food and beverage groups and major diet-related chronic diseases: an exhaustive review of pooled/meta-analyses and systematic reviews. *Nutr. Rev.* 72, 741–762. doi: 10.1111/nure.12153
- Fernandez, M. L. (2006). Dietary cholesterol provided by eggs and plasma lipoproteins in healthy populations. *Curr. Opin. Clin. Nutr. Metab. Care* 9, 8. doi: 10.1097/01.mco.0000171152.51034.bf
- Fernandez, M. L., and Calle, M. (2010). Revisiting dietary cholesterol recommendations: does the evidence support a limit of 300 mg/d? *Curr. Atheroscler. Rep.* 12, 377–383. doi: 10.1007/s11883-010-0130-7
- Financial Express (2023) *Rein in poultry-feed price hike* [WWW Document]. The Financial Express. Available at: <https://thefinancialexpress.com.bd/editorial/rein-in-poultry-feed-price-hike>.
- Fite, M. B., Tura, A. K., Yadeta, T. A., Oljira, L., and Roba, K. T. (2022). Consumption of animal source food and associated factors among pregnant women in eastern Ethiopia: A community-based study. *PloS One* 17, e0270250. doi: 10.1371/journal.pone.0270250
- Forsyth, S., Gautier, S., and Salem, N. (2017). The importance of dietary DHA and ARA in early life: a public health perspective. *Proc. Nutr. Soc* 76, 568–573. doi: 10.1017/S0029665117000313
- Gadegbeku, C., Wayo, R., Badu, G. A., Nukpe, E., and Okai, A. (2002). Food taboos among residents at Ashongman - Accra, Ghana. *Annu. Rev. Anthropol.* 31, 99–119. doi: 10.1146/annurev.anthro.32.032702.131011
- Godos, J., Micek, A., Brzostek, T., Toledo, E., Iacoviello, L., Astrup, A., et al. (2021). Egg consumption and cardiovascular risk: a dose-response meta-analysis of prospective cohort studies. *Eur. J. Nutr.* 60, 1833–1862. doi: 10.1007/s00394-020-02345-7
- Guo, J., Hobbs, D. A., Cockcroft, J. R., Elwood, P. C., Pickering, J. E., Lovegrove, J. A., et al. (2018). Association between egg consumption and cardiovascular disease events, diabetes and all-cause mortality. *Eur. J. Nutr.* 57, 2943–2952. doi: 10.1007/s00394-017-1566-0
- Headey, D. (2018). *Animal sourced foods and child nutrition in South Asia: Policy priorities* (No. Policy Brief Issue 11). LANSa: Leveraging Institutions for Nutrition in South Asia.
- Heine, R. G., Laske, N., and Hill, D. J. (2006). The diagnosis and management of egg allergy. *Curr. Allergy Asthma Rep.* 6, 145–152. doi: 10.1007/s11882-006-0053-0
- Herron, K. L., Lofgren, I. E., Adiconis, X., Ordovas, J. M., and Fernandez, M. L. (2006). Associations between plasma lipid parameters and APOC3 and APOA4 genotypes in a healthy population are independent of dietary cholesterol intake. *Atherosclerosis* 184 (1), 113–120.
- Headey, D., Hirvonen, K., and Hoddinott, J. (2018). Animal sourced foods and child stunting. *Am. J. Agric. Econ.* 100, 1302–1319. doi: 10.1093/ajae/aay053
- Hoddinott, J., Headey, D., and Dereje, M. (2015). Cows, missing milk markets, and nutrition in rural Ethiopia. *J. Dev. Stud.* 51, 958–975. doi: 10.1080/00220388.2015.1018903
- Iannotti, L. L., Lutter, C. K., Bunn, D. A., and Stewart, C. P. (2014). Eggs: the uncracked potential for improving maternal and young child nutrition among the world’s poor. *Nutr. Rev.* 72, 355–368. doi: 10.1111/nure.12107
- Iannotti, L. L., Lutter, C. K., Stewart, C. P., Gallegos Riofrio, C. A., Malo, C., Reinhart, G., et al. (2017). Eggs in early complementary feeding and child growth: A randomized controlled trial. *Pediatrics* 140, e20163459. doi: 10.1542/peds.2016-3459
- Iradukunda, F. (2020). Food taboos during pregnancy. *Health Care Women Int.* 41, 159–168. doi: 10.1080/07399332.2019.1574799
- Jo, S. Y., Lee, C. H., Kim, S. W., and Hwang, Y. H. (2019). A case of an infant diagnosed with cow’s milk allergy and concurrent meat allergy via immunoCAP ISAC®. *KMJ* 34, 72–77. doi: 10.7180/kmj.2019.34.1.72
- Julia, M. (2023) *Coop costs jump: Chicken feed 1 culprit behind rise in price of eggs* | TribLIVE.com [WWW Document]. Available at: <https://triblive.com/local/westmoreland/coop-costs-jump-chicken-feed-1-culprit-behind-rise-in-price-of-eggs/>.
- Júlia Pié Orpí, M. V. (2020). *Limitations of egg production in Sub-Saharan Africa* (Veterinaria Digital: All about veterinary medicine and animal production).
- Kariuki, L. W., Lambert, C., Purwestri, R. C., Maundu, P., and Biesalski, H. K. (2017). Role of food taboos in energy, macro and micronutrient intake of pregnant women in western Kenya. *NFS* 47, 795–807. doi: 10.1108/NFS-09-2016-0146
- Kase, B. E., Frongillo, E. A., Isanovic, S., Gonzalez, W., Wodajo, H. Y., and Djimeu, E. W. (2022). Determinants of egg consumption by infants and young children in Ethiopia. *Public Health Nutr.* 25, 3121–3130. doi: 10.1017/S1368980022001112
- Kinsley, N. (2021) *Feed costs and floods threaten Ghana’s poultry industry* [WWW Document]. All About Feed. Available at: <https://www.allaboutfeed.net/market/market-trends/feed-costs-and-floods-threaten-Ghanas-poultry-industry/>.
- Kralik, I., Zelic, A., Kristic, J., Milkovic, S. J., and Crncan, A. (2020). Factors affecting egg consumption in young consumers. *Acta Fytotechnica Zootechnica* 23, 1–6. doi: 10.15414/afz.2020.23.mi-fpap.1-6
- Krittanawong, C., Narasimhan, B., Wang, Z., Virk, H. U. H., Farrell, A. M., Zhang, H., et al. (2021). Association between egg consumption and risk of cardiovascular outcomes: A systematic review and meta-analysis. *Am. J. Med.* 134, 76–83.e2. doi: 10.1016/j.amjmed.2020.05.046



- Lee, A. J., Thalayasingam, M., and Lee, B. W. (2013). Food allergy in Asia: how does it compare? *Asia Pacif. Allergy* 3, 3. doi: 10.5415/apallergy.2013.3.1.3
- Lemos, B. S., Medina-Vera, I., Blesso, C. N., and Fernandez, M. L. (2018). Intake of 3 Eggs per Day When Compared to a Choline Bitartrate Supplement, Downregulates Cholesterol Synthesis without Changing the LDL/HDL Ratio. *Nutrients* 10, 258. doi: 10.3390/nu10020258
- Lesnierowski, G., and Stangierski, J. (2018). What's new in chicken egg research and technology for human health promotion? - A review *Trends Food Sci. Technol.* 71, 46–51. doi: 10.1016/j.tifs.2017.10.022
- Ihab, A., Rohana, A., Wan Manan, W., Wan, S. W., Zaliah, M., and Mohamed, R. A. (2014). The impact of animal source food (ASF) on the growth of malnourished children in Bachok, Kelantan: randomized controlled intervention trial. *J. Nutr. Food Sci.* 04. doi: 10.4172/2155-9600.1000321
- Li, M.-Y., Chen, J.-H., Chen, C., and Kang, Y.-N. (2020). Association between egg consumption and cholesterol concentration: A systematic review and meta-analysis of randomized controlled trials. *Nutrients* 12, 1995. doi: 10.3390/nu12071995
- Loh, W., and Tang, M. L. K. (2018). The epidemiology of food allergy in the global context. *Int. J. Environ. Res. Public Health* 15, 2043. doi: 10.3390/ijerph15092043
- Lunhui, H., Yanhong, S., Shaoshen, L., Huijing, B., Yunde, L., and Huiqiang, L. (2021). Component resolved diagnosis of egg yolk is an indispensable part of egg allergy. *Allergol. Immunopathol.* 49, 6–14. doi: 10.15586/aei.v49i2.31
- Lutter, C. K., Iannotti, L. L., and Stewart, C. P. (2018). The potential of a simple egg to improve maternal and child nutrition. *Matern. Child Nutr.* 14, e12678. doi: 10.1111/mcn.12678
- Madzime, J., Saina, H., and Ngorora, G. P. K. (2011). Market potential for Guinea fowl (*Numidia meleagris*) products. *Trop. Anim. Health Prod.* 43, 1509–1515. doi: 10.1007/s11250-011-9835-z
- McKune, S. L., Mechlowitz, K., and Miller, L. C. (2022). Dietary animal source food across the lifespan in LMIC. *Global Food Secur.* 35, 100656. doi: 10.1016/j.gfs.2022.100656
- McKune, S. L., Stark, H., Sapp, A. C., Yang, Y., Slanzi, C. M., Moore, E. V., et al. (2020). Behavior change, egg consumption, and child nutrition: A cluster randomized controlled trial. *Pediatrics* 146, e2020007930. doi: 10.1542/peds.2020-007930
- McNamara, K., and Wood, E. (2019). Food taboos, health beliefs, and gender: understanding household food choice and nutrition in rural Tajikistan. *J. Health Popul. Nutr.* 38, 17. doi: 10.1186/s41043-019-0170-8
- Meyer-Rochow, V. B. (2009). Food taboos: their origins and purposes. *J. Ethnobiol. Ethnomed.* 5, 18. doi: 10.1186/1746-4269-5-18
- Milajerdi, A., Tehrani, H., Haghighatdoost, F., Larijani, B., Surkan, P. J., and Azadbakht, L. (2018). Associations between higher egg consumption during pregnancy with lowered risks of high blood pressure and gestational diabetes mellitus. *Int. J. Vitamin Nutr. Res.* 88, 166–175. doi: 10.1024/0300-9831/a000505
- Miranda, J., Anton, X., Redondo-Valbuena, C., Roca-Saavedra, P., Rodriguez, J., Lamas, A., et al. (2015). Egg and egg-derived foods: effects on human health and use as functional foods. *Nutrients* 7, 706–729. doi: 10.3390/nu7010706
- Morou, Z., Vassilopoulou, E., Galanis, P., Tatsioni, A., Papadopoulos, N. G., and Dimoliatis, I. D. K. (2021). Investigation of quality of life determinants in children with food allergies. *Int. Arch. Allergy Immunol.* 182, 1058–1065. doi: 10.1159/000516875
- Morris, S. S., Beesabathuni, K., and Headey, D. (2018). An egg for everyone: Pathways to universal access to one of nature's most nutritious foods. *Matern. Child Nutr.* 14, e12679. doi: 10.1111/mcn.12679
- Myers, M., and Ruxton, C. H. S. (2023). Eggs: healthy or risky? A review of evidence from high quality studies on hen's eggs. *Nutrients* 15, 2657. doi: 10.3390/nu15122657
- Nahata, P. (2022) *The Chicken And Egg Challenge: Feed Prices Add to India's Inflation, Income Worries* [WWW Document]. Available at: <https://www.bqprime.com/economy-finance/the-chicken-and-egg-dilemma-feed-prices-add-to-indias-inflation-income-worries>.
- Nakamura, Y., Iso, H., Kita, Y., Ueshima, H., Okada, K., Konishi, M., et al. (2006). Egg consumption, serum total cholesterol concentrations and coronary heart disease incidence: Japan Public Health Center-based prospective study. *Br. J. Nutr.* 96, 921–928. doi: 10.1017/BJN20061937
- Narro, C., Tiongco, M., and Costales, A. (2007). "Global poultry sector trends and external drivers of structural change," in *Poultry in the 21st Century. Avian Influenza and Beyond* (Bangkok, Thailand: Food and Agriculture Organization of The United Nations (Fao)).
- Natoli, S., Markovic, T., Lim, D., Noakes, M., and Kostner, K. (2007). Unscrambling the research: Eggs, serum cholesterol and coronary heart disease. *Nutr. Dietetics* 64, 105–111. doi: 10.1111/j.1747-0080.2007.00093.x
- Natsume, O., Kabashima, S., Nakazato, J., Yamamoto-Hanada, K., Narita, M., Kondo, M., et al. (2017). Two-step egg introduction for prevention of egg allergy in high-risk infants with eczema (PETIT): a randomised, double-blind, placebo-controlled trial. *Lancet* 389, 276–286. doi: 10.1016/S0140-6736(16)31418-0
- Negash, D. (2022). Study on compound animal feed demand and animal products, supply, price and marketing in Ethiopia. *BJSTR* 41, 32808–32817. doi: 10.26717/BJSTR.2022.41.006619
- Neumann, C. G., Murphy, S. P., Gewa, C., Grillenberger, M., and Bwibo, N. O. (2007). Meat supplementation improves growth, cognitive, and behavioral outcomes in Kenyan children. *J. Nutr.* 137, 1119–1123. doi: 10.1093/jn/137.4.1119
- Nguyen, P. H., Avula, R., Ruel, M. T., Saha, K. K., Ali, D., Tran, L. M., et al. (2013). Maternal and child dietary diversity are associated in Bangladesh, Vietnam, and Ethiopia. *Am. J. Nutr.* 143, 1176–1183. doi: 10.3945/jn.112.172247
- Nishino, M., Yanagida, N., Sato, S., Nagakura, K., Takahashi, K., Ogura, K., et al. (2022). Risk factors for failing a repeat oral food challenge in preschool children with hen's egg allergy. *Pediatr. Allergy Immunol.* 33, e13895. doi: 10.1111/pai.13895
- Omer, A., Hailu, D., and Whiting, S. J. (2022). Effect of a child-owned poultry intervention providing eggs on nutrition status and motor skills of young children in Southern Ethiopia: A cluster randomized and controlled community trial. *IJERPH* 19, 15305. doi: 10.3390/ijerph192215305
- Onuorah, C. E., and Ayo, J. A. (2003). Food taboos and their nutritional implications on developing nations like Nigeria – a review. *Nutr. Food Sci.* 33, 235–240. doi: 10.1108/00346650310499767
- Papanikolaou, Y., and Fulgoni, V. (2018). Egg consumption in infants is associated with longer recumbent length and greater intake of several nutrients essential in growth and development. *Nutrients* 10, 719. doi: 10.3390/nu10060719
- Patterson, K., Bhagwat, S., Williams, J., Howe, J., and Holden, J. (2007). *USDA Database for the Choline Content of Common Foods, Release Two*. (Beltsville, Maryland).
- Pearce, K. L., Clifton, P. M., and Noakes, M. (2011). Egg consumption as part of an energy-restricted high-protein diet improves blood lipid and blood glucose profiles in individuals with type 2 diabetes. *Br. J. Nutr.* 105, 584–592. doi: 10.1017/S0007114510003983
- Polansek, T., and de la Hamaide, S. (2022) *Bird flu, Ukraine war push egg prices higher worldwide* | Reuters [WWW Document]. Available at: <https://www.reuters.com/world/bird-flu-ukraine-war-push-egg-prices-higher-worldwide-2022-04-14/>.
- Poultry World (2022). Nigerian poultry farmers suffer due to high feed costs. *Poult. World*.
- Qin, C., Lv, J., Guo, Y., Bian, Z., Si, J., Yang, L., et al. (2018). Associations of egg consumption with cardiovascular disease in a cohort study of 0.5 million Chinese adults. *Heart* 104, 1756–1763. doi: 10.1136/heartjnl-2017-312651
- Rao, P. R., Norton, H. W., and Johnson, B. C. (1964). The amino acid composition and nutritive value of proteins: V. amino acid requirements as a pattern for protein evaluation. *J. Nutr.* 82 (1), 88–92.
- Rawlins, R., Pimkina, S., Barrett, C. B., Pedersen, S., and Wydick, B. (2014). Got milk? The impact of Heifer International's livestock donation programs in Rwanda on nutritional outcomes. *Food Policy* 44, 202–213. doi: 10.1016/j.foodpol.2013.12.003
- Réault-Godbert, S., Guyot, N., and Nys, Y. (2019). The golden egg: nutritional value, bioactivities, and emerging benefits for human health. *Nutrients* 11, 684. doi: 10.3390/nu11030684
- Robb, L., Joubert, G., Jordaan, E. M., Ngounda, J., and Walsh, C. M. (2021). Choline intake and associations with egg and dairy consumption among pregnant women attending a high-risk antenatal clinic in South Africa: the NuEMI study. *BMC Pregnancy Childbirth* 21, 833. doi: 10.1186/s12884-021-04314-2
- Rong, Y., Chen, L., Zhu, T., Song, Y., Yu, M., Shan, Z., et al. (2013). Egg consumption and risk of coronary heart disease and stroke: dose-response meta-analysis of prospective cohort studies. *BMJ* 346, e8539. doi: 10.1136/bmj.e8539
- Rouhani, M. H., Rashidi-Pourfard, N., Salehi-Abargouei, A., Karimi, M., and Haghighatdoost, F. (2018). Effects of egg consumption on blood lipids: A systematic review and meta-analysis of randomized clinical trials. *J. Am. Coll. Nutr.* 37, 99–110. doi: 10.1080/07315724.2017.1366878
- Samady, W., Warren, C., Wang, J., Das, R., and Gupta, R. (2020). Egg allergy in US children. *J. Allergy Clin. Immunol. Pract.* 8, 3066–3073.e6. doi: 10.1016/j.jaip.2020.04.058
- Sanlier, N., and Üstün, D. (2021). Egg consumption and health effects: A narrative review. *J. Food Sci.* 86, 4250–4261. doi: 10.1111/1750-3841.15892
- Schnefke, C. H., Lutter, C. K., Thuita, F., Webale, A., Flax, V. L., and Bentley, M. E. (2019). Is it possible to promote egg consumption during pregnancy? Findings from a study on knowledge, perceptions, and practices in Kenya. *Food Nutr. Bull.* 40, 151–170. doi: 10.1177/0379572119839516
- Shin, J. Y., Xun, P., Nakamura, Y., and He, K. (2013). Egg consumption in relation to risk of cardiovascular disease and diabetes: a systematic review and meta-analysis. *Am. J. Clin. Nutr.* 98, 146–159. doi: 10.3945/ajcn.112.051318
- Sibbald, C. A., Nicholas, J. L., Chapnick, M., Ross, N., Gandor, P. L., Waters, W. F., et al. (2021). Fetal brain ultrasound measures and maternal nutrition: A feasibility study in Ecuador. *Am. J. Hum. Biol.* 33. doi: 10.1002/ajhb.23467
- Smith, A., and Gray, J. (2016). Considering the benefits of egg consumption for older people at risk of sarcopenia. *Br. J. Community Nurs.* 21, 305–309. doi: 10.12968/bjcn.2016.21.6.305
- Snibbe, K. (2021) *Here's a look at egg production in the U.S. and other egg facts – Orange County Register* [WWW Document]. Available at: <https://www.ocregister.com/2021/04/02/heres-a-look-at-egg-production-in-the-u-s-and-other-egg-facts/>.
- Stark, H., Omer, A., Wereme N'Diaye, A., Sapp, A. C., Moore, E. V., and McKune, S. L. (2021). The *Un Oeuf* study: Design, methods and baseline data from a cluster randomised controlled trial to increase child egg consumption in Burkina Faso. *Matern. Child Nutr.* 17. doi: 10.1111/mcn.13069
- Stevens, G. A., Finucane, M. M., De-Regil, L. M., Paciorek, C. J., Flaxman, S. R., Branca, F., et al. (2013). Global, regional, and national trends in haemoglobin concentration and prevalence of total and severe anaemia in children and pregnant and non-pregnant women

- for 1995–2011: a systematic analysis of population-representative data. *Lancet Global Health* 1, e16–e25. doi: 10.1016/S2214-109X(13)70001-9
- Stewart, M. E. (2018). *The Effects of Consuming Eggs on the Physical and Cognitive Development of Food-Insecure Haitian Children* (Fayetteville: University of Arkansas).
- Stewart, C. P., Caswell, B., Iannotti, L., Lutter, C., Arnold, C. D., Chipatala, R., et al. (2019). The effect of eggs on early child growth in rural Malawi: the Mazira Project randomized controlled trial. *Am. J. Clin. Nutr.* 110, 1026–1033. doi: 10.1093/ajcn/nqz163
- Swann, S. (2023). *The cost of eggs has increased significantly, but social media posts exaggerate the price jump* (Poynter).
- Tamez, M., Virtanen, J. K., and Lajous, M. (2016). Egg consumption and risk of incident type 2 diabetes: a dose–response meta-analysis of prospective cohort studies. *Br. J. Nutr.* 115, 2212–2218. doi: 10.1017/S000711451600146X
- TBS News (2023) *Farmers for fixing “fair prices” of broiler, eggs | The Business Standard [WWW Document]*. Available at: <https://www.tbsnews.net/economy/bazaar/farmers-seek-govt-intervention-fix-chicken-eggs-prices-594714>.
- Tibabuya, B. A., Ganle, J. K., and Ibrahim, M. (2019). Anaemia at antenatal care initiation and associated factors among pregnant women in West Gonja District, Ghana: a cross-sectional study. *Pan. Afr. Med. J.* 33. doi: 10.11604/pamj.2019.33.325.17924
- Tribune (2021). *CCP takes note of rising poultry prices [WWW Document]*. Available at: <https://tribune.com.pk/story/2298880/competition-commission-of-Pakistan-takes-note-of-rising-poultry-prices>.
- Tsegaye, D., Tamiru, D., and Belachew, T. (2021). Food-related taboos and misconceptions during pregnancy among rural communities of Illu Aba Bor zone, Southwest Ethiopia. A community based qualitative cross-sectional study. *BMC Pregnancy Childbirth* 21, 309. doi: 10.1186/s12884-021-03778-6
- Umanath, M., Paramasivam, R., Kavitha, V., and Durai, T. T. (2016). Determinants of purchase probability and consumption of egg: an evidence from Indian households. *Int. Res. J. Agric. Econ. Stat* 7, 110–115. doi: 10.15740/HAS/IRJAES/7.1/110-115
- Van Der Merwe, L. F., Moore, S. E., Fulford, A. J., Halliday, K. E., Drammeh, S., Young, S., et al. (2013). Long-chain PUFA supplementation in rural African infants: a randomized controlled trial of effects on gut integrity, growth, and cognitive development. *Am. J. Clin. Nutr.* 97, 45–57. doi: 10.3945/ajcn.112.042267
- Veena, S. R., Krishnaveni, G. V., Wills, A. K., Kurpad, A. V., Muthayya, S., Hill, J. C., et al. (2010). Association of birthweight and head circumference at birth to cognitive performance in 9- to 10-year-old children in South India: prospective birth cohort study. *Pediatr. Res.* 67, 424–429. doi: 10.1203/PDR.0b013e3181d00b45
- Vincent, G. (2023). *African egg production, consumption needs a new approach [WWW Document]* (WATTPoultry.com). Available at: <https://www.wattagnet.com/egg/egg-production/article/15537132/african-egg-production-consumption-needs-a-new-approach>.
- Wallace, T., and Fulgoni, V. (2017). Usual choline intakes are associated with egg and protein food consumption in the United States. *Nutrients* 9, 839. doi: 10.3390/nu9080839
- Wallin, A., Forouhi, N. G., Wolk, A., and Larsson, S. C. (2016). Egg consumption and risk of type 2 diabetes: a prospective study and dose–response meta-analysis. *Diabetologia* 59, 1204–1213. doi: 10.1007/s00125-016-3923-6
- Washington, N. (2015) *Eat This, Not That: Taboos and Pregnancy [WWW Document]*. *Culture*. Available at: <https://www.nationalgeographic.com/culture/article/eat-this-not-that-taboos-and-pregnancy>.
- Waswa, L. M., Jordan, I., Herrmann, J., Krawinkel, M. B., and Keding, G. B. (2015). Community-based educational intervention improved the diversity of complementary diets in western Kenya: results from a randomized controlled trial. *Public Health Nutr.* 18, 3406–3419. doi: 10.1017/S1368980015000920
- Waters, W. F., Gallegos, C. A., Karp, C., Lutter, C., Stewart, C., and Iannotti, L. (2018). Cracking the egg potential: traditional knowledge, attitudes, and practices in a food-based nutrition intervention in Highland Ecuador. *Food Nutr. Bull.* 39, 206–218. doi: 10.1177/0379572118763182
- Wei-Liang Tan, J., Valerio, C., Barnes, E. H., Turner, P. J., Van Asperen, P. A., Kakakios, A. M., et al. (2017). A randomized trial of egg introduction from 4 months of age in infants at risk for egg allergy. *J. Allergy Clin. Immunol.* 139, 1621–1628.e8. doi: 10.1016/j.jaci.2016.08.035
- WHO (2014). World health assembly global nutrition targets 2025: stunting policy brief.
- Wong, J. T., De Bruyn, J., Bagnol, B., Grieve, H., Li, M., Pym, R., et al. (2017). Small-scale poultry and food security in resource-poor settings: A review. *Global Food Secur.* 15, 43–52. doi: 10.1016/j.gfs.2017.04.003
- Wongnaa, C. A., Mbroh, J., Mabe, F. N., Abokyi, E., Debrah, R., Dzaka, E., et al. (2023). Profitability and choice of commercially prepared feed and farmers' own prepared feed among poultry producers in Ghana. *J. Agric. Food Res.* 12, 100611. doi: 10.1016/j.jafr.2023.100611
- Woo, H. W., Choi, B. Y., and Kim, M. K. (2016). Cross-sectional and longitudinal associations between egg consumption and metabolic syndrome in adults  $\geq 40$  years old: the yangpyeong cohort of the Korean genome and epidemiology study (KoGES\_Yangpyeong). *PLoS One* 11, e0147729. doi: 10.1371/journal.pone.0147729
- Wright, C. M., and Emond, A. (2015). Head growth and neurocognitive outcomes. *Pediatrics* 135, e1393–e1398. doi: 10.1542/peds.2014-3172
- Xepapadaki, P., Fiocchi, A., Grabenhenrich, L., Roberts, G., Grimshaw, K. E. C., Fiander, A., et al. (2016). Incidence and natural history of hen's egg allergy in the first 2 years of life—the EuroPrevall birth cohort study. *Allergy* 71, 350–357. doi: 10.1111/all.12801
- Zerfu, T. A., Umeta, M., and Baye, K. (2016). Dietary habits, food taboos, and perceptions towards weight gain during pregnancy in Arsi, rural central Ethiopia: a qualitative cross-sectional study. *J. Health Popul. Nutr.* 35, 22. doi: 10.1186/s41043-016-0059-8
- Zhang, X., Lv, M., Luo, X., Estill, J., Wang, L., Ren, M., et al. (2020). Egg consumption and health outcomes: a global evidence mapping based on an overview of systematic reviews. *Ann. Transl. Med.* 8, 1343. doi: 10.21037/atm-20-4243
- Zhong, W. V., Van Horn, L., Cornelis, M. C., Wilkins, J. T., Ning, H., Carnethon, M. R., et al. (2019). Associations of dietary cholesterol or egg consumption with incident cardiovascular disease and mortality. *JAMA* 321, 1081–1095. doi: 10.1001/jama.2019.1572





## OPEN ACCESS

## EDITED BY

Jeff Wood,  
University of Bristol, United Kingdom

## REVIEWED BY

Mayra A. D. Saleh,  
University of the Azores, Portugal  
Lijun Chen,  
University of Florida, United States

## \*CORRESPONDENCE

Klaus G. Grunert  
✉ klg@mgmt.au.dk

RECEIVED 24 October 2023

ACCEPTED 12 December 2023

PUBLISHED 03 January 2024

## CITATION

Mulders MDGH, Grunert KG, Pedersen S,  
Brunso K and Zhou Y (2024) Pleasure, quality  
or status? an analysis of drivers of purchase of  
fresh pork in China.  
*Front. Anim. Sci.* 4:1327105.  
doi: 10.3389/fanim.2023.1327105

## COPYRIGHT

© 2024 Mulders, Grunert, Pedersen, Brunso  
and Zhou. This is an open-access article  
distributed under the terms of the [Creative  
Commons Attribution License \(CC BY\)](#). The  
use, distribution or reproduction in other  
forums is permitted, provided the original  
author(s) and the copyright owner(s) are  
credited and that the original publication in  
this journal is cited, in accordance with  
accepted academic practice. No use,  
distribution or reproduction is permitted  
which does not comply with these terms.

# Pleasure, quality or status? an analysis of drivers of purchase of fresh pork in China

Maartje D. G. H. Mulders<sup>1</sup>, Klaus G. Grunert<sup>1,2\*</sup>,  
Susanne Pedersen<sup>1</sup>, Karen Brunso<sup>1</sup> and Yanfeng Zhou<sup>3</sup>

<sup>1</sup>MAPP Centre, Department of Management, Aarhus University, Aarhus, Denmark, <sup>2</sup>School of Marketing and Communication, University of Vaasa, Vaasa, Finland, <sup>3</sup>Sun Yat-sen Business School, Sun Yat-sen University, Guangzhou, China

What are consumers aiming to get when they buy fresh meat? Is it the emotional pleasure, the nutritional quality and functionality, or the status that goes with it? We examine this question for Chinese consumers buying fresh pork. In order to understand the driving forces for pork purchases, we use the concept of perceived value of a product, and distinguish emotional value, quality/performance and social value, together with price/value for money. We look at how perceived value of pork products in China is related to consumers' attitude to these products and to their repeated purchase of these products. In addition, we look at how value perception and its role in determining attitude and purchase behavior differ between different consumer segments, distinguished based on their shopping behavior. An online survey was carried out in 5 Chinese 1st and 2nd tier cities. Respondents were segmented based on their usage of different ways of shopping for pork using latent class cluster analysis. Relationships between constructs were estimated using PLS. Quality/functional value was the strongest determinant of attitude, but emotional value was both the strongest direct determinant of purchase behavioral and the strongest determinant overall when taking effects mediated by attitude into account. Customer journey segments differed in their pattern of determinants of attitudinal and behavioral loyalty. We conclude that buying fresh meat is, for Chinese consumers, mostly driven by the expected pleasure and to a lesser degree by quality and functional properties like safety and healthiness. The latter do have an impact on consumers' attitude to the product, but less so on their buying behavior, suggesting that attitude and purchase are driven by different mental processes. We discuss implications for future demand for fresh pork in China.

## KEYWORDS

fresh pork, China, customer perceived value, loyalty, segmentation, customer journey

# 1 Introduction

What are consumers aiming to get when they buy fresh meat? It is a widely accepted tenet in marketing that if a customer does not perceive value in a market offering, the customer is not likely to buy (Day and Wensley, 1988; Woodruff, 1997). As the concept of *value* has many meanings both in science and in everyday language (Loebler and Wloka, 2019), considerable effort has been made in exploring the concept of customer perceived value, from the simple notion that value is the perceived balance between what you get and what you have to give, to multi-dimensional conceptualizations of customer value, where different aspects of the gain component are distinguished (for example functional, emotional and social gains, see Zeithaml et al. (2020), for an overview). When customer perceived value becomes a multi-dimensional concept, the importance of the various dimensions for creating customer loyalty can differ, and these differences may be dependent on characteristics of both the market offering and the customer, a notion that has been amply supported by research (Swait and Sweeney, 2000; Leroi-Werelds et al., 2014). This also goes for value perception of fresh meat.

When consumers consistently perceive high value in a product, they may become loyal customers, buying the product again and again and praising it when talking to others. Loyalty as well is not unidimensional. It is common to distinguish between attitudinal and behavioral loyalty, and it has been shown that these two components do not always align (Dick and Basu, 1994). With both customer value and loyalty being multidimensional concepts, what if the way dimensions of customer value affect customer loyalty is different for attitudinal and behavioral loyalty? This question has received only scant attention in the literature, even though it is of obvious importance for practice. Purchases – the manifestation of behavioral loyalty – are the ultimate aim of all sellers, but without underlying attitudinal loyalty even repeated purchases may be unstable and easily influenced by, for example, competitor activities. When different dimensions of customer value affect attitudinal and behavioral loyalty, how can a seller ensure a strong positive attitude that also will translate into strong behavioral loyalty?

With multiple channels for sales, delivery and communication proliferating in the meat industry, the way customers perceive value can be linked to the multiples ways in which the customer can come into contact with the product and the brand over time. Every occasion in which the customer has such contact – for example, when seeing advertising, having the product discussed in social media, seeing it in the store – can be defined as a touchpoint between the customer and the product, and the sequence of touchpoints that the customer experiences over time is dubbed the customer journey. The concept of customer journey segments has been proposed in order to capture differences in customers' use of these different touchpoints (Herhausen et al., 2019). Different touchpoints differ in their ability to convey information to the customer and in their ability to contribute to the value creation process, and will in many cases attract different types of customers. We therefore argue that the way in which dimensions of customer value perception are linked to attitudinal and behavior loyalty will differ between customer journey segments.

In the following, we present a study on how dimensions of customer perceived value for fresh pork meat are linked to attitudinal and behavior loyalty for different customer journey segments in China. Fresh pork in China is an interesting case for several reasons. The market for fresh pork in China is a good example of multi-channel marketing, with a multitude of brands being available across a range of channels ranging from brick-and-mortar stores via online channels to wet markets. Pork is a highly competitive market in China, with many brands competing for consumer demand, and is a frequently bought staple, which is interesting from the customer journey point of view. Most existing research on customer journeys is on services or durable products, where a journey across several touchpoints can be categorized into a pre-purchase, purchase and post-purchase phase (Lemon and Verhoef, 2016). This perspective is not applicable in relation to fast moving consumer goods like pork, where consumers are in almost continuous contact with a variety of touchpoints and where the customer journey becomes an ongoing process with single purchases being just elements in this process. Pork in China is a fast moving consumer good, but is still (in contrast to the situation in Europe or the USA) heavily, such that the consumer can get into contact with the brand on multiple occasions, for example in advertising and on social media. While mapping individual consumer journeys for a fast-moving consumer good like pork is difficult, the concept of customer journey segments, defined based on the patterns of channel usage, is a promising way of making the customer journey concept usable for such a product.

Our contribution to the literature is twofold. First, we add to the literature on attitudinal and behavioral loyalty by showing that discrepancies between the two can be attributed to attitudinal and behavioral loyalty being affected by different components of customer perceived value. Third, we show how the concept of customer journey segments can be related to loyalty formation by invoking the customer value construct, responding to the Marketing Science Institute's (2018) call for more research on sources of loyalty during the customer journey.

## 2 Conceptual development

### 2.1 Customer value

In a widely cited paper, Zeithaml (1988) defined customer perceived value (CPV) as the balance between the perceived gains and the perceived sacrifice linked to a market offering, a notion that has become widely adopted. The concept of customer perceived value has since been recognized as a cornerstone in understanding consumer behavior. The two-dimensional view of CPV has been developed into a multi-dimensional view, mostly based on distinguishing different types of gains. Sweeney and Soutar (2001), building on earlier work from Sheth et al. (1991), proposed a four-dimensional conceptualization of CPV, distinguishing the components emotional value, social value, quality/performance value and price/value for money. This conceptualization and the scale that has been developed for measuring it has been widely adopted in subsequent studies on

CPV (Wang et al., 2004; Smith and Colgate, 2007; Papista and Krystallis, 2013; Hernandez-Ortega et al., 2017; Fazal-E-Hasan et al., 2018), although other multi-dimensional approaches have appeared in the literature (see Zeithaml et al. (2020), for an overview).

In our study, we adopt the concept of CPV of Sweeney and Soutar (2001) and investigate how the four dimensions of emotional value, social value, quality/performance value and price/value for money affect both attitudinal and behavioral customer loyalty to fresh pork brands. Important to note is that we validated that these four dimensions covered the main aspects of value perception for consumers in a Chinese context by conducting two preparatory focus groups. For example, one participant in these focus groups stated that one of the pork brands they knew was *Economical, cost-effective, high-class meat quality, it is clean and makes you feel assured*.

## 2.2 Attitudinal and behavioral loyalty

It seems intuitive that customer perceived value and customer loyalty should be related, although research has shown that this relationship is actually complex (Leroi-Werelds et al., 2014). For example, Floh et al. (2014) found that different dimensions of CPV are drivers of repurchase intention for different types of customers. In analyzing this relationship, it is important to address the distinction between attitudinal and behavioral loyalty. It has long been argued that loyalty as measured by repeated purchases may be based on 'inertia' rather than on a conviction of brand superiority (Assael, 1984). Dick and Basu (1994), in a widely cited contribution, have therefore argued that loyalty has two components, relative attitude and repeat patronage, and that these two need not be aligned. When they are not aligned, there can be cases of 'latent loyalty' (when attitude is positive but does not translate into repeat patronage) or of 'spurious loyalty' (when repeat purchases occur without being based on positive attitude). The existence of such cases of non-alignment has been demonstrated also for the grocery sector (Møller Jensen, 2011; Ngobo, 2017). Potential discrepancies between relative attitude and repeat patronage can be analyzed as a special case of the attitude-behavior gap (Boulstridge and Carrigan, 2000; Carrigan and Attalla, 2001; Sheeran, 2002; Auger et al., 2007; Papaioikonomou et al., 2011). This attitude-behavior gap has been clearly documented also with regard to food-related behaviors (for example for purchasing organic food, (Shepherd et al., 2005); environmentally friendly products (Moraes et al., 2012); or fair-trade foods (Chatzidakis et al., 2007). A number of reasons for this gap have been discussed in the literature, including the role of social norms (Fishbein and Ajzen, 1975), a lack of control over the behavior (Ajzen, 2002), the advent of unforeseen circumstances, or a lack of attitude activation at the time of the behavior, especially when the attitude is weakly grounded in a belief structure (Fazio et al., 1989).

We would like to argue that an additional possible reason for discrepancies between attitudinal and behavioral loyalty is that they are affected by different dimensions of customer perceived value. There is some patchy existing evidence to support this notion. Pura (2005), in a study on mobile services, found support for her

hypotheses that different dimensions of CPV affect commitment and behavior intentions, although her hypotheses were specific to the service investigated. Also, there was no attempt at generalizations regarding which CPV dimensions would generally have more impact on the one or the other. Wang et al. (2004), studying an unspecified service, looked at how CPV dimensions related to, among other constructs, behavioral intentions and felt loyalty, and found that not all effects of CPV dimensions on behavioral intentions were completely mediated by felt loyalty.

Differential effects of CPV dimensions on attitudinal and behavioral loyalty may be related to attitude functions. Attitudes cannot only guide behavior but can also help define one's identity (Maio and Olson, 1999; Briñol et al., 2019). If a consumer defines him/herself as quality conscious and thrifty, the quality/performance and price/value for money dimensions of CPV may have most influence on that consumer's attitudinal loyalty, because it provides consistency with that person's self-perception. Still, the emotional and social dimensions of CPV may have an impact on that person's behavioral loyalty, based on the emotional and social gratification that these dimensions of CPV bring about.

## 2.3 Customer journey segments

Consumer decision-making and purchasing often occurs in a multi-channel setting, where consumers travel between different touchpoints where they encounter the products that they decide between. The sequence of these interactions is often called 'the customer journey' in the marketing literature (Lemon and Verhoef, 2016). For frequently bought consumer products like fresh pork, the customer journey will be expressed by the pattern of usage of different sales channels and other touchpoints where the consumer meets the competing brand across an ongoing sequence of purchases (Ieva and Ziliani, 2018). Consumers will differ in touchpoint usage during the customer journey, and these differences can be captured by distinguishing customer journey segments. Herhausen et al. (2019) showed that drivers of loyalty differed between customer journey segments, which they identified across a range of different product categories, though not including groceries, which they argued are still too much dominated by offline selling. We extend this research into the grocery sector in a market, China, where multi-channel selling of groceries is widespread, and provide additional insights by linking drivers of loyalty to the customer perceived value construct. For example, it could be the case that price/value for money is more important for those who shop more via online supermarkets vs. regular supermarkets, and that for those who shop in high-end supermarkets more than regular supermarkets quality and social recognition is more important.

## 2.4 Research context

Fresh pork in China is distributed through different sales channels, of which different variations of brick-and-mortar supermarkets and online retail stores are the most important,

and in addition is heavily branded, allowing consumers to identify competing products across different channels and touchpoints. The Chinese food retailing system has changed quite drastically and rapidly during the past decades (Veeck and Veeck, 2000; Si et al., 2016). While the traditional wet markets still have a large share of fresh food retailing, other channels such as super- and hypermarkets are now dominant channels for purchasing fresh food (Veeck and Veeck, 2000; Si et al., 2016). Moreover, online purchasing channels have proliferated greatly in the last years and provide consumers with easy means of purchasing food and having it delivered to their doorsteps quickly (Maimaiti et al., 2018).

## 2.5 Hypotheses and conceptual model

This study aims to gain an understanding of how different dimensions of customer perceived value of pork affect attitudinal and behavioral loyalty for different customer journey segments. Overall, we hypothesize that:

- H1: The four dimensions of customer perceived value – emotional value, social value, quality/performance value and price/value for money – affect attitudinal loyalty.
- H2: The four dimensions of customer perceived value affect behavioral loyalty both directly and indirectly via attitudinal loyalty.
- H3: The pattern of direct influence of the four dimensions of perceived value on attitudinal loyalty differs from the pattern of direct influence of the four dimensions of perceived value on behavioral loyalty.
- H4: Different customer journey segments differ in the relationship between customer perceived value, attitudinal loyalty and behavioral loyalty.

See Figure 1 for a graphical presentation of our conceptual model.

## 3 Materials and methods

### 3.1 Sample

Data were collected by means of an online survey with consumers in the 1<sup>st</sup> tier cities Guangzhou, Shanghai, Shenzhen, and the 2<sup>nd</sup> tier cities Hangzhou and Nanjing,  $n = 400$  per city, resulting in a total sample size of 2000. Respondents were recruited through a major commercial consumer panel provider. Respondents were included if they were at least partly responsible for food shopping in the household and if they had bought pork at least once during the last month. Limiting the sampling to 1<sup>st</sup> and 2<sup>nd</sup> tier cities is meaningful as this is where purchasing power is concentrated, and this is where multiple channels in the distribution of pork are most clearly visible.

### 3.2 Measures

Brand awareness for eleven major brands of fresh pork in China was measured by asking the participants which of these 11 pork brands they had seen previously. This was used as a filter for measuring customer perceived value, attitudinal loyalty and behavior loyalty. Buying frequency for each of these brands was measured by asking participants how frequently they bought any of these brands in their last 10 purchases of pork meat. Out of all the brands that participants were familiar with, participants were asked questions about customer perceived value, attitudinal and behavioral loyalty for two randomly selected brands.

*Customer perceived value* was measured for the four dimensions: quality/performance, price/value for money, emotional value and social value with items adapted from Sweeney and Soutar (2001), e.g., *brand X has consistent quality* or *brand X offers value for money* rated on a 1-7 Likert scale ('strongly disagree' – 'strongly agree'). The items and their loadings can be seen in Table 1.

*Attitudinal loyalty* was measured with four items, e.g., *Purchasing meat from brand X is ...* where participants could rate the answers on a 1-7 scale ranging from e.g., harmful (1) to beneficial (7); see Table 1.

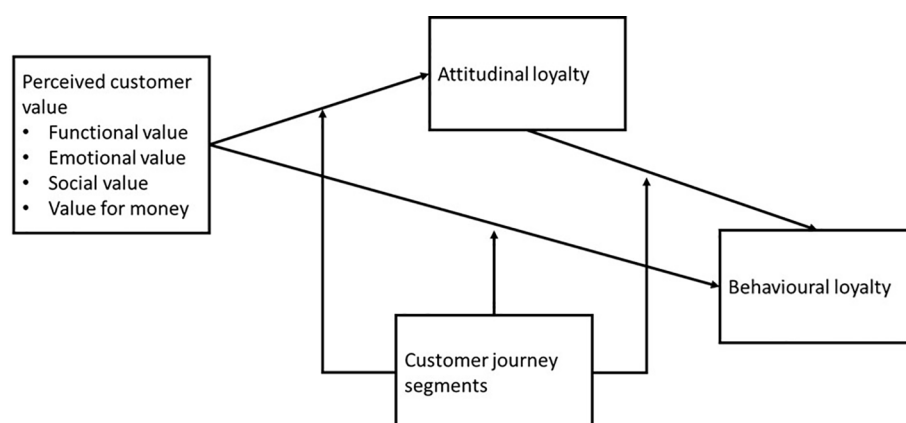


FIGURE 1  
Conceptual approach.

TABLE 1 Measurement model for PLS analysis (n=4000).

Constructs/Items	M	SD	Loadings
<b>Customer Perceived Value: Quality/performance</b>			
X has consistent quality	5.74	1.10	.82
X is trustworthy	5.74	1.10	.81
X is good quality	5.69	1.09	.81
X is safe	5.78	1.10	.82
X is healthy	5.72	1.11	.82
<b>Customer Perceived Value: Price/value for money</b>			
X is reasonably priced	5.51	1.16	.83
X is value for money	5.59	1.13	.81
X is a good product for the price	5.46	1.20	.84
X is economical	5.48	1.20	.84
<b>Customer Perceived Value: Emotional value</b>			
I will enjoy eating X	5.63	1.15	.80
I will feel relaxed about eating X	5.54	1.18	.82
X will make me feel good	5.53	1.16	.83
X will give me pleasure	5.39	1.26	.81
<b>Customer Perceived Value: Social value</b>			
X will help me to feel acceptable	5.19	1.40	.87
X will improve the way I am perceived	5.10	1.43	.88
X will make a good impression other people	5.22	1.37	.87
X will give me social approval	5.19	1.37	.86
<b>Attitudinal loyalty</b>			
Purchasing meat from brand X is ... (foolish-wise)	5.56	1.13	.69
Purchasing meat from brand X is ... (bad-good)	4.71	1.64	.79
Purchasing meat from brand X is ... (harmful-beneficial)	5.52	1.12	.73
Purchasing meat from brand X is ... (punishing-rewarding)	4.56	1.75	.82
<b>Behavioral loyalty: Future purchase intention</b>			
In the future, X will be the brand that I buy most often	5.42	1.16	

n=4000, as each participant answered each question for two randomly selected known brands. The measurement model for the segment-specific subgroups is available from the authors upon request.

In this study, we measured *behavioral loyalty* in two different ways: First, we measured future purchase intention. This was measured with the question *In the future, when I buy pork, brand X will be the brand I buy most often* on a 1-7 scale ('not at all likely' – 'very likely'). Secondly, we measured whether respondents had one particular brand that they bought more often than any other brand during their last 10 pork purchases. We coded this as follows: If one brand was chosen more frequently than all other brands, then this

was listed as the respondent's favorite (e.g., a brand was coded as a consumer's 'favorite brand' if it was bought most frequently, for example 6 times out of the last 10, whereas the remaining 4 choices were made for several other different brands). However, if several brands were chosen equally frequently (e.g., multiple brands being chosen twice in the last 10 purchases, yet none being chosen more than twice), then this respondent was classified as having 'no favorite'.

*Channel usage patterns.* In relation to channel use, consumers were asked to think of the last ten times that they purchased pork meat. For each of these purchases, respondents had to select from a list of common shopping channels where they had bought the pork: mainstream supermarkets, wet markets, convenience stores, high-end supermarkets, online stores, and imported-goods stores. The responses thus show how the last ten purchases were distributed across the different channels. We use these data to identify customer journey segments.

## 4 Results

Below, we will first elaborate on the sample composition and the reliability of our measures. This is followed by our segmentation analysis and the investigation of the effects of customer perceived value on attitudinal and behavioral loyalty.

### 4.1 Sample composition and reliability of measures

We collected data from 2000 participants. The sample consisted of 70% females, indicating that there are still more females than males doing the household shopping. All demographic characteristics of the sample can be seen in [Table 2](#).

We also computed Cronbach's  $\alpha$  for the measures for customer perceived value and attitudinal loyalty. For CPV we found that all four dimensions had good reliability (perceived quality= .87; value for money= .85; expected enjoyment= .83; social recognition= .89). Attitudinal loyalty (.75) also had good reliability.

### 4.2 Identification of customer journey segments

We identified segments according to differences in their channel usage. Most respondents reported buying pork at a mainstream supermarket (94%) at least 1 out of 10 purchases, but differed in the frequency with which they used other channels. Respondents were grouped according to their channel usage by performing a latent class analysis in LatentGold ([Vermunt and Magidson, 2013](#)). A four-cluster solution was adopted as a compromise between analysis of the information criteria AIC and BIC and interpretability.

A large segment of consumers buys most frequently at mainstream supermarkets, and does not use other channels very frequently, except for the wet markets. We termed this group the



TABLE 2 Sample characteristics.

Demographic profile	Total n (%)	Guangzhou n (%)	Shanghai n (%)	Shenzhen n (%)	Nanjing n (%)	Hangzhou n (%)
<i>Gender</i>						
Male	589 (29.5)	99 (24.8)	106 (26.5)	120 (30)	133 (33.25)	131 (32.8)
Female	1402 (70.1)	301 (75.3)	294 (73.5)	278 (69.5)	265 (66.25)	264 (66.0)
Not applicable/Prefer not to say	9 (.4)	0 (0)	0 (0)	2 (.5)	2 (.5)	5 (1.3)
<i>Age</i>						
18-24	69 (3.5)	26 (6.5)	10 (2.5)	17 (4.3)	9 (2.3)	7 (1.8)
25-34	677 (33.9)	193 (48.3)	194 (48.5)	130 (32.5)	97 (24.3)	63 (15.8)
35-40	254 (12.7)	83 (20.8)	75 (18.8)	42 (10.5)	33 (8.3)	21 (5.3)
41-44	749 (37.5)	84 (21.0)	96 (24.0)	185 (46.3)	180 (45.0)	204 (51.0)
45-54	210 (10.5)	14 (3.5)	16 (4.0)	25 (6.3)	136 (17.0)	87 (21.8)
55-64	37 (1.9)	0 (0)	8 (2.0)	1 (.3)	10 (2.5)	18 (4.5)
65 or more	4 (.2)	0 (0)	1 (.3)	0 (0)	3 (.8)	0 (0)
<i>Marital status</i>						
Married/Cohabiting	1745 (87.3)	346 (86.5)	352 (88.0)	349 (87.3)	351 (87.8)	347 (86.8)
Single	213 (10.7)	51 (12.8)	44 (11.0)	39 (9.8)	37 (9.3)	42 (10.5)
Divorced/Widowed	17 (.9)	2 (.5)	2 (.5)	3 (.8)	7 (1.8)	3 (.8)
Other	10 (.5)	0 (0)	1 (.3)	4 (1.0)	2 (.5)	3 (.8)
Do not wish to disclose	15 (.8)	1 (.25)	1 (.3)	5 (1.3)	3 (.8)	5 (1.3)
<i>Highest education level</i>						
Primary school or below	5 (.3)	1 (.3)	1 (.3)	1 (.25)	1 (.3)	1 (.3)
Junior high school	26 (1.3)	3 (.8)	1 (.3)	4 (1.0)	8 (2.0)	10 (2.5)
High school/Vocational school/Technical school	114 (5.7)	14 (3.5)	10 (2.5)	24 (6.0)	27 (6.8)	39 (9.8)
College	295 (14.8)	49 (12.3)	38 (9.5)	73 (18.3)	71 (17.8)	64 (16.0)
University	1349 (67.5)	288 (72.0)	296 (74.0)	262 (65.5)	255 (63.7)	248 (62.0)
Master or higher	210 (10.5)	45 (11.3)	54 (13.5)	35 (8.8)	38 (9.5)	38 (9.5)
Other	1 (.1)	0 (0)	0 (0)	1 (.25)	0 (0)	0 (0)
<i>Household size (including only adults over 18)</i>						
1 individual	115 (5.8)	18 (4.5)	16 (4.0)	23 (5.8)	30 (7.5)	28 (7.0)
2 individuals	909 (45.5)	193 (48.3)	210 (52.5)	173 (43.4)	171 (42.8)	164 (40.5)
3 individuals	574 (28.7)	98 (24.5)	112 (28.0)	116 (29.0)	125 (31.3)	123 (30.8)
4 individuals	304 (15.2)	66 (16.5)	50 (12.5)	66 (16.5)	56 (14.0)	66 (16.5)
5 individuals or more	98 (4.9)	25 (6.4)	12 (3.0)	22 (5.5)	18 (4.5)	21 (5.3)
<i>Children in the household</i>						
No children	410 (20.5)	64 (16.0)	77 (19.3)	74 (18.5)	87 (21.8)	108 (27.0)
One child	1240 (62.0)	257 (64.3)	259 (64.8)	228 (57.5)	251 (62.7)	245 (61.3)
Two children	294 (14.7)	65 (16.3)	62 (14.2)	82 (20.5)	53 (13.3)	37 (9.3)
Three children	47 (2.4)	11 (2.8)	5 (1.3)	15 (3.8)	7 (1.8)	9 (2.3)
Four children or more	9 (.5)	3 (.8)	2 (.5)	2 (.3)	4 (.5)	1 (.3)
<i>Self-described economic status of the household</i>						
Difficult	46 (2.3)	10 (2.5)	4 (1.0)	16 (4.0)	7 (1.8)	9 (2.3)
Modest	1110 (55.5)	216 (54.0)	212 (53.0)	217 (54.3)	217 (54.3)	248 (62.0)
Reasonable	769 (38.5)	160 (40.0)	166 (41.5)	155 (38.8)	161 (40.3)	127 (31.8)
Well off	75 (3.8)	14 (3.5)	36 (4.5)	12 (3.0)	15 (3.8)	16 (4.0)

‘mainstream buyers’, and they make up for 46% of our sample. The second segment was termed ‘online buyers’ as the people in this segment use online channels much more frequently than the other groups (16% of our respondents). Third, there is a consumer group who purchase using all channels, which we named ‘channel nomads’ (17% of our respondents). Finally, there is a group of consumers, who next to mainstream supermarkets buy most frequently in high-end supermarkets, convenience stores and imported goods stores, which are arguably more upscale channels than wet markets or online, and thus we termed this group the ‘high-end buyers’. This final cluster makes up 21% of our respondents (see Figure 2).

### 4.3 Effect of customer perceived value on attitudinal and behavioral loyalty

In order to analyze the effect of the four dimensions of CPV on attitudinal and behavioral loyalty, we performed a partial least squares structural equation model (PLS-SEM) analysis in SmartPLS 3 (Ringle et al., 2015). The structural model consisted of six correlated constructs (quality/performance, emotional value, social value, price/value for money, attitudinal loyalty, and behavioral loyalty). The convergent validity of our measurement model was acceptable (i.e., the average variance extracted, AVE, is larger than .5). as our AVEs ranged from .54-.75. Moreover, the

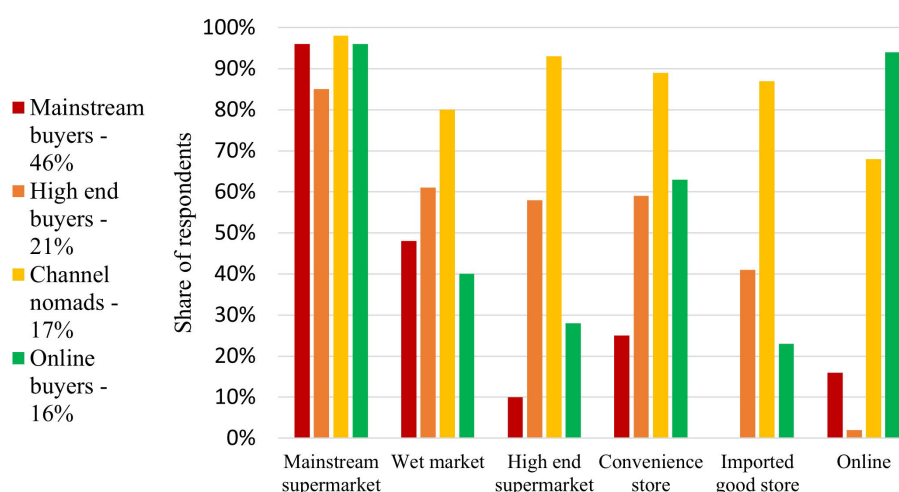


FIGURE 2  
Customer journey segments.

Cronbach's alphas, as reported previously, are all satisfactory, as are all values for Jöreskog's composite reliability ( $>0.82$ ). With regard to discriminant validity, the heterotrait-monotrait (HTMT) ratio of the correlations should be under 0.90 for conceptually similar constructs, which was the case in our study (ranging from 0.32 to 0.89). The complete measurement model can be seen in Table 1.

As PLS-SEM is a nonparametric method, bootstrapping is required to determine statistical significance of the path coefficients (Hair et al., 2019). In our study, we used a bootstrapping of 5000. The results of the model for the full sample can be found in Table 3.

When looking at the effect of dimensions of CPV on attitudinal and behavioral loyalty, we see that perceived quality/performance is a positive predictor of attitudinal loyalty, but does not directly predict behavioral loyalty. Price/value for money and emotional value also have a direct positive influence on attitudinal loyalty. Social value had a small - but negative - influence on attitudinal loyalty. Overall, three out of four dimensions of PCV have a strong positive effect on attitudinal loyalty. Furthermore, we find the same pattern for the indirect effects of all four PCV measures on behavioral loyalty, mediated by attitudinal loyalty.

Additionally, price/value for money is a stronger predictor for behavioral than for attitudinal loyalty. Moreover, social value is a positive predictor for behavioral loyalty, yet a negative predictor for attitudinal loyalty. All three results combined give a clear indication that attitudinal and behavioral loyalty indeed have different determinants. This will be further elaborated on in the discussion section.

We then investigated if these relationships differ for the customer journey segments distinguished based on their channel usage. In order to do this, we conducted a multi-group path analysis using SmartPLS. The results for the different segments can also be found in Table 3. We found the following significant differences

between the path coefficients for the customer journey segments: High-end buyers differ from mainstream buyers in that emotional value was a larger predictor of behavioral loyalty for mainstream buyers than for high-end buyers. Moreover, quality/performance was a significant predictor of behavioral loyalty only for the high-end buyers, making them significantly different from the mainstream and online buyers (but not from channel nomads). Finally, channel nomads were significantly different from mainstream buyers as well as online buyers in the relation between attitudinal and behavioral loyalty, as for mainstream and online buyers' attitudinal loyalty is a stronger predictor of behavioral loyalty than for channel nomads. This may hint towards channel nomads also being more likely brand nomads. This will be addressed in the following section.

#### 4.4 Customer journey segments and behavioral loyalty

When looking at current behavioral loyalty, the results show that one third of the respondents did not have a favorite brand, meaning that current behavioral loyalty for pork meat in China is rather low. We investigated if the four consumer segments distinguished earlier differ in terms of their patterns of preferred brands, see Figure 3. The results show that the distribution of purchases on different brands differs between consumer segments: channel nomads purchased 5.5 different brands on average in their last 10 purchases, the online buyers 4.1, the high-end buyers 3.8 and the mainstream buyers 3.3. Interesting to note, however, is that the channel nomads are the ones who do not favor one brand over another the most, meaning that they are indeed also most likely to be 'brand nomads'. This may be partly explained due to the smaller effect that attitudinal loyalty has in predicting behavioral loyalty.

TABLE 3 Direct, indirect and total effects table for model on full sample and segment-specific subsamples.

	Total Effects	Direct Effects	Indirect Effects
<b>Whole sample</b>			
Quality/performance → Attitudinal loyalty		.387***	
Quality/performance → Attitudinal loyalty → Behavioral loyalty	.113***	.014 <sup>NS</sup>	.099***
Price/value for money → Attitudinal loyalty		.080***	
Price/value for money → Attitudinal loyalty → Behavioral loyalty	.189***	.168***	.021***
Emotional value → Attitudinal loyalty		.214***	
Emotional value → Attitudinal loyalty → Behavioral loyalty	.344***	.289***	.055***
Social value → Brand attitude		-.076***	
Social value → Brand attitude → Behavioral loyalty	.056**	.076***	-.019***
Attitudinal loyalty → Behavioral loyalty		.255***	
<b>Mainstream buyers</b>			
Quality/performance → Attitudinal loyalty		.412***	
Quality/performance → Attitudinal loyalty → Behavioral loyalty	.069 <sup>NS</sup>	-.052 <sup>NS</sup>	.121***
Price/value for money → Attitudinal loyalty		.097**	
Price/value for money → Attitudinal loyalty → Behavioral loyalty	.189***	.160***	.028**
Emotional value → Attitudinal loyalty		.209***	
Emotional value → Attitudinal loyalty → Behavioral loyalty	.406***	.345***	.062***
Social value → Brand attitude		-.086**	
Social value → Brand attitude → Behavioral loyalty	.011 <sup>NS</sup>	.037 <sup>NS</sup>	-.025**
Attitudinal loyalty → Behavioral loyalty		.294***	
<b>High end buyers</b>			
Quality/performance → Attitudinal loyalty		.332***	
Quality/performance → Attitudinal loyalty → Behavioral loyalty	.204***	.124 <sup>NS</sup>	.080***
Price/value for money → Attitudinal loyalty		.058 <sup>NS</sup>	
Price/value for money → Attitudinal loyalty → Behavioral loyalty	.213***	.200**	.014 <sup>NS</sup>

(Continued)

TABLE 3 Continued

	Total Effects	Direct Effects	Indirect Effects
Emotional value → Attitudinal loyalty		.219***	
Emotional value → Attitudinal loyalty → Behavioral loyalty	.202**	.149**	.053**
Social value → Brand attitude		-.012 <sup>NS</sup>	
Social value → Brand attitude → Behavioral loyalty	.110*	.113*	-.003 <sup>NS</sup>
Attitudinal loyalty → Behavioral loyalty		.241***	
<b>Channel nomads</b>			
Quality/performance → Attitudinal loyalty		.359***	
Quality/performance → Attitudinal loyalty → Behavioral loyalty	.165*	.108 <sup>NS</sup>	.057***
Price/value for money → Attitudinal loyalty		.092 <sup>NS</sup>	
Price/value for money → Attitudinal loyalty → Behavioral loyalty	.148**	.133**	.015 <sup>NS</sup>
Emotional value → Attitudinal loyalty		.158**	
Emotional value → Attitudinal loyalty → Behavioral loyalty	.302***	.277***	.025*
Social value → Brand attitude		-.088 <sup>NS</sup>	
Social value → Brand attitude → Behavioral loyalty	.066 <sup>NS</sup>	.080*	-.014 <sup>NS</sup>
Attitudinal loyalty → Behavioral loyalty		.160***	
<b>Online buyers</b>			
Quality/performance → Attitudinal loyalty		.364***	
Quality/performance → Attitudinal loyalty → Behavioral loyalty	.088 <sup>NS</sup>	-.018 <sup>NS</sup>	.106***
Price/value for money → Attitudinal loyalty		.059 <sup>NS</sup>	
Price/value for money → Attitudinal loyalty → Behavioral loyalty	.215***	.198***	.017 <sup>NS</sup>
Emotional value → Attitudinal loyalty		.262***	
Emotional value → Attitudinal loyalty → Behavioral loyalty	.391***	.314***	.076**
Social value → Brand attitude		-.046 <sup>NS</sup>	
Social value → Brand attitude → Behavioral loyalty	.058 <sup>NS</sup>	.072 <sup>NS</sup>	-.013 <sup>NS</sup>
Attitudinal loyalty → Behavioral loyalty		.292***	

NS, non-significant; \*p&lt;.05, \*\*p&lt;.01, \*\*\*p&lt;.001.

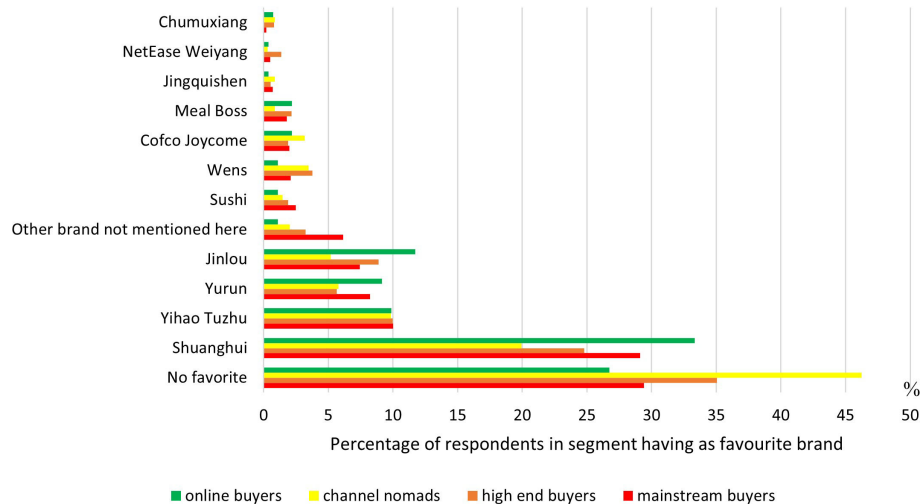


FIGURE 3  
Behavioural loyalty, measured as brand most frequently purchased, by customer journey segment.

## 5 Discussion

In this study we investigated how different dimensions of customer perceived value for fresh pork affect attitudinal and behavioral loyalty and how this differs between customer journey segments. Overall, we found support for our four hypotheses: the four dimensions of CPV, quality/performance value, emotional value, social value and price/value for money, were predictors of both attitudinal and behavioral loyalty, but the pattern of influence was different between attitudinal and behavioral loyalty. In addition, the patterns differed between different customer journey segments.

### 5.1 Discussion of findings

We looked at four dimensions of CPV: quality/performance, price/value for money, emotional value and social value. We find that quality/performance is the strongest predictor of attitudinal loyalty, whereas expected emotional value is the strongest predictor of behavioral loyalty. Further, the effect of quality/performance on behavioral loyalty is fully mediated by attitudinal loyalty, whereas the other three dimensions of CPV have both direct and indirect effects on behavioral loyalty. Overall, this confirms our expectation that the four dimensions of CPV affect attitudinal and behavioral loyalty differently, strengthening the preliminary evidence provided by Pura (2005) and Wang et al. (2004).

We may interpret these findings based on theories of attitude functions (Shavitt and Nelson, 2002). Attitude to the brand may in this case primarily serve a self-assertive function, reinforcing consumers' self-perception of being a quality conscious and thrifty buyer. This does to some extent translate to behavioral loyalty, but in addition behavioral loyalty is affected by the perceived emotional value of the product, which becomes the dominant driver of behavioral loyalty. That affective reactions can

affect purchase intention for a meat product besides or on top of its quality evaluation has been shown before (Saeed and Grunert, 2014).

Another interesting finding was that the perceived social value had a negative direct effect on attitudinal loyalty, yet a positive direct effect on behavioral loyalty. Social value pertains to the social recognition that people perceive being linked to using the product. It is thus close to the construct of social norm, which has been widely used to explain gaps in the link between attitude and behavior, also with regard to food (e.g., Vermeir & Verbeke, 2006). Hence, our results are in line with the common finding of a positive effect of perceived social pressure or encouragement on behavior and behavioral intentions. In addition to that, however, our findings suggest that buying a meat brand because of the perceived social recognition coming with it, is something that detracts from the attitude to the brand. A possible explanation for this is because buying a brand for such a reason is not in line with one's self-perception as an autonomous decision-maker, which again would be in line with the view of attitude as having a self-expressive function.

We also looked at how different patterns of customer journeys across different channels may affect the way in which CPV affects attitudinal and behavioral loyalty. Our results show that the pattern of influence of dimensions of CPV on attitudinal and behavioral loyalty differs between the segments. Two aspects are worth emphasizing. First, the overall finding that quality/performance is the strongest direct predictor of attitudinal loyalty, whereas emotional value is the strongest predictor of behavioral loyalty, holds for most of the customer journey segments, but not for the *high end buyers*, where the effect of these two dimensions on behavioral loyalty is about equal, which is in good correspondence with the defining criterion for these customers, namely that they shop a lot in high-end outlets. Second, the ambivalent effects of social value discussed above work differently in the different segments. The negative effect of social value on attitudinal loyalty is found only for the *mainstream buyers*

segment. The positive effect of social value on behavioral loyalty occurs only for *high end buyers* and for *channel nomads*. Thus, the segments react differently on the perception of social value of the different brands.

Our results have some implications for loyalty building on the market for fresh pork in China. China is unique in their heavy branding of fresh meat, whereas in most Western countries fresh meat is sold unbranded or under retailer labels. Still, brand loyalty of the Chinese consumers with regard to pork brands appears to be low. This could mirror the fact that, apart from a distinction of some premium brands mostly distinguished by the use of a particular pig race (black pigs), brand differentiation is rather low, with most brands having similar brand positioning based on safety and good taste (Pedersen et al., 2020). Our results underline the importance of creating customer value both in terms of quality and in terms of emotional benefits. In addition, our results indicate that the use of different channels has an effect on brand image; therefore, ensuring consistent brand encounters across the different channels may be very important.

## 5.2 Limitations and future research

Some limitations should be considered when interpreting the results of this study. Most importantly, this is a single country study and the results therefore do not easily generalize. Future research could experimentally investigate the effect of different value propositions, defined in terms of the dimensions of CPV distinguished here, on attitudinal and behavioral loyalty. This could be combined with measures of attitude function in order to be able to test the soundness of our interpretation that attitude function is a major factor in explaining these differential effects.

Second, the investigation is based on a cross-sectional online survey, which means that interpretations in terms of causality should be made with caution. A third limitation is that all behaviors measured in this study are based on self-report and not on direct observations.

## 5.3 Conclusion

We conclude that buying fresh meat is, for Chinese consumers, mostly driven by the expected pleasure and to a lesser degree by quality and functional properties like safety and healthiness. The latter do have an impact on consumers' attitude to the product, but less so on their buying behavior, suggesting that attitude and purchase are driven by different mental processes. Moreover, we find that these relationships differ between different segments of consumers distinguished based on their customer journey patterns.

## 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 studies involving humans were approved by Aarhus University Research Ethics Committee. The studies were conducted in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study.

## Author contributions

MM: Conceptualization, Formal Analysis, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing. KG: Conceptualization, Formal Analysis, Funding acquisition, Investigation, Methodology, Supervision, Writing – original draft, Writing – review & editing. SP: Conceptualization, Methodology, Project administration, Writing – review & editing. KB: Conceptualization, Data curation, Writing – review & editing. YZ: Conceptualization, Data curation, Project administration, Writing – review & editing.

## Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. This study has received financial support from the Danish Agricultural and Food Council.

## 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.

## Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.



## References

- Ajzen, I. (2002). Perceived behavioral control, self-efficacy, locus of control, and the theory of planned behavior 1. *J. Appl. Soc. Psychol.* 32, 665–683. doi: 10.1111/j.1559-1816.2002.tb00236.x
- Assael, H. (1984). Consumer behavior and market action. *Boston MA: Kent.*
- Auger, P., Devinney, T. M., and Louviere, J. J. (2007). Using best–worst scaling methodology to investigate consumer ethical beliefs across countries. *J. business ethics* 70, 299–326. doi: 10.1007/s10551-006-9112-7
- Boulstridge, E., and Carrigan, M. (2000). Do consumers really care about corporate responsibility? Highlighting the attitude–behaviour gap. *J. communication Manage.* 4, 355–368. doi: 10.1108/eb023532
- Briñol, P., Petty, R. E., and Stavrakaki, M. (2019). “Structure and function of attitudes,” in *Oxford research encyclopedia of psychology*. (Oxford: Oxford University Press).
- Carrigan, M., and Attalla, A. (2001). The myth of the ethical consumer—do ethics matter in purchase behaviour? *J. consumer marketing* 18, 560–578. doi: 10.1108/07363760110410263
- Chatzidakis, A., Hibbert, S., and Smith, A. P. (2007). Why people don’t take their concerns about fair trade to the supermarket: The role of neutralisation. *J. business ethics* 74, 89–100. doi: 10.1007/s10551-006-9222-2
- Day, G. S., and Wensley, R. (1988). Assessing advantage: a framework for diagnosing competitive superiority. *J. marketing* 52, 1–20. doi: 10.1177/002224298805200201
- Dick, A. S., and Basu, K. (1994). Customer loyalty: toward an integrated conceptual framework. *J. Acad. marketing Sci.* 22, 99–113. doi: 10.1177/0092070394222001
- Fazal-E-Hasan, S. M., Ahmadi, H., Mortimer, G., Grimmer, M., and Kelly, L. (2018). Examining the role of consumer hope in explaining the impact of perceived brand value on customer–brand relationship outcomes in an online retailing environment. *J. Retailing Consumer Serv.* 41, 101–111. doi: 10.1016/j.jretconser.2017.12.004
- Fazio, R. H., Powell, M. C., and Williams, C. J. (1989). The role of attitude accessibility in the attitude-to-behavior process. *J. consumer Res.* 16, 280–288. doi: 10.1086/209214
- Fishbein, M., and Ajzen, I. (1975). *Belief, attitude, intention, and behavior: An introduction to theory and research*. (Reading, MA: Addison-Wesley).
- Floh, A., Zauner, A., Koller, M., and Rusch, T. (2014). Customer segmentation using unobserved heterogeneity in the perceived-value–loyalty–intentions link. *J. Business Res.* 67, 974–982. doi: 10.1016/j.jbusres.2013.08.003
- Hair, J. F., Risher, J. J., Sarstedt, M., and Ringle, C. M. (2019). When to use and how to report the results of PLS-SEM. *Eur. Bus. Rev.* 26, 106–121.
- Herhausen, D., Kleinlercher, K., Verhoef, P. C., Emrich, O., and Rudolph, T. (2019). Loyalty formation for different customer journey segments. *J. Retailing* 95, 9–29. doi: 10.1016/j.jretai.2019.05.001
- Hernandez-Ortega, B., Aldas-Manzano, J., Ruiz-Mafe, C., and Sanz-Blas, S. (2017). Perceived value of advanced mobile messaging services: A cross-cultural comparison of Greek and Spanish users. *Inf. Technol. People* 30, 324–355. doi: 10.1108/ITP-01-2014-0017
- Ieva, M., and Ziliani, C. (2018). Mapping touchpoint exposure in retailing: Implications for developing an omnichannel customer experience. *Int. J. Retail Distribution Manage.* 46, 304–322. doi: 10.1108/IJRDM-04-2017-0097
- Lemon, K. N., and Verhoef, P. C. (2016). Understanding customer experience throughout the customer journey. *J. marketing* 80, 69–96. doi: 10.1509/jm.15.0420
- Leroi-Werelds, S., Streukens, S., Brady, M. K., and Swinnen, G. (2014). Assessing the value of commonly used methods for measuring customer value: A multi-setting empirical study. *J. Acad. marketing Sci.* 42, 430–451. doi: 10.1007/s11747-013-0363-4
- Loebler, H., and Wloka, M. (2019). Customers’ everyday understanding of ‘value’ from a second-order cybernetic perspective. *J. Marketing Manage.* 35, 992–1014. doi: 10.1080/0267257X.2019.1632374
- Maimaiti, M., Zhao, X., Jia, M., Ru, Y., and Zhu, S. (2018). How we eat determines what we become: opportunities and challenges brought by food delivery industry in a changing world in China. *Eur. J. Clinical Nut.* 72, 1282–1286.
- Maio, G. R., and Olson, J. M. (1999). *Why we evaluate: Functions of attitudes*. (London: Psychology Press).
- Marketing Science Institute. (2018). *Research Priorities 2018-2020*. Cambridge, MA: Marketing Science Institute.
- Møller Jensen, J. (2011). Consumer loyalty on the grocery product market: an empirical application of Dick and Basu’s framework. *J. Consumer Marketing* 28, 333–343. doi: 10.1108/07363761111149983
- Moraes, C., Carrigan, M., and Szmigin, I. (2012). The coherence of inconsistencies: Attitude–behaviour gaps and new consumption communities. *J. Marketing Manage.* 28, 103–128. doi: 10.1080/0267257X.2011.615482
- Ngobo, P. V. (2017). The trajectory of customer loyalty: an empirical test of Dick and Basu’s loyalty framework. *J. Acad. Marketing Sci.* 45, 229–250. doi: 10.1007/s11747-016-0493-6
- Papaoikonomou, E., Ryan, G., and Ginieis, M. (2011). Towards a holistic approach of the attitude behaviour gap in ethical consumer behaviours: Empirical evidence from Spain. *Int. Adv. Economic Res.* 17, 77–88. doi: 10.1007/s11294-010-9288-6
- Papista, E., and Krystallis, A. (2013). Investigating the types of value and cost of green brands: Proposition of a conceptual framework. *J. business ethics* 115, 75–92. doi: 10.1007/s10551-012-1367-6
- Pedersen, S., Grunert, K. G., and Zhou, Y. (2020). *PORKBRAND WPI: Mapping Present Sales Channels for Pork in China*. Available at: [https://mgmt.au.dk/fileadmin/Busines\\_Administration/MAPP/Porkbrand\\_WPI\\_report.pdf](https://mgmt.au.dk/fileadmin/Busines_Administration/MAPP/Porkbrand_WPI_report.pdf).
- Pura, M. (2005). Linking perceived value and loyalty in location-based mobile services. *Managing Service Quality: Int. J.* 15, 509–538. doi: 10.1108/09604520510634005
- Ringle, C. M., Wende, S., and Becker, J. M. (2015). *SmartPLS 3*. (Bönningstedt: SmartPLS). Available at: <http://www.smartpls.com>.
- Saeed, F., and Grunert, K. G. (2014). Expected and experienced quality as predictors of intention to purchase four new processed beef products. *Br. Food J.* 116, 451–471. doi: 10.1108/BFJ-10-2011-0262
- Shavitt, S., and Nelson, M. R. (2002). The role of attitude functions in persuasion and social judgment. In: J. P. Dilliar and L. Shen (Eds.). *The Sage Handbook of Persuasive Communication*. (Thousand Oaks, CA: Sage). 137–153.
- Sheeran, P. (2002). Intention—behavior relations: a conceptual and empirical review. *Eur. Rev. Soc. Psychol.* 12, 1–36. doi: 10.1080/14792772143000003
- Shepherd, R., Magnusson, M., and Sjöden, P.-O. (2005). Determinants of consumer behavior related to organic foods. *AMBIO: A J. Hum. Environ.* 34, 352–359. doi: 10.1579/0044-7447-34.4.352
- Sheth, J. N., Newman, B. L., and Gross, B. L. (1991). Why we buy what we buy: A theory of consumption values. *J. business Res.* 22, 159–170. doi: 10.1016/0148-2963(91)90050-8
- Si, Z., Scott, S., and McCordic, C. (2016). *Supermarkets, Wet Markets and Food Patronage in Nanjing, China*. Hungry Cities Partnership Report).
- Smith, J. B., and Colgate, M. (2007). Customer value creation: a practical framework. *J. marketing Theory Pract.* 15, 7–23. doi: 10.2753/MTP1069-6679150101
- Swait, J., and Sweeney, J. C. (2000). Perceived value and its impact on choice behavior in a retail setting. *J. Retailing Consumer Serv.* 7, 77–88. doi: 10.1016/S0969-6989(99)00012-0
- Sweeney, J. C., and Soutar, G. N. (2001). Consumer perceived value: The development of a multiple item scale. *J. retailing* 77, 203–220. doi: 10.1016/S0022-4359(01)00041-0
- Veeck, A., and Veeck, G. (2000). Consumer segmentation and changing food purchase patterns in Nanjing, PRC. *World Development*. 28, 457–471.
- Vermunt, J. K., and Magidson, J. (2013). *Technical Guide for Latent GOLD 5.0: Basic, Advanced, and Syntax*. (Belmont, MA: Statistical Innovations Inc).
- Wang, Y., Po Lo, H., Chi, R., and Yang, Y. (2004). An integrated framework for customer value and customer-relationship-management performance: a customer-based perspective from China. *Managing Service Quality: Int. J.* 14, 169–182. doi: 10.1108/09604520410528590
- Woodruff, R. B. (1997). Customer value: the next source for competitive advantage. *J. Acad. marketing Sci.* 25, 139–153. doi: 10.1007/BF02894350
- Zeithaml, V. A. (1988). Consumer perceptions of price, quality, and value: a means-end model and synthesis of evidence. *J. marketing* 52, 2–22. doi: 10.1177/002224298805200302
- Zeithaml, V. A., Verleye, K., Hatak, I., Koller, M., and Zauner, A. (2020). Three decades of customer value research: paradigmatic roots and future research avenues. *J. Service Res.* 23, 409–432. doi: 10.1177/1094670520948134



## OPEN ACCESS

## EDITED BY

Jeff Wood,  
University of Bristol, United Kingdom

## REVIEWED BY

Stefaan De Smet,  
Ghent University, Belgium  
Jerrad Legako,  
Texas Tech University, United States

## \*CORRESPONDENCE

Stephen B. Smith  
✉ sbsmith@tamu.edu

RECEIVED 03 November 2023

ACCEPTED 03 January 2024

PUBLISHED 29 January 2024

## CITATION

Smith SB (2024) Oleic acid concentration in bovine adipose tissues: impact on human health, sensory attributes, and genetic regulation. *Front. Anim. Sci.* 5:1332861. doi: 10.3389/fanim.2024.1332861

## COPYRIGHT

© 2024 Smith. This is an open-access article distributed under the terms of the [Creative Commons Attribution License \(CC BY\)](#). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.

# Oleic acid concentration in bovine adipose tissues: impact on human health, sensory attributes, and genetic regulation

Stephen B. Smith\*

Department of Animal Science, Texas A&M University, College Station, TX, United States

Fatty acids are important components of foods derived from livestock species, as they contribute to the healthfulness and benefits of beef and beef products. Oleic acid (18:1n-9) is the most highly regulated and most abundant fatty acid in animal tissue. The greatest risk factor for cardiovascular disease (CVD) is low circulating high-density lipoprotein cholesterol (HDL-C), and consumption of beef naturally enriched with oleic acid increases plasma HDL-C concentrations in men and women. Oleic acid is synthesized by the activity of stearoyl-coenzyme A (CoA) desaturase (SCD). In cattle, SCD activity and *SCD1* gene expression are highest in adipose tissue depots, followed by skeletal muscle, intestinal mucosa, and the liver. Early studies demonstrated that the concentration of oleic acid beef contributes to positive flavor attributes, but this finding has been difficult to replicate in more recent studies. Including grain (especially corn) in the finishing diets of cattle is essential for the upregulation of *SCD1* expression and activity. The measurement of SCD activity is technically difficult, but quantifying *SCD* gene expression or the concentration of palmitoleic acid (16:1n-7) in beef often provides insight into SCD activity. DNA polymorphisms in *SCD1*, the sterol regulatory element binding protein-1, the fatty acid synthase, and the growth hormone are associated with oleic acid concentration in the muscle of Japanese Black cattle, indicating a strong genetic component to the regulation of fatty acid composition of beef.

## KEYWORDS

oleic acid, SCD, HDL-C, cardiovascular risk, genetic regulation of SCD

## Introduction

Unlike the essential fatty acids, linoleic acid (18:2n-6) and  $\alpha$ -linolenic acid (18:3n-3), the concentration of oleic acid (18:1n-9) can readily be increased in bovine adipose tissue and muscle. Oleic acid is the most abundant fatty acid in the bovine muscle, subcutaneous adipose tissue, and intramuscular adipose tissue (Westerling and Hedrick, 1979; St. John et al., 1987; Sturdivant et al., 1992; May et al., 1993; Smith et al., 1998; Chung et al., 2006; Brooks et al., 2011). Oleic acid is produced by the activity of the  $\Delta 9$  desaturase, stearoyl-coenzyme A (CoA) desaturase (SCD), and SCD is encoded by *stearoyl-CoA desaturase-1 (SCD1)*, which is expressed in virtually all bovine tissues. This mini-review describes the effects of oleic acid-enriched beef on risk factors for cardiovascular disease (CVD); the relationship between oleic acid and sensory attributes in beef; and dietary and genetic factors regulating *SCD1* gene expression and SCD activity in bovine tissues.

## Oleic acid and risk factors for CVD

We have demonstrated that the increased consumption of oleic acid-enriched ground beef increases plasma high-density lipoprotein cholesterol (HDL-C) concentration from baseline (Adams et al., 2010; Gilmore et al., 2011; Gilmore et al., 2013). The subjects for Adams et al. (2010) were mildly hypercholesterolemic men; those for Gilmore et al. (2011) were normocholesterolemic men; those for Gilmore et al. (2013) were normocholesterolemic, postmenopausal women; and those for Choi et al. (2018) were normocholesterolemic, postmenopausal women and mildly hypercholesterolemic, older men. Adams et al. (2010) compared the effects of ground beef formulated from lean and fat trim from grass-fed (low oleic acid) and grain-fed (high oleic acid) Wagyu steers and conventional cattle (Table 1). Gilmore et al. (2011) prepared ground beef patties from lean and fat trim from 20-month-old Angus steers raised solely on pasture and hay (low oleic acid) and Angus steers fed a corn-based feedlot diet for 8 months following weaning (high oleic acid). Gilmore et al. (2013) produced patties from retail chub pack ground beef (low oleic acid) and utilized premade ground beef patties formulated from Akaushi (American Red Wagyu) steers (high oleic acid). For Trials 1–3, the high oleic-acid ground beef patties contained 2–3 g more oleic acid per patty than the low oleic-acid patties (Table 1).

In an effort to create ground beef patties that contained similar amounts of oleic acid, we formulated patties from chub pack ground beef (low oleic acid; 25% fat) and used premade Akaushi patties (high oleic acid; 20% fat) (Choi et al., 2018). However, after fatty acid analysis of the patties, we found that the chub pack patties contained more oleic acid (9.66 g/patty) than the Akaushi patties (7.72 g oleic acid/patty). We continue to refer to the Akaushi ground beef as high oleic acid because the monounsaturated fatty acid (MUFA):saturated fatty acid (SFA) ratio was higher in Akaushi patties (1.24) than in chub pack patties (0.96).

In Trial 1, men first consumed low oleic-acid ground beef (5 patties/week for 5 weeks) followed by a 3-week washout, during which they returned to their habitual diet. Following the washout period, the men consumed the high oleic-acid ground beef (5 patties/week for 5 weeks). During the first ground beef intervention period, the low oleic-ground beef decreased the plasma HDL-C concentration. During the second ground beef intervention period, the high oleic-acid intervention increased the plasma HDL-C concentration to pretrial levels. Trials 2–4 were randomized crossover trials in which participants consumed low oleic-acid or high oleic-acid ground beef (five 114-g patties/week for 5 weeks) and following a 4-week washout period, consumed the opposite type of ground beef. In Trials 2 and 3, the high oleic-acid ground beef increased plasma HDL-C concentration (Gilmore et al., 2011; Gilmore et al., 2013). Choi et al. (2018) demonstrated that high oleic-acid (Akaushi) ground beef had no effect on HDL-C concentration but increased the plasma concentration of the most buoyant and more healthful low-density lipoprotein cholesterol (LDL-C) fractions, LDL<sub>1</sub>-C plus LDL<sub>2</sub>-C, by over 4 mg/dL. On average, Trials 1–4 demonstrated a 3–4 mg/dL increase in HDL-C concentration when men and women consumed high oleic-acid ground beef as compared to conventional ground beef (Smith et al., 2020). A combined analysis of the Framingham Heart Study (1,428 participants), the Lipid Research Clinics Prevalence Mortality Follow-up Study (6,234 participants), the Lipid Research Clinics Coronary Primary Prevention Trial (1,808 participants), and the Multiple Risk Factor Intervention Trial (5,792 participants) concluded that a 1 mg/dL increase in HDL-C was associated with a 2%–3% depression in CVD mortality (Gordon et al., 1989). Therefore, even a relatively small increase in HDL-C concentration might reduce risk for CVD.

In Trial 2, both low and high oleic-acid ground beef decreased HDL<sub>2</sub>-C and HDL<sub>3</sub> particle diameters (Gilmore et al., 2011). Roussel et al. (2012) reported that a Beef in an Optimal Lean Diet (BOLD) depressed HDL-C concentrations in men and women, and Wu et al. (2021) documented that BOLD decreased the abundance of the larger HDL<sub>2b</sub> lipoprotein particles. Lytle et al. (2023) reported that consumption of lean ground beef (5% fat) decreased HDL-C concentration in men and depressed the abundance of the larger HDL<sub>2b</sub> and HDL<sub>2a</sub> lipoprotein particles. The effects of these lean beef interventions might explain the decreased HDL<sub>2</sub> and HDL<sub>3</sub> particle size reported by Gilmore et al. (2011).

## Fatty acids and beef sensory attributes

For over six decades, researchers have attempted to establish a relationship between fatty acid composition and beef palatability. Waldman et al. (1968) investigated the relationship of palatability traits with the percentage of fatty acids in lipids from three adipose tissue depots and the longissimus muscle (LM) but there were no significant associations among fatty acid composition, LM tenderness, juiciness, or flavor. Dryden and Marchello (1970)

TABLE 1 Characteristics of low oleic-acid (Low) and high oleic-acid (High) ground beef used in four randomized, controlled trials<sup>1</sup>.

Item	Trial 1		Trial 2		Trial 3		Trial 4	
	Low	High	Low	High	Low	High	Low	High
<b>Fatty acid, g/114-g patty</b>								
Myristic, 14:0	1.00	1.08	0.99	0.66	0.74	0.58	0.86	0.55
Myristoleic, 14:1n-5	0.44	0.29	0.28	0.22	0.18	0.24	0.19	0.28
Palmitic, 16:0	9.67	9.28	8.78	7.89	6.06	5.32	6.46	4.53
Palmitoleic, 16:1n-7	1.24	1.76	0.85	0.97	0.64	1.00	0.91	0.90
Stearic, 18:0	6.14	4.01	5.57	4.31	4.46	2.67	4.05	2.15
Oleic, 18:1n-9	15.1	17.3	10.1	13.3	8.62	10.6	9.66	7.72
<i>cis</i> -Vaccenic, 18:1n-7	0.58	0.82	0.30	0.47	0.35	0.54	0.35	0.48
Linoleic, 18:2n-6	0.91	0.92	0.55	0.56	0.31	0.34	0.54	0.39
$\alpha$ -Linolenic, 18:3n-3	0.06	0.03	0.09	0.03	0.01	0.02	0.06	0.03
Total 18:1 <i>trans</i> <sup>2</sup>	1.73	1.25	1.07	0.69	1.59	1.09	1.59	0.83
Total fat, g/114 g patty	40		29		24		25	18
MUFA : SFA <sup>3</sup>	0.95	1.31	0.71	1.10	0.86	1.43	0.96	1.24

<sup>1</sup>Data are the means for at least n = 3 batches of ground beef for each trial. Trial 1, Adams et al. (2010); Trial 2, Gilmore et al. (2011); Trial 3, Gilmore et al. (2013); and Trial 4, Choi et al. (2018).

<sup>2</sup>Sum of 18:1*trans*-10 and 18:1*trans*-11.

<sup>3</sup>MUFA : SFA = (14:1n-5 + 16:1n-5 + 18:1n-7 + 18:1n-9)/(14:0 + 16:0 + 17:0 + 18:0 + 20:0).

reported that the percentage of oleic acid was positively correlated with beef flavor, but not juiciness, in LM intramuscular lipid (IML), whereas linoleic acid was negatively correlated with juiciness. Westerling and Hedrick (1979) compared fatty acid composition and the flavor characteristics of steers and heifers fed fescue pasture or fescue pasture plus grain. Beef flavor score increased with time for those fed the grain-based diet and was positively correlated with oleic acid and negatively correlated with palmitic acid (16:0), stearic acid (18:0), and linoleic acid. Melton et al. (1982a) reported a significant, positive correlation with flavor score and oleic acid in beef from grass-finished, forage-grain-finished, and grain-finished steers. Melton et al. (1982b) demonstrated that the percentage of oleic acid was low and that stearic acid was higher in ground beef from steers backgrounded on pasture than in ground beef from steers that had been fed a cracked corn finishing diet. Positive flavor descriptors increased with days on feed and negative flavor descriptors declined with days on feed, and oleic acid was negatively correlated with negative flavor descriptors. Conversely, stearic and  $\alpha$ -linolenic acids were positively correlated with negative flavor descriptors. Mandell et al. (1998) compared beef from forage-fed cattle to beef from grain-fed cattle and surmised that higher concentrations of linoleic acid and lower concentrations of oleic acid may have been responsible for the differences in beef flavor.

It has been more difficult to establish a relationship between fatty acid composition and beef flavor attributes when cattle are feedlot-finished the same number of days. Gilbert et al. (2003) fed Brangus steers cracked corn, casein-formaldehyde-protected canola

lipid (high in oleic acid), or casein-formaldehyde-protected starch (which also contained canola oil). There was no difference in the oleic acid concentration of subcutaneous or intramuscular adipose tissue or in descriptive meat sensory or flavor attributes among treatments. Blackmon et al. (2015) produced ground beef from beef brisket, flank, and plate primals. Brisket is especially high in oleic acid (Turk and Smith, 2009; Smith et al., 2012; Smith et al., 2020) and the ground beef formulated from the brisket primal contained more oleic acid than ground beef from the flank or plate (Blackmon et al., 2015). Brisket ground beef had greater bloody/serumy and fat-like sensory attributes than ground beef from the flank, but there was no correlation between oleic acid concentration and any sensory panel flavor attributes. Kerth et al. (2015) formulated ground beef containing fat trim from the brisket, chuck, flank, and round. Brisket ground beef contained slightly more oleic acid than ground beef formulated from the other fat trims but there were no differences in consumer sensory traits.

Frank et al. (2016) reported the influence of intramuscular fat, animal feed, and breed type on sensory characteristics, chemical characteristics, and fatty acid composition of Australian Angus and Wagyu cattle. Although they observed several significant relationships between the percentages of IML, sensory attributes, and headspace volatile compounds, Frank et al. (2016) did not report associations among fatty acids and sensory characteristics. Chen et al. (2022) documented muscle fatty acids, beef flavor compounds, and beef flavors in Angus and Xianxi Yellow cattle. Although they reported principal component analysis (PCA) for flavor compounds and flavor attributes, a PCA was not reported for



beef fatty acids and flavor attributes. We interpret the results of Frank et al. (2016) and Chen et al. (2022) to mean that there was no relationship between beef fatty acids and any sensory attributes. We conclude that there is little correlation between the concentration of fatty acids and flavor attributes of beef unless there are differences in the production of cattle (e.g., grass feeding vs. grain feeding).

## Fatty acid composition, SCD activity, and SCD1 gene expression

As marbling score increases across a broad range of production conditions, the concentration and amount of oleic acid increase, and there is a concomitant decrease in stearic acid in bovine adipose tissue (Waldman et al., 1968; Chung et al., 2006; Brooks et al., 2011; Legako et al., 2015; Frank et al., 2016). In ruminants, dietary oleic acid is largely hydrogenated to stearic acid by ruminal microorganisms before reaching the abomasum (St. John et al., 1991; Ekeren et al., 1992). For bovine tissues, SCD activity is highest in adipose tissues but readily detectable in intestinal mucosal cells (St. John et al., 1991; Chang et al., 1992; Page et al., 1997; Archibeque et al., 2005). We interpret this to mean that duodenal stearic acid is converted in large part to oleic acid before being incorporated into chylomicrons. The primary source of oleic acid in bovine adipose tissue is *de novo* synthesis. Glucose, acetate, and lactate can be incorporated in fatty acid in bovine subcutaneous and intramuscular adipose tissues (Whitehurst et al., 1978; Smith and Prior, 1981; Smith, 1983; Smith and Crouse, 1984). The fatty acid synthase reaction produces palmitic acid and a small amount of myristic acid (14:0); stearic acid is synthesized by fatty acid elongase; and oleic acid is produced by desaturating stearic acid via SCD. Small amounts of palmitoleic acid (16:1n-7) are also generated by the desaturation of palmitic acid.

Percentages of palmitoleic acid in bovine tissues may provide evidence for current and/or past SCD activity (Smith et al., 1998). Subcutaneous adipose tissue from Japanese Black steers produced in Japan contained 5.2% palmitoleic acid, and subcutaneous adipose tissues from cattle raised in Australia and fed wheat and/or barley contained 1.6% palmitoleic acid (Smith et al., 1998). The proportions of stearic acid for these two groups of steers were 7.6% and 26.1%, respectively. These results illustrate the impact of finishing diets on the fatty acid composition of bovine adipose tissue.

Several studies have documented higher *SCD1* gene expression and/or higher SCD activity in subcutaneous adipose tissue is associated with higher concentrations of MUFA (Yang et al., 1999; Archibeque et al., 2005; Chung et al., 2007; Duckett et al., 2009; Brooks et al., 2011). Yang et al. (1999) measured SCD activity in subcutaneous adipose tissue from Australian pasture-finished and feedlot cattle, in which feedlot cattle were fed sorghum-based finishing diets in the absence and presence of rumen-protected cottonseed oil (CSO). Subcutaneous adipose tissue from pasture-finished cattle had higher SCD activity than adipose tissue from grain-finished cattle, and protected CSO strongly depressed SCD activity relative to grain-

finished cattle that were not fed CSO. The results of Smith et al. (1998) (which also included Australian grain-finished cattle) and Yang et al. (1999) were quite the opposite of the effects of grain finishing of cattle in the US. Research from the US has consistently demonstrated that MUFA increased over time in adipose tissue from grain-finished steers (Westerling and Hedrick, 1979; Huerta-Leidenz et al., 1996; Chung et al., 2006). *SCD1* gene expression is not upregulated until cattle are fed a grain-based diet (Brooks et al., 2011) and *SCD1* gene expression increases in LM and most adipose tissue depots the longer the steers are fed a corn-based finishing diet (Martin et al., 1999; Chung et al., 2007; Smith et al., 2012; Li et al., 2018).

## Genetic regulation of fatty acid composition in beef cattle

Adipose tissue and muscle from Japanese Black, Hanwoo, and Yanbian Yellow cattle (raised in Japan, Korea, and China, respectively) contain an unusually high concentration of oleic acid (Sturdivant et al., 1992; Zembayashi et al., 1995; Smith et al., 2001; Smith et al., 2009; Maharani et al., 2012; Li et al., 2018). Comparisons of beef from Black Wagyu, Akaushi (Red Wagyu), Angus, and commercial beef raised in the US have confirmed that beef from Wagyu and Akaushi cattle fed a grain-based diet contains a higher concentration of MUFA than beef from domestic cattle (May et al., 1993; Chung et al., 2006; Adams et al., 2010; Gilmore et al., 2013; Choi et al., 2018).

Lunt et al. (1993) were the first to compare American Wagyu and Angus steers under the same management conditions. The Wagyu's subcutaneous adipose tissue contained more MUFA and less SFA (MUFA : SFA ratio = 1.50) than adipose tissue from Angus steers (MUFA : SFA ratio = 1.17) (May et al., 1993). Subsequently, we documented USDA quality grade, fatty acid composition, SCD activity, and *SCD1* gene expression in Angus and Wagyu slaughtered at a targeted final body weight of 525 kg and 650 kg (Chung et al., 2006; Chung et al., 2007). The MUFA : SFA ratio increased over time in Wagyu and Angus subcutaneous adipose tissues and was higher in adipose tissues from corn-fed steers than in hay/corn-fed steers (Chung et al., 2006) (Figure 1A). The MUFA : SFA ratio was higher in adipose tissue from Wagyu steers and the slip point (a measure of melting point) was lower in subcutaneous adipose tissue lipids from cattle raised to the Japanese endpoint than in cattle raised to the US endpoint (Chung et al., 2006) (Figure 1B). These findings illustrate the importance of the duration of feeding a finishing diet for adipose MUFA and lipid slip point. SCD activity increased over time in subcutaneous adipose tissue from corn-fed Angus and Wagyu steers and in hay/corn-fed Wagyu steers (Figure 1C) (Chung et al., 2007), and *SCD1* expression increased over time in adipose tissue from Wagyu steers (but not Angus steers) fed either the corn or the hay/corn diet (Figure 1D).

Taniguchi et al. (2004) demonstrated single-nucleotide polymorphisms in the open-reading frame (exon 5) of an *SCD1* cDNA generated from Japanese Black cattle, in which valine was replaced with alanine. The VA and AA genotypes contributed to higher MUFA and lower melting points in intramuscular adipose tissue than



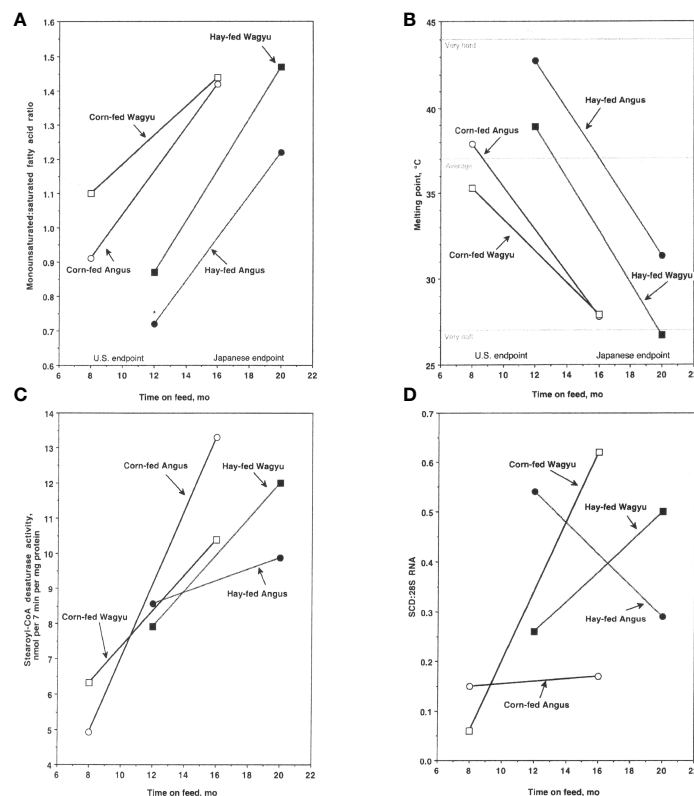


FIGURE 1

Monounsaturated fatty acid (MUFA):saturated fatty acid (SFA) ratio (A), slip point (B), stearoyl-CoA desaturase activity (C), and *SCD1* gene expression (D) in subcutaneous adipose tissues of Angus steers fed a corn-based diet; Angus steers fed a hay/corn diet; Wagyu steers fed a corn-based diet; and Wagyu steers fed a hay/corn diet ( $n = 4$  at all sampling times). All steers were weaned at 8 months of age. The US endpoint steers weighed 525 kg on average at sampling and the Japanese endpoint steers weighed 620 kg on average at sampling. The corn-based diet (Corn-fed) was designed to yield an average daily gain of 1.36 kg/d and the hay-based diet (Hay-fed) was supplemented with the same corn-based diet to yield an average daily gain of 0.9 kg/d. Marbling score was based on USDA marbling standards, and slip point is an estimate of the subcutaneous adipose tissue melting point. Stearoyl-CoA desaturase activity is expressed in nanomoles (nmol) stearic acid converted to oleic acid/(7 min•mg protein) and *SCD1* gene expression is the *SCD*:28S ratio; both were measured in subcutaneous adipose tissues overlying the longissimus muscle. Data were derived from Chung et al. (2006), and Chung et al. (2007).

the more infrequent VV genotype (Hoashi et al., 2007). Matsuhashi et al. (2011), Narukami et al. (2011), and Yokota et al. (2012) subsequently confirmed that these *SCD1* polymorphisms contributed to variations in fatty acid composition across populations of Japanese Black cattle. In contrast, Maharani et al. (2012) reported that *SCD1* TT, CC, and CT genotypes in exon 5 had no effect on oleic acid or total MUFA in beef from Korean Hanwoo cattle.

Taylor et al. (1998) first reported quantitative trait loci for stearic and oleic acids flanking the region in BTA19 between 28 cM and 51 cM. This region includes growth hormone (*GH*; 48.8 cM) but Taylor et al. (1998) were unable to identify the other genes in BTA19 responsible for the differences in stearic and oleic acids. Kawaguchi et al. (2021) reported fatty acid synthase (*FASN*; 51.4 cM) and sterol regulatory element-binding protein 1 (*SREBP1*; 35.2 cM) are located on BTA19. *FASN* regulates myristic acid and palmitic acid synthesis and *SREBP1* is a transcription factor that

regulates expression of *FASN* and *SCD1* (located on BTA26; Campbell et al., 2001). Hoashi et al. (2007) and Matsuhashi et al. (2011) reported that the genotypes of *SREBP1* and *SCD1* are associated with the concentration of MUFA in beef from Japanese Black cattle, and Matsuhashi et al. (2011) reported that genotypes of *FASN* and *GH* are also associated with the concentration of MUFA.

## Summary

Oleic-acid-enriched beef may reduce the risk for CVD but the effect of oleic acid on sensory attributes of beef has been difficult to demonstrate. Oleic acid increases in beef if cattle are raised to heavier weights and fed corn-based diets. Stearic acid in adipose tissue samples predicts the lipid melting point and may be negatively associated with beef sensory attributes. Although considerable research has focused on *SCD1* gene expression,

genetic polymorphisms in *GH*, *FASN*, and *SREBP1* also contribute significantly to the fatty acid composition of beef.

## Author contributions

SS: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, and Writing – review & editing.

## Funding

The author(s) declare that no financial support was received for the research, authorship, and/or publication of this article.

## References

- Adams, T. H., Walzem, R. L., Smith, D. R., Tseng, S., and Smith, S. B. (2010). Hamburger high in total, saturated and *trans*-fatty acids decreases HDL cholesterol and LDL particle diameter, and increases plasma TAG, in mildly hypercholesterolaemic men. *Br. J. Nutr.* 103, 91–98. doi: 10.1017/S000714509991516
- Archibeque, S. L., Lunt, D. K., Tume, R. K., and Smith, S. B. (2005). Fatty acid indices of stearoyl Co-A desaturase activity do not reflect actual stearoyl Co-A desaturase enzyme activity in adipose tissues of beef steers finished with corn-, flaxseed-, or sorghum-based diets. *J. Anim. Sci.* 83, 1153–1166. doi: 10.2527/2005.8351153x
- Blackmon, T., Miller, R. K., Kerth, C., and Smith, S. B. (2015). Ground beef patties prepared from brisket, flank and plate have unique fatty acid and sensory characteristics. *Meat Sci.* 103, 46–53. doi: 10.1016/j.meatsci.2015.01.004
- Brooks, M. A., Choi, C. W., Lunt, D. K., Kawachi, H., and Smith, S. B. (2011). Subcutaneous and intramuscular adipose tissue stearoyl-coenzyme A desaturase gene expression and fatty acid composition in calf- and yearling-fed Angus steers. *J. Anim. Sci.* 89, 2556–2570. doi: 10.2527/jas.2010-3369
- Campbell, E. M. G., Gallagher, D. S., Davis, S. K., Taylor, J. F., and Smith, S. B. (2001). Rapid communication: Mapping of the bovine stearoyl-coenzyme A desaturase (*SCD*) gene to BTA26. *J. Anim. Sci.* 79, 1954–1955. doi: 10.2527/2001.7971954x
- Chang, J. H. P., Lunt, D. K., and Smith, S. B. (1992). Fatty acid composition and fatty acid elongase and stearoyl-CoA desaturase activities in tissues of steers fed high oleate sunflower seed. *J. Nutr.* 122, 2074–2080. doi: 10.1093/jn/122.11.2074
- Chen, D., Wang, X., Guo, Q., Deng, H., Luo, J., Yi, K., et al. (2022). Muscle fatty acids, meat flavor compounds and sensory characteristics of Xiangxi Yellow cattle in comparison to Aberdeen Angus. *Anim. (Basel)* 12, 1161. doi: 10.3390/ani12091161
- Choi, S. H., Gharahmany, G., Walzem, R. L., Meade, T. H., and Smith, S. B. (2018). Ground beef high in total fat and saturated fatty acids decreases x receptor signaling targets in peripheral blood mononuclear cells of men and women. *Lipids* 53, 279–290. doi: 10.1002/lipd.12028
- Chung, K. Y., Lunt, D. K., Choi, C. B., Chae, S. H., Rhoades, R. D., Adams, T. L., et al. (2006). Lipid characteristics of subcutaneous adipose tissue and M. longissimus thoracis of Angus and Wagyu steers fed to U.S. and Japanese endpoints. *Meat Sci.* 73, 432–441. doi: 10.1016/j.meatsci.2006.01.002
- Chung, K. Y., Lunt, D. K., Kawachi, H., and Yano, H. (2007). Lipogenesis and stearoyl-CoA desaturase gene expression and enzyme activity in adipose tissue of short- and long-fed Angus and Wagyu steers fed corn- or hay-based diets. *J. Anim. Sci.* 85, 380–387. doi: 10.2527/jas.2006-498
- Dryden, F. D., and Marchello, J. A. (1970). Influence of total lipid and fatty acid composition upon the palatability of three bovine muscles. *J. Anim. Sci.* 31, 36–41. doi: 10.2527/jas1970.31136x
- Duckett, S. K., Pratt, S. L., and Pavan, E. (2009). Corn oil or corn grain supplementation to steers grazing endophyte-free tall fescue. II. Effects on subcutaneous fatty acid content and lipogenic gene expression. *J. Anim. Sci.* 87, 1120–1128. doi: 10.2527/jas.2008-1420
- Ekeren, P. A., Smith, D. R., Lunt, D. K., and Smith, D. R. (1992). Ruminant biohydrogenation of fatty acids from high-oleate sunflower seeds. *J. Anim. Sci.* 70, 2574–2580. doi: 10.2527/1992.7082574x
- Frank, D., Ball, A., Hughes, J., Krishnamurthy, R., Piyasiri, U., Stark, J., et al. (2016). Sensory and flavor chemistry characteristics of Australian beef: Influence of intramuscular fat, feed, and breed. *J. Agric. Food Chem.* 64, 4299–4311. doi: 10.1021/acs.jafc.6b00160
- Gilbert, C. D., Lunt, D. K., Miller, R. K., and Smith, S. B. (2003). Carcass, sensory, and adipose tissue traits of Brangus steers fed casein-formaldehyde-protected starch and/or canola lipid. *J. Anim. Sci.* 81, 2457–2468. doi: 10.2527/2003.81102457x
- Gilmore, L. A., Crouse, S. F., Carbuhn, A., Klooster, J., Calles, J. A. E., Meade, T., et al. (2013). Exercise attenuates the increase in plasma monounsaturated fatty acids and high-density lipoprotein but not high-density lipoprotein 2b cholesterol caused by high-oleic ground beef in women. *Nutr. Res.* 33, 1003–1011. doi: 10.1016/j.nutres.2013.09.003
- Gilmore, L. A., Walzem, R. L., Crouse, S. F., Smith, D. R., Adams, T. H., Vaidyanathan, V., et al. (2011). Consumption of high-oleic acid ground beef increases HDL cholesterol concentration but both high- and low-oleic acid ground beef decrease HDL particle diameter in normocholesterolemic men. *J. Nutr.* 141, 1188–1194. doi: 10.3945/jn.110.136085
- Gordon, D. J., Probstfield, J. L., Garrison, R. J., Neaton, J. D., Castelli, W. P., Knoke, J. D., et al. (1989). High-density lipoprotein cholesterol and cardiovascular disease: Four prospective American studies. *Circulation* 79, 8–15. doi: 10.1161/01.cir.79.1.8
- Hoashi, S., Ashida, N., Ohsaki, H., Utsugi, T., Sasazaki, S., Taniguchi, M., et al. (2007). Genotype of bovine sterol regulatory element binding protein-1 (*SREBP-1*) is associated with fatty acid composition in Japanese Black cattle. *Mamm Genome* 18, 880–886. doi: 10.1007/s00335-007-9072-y
- Huerta-Leidenz, N. O., Cross, H. R., Savell, J. W., Belk, K. E., Lunt, D. K., Baker, J. F., et al. (1996). Fatty acid composition of adipose tissues of male calves at different stages of growth. *J. Anim. Sci.* 74, 1256–1264. doi: 10.2527/1996.7461256x
- Kawaguchi, F., Kakiuchi, F., Oyama, K., Mannen, H., and Sasazaki, S. (2021). Effect of five polymorphisms on percentage of oleic acid in beef and investigation of linkage disequilibrium to confirm the locations of quantitative trait loci on BTA19 in Japanese Black cattle. *Life (Basel)* 11, 597. doi: 10.3390/life11070597
- Kerth, C. R., Harbison, A. L., Smith, S. B., and Miller, R. K. (2015). Consumer sensory evaluation, fatty acid composition, and shelf-life of ground beef with subcutaneous fat trimmings from different carcass locations. *Meat Sci.* 104, 30–36. doi: 10.1016/j.meatsci.2015.01.014
- Legako, J. F., Dinh, T. T., Miller, M. F., and Brooks, J. C. (2015). Effects of USDA beef quality grade and cooking on fatty acid composition of neutral and polar lipid fractions. *Meat Sci.* 100, 246–255. doi: 10.1016/j.meatsci.2014.10.013
- Li, X. Z., Yan, C. G., Gao, Q. S., Yan, Y., Choi, S. H., and Smith, S. B. (2018). Adipogenic/lipogenic gene expression and fatty acid composition in chuck, loin, and round muscles in response to grain feeding of Yanbian Yellow cattle. *J. Anim. Sci.* 96, 2698–2709. doi: 10.1093/jas/sky161
- Lunt, D. K., Riley, R. R., and Smith, S. B. (1993). Growth and carcass characteristics of Angus and American Wagyu steers. *Meat Sci.* 34, 327–334. doi: 10.1016/0309-1740(93)90081-R
- Lytle, J. R., Price, T., Crouse, S. F., Smith, D. R., Walzem, R. L., and Smith, S. B. (2023). Consuming high-fat and low-fat ground beef depresses high-density and low-density lipoprotein cholesterol concentrations, and reduces small, dense low-density lipoprotein particle abundance. *Nutrients* 15, 337. doi: 10.3390/nu15020337
- Maharani, D., Jung, Y., Jung, W. Y., Jo, C., Ryoo, S. H., Lee, S. H., et al. (2012). Association of five candidate genes with fatty acid composition in Korean cattle. *Mol. Biol. Rep.* 39, 6113–6121. doi: 10.1007/s11033-011-1426-6

## Conflict of interest

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

## Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

- Mandell, I. B., Buchanan-Smith, J. G., and Campbell, C. P. (1998). Effects of forage vs grain feeding on carcass characteristics, fatty acid composition, and beef quality in Limousin-cross steers when time on feed is controlled. *J. Anim. Sci.* 76, 2619–2630. doi: 10.2527/1998.76102619x
- Martin, G. S., Lunt, D. K., Britain, K. G., and Smith, S. B. (1999). Postnatal development of stearoyl coenzyme A desaturase gene expression and adiposity in bovine subcutaneous adipose tissue. *J. Anim. Sci.* 77, 630–636. doi: 10.2527/1999.773630x
- Matsushashi, T., Maruyama, S., Uemoto, Y., Kobayashi, N., Mannen, H., Abe, T., et al. (2011). Effects of bovine fatty acid synthase, stearoyl-coenzyme A desaturase, sterol regulatory element-binding protein 1, and growth hormone gene polymorphisms on fatty acid composition in Japanese Black Cattle. *J. Anim. Sci.* 89, 12–22. doi: 10.2527/jas.2010-3121
- May, S. G., Sturdivant, C. A., Lunt, D. K., Miller, R. K., and Smith, S. B. (1993). Comparison of sensory characteristics and fatty acid composition between Wagyu crossbred and Angus steers. *Meat Sci.* 35, 289–298. doi: 10.1016/0309-1740(93)90034-F
- Melton, S. L., Amiri, M., Davis, G. W., and Backus, W. R. (1982a). Flavor and chemical characteristics of ground beef from grass-, forage-grain and grain-finished steers. *J. Anim. Sci.* 55, 71–87. doi: 10.2527/jas1982.55177x
- Melton, S. L., Black, J. M., Davis, G. W., and Backus, W. R. (1982b). Flavor and selected chemical components of ground beef from steers backgrounded on pasture and fed corn up to 140 days. *J. Food Sci.* 47, 699–704. doi: 10.1111/j.1365-2621.1982.tb12694.x
- Narukami, T., Sasazaki, S., Oyama, K., Nogi, T., Taniguchi, M., and Mannen, H. (2011). Effect of DNA polymorphisms related to fatty acid composition in adipose tissue of Holstein cattle. *Anim. Sci. J.* 82, 406–411. doi: 10.1111/j.1740-0929.2010.00855.x
- Page, A. M., Sturdivant, C. A., Lunt, D. K., and Smith, S. B. (1997). Dietary whole cottonseed depresses lipogenesis but has no effect on stearoyl coenzyme desaturase activity in bovine subcutaneous adipose tissue. *Comp. Biochem. Physiol. B Biochem. Mol. Biol.* 118, 79–84. doi: 10.1016/s0305-0491(97)00027-8
- Roussel, M. A., Hill, A. M., Gaugler, T. L., West, S. G., Heuvel, J. P., and Alaupovic, P. (2012). Beef in an Optimal Lean Diet study: effects on lipids, lipoproteins, and apolipoproteins. *Am. J. Clin. Nutr.* 95, 9–16. doi: 10.3945/ajcn.111.016261
- Smith, S. B. (1983). Contribution of the pentose cycle to lipogenesis in bovine adipose tissue. *Arch. Biochem. Biophys.* 221, 46–56. doi: 10.1016/0003-9861(83)90120-0
- Smith, S. B., and Crouse, J. D. (1984). Relative contributions of acetate, lactate and glucose to lipogenesis in bovine intramuscular and subcutaneous adipose tissue. *J. Nutr.* 114, 792–800. doi: 10.1093/jn/114.4.792
- Smith, S. B., Go, G. W., Johnson, B. J., Chung, K. Y., Choi, S. H., Sawyer, J. E., et al. (2012). Adipogenic gene expression and fatty acid composition in subcutaneous adipose tissue depots of Angus steers between 9 and 16 months of age. *J. Anim. Sci.* 90, 2505–2514. doi: 10.2527/jas.2011-4602
- Smith, S. B., Kawachi, H., Choi, C. B., Choi, C. W., Wu, G., and Sawyer, J. E. (2009). Cellular regulation of bovine intramuscular adipose tissue development and composition. *J. Anim. Sci.* 87 (E Suppl.), E72–E82. doi: 10.2527/jas.2008-1340
- Smith, S. B., Lunt, D. K., Smith, D. R., and Walzem, R. L. (2020). Producing high-oleic acid beef and the impact of ground beef consumption on risk factors for cardiovascular disease: A review. *Meat Sci.* 163, 108076. doi: 10.1016/j.meatsci.2020.108076
- Smith, S. B., and Prior, R. L. (1981). Evidence for a functional ATP-citrate lyase: NADP-malate dehydrogenase pathway in bovine adipose tissue: enzyme and metabolite levels. *Arch. Biochem. Biophys.* 211, 192–201. doi: 10.1016/0003-9861(81)90444-6
- Smith, S. B., Yang, A., Larsen, T. W., and Tume, R. K. (1998). Positional analysis of triacylglycerols from bovine adipose tissue lipids varying in degree of unsaturation. *Lipids* 33, 197–207. doi: 10.1007/s11745-998-0196-8
- Smith, S. B., Zembayashi, M., Lunt, D. K., Sanders, J. O., and Gilbert, C. D. (2001). Carcass traits and microsatellite distributions in offspring of sires from three graphical regions of Japan. *J. Anim. Sci.* 79, 3041–3051. doi: 10.2527/2001.79123041x
- St. John, L. C., Lunt, D. K., and Smith, S. B. (1991). Fatty acid elongase and desaturase activities in bovine liver and adipose tissue microsomes. *J. Anim. Sci.* 69, 1064–1073. doi: 10.2527/1991.6931064x
- St. John, L. C., Young, C. R., Knabe, D. A., Schelling, G. T., Grundy, S. M., and Smith, S. B. (1987). Fatty acid profiles and sensory and carcass traits of tissues from steers and swine fed an elevated monounsaturated fat diet. *J. Anim. Sci.* 64, 1441–1447. doi: 10.2527/jas1987.6451441x
- Sturdivant, C. A., Lunt, D. K., and Smith, S. B. (1992). Fatty acid composition of longissimus muscle and subcutaneous and intramuscular adipose tissues of Japanese Wagyu cattle. *Meat Sci.* 32, 449–458. doi: 10.1016/0309-1740(92)90086-J
- Taniguchi, M., Utsugi, T., Oyama, K., Mannen, H., Kobayashi, M., Tanabe, Y., et al. (2004). Genotype of stearoyl-coA desaturase is associated with fatty acid composition in Japanese Black cattle. *Mamm Genome* 15, 142–148. doi: 10.1007/s00335-003-2286-8
- Taylor, J. F., Coutinho, L. L., Herring, K. L., Gallagher, D. S. Jr, Brenneman, R. A., Burney, N., et al. (1998). Candidate gene analysis of *GHI* for effects on growth and carcass composition of cattle. *Anim. Genet.* 29, 194–201. doi: 10.1046/j.1365-2052.1998.00317.x
- Turk, S. N., and Smith, S. B. (2009). Carcass fatty acid mapping. *Meat Sci.* 81, 658–663. doi: 10.1016/j.meatsci.2008.11.005
- Waldman, R. C., Suess, G. G., and Brungardt, J. M. (1968). Fatty acids of certain bovine tissues and their association with growth, carcass and palatability traits. *J. Anim. Sci.* 48, 1368–1379. doi: 10.2527/jas1968.273632x
- Westerling, D. B., and Hedrick, H. B. (1979). Fatty acid composition of bovine lipids as influenced by diet, sex and anatomical location and relationship to sensory characteristics. *J. Anim. Sci.* 48, 1343–1348. doi: 10.2527/jas1979.4861343x
- Whitehurst, G. B., Beitz, D. C., Pothoven, M. A., Ellison, W. R., and Crump, M. H. (1978). Lactate as a precursor of fatty acids in bovine adipose tissue. *J. Nutr.* 108, 1806–1811. doi: 10.1093/jn/108.11.1806
- Wu, X., Roussel, M. A., Hill, A. M., Kris-Etherton, P. M., and Walzem, R. L. (2021). Baseline insulin resistance is a determinant of the small, dense low-density lipoprotein response to diets differing in saturated fat, protein, and carbohydrate contents. *Nutrients* 13, 4328. doi: 10.3390/nu13124328
- Yang, A., Larsen, T. W., Smith, S. B., and Tume, R. K. (1999).  $\Delta^9$  desaturase activity in bovine subcutaneous adipose tissue of different fatty acid composition. *Lipids* 34, 971–978. doi: 10.1007/s11745-999-0447-8
- Yokota, S., Sugita, H., Ardiyanti, A., Shoji, N., Nakajima, H., Hosono, M., et al. (2012). Contributions of FASN and SCD gene polymorphisms on fatty acid composition in muscle from Japanese Black cattle. *Anim. Genet.* 43, 790–792. doi: 10.1111/j.1365-2052.2012.02331.x
- Zembayashi, M., Nishimura, K., Lunt, D. K., and Smith, S. B. (1995). Effect of breed type and sex on the fatty acid composition of subcutaneous and intramuscular lipids of finishing steers and heifers. *J. Anim. Sci.* 73, 3325–3332. doi: 10.2527/1995.73113325x



## OPEN ACCESS

## EDITED BY

Jeff Wood,  
University of Bristol, United Kingdom

## REVIEWED BY

Payam Vahmani,  
University of California, Davis, United States

## \*CORRESPONDENCE

Daniel Anthony Dias  
✉ dan.dias@deakin.edu.au

RECEIVED 09 December 2023

ACCEPTED 08 February 2024

PUBLISHED 23 February 2024

## CITATION

Edirisinghe N, Flavel M, Pouniotis D, Zakaria R,  
Lim KF and Dias DA (2024) From feed to fork:  
immunity, performance and quality of  
products from farm animals fed  
sugarcane products.  
*Front. Anim. Sci.* 5:1352961.  
doi: 10.3389/fanim.2024.1352961

## COPYRIGHT

© 2024 Edirisinghe, Flavel, Pouniotis, Zakaria,  
Lim and Dias. This is an open-access article  
distributed under the terms of the [Creative  
Commons Attribution License \(CC BY\)](#). The  
use, distribution or reproduction in other  
forums is permitted, provided the original  
author(s) and the copyright owner(s) are  
credited and that the original publication in  
this journal is cited, in accordance with  
accepted academic practice. No use,  
distribution or reproduction is permitted  
which does not comply with these terms.

# From feed to fork: immunity, performance and quality of products from farm animals fed sugarcane products

Nee Edirisinghe<sup>1</sup>, Matthew Flavel<sup>2,3</sup>, Dodie Pouniotis<sup>1</sup>,  
Rosita Zakaria<sup>1,4</sup>, Kosta Fremiellie Lim<sup>2</sup>  
and Daniel Anthony Dias<sup>5\*</sup>

<sup>1</sup>School of Health and Biomedical Sciences, Royal Melbourne Institute of Technology (RMIT) University, Bundoora, VIC, Australia, <sup>2</sup>Bioactives Division, The Product Makers Australia Pty. Ltd, Keysborough, VIC, Australia, <sup>3</sup>Department of Microbiology, Anatomy, Physiology and Pharmacology, La Trobe University, Bundoora, VIC, Australia, <sup>4</sup>Centre for Food Allergy Research, Murdoch Children Research Institute, Parkville, VIC, Australia, <sup>5</sup>ARC Training Centre for Hyphenated Analytical Separation Technologies (HyTECH), CASS Food Research Centre, School of Exercise and Nutrition Sciences, Deakin University, Burwood, VIC, Australia

Sugarcane extracts have generated a growing interest due to their potential applications that extend beyond conventional sugar and ethanol production. These by-products, along with sugarcane extracts offer valuable nutrients and compounds that can be utilized in animal feed supplementation, aiming to improve immunity and growth performance, and the quality of animal-derived products consumed by humans. The immune-boosting properties of sugarcane supplementation have been documented through several studies highlighting enhanced cytotoxicity, increased phagocytic capacity, and modulation of immune cells and cytokine production. Abundant in polyphenols and bioactive compounds, sugarcane products are believed to contribute to these immunological effects. However, further research is required to unravel the specific mechanisms underlying these actions. Supplementing sugarcane by-products in animal feed has shown promising results of improved growth rates and weight gains in various animal species. Sugarcane supplementation positively influences animal performance by optimizing nutrient intake and utilization, enhancing feed conversion efficiency, and promoting healthy growth. Moreover, sugarcane supplementation has been associated with improved meat tenderness and overall quality in animal-derived products. To optimize the utilization of sugarcane products, future research will need to focus on determining optimal inclusion quantities and product or extract combinations, identifying specific compound classes, and balancing nutritional profiles in animal feed formulations. Additionally, studies should focus on evaluating long-term effects on animal health and subsequent product quality, and explore the environmental sustainability of sugarcane product supplementation in feed. This mini-review explores the impact of sugarcane product supplementation on swine, poultry, aquaculture species and ruminants, focusing on its effects on immunity, growth performance, and product quality.

## KEYWORDS

sugarcane, feed, farm animals, immunity, growth, performance, quality



# 1 Introduction

Given the significant increase in the demand for food in recent years, sustainable animal production has progressively become important (Aland and Madec, 2009). Ensuring peak animal health, growth and performance is therefore of importance to maintain the global demand for animal-based products. In livestock industry, antibiotics are often added into animal feed to avoid infectious diseases and subsequently, increasing their production (Barton, 2000). However, there is a growing apprehension regarding the consequences of the continual usage of antibiotics in farm animals in relation to public health, with evidence demonstrating antibiotic resistance in associated food products originating from animals administered with antibiotics (Papatsiros et al., 2014; Marshall and Levy, 2011). This has the potential to result in significant health consequences for humans who consume animal products further down the food chain. To address this requirement, environmentally sustainable alternatives need to be explored, to not only protect the well-being of farm animals but also optimize their growth and performance. By doing so, the overall quality of products destined for human consumption can be enhanced.

For example, given the influence of the gut microbiota on immune responses and gut health, plant-based antibiotic alternatives are expected to do more than combat pathogens; these are expected to also foster the proliferation of beneficial microbes. This symbiotic relationship between the host animal and its microbial inhabitants emphasizes the importance of interventions that promote a balanced and resilient microbiome, thereby enhancing overall physiological well-being (Kim and Lillehoj, 2019). Furthermore, the systemic effects of plant-based antibiotic alternatives on livestock extend beyond their antimicrobial properties to encompass improvements in digestive processes. These alternatives play a pivotal role in stimulating the production of endogenous enzymes, thereby enhancing feed digestibility and nutrient absorption (Bagno et al., 2018). This highlights their value as integral components in promoting optimal health and performance in animal agriculture. Exploring sugarcane products as environmentally friendly alternatives to antibiotics in animal feed can hold promise for sustainable animal farming practices.

Sugarcane (*Saccharum officinarum*) serves as a significant economic contributor in the production of sugar and ethanol, as well as food processing and preservation industries (Prakash et al., 2021). There is also an increasing awareness in exploring the commercial potential of sugarcane by-products beyond their traditional use in sugar and ethanol production (de Paula et al., 2021). Sugar processing yields valuable major by-products such as molasses and bagasse, along with other economically beneficial products such as tops, ash, and press-mud (Solomon, 2011). In addition to its diverse applications, sugarcane plays a fundamental role as a primary source of roughage in animal feed supplementation, whether utilized in its entirety, through fermentation, or in the form of its by-products (Almazán et al., 1999; Carvalho et al., 2022).

In the pursuit of delivering animal-based foods of superior quality and high nutritional value, the field of animal nutrition focuses on optimizing the ingredients and refining the manufacturing processes involved in producing high-quality animal feed (Van der Poel et al., 2020). Additionally, the interest in a circular economy model is growing, where combined interdisciplinary approaches to completely utilize beneficial by-products, and minimize waste reduction are increasingly applied in agri-food systems (Hamam et al., 2021). Figure 1 illustrates the interconnectedness of livestock health, human consumption of animal derived products and the environmental sustainability impacts. In addressing the nutritional value of sugarcane products and by products, for example, sugarcane molasses is known to be rich in nutrients with proximate composition analysis showing molasses to be high in carbohydrates and sucrose (Khairul et al., 2022). Similarly, non-centrifugal cane sugar is also high in carbohydrates and sucrose, while also having a high mineral content (Jaffé, 2015). Despite the efforts to incorporate sugarcane products in animal feed, there is still scope for optimization in their effective utilization (Yanti et al., 2021). Particularly, sugarcane's nutritional value can be limited when used as a standalone feed, due to its low protein content and the fibrous characteristics of its cell wall (Cabral et al., 2020). The benefits of including sugarcane products is therefore largely evident when supplemented with other highly digestible feed components in livestock diets (Cabello et al., 2008; Preston, 1983). Additionally, it is important to consider data beyond the macronutrient composition of sugarcane products and by-products in order to assess the impact of including them as animal feed components.

The effective management of farm animal diseases is a constant priority, and maximizing animals' immunological defence capabilities can significantly enhance their overall health and welfare (Novák, 2014). The demand for raising farm animals without synthetic products and pharmaceuticals, especially antibiotics, has prompted feed producers to consider more naturally derived supplementation in feed (Burdick Sanchez et al., 2021). In addition to their role in protecting plants from pests, phytochemicals are considered to have positive effects on animal health and nutrition (Provenza and Villalba, 2010). This mini-review explores the impact of sugarcane product supplementation as by-products (bagasse, molasses) or as extracts in the diets of swine, poultry and aquaculture species raised for human consumption, particularly focusing on its effects on their immunity and growth, alongside examples from ruminant studies.

# 2 Impact on immunity

Given the important implication of oxidative stress in inflammation in farm animals, the inclusion of polyphenols as feed additives in animal nutrition holds great potential (Gessner et al., 2017). The by-products of sugar production, for example, sugarcane juice and molasses, are sources of valuable phenolic compounds known for their potent antioxidant properties



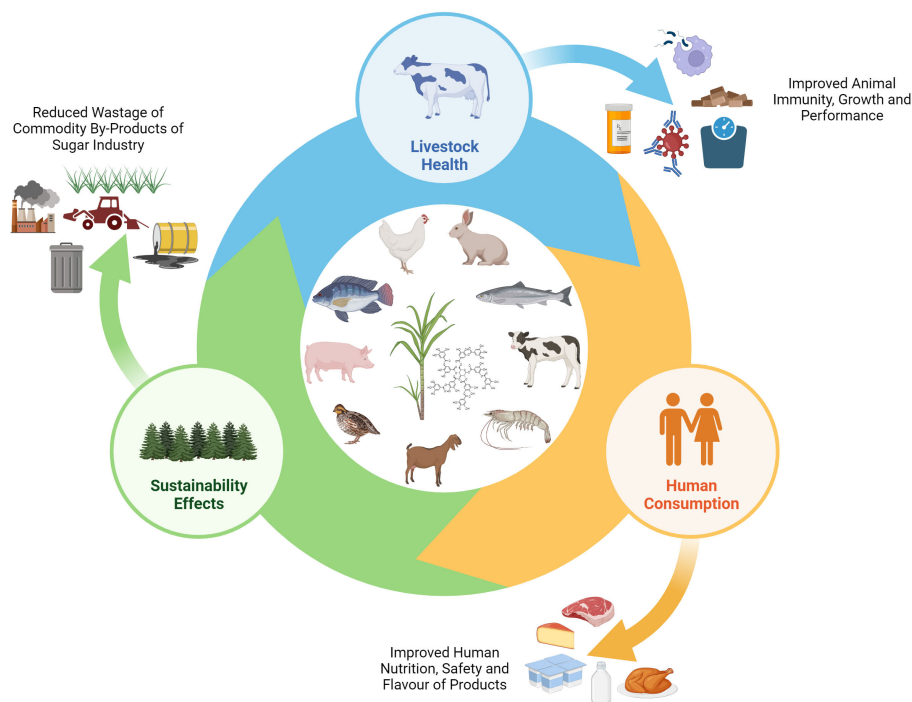


FIGURE 1

The effects of sugarcane supplementation in animal feed on livestock health, impact of human consumption of animal products, and implications on environmental sustainability.

(Prakash et al., 2021). Consequently, there is an increasing awareness in exploring the potential benefits of these products from both animal and human health perspectives (Bucio-Noble et al., 2018; Deseo et al., 2020). Various types of Reactive Oxygen Species (ROS), including hydrogen peroxide, nitrogen dioxide, superoxide and hydroxyl radicals generated in the body, have the potential to cause damage to biomolecules such as DNA, RNA and proteins (Halliwell, 2013; Feig et al., 1994). Unregulated oxidative stress, particularly long term, is understood to be contributing to the progression of inflammatory diseases (Mittal et al., 2014; Oyinloye et al., 2015). Intestinal diseases in young pigs and chickens, including diarrhoea and enteritis, are associated with oxidative stress and inflammatory reactions, underlining the importance of addressing these factors in managing and preventing such diseases (Lauridsen, 2019). ROS serve as cellular response mediators that can trigger the production of cytokines from many types of cells (Vassilakopoulos et al., 2002). Cytokines, which are proteins generated by several types of immune cells, play vital roles in the immune response by coordinating both physiological as well as behavioural changes required for the immunological challenges faced by animals (Nordgreen et al., 2020). Inflammatory cytokines are rapidly induced in initial stages of disease or injury processes, without the reliance on specific antigens, highlighting their significance in the early phases of immune activation (Murtaugh et al., 1996). Phenolic compounds derived from sugarcane demonstrate that the efficacy in mitigating oxidative stress and inflammation. Bucio-Noble et al. demonstrated ethanol extracts obtained from whole dried sugarcane consisting of polyphenols such as flavonoids displayed potent antioxidant

activity, with these bioactive compounds playing a significant role in modulating inflammatory mediator proteins (Bucio-Noble et al., 2018).

Upon examining the impact of a sugarcane juice extract into weanling pig feed on immune responses, a study by Lo et al. showed enhanced cytotoxicity by natural killer (NK) cells, accompanied by up to 58% increase in the phagocytic activity of monocytes (Lo et al., 2005). In another study, the effect of inclusion of the same extract in feed against pseudorabies infection in pigs revealed additional immunological effects. These effects included a 76% increase in lymphocyte proliferation, and up to 52% increase in interferon-gamma (IFN- $\gamma$ ) producing cells. Additionally, the supplementation of a sugarcane juice extract in the diet also resulted in milder clinical signs of pseudorabies infection in these weanling pigs, as well as reduced severity of non-suppurative encephalitis (Lo et al., 2006). Results from these two studies indicate the ability of sugarcane extracts in modulating both the innate immune response, as well as regulating the adaptive immune cells and cytokine production. Collectively, these studies can be used to suggest possibilities of utilizing sugarcane extracts in minimizing the use of antibiotics in farmed pigs. This is a valuable implication of sugarcane product supplementation to pig feed, as the use of antibiotics in livestock have been linked to high levels of antimicrobial resistant bacteria in animals, which has a subsequent detrimental effect on public health (Wegener, 2003; Chang et al., 2015). While sugarcane products hold the potential to serve as an antibiotic alternative, there needs to be a comprehensive comparison between sugarcane extracts and conventional antibiotics, evaluating their impact on pig health, growth, and overall well-being.

In a study carried out by Matsumoto et al. (2021), the authors evaluated the ability of a sugarcane extract to suppress *Escherichia coli* induced diarrhoea in weaning pigs of 21 days old, which showed 0% mortality in the pigs fed 1.0% (w/w) sugarcane extract supplemented to their basal diet. Sugarcane supplementation also improved both the incidence and duration of diarrhoea in these pigs, while reducing the relative abundance of *Enterobacteriaceae* in the jejunum and ileum (Matsumoto et al., 2021). The *Enterobacteriaceae* family comprises of pathogens that pose a significant threat to the livestock industry and can lead to foodborne outbreaks, thereby jeopardizing human health (Wang et al., 2021). While the authors attributed the presence of polyphenols in the sugarcane extract to the observed improvement in immunity, there was no comprehensive chemical profiling of the extract to identify or quantify the polyphenols present. Results of this study carry significant implications such as promising improvements in the wellbeing of pigs. This can potentially have positive downstream implication on meat safety, and human health, therefore, a more comprehensive exploration of the identity of polyphenols responsible for these beneficial effects is crucial to gain an improved understanding of the functional components within these extracts.

It is necessary to consider the supplementation dosage of sugarcane products in pig diets when assessing their potential benefits. In a study conducted by Wijesiriwardana et al. (2020), the authors revealed interesting findings of gilts and sows. Despite an 11% increase in the dietary polyphenol content due to the supplementation of a sugarcane extract that was fed from day 110 of gestation to lactation stages, there was no discernible impact on the inflammatory marker Interleukin-1 $\beta$  in pigs (Wijesiriwardana et al., 2020). It is worth noting that this study utilized a single dose of the extract and did not employ a dose-response design, which leaves room for consideration that the tested dose may not have been sufficient to trigger an immune response. Moreover, in this study, a single cytokine, Interleukin-1 $\beta$ , was employed to evaluate the inflammatory response. Interleukin-1 $\beta$  is a key pro-inflammatory cytokine associated with both acute and chronic inflammatory conditions (Ren and Torres, 2009). It is worth considering that the sugarcane extract may potentially modulate the inflammatory response through other pro-inflammatory cytokines. These results highlight the complexity of nutritional strategies in pig diets, the potential for precision feeding, and the multifaceted nature of immune and inflammatory responses in pigs, all warranting the prerequisite for further investigation.

In a study by Amer et al. (2004), the authors investigated the effects of a sugarcane juice extract supplemented at 500 mg/kg/day to the crop of immunosuppressed 3-weeks old chickens, which resulted in increased levels of total antibodies in response to *Brucella abortus* and sheep red blood cells. Additionally, it demonstrated an improved delayed-type hypersensitivity (DTH) response to Human  $\gamma$  Globulin (Amer et al., 2004). This suggests the enhanced ability of these chickens to fight specific pathogens and exerting cell mediated reactions, particularly with regards to the DTH response (Black, 1999). The authors' omission of specific mechanisms underlying the observed protective effects of sugarcane extract against immunosuppression underlines the value of

comprehensively chemically profiling the extract, such as using High Resolution Liquid Chromatography-Mass Spectrometry approaches, to gain insights into the compounds responsible for these immunological effects.

In a study by Awais and Akhtar (2012), the authors focused on the administration of an aqueous extract of sugarcane juice and an ethanoic extract of sugarcane bagasse at 4 mL/kg of body weight/day to 5-7 days old broiler chickens. The results showed an increased lymphoproliferative response against Concanavalin-A both *in vivo* and *in vitro*. The study also reported findings of increased Immunoglobulin (Ig) titers (i.e. IgG, IgM and total Ig) against sheep red blood cells, along with increased organ-body weight ratios of lymphoid organs, indicative of immune cell activation and proliferation in chickens (Awais and Akhtar, 2012). Specifically, the Ig responses propose an antigen binding and effector immune role as a result of bagasse administration (Lefranc and Lefranc, 2001). Awais et al. (2011) also investigated the anti-coccidial effects of the same two extracts at 4 mL/kg of body weight/day in 5-7 days old broiler chickens, where both extracts increased the resistance against coccidiosis. Notably, the protective effects were more prominent in the ethanolic bagasse extract, followed by the aqueous juice extract. Both extracts also improved the humoral antibody response, where the serum antibody titers were significantly increased when the extracts were supplemented (Awais et al., 2011). These studies encompassed two separate extracts from different sugarcane products, therefore, a comprehensive chemical analysis becomes imperative to determine and quantify the specific constituents within each extract and product, offering insights into how these components may be contributing to the observed immunological effects. The need for a comprehensive chemical analysis is particularly crucial in this case, considering that different extraction solvents have the ability to extract different components from the products, potentially influencing the observed immunological effects. Together, these studies offer the promising prospect of sugarcane product supplementation in enhancing the immune response in broiler chickens.

When sugarcane bagasse at 10 g/Kg was used in a study by Lumsangkul et al. (2021) as a dietary supplement for Nile Tilapia fish, it was able to demonstrate an increase in the expression of Interleukin (IL) cytokines, including IL-1 and IL-8. Additionally, lipopolysaccharide binding protein (LBP), glutathione enzymes and genes were also increased in response to bagasse supplementation (Lumsangkul et al., 2021). In addition to the indications of stimulating an inflammatory response as evident by the production of cytokines, increased LBP, and glutathione enzymes and genes suggest improved protection against infection, and oxidative stress, respectively (Hayes and McLellan, 1999; Lamping et al., 1998). These results suggest that supplementation with sugarcane bagasse may have immunomodulatory and antioxidant effects, contributing to improved overall health and resilience in Nile Tilapia fish.

In the investigation of livestock immunity, gut immunity also plays a dominant role in understanding its overall impact on animal health and well-being. The complex and diverse community of microorganisms residing in the animal intestinal organs, known as the gut microbiome, has been shown to have significant implications for immune function (Chen et al., 2021; Kraimi

et al., 2019). An *in vitro* study by Loo et al. (2022) carried out on a pig faecal fermentation model revealed that a 1g mixture of sugarcane extract and sugarcane fibre altered the pig faecal microbiome, increasing the abundance of probiotic bacteria such as *Lactobacillus*, and decreasing the abundance of harmful bacteria such as *Escherichia-Shigella*. With the sugarcane extract having a total phenolic content of 18 mg (GAE)/mL and a total flavonoids content of 4.2 mg (CE)/mL, this study highlights the beneficial incorporation of sugarcane polyphenols and fibre in the positive alteration of pig gut physiology (Loo et al., 2022). Another *in vitro* study carried out by Loo et al. (2023) demonstrated a similar effect on the pig gut microbiome following the introduction of 0.5 g of sugarcane extract and sugarcane fibre with a total phenolic content of 57.6 mg GAE, where the mixture resulted in the abundance in *Lactobacillus*, while reducing the harmful bacteria of the genus *Streptococcus*. While this study also reinforces the positive effects of polyphenols on the pig gut microbiome, the incorporation of polyphenols and fibre mixture resulted in greater beneficial effects than sugarcane polyphenols or sugarcane fibre alone (Loo et al., 2023). Taken together, the results of these two *in vitro* studies show a potential way to maximise the beneficial effects of sugarcane polyphenols on the pig gut microbiome by the incorporation of other products. Further investigations are required to elucidate the specific polyphenols present in the sugarcane extract and to determine the precise fibre content. Understanding these components in greater detail is crucial for deciphering how they may contribute to positively modulating the pig gut microbiome.

The gut microbiome has a lesser reliance on feed intake, while the structure of the rumen microbiome exhibits a clear correlation with feed intake, highlighting its sensitivity to dietary patterns (Monteiro et al., 2022). In a study by Li et al. (2021), the authors examined the inclusion of sugarcane tops in goat diets. It was observed that the addition of sugarcane tops positively impacted the community structure and diversity of the goat rumen microbiota (Li et al., 2021). The incorporation of sugarcane tops led to increased alpha and beta diversity, metrics used to analyse microbiome diversity within and between samples, indicating its potential as a valuable feed additive for goats (Li et al., 2021; Kers and Saccenti, 2022). To further highlight the importance of these findings, it is essential to conduct chemical analyses aimed at delineating the exact composition of the sugarcane top extract. Akhtar et al. (2008) reported enhanced cell-mediated immunity involving neutrophils, macrophages, and NK cells, as well as improved antibody response to sheep red blood cells against *Eimeria*, following sugarcane juice supplementation in 12-day-old broiler chickens (Akhtar et al., 2008). In a study by Shakeri et al. (2020), the authors reported the anti-oxidant effects against heat stress with sugarcane extract supplementation for broiler chickens of one-day age measured by breast muscle lipid peroxidase (TBARS). The authors reported a linear reduction in breast muscle TBARS as the dose of sugarcane extract increased from 0-10 g/Kg (Shakeri et al., 2020). The TBARS assay is a widely employed method for assessing lipid oxidation and determining antioxidant activity in food analysis (Ghani et al., 2017). While both studies encompassed a dose-response design, once again, the absence of chemical profiling for both supplemented extracts emphasize a key research gap, impeding the capacity to identify the specific components accountable for the

observed positive effects. Furthermore, immunological effects of a sugarcane juice extract were extensively studied on chickens, where it revealed improved humoral immune responses, improved lymphoid organ morphology and weight, protection against *Eimeria tenella*, and improved delayed-hypersensitivity responses (El-Abasy et al., 2003a; El-Abasy et al., 2004; El-Abasy et al., 2003b; El-Abasy et al., 2002).

It is also worth noting that antibiotics incorporated into animal feed can have an impact on the environment. Antibiotics employed in animal agriculture can navigate their way into the environment through various channels, from the drug manufacturing phase to the disposal of unused medications and containers. Additionally, their presence in animal waste materials used or applied in agricultural practices further contributes to environmental contamination (Chee-Sanford et al., 2012). Therefore, considering sugarcane products as an alternative to current antibiotics hold potential to be a more environmentally friendly approach in animal feed considerations.

Where sugarcane products have undergone chemical profiling to identify the specific types of polyphenols present, it unveiled the occurrence of flavonoids and phenolic acids in these products (Oliveira et al., 2022). Flavonoids such as quercetin, apigenin, and luteolin (sub-classes: flavonols and flavones), and phenolic acids such as vanillic acid, syringic acid, and ferulic acid (sub classes: hydroxybenzoic and hydroxycinnamic acids), are amongst the different polyphenols found in various sugarcane derivatives. Molina-Cortés et al. (2023)). reported a quantitative heatmap of polyphenols present in different sugarcane products, where flavones were the most enriched polyphenol type in sugarcane leaves, molasses and juice. Additionally, sugarcane rind and bagasse were abundant in anthocyanins and phytosterols, respectively (Molina-Cortés et al., 2023). The observed immunological effects of sugarcane products or extract supplementation may be attributed to the enrichment of polyphenols in these products. These polyphenols are known for their potential to enhance immunity. For example, in a study by Prakash et al., the researchers demonstrated the anti-inflammatory effects of a polyphenol-rich sugarcane extract on *in vitro* human and mouse cell lines in reducing the levels of a range of inflammatory cytokines including TNF- $\alpha$ , IL-4, IL-8 and IFN- $\gamma$  cytokines, attributing their mechanisms of action to NF- $\kappa$ B and VEGF-1 regulatory pathways (Prakash et al., 2021). Furthermore, Rueda-Gensini et al. examined the anti-inflammatory effects of non-centrifugal cane sugar where they reported the immunomodulatory activities to function via the TLR-4 pathway in human monocytes (Rueda-Gensini et al., 2022). However, further research is warranted to gain a deeper understanding and a broader perspective of the exact targets in these pathways underlying these actions. Exploring the intricate mechanisms by which polyphenols influence immune response in pigs and chickens can provide valuable insights into their potential as immunomodulatory agents. It is important to unravel the specific molecular pathways and cellular interactions involved, in order to comprehensively understand the immunological benefits conferred by sugarcane supplementation. Such knowledge can inform the development of targeted strategies to optimize the immunomodulatory effects of sugarcane products in swine and poultry.

### 3 Impact on animal growth performance

The key factor in selecting suitable feed additives is the priority of animal health and well-being, as feed additives perform a variety of functions, including fulfilling essential nutrient requirements, optimising growth performance, and improving feed utilization (Wenk, 2003). To meet the increasing demand for high-quality feed ingredients while managing the associated costs, it is necessary to also explore alternative ingredients that offer animal feed the superior quality, while also being economically affordable (Saadaoui et al., 2021). Having access to abundant feed throughout the year is a critical aspect in defining the success in the farm animal industry, and particularly sugarcane, given that it is typically available during seasons where other feedstuffs are in limited supply (Akinbode et al., 2017). When utilising different types of sugarcane by-products including molasses, bagasse, straw and cane tops, either in isolation or in combination in livestock feed, various pre-treatment strategies are also available to maximise digestibility and enhance the dietary quality of the feed (Bordonal et al., 2018).

Several studies have assessed the growth performance of pigs, chicken and aquaculture species as a result of sugarcane product, by-product or extract supplementation in feed. Observed positive outcomes suggest that sugarcane supplementation in feed can contribute to enhanced growth rates and improved weight gain in these animals. In a study by Matsumoto et al. (2021), the authors demonstrated enhanced final body weight in 21-days old male pigs through sugarcane extract supplementation at 1.0% w/w and 0.1% w/w doses compared to a basal (control) diet, while Akhtar et al. (2008) similarly observed improved growth in 12-days old broiler chickens with sugarcane juice supplementation, with the maximum weight gain observable at 400 mg/kg body weight compared to the control condition (Matsumoto et al., 2021; Akhtar et al., 2008). Growth performance in seafood animals was also examined across various studies. For example, Shimul et al. (2018) found enhanced growth in tilapia fingerling with sugarcane extract supplementation at 120 mg/Kg feed compared to a 0% polyphenol (control) diet, Moriyama et al. (2021) observed dose-dependent weight gain in rainbow trout and coho salmon with sugarcane bagasse supplementation at 100 mg/Kg and 500 mg/Kg doses compared to a 0 mg/Kg (control) condition, whilst Penglase et al. (2022) reported a 54% amplified growth in post-larvae black tiger shrimp following sugarcane extract supplementation at 6 g/Kg diet dose, compared to a sugarcane extract-free (control) diet (SHIMUL et al., 2018; Moriyama et al., 2021; Penglase et al., 2022). The specific components of sugarcane, such as polyphenols and other nutrients, may play a role in promoting growth and development. For example, sugarcane leaves are high in its level of crude fibre, and are enriched in soluble carbohydrates (Mahala et al., 2013). Further exploration is necessary to discern whether these observed variations in growth performance are attributable to the palatability of the extracts, potentially influencing the feed intake of these animals.

Where growth investigations were carried out by supplementing sugarcane products, and either no observable effects or no detrimental effects were demonstrated on the animals, it could suggest the influence of various factors,

including animal species, dosage, duration of supplementation, and other dietary components added to the feed on growth performance. It is important to consider these factors when formulating pig, chicken or fish diets with sugarcane products to optimise growth outcomes, alongside improving immunity. Moreover, these extracts vary in chemical composition, and therefore, chemically profiling them using chromatographical and spectroscopical means to identify the constituents will provide useful insights into their biological functions.

Regarding animal performance, a study by Pu et al. (2022) was carried out on male quail after supplementing their feed with an extract derived from sugarcane molasses, where the effects of reproductive endocrine activity was evaluated. The study reported a decrease in serum testosterone, and testicular and epididymal weight, an inhibition of hydroxysteroid dehydrogenase and suppressed sexual behaviour, suggesting the ability of sugarcane molasses supplementation on impeding steroidogenesis (Pu et al., 2022). The authors concluded that this was useful in the poultry industry in managing livestock, as decreased testosterone leads to efficient feed to growth conversion, as well as contributing to improved quality of meat (Rikimaru et al., 2009). While this study focused on quail, a component of the poultry industry, further research across other sectors such as broilers is imperative. Extending the positive implications of this study to the entire poultry industry necessitates comprehensive exploration across various poultry branches. Research exploring the impact of sugarcane supplementation in farm animal feed frequently delves into both growth and performance, highlighting a possible correlation between the two aspects. Additionally, animal performance was assessed in tandem with immune health, suggesting an interconnected relationship between immunity and overall performance. In a recent dairy study conducted by Ahmed et al. (2023), Holstein x Friesian cows ranging from early, mid and late phases of lactation were supplemented with a sugarcane extract at a low dosage of 0.25% of the dry matter intake, which showcased an increase in milk yield, a reduction in methane emission, and an improvement in their mastitis condition. The results for each of these aspects following the treatment with the sugarcane extract were compared to that of pre-treatment results (Ahmed et al., 2023). It is important to comprehensively profile this sugarcane extract to identify the specific compounds, including polyphenols responsible for the observed positive outcomes. Moreover, additional research on ruminants and sugarcane supplementation is essential to establish conclusive evidence regarding the positive effects of sugarcane product supplementation on ruminant performance.

Furthermore, methane stands as the primary greenhouse gas emitted during the natural digestive processes of ruminants and it is crucial to highlight that the release of greenhouse gases by animals and its consequential influence on climate change represent significant global concerns (Broucek, 2014). Therefore, the authors' finding relating to the methane reduction in response to sugarcane extract supplementation can have significant positive environmental impact.

The incorporation of sugarcane by-products into feed has been shown to improve the quality of chicken, as evidenced by a study by Shakeri et al., where sugarcane extract supplementation for one-day



old broiler chickens improved the tenderness of meat compromised by heat stress (Shakeri et al., 2020). Texture is one of the predominant aspects relating to the quality of animal products, and it represents one of the critical sensory properties contributing to the assessment of final quality of poultry meat (Fletcher, 2002). Although the exact aetiology is unclear, several factors affect meat tenderness including temperature, length of sarcomeres and proteolysis as these factors evidently affect the conversion of muscle to meat process (Maltin et al., 2003). The authors utilised four doses of the sugarcane extract ranging from 2–10 mg/Kg and compared the effects to a sugarcane-free control diet. This study demonstrated the positive effects of the inclusion of sugarcane with respect to meat quality, as the authors reported an increase in muscle myofibrillar fragmentation index and decrease in shear force in a dose-dependent manner, both of which correlate with increased meat tenderness. Furthermore, it was also able to negate the consequences of heat stress on multiple aspects including pH, water content and muscle colour (Shakeri et al., 2020; Bencini and Purvis, 1990). Additionally, regarding the quality of milk from early, mid and late phases of lactation cows in response to sugarcane extract supplementation, the study by Ahemd et al. can be considered, where the authors reported a 53% reduction in the somatic cell count (Ahmed et al., 2023). Minimizing mastitis and

ensuring the production of high-quality milk are essential for dairy farmers aiming to maintain competitiveness in the marketplace. Somatic cell count of milk has served as a longstanding tool in achieving this goal (Ruegg and Pantoja, 2013). Milk from infected cows typically exhibits an elevated raw milk somatic cell count, indicating potential mastitis issues (Ma et al., 2000). Hence, incorporating sugarcane extract at a dosage of 0.25% of the dry matter intake holds promise for enhancing dairy quality. The integration of sugarcane by-products into animal feed presents a promising avenue to enhance the quality of animal-derived products. These findings underline the potential for improved meat tenderness, milk yield, and overall product quality while aligning with modern consumer expectations for nutritious, safe, and affordable food choices, thus contributing to the sustainable advancement of the livestock industry. Therefore, it is crucial to investigate the quality attributes of animal-derived products when sugarcane supplementation is integrated into feed. Further research is essential to elucidate how the favourable outcomes of sugarcane supplementation can influence product quality.

Table 1 provides an overview of the recent studies conducted on different farm animals raised for human consumption, and the effects of immunity, growth and quality upon feed supplementation with sugarcane products, with a particular focus on swine and poultry.

TABLE 1 Impact of sugarcane product supplementation on animal immunity, growth, performance, and quality of derived products.

Food Type	Animal	Theme	Sugarcane Products Supplemented in Feed	Effect of Supplementation	References
Red meat	Pig	Immunity Growth	Extract derived from sugarcane juice	Enhanced immune response Reduced disease severity No significant growth improvement	(Lo et al., 2006; Lo et al., 2005)
		Gut Immunity Growth	Sugarcane extract	Improved gastrointestinal health  Microbiota modulation Metabolic improvements Improved growth	(Matsumoto et al., 2021)
		Immunity Growth	Patented sugarcane extract	No significant effect on the inflammatory response No observed improvement in growth performance	(Wijesiriwardana et al., 2020)
	Goat	Gut Immunity Growth	Sugarcane top	Different diversity and community structures of rumen microbiota No effect on growth performance and plasma biochemical parameters	(Li et al., 2021)
Poultry	Chicken	Immunity Growth	Extract derived from sugarcane juice	Enhanced antibody production Improved delayed-hypersensitivity responses Improved body weight	(Amer et al., 2004)
		Immunity Growth	Sugarcane juice, bagasse	Enhanced immune response Improved organ-body weight ratios Improved body weight gain Improved feeding efficiency	(Awais and Akhtar, 2012)
		Immunity Growth	Sugarcane juice	Increased antibody response, improved cell-mediated immune response Decreased mortality, decreased lesion scores, decreased oocysts in faeces, mild haemorrhages Increased body weight gain	(Akhtar et al., 2008)
		Immunity Quality	Patented sugarcane extract		(Shakeri et al., 2020)

(Continued)



TABLE 1 Continued

Food Type	Animal	Theme	Sugarcane Products Supplemented in Feed	Effect of Supplementation	References
				Anti-oxidant effect Improved meat tenderness Mitigation of heat stress	
		Immunity Growth	Sugarcane juice, bagasse	Anti-coccidial effect Enhanced humoral immune response Improved body weight gain	(Awais et al., 2011)
		Immunity Growth	Extract derived from sugarcane juice	Enhanced immune response, improved humoral immune response Improved body weight gain	(El-Abasy et al., 2002)
		Immunity Growth	Extract derived from sugarcane juice	Enhanced immune response Improved body weight gain Improved lymphoid organ morphology and weight	(El-Abasy et al., 2004)
		Immunity Growth	Extract derived from sugarcane juice	Enhanced immune response Improved body weight gain Decreased mortality, decreased lesion scores, decreased oocysts in faeces, mild haemorrhages	(El-Abasy, 2003a)
		Immunity	Extract derived from sugarcane juice	Enhanced immune response Improved delayed-hypersensitivity responses	(El-Abasy, 2003b)
	Quail	Growth	Extract derived from sugarcane molasses	Suppressed sexual behaviour Decreased testosterone levels Altered reproductive organ characteristics Inhibition of Hydroxysteroid Dehydrogenase	(Pu et al., 2022)
Seafood	Tilapia	Immunity Growth	Sugarcane bagasse	Enhanced immune response Improved mucosal defence Enhanced respiratory burst activity Increased growth performance	(Lumsangkul et al., 2021)
		Growth Performance	Patented sugarcane extract	Improved growth performance Enhanced condition factor Improved feed conversion ratio	(SHIMUL et al., 2018)
	Salmon	Growth	Sugarcane bagasse	Dose-dependent weight gain Increased Insulin-like Growth Factor-1 mRNA levels	(Moriyama et al., 2021)
	Shrimp	Growth	Patented sugarcane extract	Increased growth Increased feed conversion ratio Increased survival	(Penglase et al., 2022)
Diary	Cow	Quality Performance	Patented sugarcane extract	Increased milk yield Decreased Methane emission Improved mastitis	(Ahmed et al., 2023)

## 4 Conclusions and future perspectives

The exploration of sugarcane products as viable supplements in the diets of swine, poultry and fish raised for human consumption presents a multifaceted strategy with potential benefits for immunity and growth. The increasing global demand for animal-based products necessitates a sustainable approach to production that prioritizes animal health while ensuring optimal growth and performance. This mini-review highlights the potential of sugarcane products as valuable additions to swine, poultry, aquaculture species and ruminant feed. These products contain bioactive compounds, including polyphenols, known for their antioxidant properties. The studies discussed here demonstrate the positive impact of sugarcane supplementation on various aspects of immunity, including modulation of inflammatory responses, enhanced immune cell activities, and improved resistance against infections.

Furthermore, sugarcane supplementation shows promise in promoting growth and performance in swine, poultry and fish. Several studies spanning different species, including pigs, chickens, tilapia fish, and quail, consistently reveal positive outcomes in terms of enhanced weight gain, improved growth rates, and increased reproductive efficiency. The observed benefits suggest the potential of sugarcane products to serve as alternative feed ingredients, contributing to the overall well-being of these animals.

The quality of animal-derived products, such as meat and milk, is a critical aspect of modern food production. The inclusion of sugarcane products in animal diets has demonstrated positive effects on meat tenderness and milk yield. These findings align with evolving consumer expectations for high-quality, nutritious, and sustainable food choices.

Despite the promising results, it is essential to acknowledge the existing gaps in research, such as the necessity for comprehensively

applying analytical chemical profiling techniques to identify specific bioactive compounds responsible for observed effects in sugarcane products. Additionally, dose-response studies and investigations into the potential variations based on animal species, duration of supplementation, and other dietary components are necessary for optimizing the outcomes of sugarcane supplementation.

## Author contributions

NE: Conceptualization, Writing – original draft, Writing – review & editing. MF: Conceptualization, Writing – review & editing. DP: Supervision, Writing – review & editing. RZ: Supervision, Writing – review & editing. KL: Writing – review & editing. DD: Conceptualization, Supervision, Writing – review & editing.

## Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. This mini-review was funded by The Product Makers (TPM) Australia Pty. Ltd., Keysborough, Victoria, Australia. The funder had no role in conceptualizing the topics presented in this review apart from

reviewing and editing. The funder agreed for the study to be submitted for publication.

## Conflict of interest

Author MF and KL are employed by the company The Product Makers Australia Private Limited. The remaining 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.

The authors declare that this study received funding from The Product Makers Australia Private Limited. The funder had the following involvement in the study: payment of the publication charges.

## Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

## References

- Ahmed, A., Flavel, M., Mitchell, S., Macnab, G., Dunuarachchige, M. D., Desai, A., et al. (2023). Increased milk yield and reduced enteric methane concentration on a commercial dairy farm associated with dietary inclusion of sugarcane extract (*Saccharum officinarum*). *Animals* 13, 3300. doi: 10.3390/ani13203300.
- Akhtar, M., Hafeez, M. A., Muhammad, F., Haq, A. U., and Anwar, M. I. (2008). Immunomodulatory and protective effects of sugar cane juice in chickens against *Eimeria* infection. *Turkish J. Vet. Anim. Sci.* 32, 463–467.
- Akinbode, R., Isah, O., Oni, A., Arigbede, O., and Ojo, V. (2017). Nutritional evaluation of sugarcane top ensiled with varying proportion of broiler litter. *Livestock Res. Rural Dev.* 29, 2017. Available at: <http://www.lrrd.org/lrrd29/1/akin29006.html>
- Aland, A., and Madec, F. (2009). *Sustainable animal production: the challenges and potential developments for professional farming* (Wageningen, Netherlands: Wageningen Academic Publishers). doi: 10.3920/978-90-8686-685-4.
- O. Almazán, L. Gonzalez and L. Galvez (Eds.) (1999). *The sugar cane, its by-products and co-products. Proceedings of the Third Annual Meeting of Agricultural Scientists, Réduit, Mauritius, 17-18 November 1998* (Réduit, Mauritius: Food and Agricultural Research Council).
- Amer, S., Na, K.-J., El-Abasy, M., Motobu, M., Koyama, Y., Koge, K., et al. (2004). Immunostimulating effects of sugar cane extract on X-ray radiation induced immunosuppression in the chicken. *Int. Immunopharmacol.* 4, 71–77. doi: 10.1016/j.intimp.2003.10.006.
- Awais, M. M., and Akhtar, M. (2012). Evaluation of some sugarcane (*Saccharum officinarum* L.) extracts for immunostimulatory and growth promoting effects in industrial broiler chickens. *Pakistan Vet. J.* 32, 398–402.
- Awais, M. M., Akhtar, M., Muhammad, F., ul Haq, A., and Anwar, M. I. (2011). Immunotherapeutic effects of some sugar cane (*Saccharum officinarum* L.) extracts against coccidiosis in industrial broiler chickens. *Exp. Parasitol.* 128, 104–110. doi: 10.1016/j.exppara.2011.02.024.
- Bagno, O., Prokhorov, O., Shevchenko, S., Shevchenko, A., and Dyadichkina, T. (2018). Use of phytobiotics in farm animal feeding. *Agric. Biol.* 53, 687–697. doi: 10.15389/agrobiol.2018.4.687eng
- Barton, M. D. (2000). Antibiotic use in animal feed and its impact on human health. *Nutr. Res. Rev.* 13, 279–299. doi: 10.1079/095442200108729106.
- Bencini, R., and Purvis, I. (1990). The yield and composition of milk from Merino sheep. *Wool Technol. Sheep Breeding* 38, 71–73.
- Black, C. A. (1999). Delayed type hypersensitivity: Current theories with a historic perspective. *Dermatol. Online J.* 5. doi: 10.5070/D32fw0g1xx).
- Bordonal, R., Carvalho, J. L. N., Lal, R., de Figueiredo, E. B., de Oliveira, B. G., and La Scala, N. (2018). Sustainability of sugarcane production in Brazil. A review. *Agron. Sustain. Dev.* 38, 1–23. doi: 10.1007/s13593-018-0490-x.
- Broucek, J. (2014). Production of methane emissions from ruminant husbandry: a review. *J. Environ. Protect.* 5, 1482. doi: 10.4236/jep.2014.515141.
- Bucio-Noble, D., Kautto, L., Krisp, C., Ball, M. S., and Molloy, M. P. (2018). Polyphenol extracts from dried sugarcane inhibit inflammatory mediators in an *in vitro* colon cancer model. *J. Proteom.* 177, 1–10. doi: 10.1016/j.jprot.2018.02.009.
- Burdick Sanchez, N. C., Broadway, P. R., and Carroll, J. A. (2021). Influence of yeast products on modulating metabolism and immunity in cattle and swine. *Animals* 11, 371. doi: 10.3390/ani11020371
- Cabello, A., Torres, A., and Almazán, O. (2008). The economical viability of animal production based on sugarcane co-products under the present prices of commodities. *Sugar Tech.* 10, 25–28. doi: 10.1007/s12355-008-0004-2.
- Cabral, A., Carvalho, F., Santos, G., Ferreira, J., Silva, M., Santos, G., et al. (2020). Use of sugar cane to feed lactating dairy goats. *Arquivo Brasileiro Medicina Veterinária e Zootecnia* 72, 2297–2307. doi: 10.1590/1678-4162-12022.
- Carvalho, C., Zuccari, A. M., Pereira, W., Moura, A. M., Schultz, N., Paiva, A. J., et al. (2022). Evaluation of sugarcane for animal feed in the Baixada Fluminense-RJ. *Rev. Ciec. Agron.* 53. doi: 10.5935/1806-6690.20220055.
- Chang, Q., Wang, W., Regev-Yochay, G., Lipsitch, M., and Hanage, W. P. (2015). Antibiotics in agriculture and the risk to human health: how worried should we be? *Evol. Appl.* 8, 240–247. doi: 10.1111/eva.12185.
- Chee-Sanford, J. C., Krapac, I. J., Yannarell, A. C., and Mackie, R. I. (2012). 29. *Environmental Impacts of Antibiotic Use in the Animal Production Industry* (Sweden: Baltic University Press).
- Chen, S., Luo, S., and Yan, C. (2021). Gut microbiota implications for health and welfare in farm animals: A review. *Animals* 12, 93. doi: 10.3390/ani12010093.

- de Paula, C. B. C., de Paula-Elias, F. C., Rodrigues, M. N., Coelho, L. F., de Oliveira, N. M. L., de Almeida, A. F., et al. (2021). Polyhydroxyalkanoate Synthesis by *Burkholderia glumae* into a sustainable sugarcane biorefinery concept. *Front. Bioeng. Biotechnol.* 8, 631284. doi: 10.3389/fbioe.2020.631284.
- Deseo, M. A., Elkins, A., Rochfort, S., and Kitchen, B. (2020). Antioxidant activity and polyphenol composition of sugarcane molasses extract. *Food Chem.* 314, 126180. doi: 10.1016/j.foodchem.2020.126180.
- El-Abasy, M., Motobu, M., Na, K.-J., Shimura, K., Nakamura, K., Koge, K., et al. (2003a). Protective effects of sugar cane extracts (SCE) on *Eimeria tenella* infection in chickens. *J. Vet. Med. Sci.* 65, 865–871. doi: 10.1292/jvms.65.865.
- El-Abasy, M., Motobu, M., Nakamura, K., Koge, K., Onodera, T., Vainio, O., et al. (2004). Preventive and therapeutic effects of sugar cane extract on cyclophosphamide-induced immunosuppression in chickens. *Int. Immunopharmacol.* 4, 983–990. doi: 10.1016/j.intimp.2004.01.019.
- El-Abasy, M., Motobu, M., Sameshima, T., Koge, K., Onodera, T., and Hirota, Y. (2003b). Adjuvant effects of sugar cane extracts (SCE) in chickens. *J. Vet. Med. Sci.* 65, 117–119. doi: 10.1292/jvms.65.117.
- El-Abasy, M., Motobu, M., Shimura, K., Na, K. J., Kang, C. B., Koge, K., et al. (2002). Immunostimulating and growth-promoting effects of sugar cane extract (SCE) in chickens. *J. Vet. Med. Sci.* 64, 1061–1063. doi: 10.1292/jvms.64.1061.
- Feig, D. I., Reid, T. M., and Loeb, L. A. (1994). Reactive oxygen species in tumorigenesis. *Cancer Res.* 54, 1890s–1894s.
- Fletcher, D. (2002). Poultry meat quality. *World's Poult. Sci. J.* 58, 131–145. doi: 10.1079/WPS20020013.
- Gessner, D., Ringseis, R., and Eder, K. (2017). Potential of plant polyphenols to combat oxidative stress and inflammatory processes in farm animals. *J. Anim. Physiol. Anim. Nutr.* 101, 605–628. doi: 10.1111/jpn.12579.
- Ghani, M. A., Barril, C., Bedgood, D. R. Jr., and Prenzler, P. D. (2017). Measurement of antioxidant activity with the thiobarbituric acid reactive substances assay. *Food Chem.* 230, 195–207. doi: 10.1016/j.foodchem.2017.02.127.
- Halliwell, B. (2013). The antioxidant paradox: less paradoxical now? *Br. J. Clin. Pharmacol.* 75, 637–644. doi: 10.1111/j.1365-2125.2012.04272.x.
- Hamam, M., Chinnici, G., Di Vita, G., Pappalardo, G., Pecorino, B., Maesano, G., et al. (2021). Circular economy models in agro-food systems: A review. *Sustainability* 13, 3453. doi: 10.3390/su13063453.
- Hayes, J. D., and McLellan, L. I. (1999). Glutathione and glutathione-dependent enzymes represent a co-ordinately regulated defence against oxidative stress. *Free Radical Res.* 31, 273–300. doi: 10.1080/10715769900300851.
- Jaffé, W. R. (2015). Nutritional and functional components of non centrifugal cane sugar: a compilation of the data from the analytical literature. *J. Food Compos. Anal.* 43, 194–202. doi: 10.1016/j.jfca.2015.06.007.
- Kers, J. G., and Saccenti, E. (2022). The power of microbiome studies: Some considerations on which alpha and beta metrics to use and how to report results. *Front. Microbiol.* 12, 796025. doi: 10.3389/fmicb.2021.796025.
- Khairul, S.-A. M., Mahyudin, N. A., Abas, F., and Ab Rashid, N. K. M. (2022). The proximate composition and metabolite profiling of sugarcane (*Saccharum officinarum*) molasses. *Malaysian Appl. Biol.* 51, 63–68. doi: 10.55230/mabjournal.v51i2.2259.
- Kim, W. H., and Lillehoj, H. S. (2019). Immunity, immunomodulation, and antibiotic alternatives to maximize the genetic potential of poultry for growth and disease response. *Anim. Feed Sci. Technol.* 250, 41–50. doi: 10.1016/j.janifedsci.2018.09.016.
- Kraimi, N., Dawkins, M., Gebhardt-Henrich, S. G., Velge, P., Rychlik, I., Volf, J., et al. (2019). Influence of the microbiota-gut-brain axis on behavior and welfare in farm animals: A review. *Physiol. Behav.* 210, 112658. doi: 10.1016/j.physbeh.2019.112658.
- Lamping, N., Dettmer, R., Schröder, N., Pfeil, D., Hallatschek, W., Burger, R., et al. (1998). LPS-binding protein protects mice from septic shock caused by LPS or gram-negative bacteria. *J. Clin. Invest.* 101, 2065–2071. doi: 10.1172/JCI2338.
- Lauridsen, C. (2019). From oxidative stress to inflammation: Redox balance and immune system. *Poult. Sci.* 98, 4240–4246. doi: 10.3382/ps/pey407.
- Lefranc, M.-P., and Lefranc, G. (2001). *The immunoglobulin factsbook* (California, USA: Academic press).
- Li, M., Zi, X., Yang, H., Ji, F., Tang, J., Lv, R., et al. (2021). Effects of king grass and sugarcane top in the absence or presence of exogenous enzymes on the growth performance and rumen microbiota diversity of goats. *Trop. Anim. Health Prod.* 53, 1–13. doi: 10.1007/s11250-020-02544-8.
- Lo, D.-Y., Chen, T.-H., Chien, M.-S., Koge, K., Hosono, A., Kaminogawa, S., et al. (2005). Effects of sugar cane extract on the modulation of immunity in pigs. *J. Vet. Med. Sci.* 67, 591–597. doi: 10.1292/jvms.67.591.
- Lo, D.-Y., Chien, M.-S., Yeh, K.-S., Koge, K., Lin, C.-C., Hsuan, S.-L., et al. (2006). Effects of sugar cane extract on pseudorabies virus challenge of pigs. *J. Vet. Med. Sci.* 68, 219–225. doi: 10.1292/jvms.68.219.
- Loo, Y. T., Howell, K., Suleria, H., Zhang, P., Gu, C., and Ng, K. (2022). Sugarcane polyphenol and fiber to affect production of short-chain fatty acids and microbiota composition using *in vitro* digestion and pig faecal fermentation model. *Food Chem.* 385, 132665. doi: 10.1016/j.foodchem.2022.132665.
- Loo, Y. T., Howell, K., Suleria, H., Zhang, P., Liu, S., and Ng, K. (2023). Fibre fermentation and pig faecal microbiota composition are affected by the interaction between sugarcane fibre and (poly) phenols *in vitro*. *Int. J. Food Sci. Nutr.* 74, 219–233. doi: 10.1080/09637486.2023.2187329.
- Lumsangkul, C., Tapingkae, W., Sringarm, K., Jaturasitha, S., Le Xuan, C., Wannavijit, S., et al. (2021). Effect of dietary sugarcane bagasse supplementation on growth performance, immune response, and immune and antioxidant-related gene expressions of Nile tilapia (*Oreochromis niloticus*) cultured under Biofloc system. *Animals* 11, 2035. doi: 10.3390/ani11072035.
- Ma, Y., Ryan, C., Barbano, D., Galton, D., Rudan, M., and Boor, K. (2000). Effects of somatic cell count on quality and shelf-life of pasteurized fluid milk. *J. Dairy Sci.* 83, 264–274. doi: 10.3168/jds.S0022-0302(00)74873-9.
- Mahala, A., Mokhtar, A., Amasiab, E., and AttaElmnan, B. (2013). Sugarcane tops as animal feed. *Int. Res. J. Agric. Sci. Soil Sci.* 3, 147–151.
- Maltin, C., Balcerzak, D., Tilley, R., and Delday, M. (2003). Determinants of meat quality: tenderness. *Proc. Nutr. Soc.* 62, 337–347. doi: 10.1079/PNS2003248.
- Marshall, B. M., and Levy, S. B. (2011). Food animals and antimicrobials: impacts on human health. *Clin. Microbiol. Rev.* 24, 718–733. doi: 10.1128/CMR.00002-11.
- Matsumoto, H., Miyagawa, M., Yin, Y., and Oosumi, T. (2021). Effects of organic acid, *Enterococcus faecalis* strain EC-12 and sugar cane extract in feed against enterotoxigenic *Escherichia coli*-induced diarrhea in pigs. *AMB Express* 11, 1–10. doi: 10.1186/s13568-021-01228-2.
- Mittal, M., Siddiqui, M. R., Tran, K., Reddy, S. P., and Malik, A. B. (2014). Reactive oxygen species in inflammation and tissue injury. *Antioxid. Redox Signaling* 20, 1126–1167. doi: 10.1089/ars.2012.5149.
- Molina-Cortés, A., Quimbaya, M., Toro-Gomez, A., and Tobar-Tosse, F. (2023). Bioactive compounds as an alternative for the sugarcane industry: Towards an integrative approach. *Heliyon* 9, 1–20. doi: 10.1016/j.heliyon.2023.e13276.
- Monteiro, H. F., Zhou, Z., Gomes, M. S., Peixoto, P. M., Bonsaglia, E. C., Canisso, I. F., et al. (2022). Rumen and lower gut microbiomes relationship with feed efficiency and production traits throughout the lactation of Holstein dairy cows. *Sci. Rep.* 12, 4904. doi: 10.1038/s41598-022-08761-5.
- Moriyama, S., Miyasaka, K., and Furuta, T. (2021). Effects of somatic growth and insulin-like growth factor mRNA expression in the liver of salmon by feeding with sugarcane bagasse extract. *Aquac. Sci.* 69, 195–202.
- Murtaugh, M. P., Baarsch, M. J., Zhou, Y., Scamurra, R. W., and Lin, G. (1996). Inflammatory cytokines in animal health and disease. *Vet. Immunol. Immunopathol.* 54, 45–55. doi: 10.1016/S0165-2427(96)05698-X.
- Nordgreen, J., Edwards, S. A., Boyle, L. A., Bolhuis, J. E., Veit, C., Sayyari, A., et al. (2020). A proposed role for pro-inflammatory cytokines in damaging behavior in pigs. *Front. Vet. Sci.* 7, 646. doi: 10.3389/fvets.2020.00646.
- Novák, K. (2014). Functional polymorphisms in Toll-like receptor genes for innate immunity in farm animals. *Vet. Immunol. Immunopathol.* 157, 1–11. doi: 10.1016/j.vetimm.2013.10.016.
- Oliveira, A. L., Carvalho, M. J., Oliveira, D. L., Costa, E., Pintado, M., and Madureira, A. R. (2022). Sugarcane straw polyphenols as potential food and nutraceutical ingredient. *Foods* 11, 4025. doi: 10.3390/foods11244025.
- Oyinloye, B. E., Adenowo, A. F., and Kappo, A. P. (2015). Reactive oxygen species, apoptosis, antimicrobial peptides and human inflammatory diseases. *Pharmaceuticals* 8, 151–175. doi: 10.3390/ph8020151.
- Papatsiros, V., Katsoulos, P.-D., Koutoulis, K., Karatzia, M., Dedousi, A., and Christodoulou, G. (2014). Alternatives to antibiotics for farm animals. *CABI Rev.* 2013, 1–15. doi: 10.1079/PAVSNNR20138032.
- Penglas, S., Ackery, T., Kitchen, B., Flavel, M., and Condon, K. (2022). The Effects of a Natural Polyphenol Extract from Sugarcane (*Saccharum officinarum*) on the Growth, Survival, and Feed Conversion Efficiency of Juvenile Black Tiger Shrimp (*Penaeus monodon*). *Appl. Sci.* 12, 8090. doi: 10.3390/app12168090.
- Prakash, M. D., Stojanovska, L., Feehan, J., Nurgali, K., Donald, E. L., Plebanski, M., et al. (2021). Anti-cancer effects of polyphenol-rich sugarcane extract. *PLoS One* 16, e0247492. doi: 10.1371/journal.pone.0247492.
- Preston, T. (1983). The use of sugar cane and by-products for livestock. Chemistry and World Food Supplies: The New Frontiers, Chemrawn II: Invited Papers Presented at the International Conference on Chemistry and World Food Supplies, Manila, Philippines, 6–10 December 1982. *Int. Rice Res. Inst.* 337–348.
- Provenza, F. D., and Villalba, J. J. (2010). The role of natural plant products in modulating the immune system: an adaptable approach for combating disease in grazing animals. *Small Ruminant Res.* 89, 131–139. doi: 10.1016/j.smallrumres.2009.12.035.
- Pu, S., Kobayashi, S., Mizu, M., Furuta, T., Nagaoka, K., Gore, A. C., et al. (2022). Effects of sugar cane extract on steroidogenesis in testicular interstitial cells of male Japanese quail (*Coturnix japonica*). *J. Exp. Zoology Part A: Ecol. Integr. Physiol.* 337, 760–767. doi: 10.1002/jez.2633.
- Ren, K., and Torres, R. (2009). Role of interleukin-1 $\beta$  during pain and inflammation. *Brain Res. Rev.* 60, 57–64. doi: 10.1016/j.brainresrev.2008.12.020.
- Rikimaru, K., Yasuda, M., Komastu, M., and Ishizuka, J. (2009). Effects of caponization on growth performance and carcass traits in Hinai-jidori chicken. *J. Poult. Sci.* 46, 351–355. doi: 10.2141/jpsa.46.351.
- Rueda-Gensini, L., Serna, J. A., Bolaños, N. I., Rodriguez, J., Cruz, J. C., and Muñoz-Camargo, C. (2022). Evaluating the impact of thermal processing on the anti-inflammatory activity of non-centrifugal cane sugar: implications on cytokine

- secretion and TLR4 signaling. *Front. Pharmacol.* 13, 905347. doi: 10.3389/fphar.2022.905347.
- Ruegg, P., and Pantoja, J. (2013). Understanding and using somatic cell counts to improve milk quality. *Irish J. Agric. Food Res.* 52, 101–117. Available at: <https://www.jstor.org/stable/23631024>
- Saadaoui, I., Rasheed, R., Aguilar, A., Cherif, M., Al Jabri, H., Sayadi, S., et al. (2021). Microalgal-based feed: promising alternative feedstocks for livestock and poultry production. *J. Anim. Sci. Biotechnol.* 12, 76. doi: 10.1186/s40104-021-00593-z.
- Shakeri, M., Cottrell, J. J., Wilkinson, S., Le, H. H., Suleria, H. A., Warner, R. D., et al. (2020). A dietary sugarcane-derived polyphenol mix reduces the negative effects of cyclic heat exposure on growth performance, blood gas status, and meat quality in broiler chickens. *Animals* 10, 1158. doi: 10.3390/ani10071158.
- SHIMUL, S. A. A., SOUHARDYA, S. M., and AL NAHID, S. A. (2018). Effects of polyphenols from sugarcane on the growth performances of farmed tilapia (*Oreochromis niloticus*). *Bangladesh J. Fisheries* 30, 153–162.
- Solomon, S. (2011). Sugarcane by-products based industries in India. *Sugar Tech.* 13, 408–416. doi: 10.1007/s12355-011-0114-0.
- Van der Poel, A., Abdollahi, M., Cheng, H., Colovic, R., Den Hartog, L., Miladinovic, D., et al. (2020). Future directions of animal feed technology research to meet the challenges of a changing world. *Anim. Feed Sci. Technol.* 270, 114692. doi: 10.1016/j.anifeedsci.2020.114692.
- Vassilakopoulos, T., Katsounou, P., Karatza, M.-H., Kollintza, A., Zakynthinos, S., and Roussos, C. (2002). Strenuous resistive breathing induces plasma cytokines: role of antioxidants and monocytes. *Am. J. Respir. Crit. Care Med.* 166, 1572–1578. doi: 10.1164/rccm.200203-177OC.
- Wang, F., Zhang, W., and Niu, D. (2021). foodborne Enterobacteriaceae of animal origin. *Front. Cell. Infect. Microbiol.* 11, 772359. doi: 10.3389/fcimb.2021.772359.
- Wegener, H. C. (2003). Antibiotics in animal feed and their role in resistance development. *Curr. Opin. Microbiol.* 6, 439–445. doi: 10.1016/j.mib.2003.09.009.
- Wenk, C. (2003). Herbs and botanicals as feed additives in monogastric animals. *Asian-Australasian J. Anim. Sci.* 16, 282–289. doi: 10.5713/ajas.2003.282.
- Wijesiriwardana, U. A., Pluske, J. R., Craig, J. R., Cottrell, J. J., and Dunshea, F. R. (2020). Evaluation of sugarcane-derived polyphenols on the pre-weaning and post-weaning growth of gilt progeny. *Animals* 10, 984. doi: 10.3390/ani10060984.
- Yanti, G., Jamarun, N., and Astuti, T. (2021). Quality improvement of sugarcane top as animal feed with biodelignification by *phanerochaete chrysosporium* fungi on in-vitro digestibility of NDF, ADF, Cellulose and hemicellulose. *J. Phys.: Conf. Ser.* 1940, 1–6.



## OPEN ACCESS

## EDITED BY

Marzena Helena Zajac,  
University of Agriculture in Krakow, Poland

## REVIEWED BY

Piotr Kulawik,  
University of Agriculture in Krakow, Poland  
Monika Modzelewska-Kapitula,  
University of Warmia and Mazury in Olsztyn,  
Poland

## \*CORRESPONDENCE

J. D. Wood

✉ jeff.wood@bristol.ac.uk

RECEIVED 03 November 2023

ACCEPTED 15 February 2024

PUBLISHED 01 March 2024

## CITATION

Wood JD, Giromini C and Givens DI (2024)  
Animal-derived foods: consumption,  
composition and effects on health and the  
environment: an overview.  
*Front. Anim. Sci.* 5:1332694.  
doi: 10.3389/fanim.2024.1332694

## COPYRIGHT

© 2024 Wood, Giromini and Givens. This is an  
open-access article distributed under the terms  
of the [Creative Commons Attribution License](#)  
(CC BY). The use, distribution or reproduction  
in other forums is permitted, provided the  
original author(s) and the copyright owner(s)  
are credited and that the original publication  
in this journal is cited, in accordance with  
accepted academic practice. No use,  
distribution or reproduction is permitted  
which does not comply with these terms.

# Animal-derived foods: consumption, composition and effects on health and the environment: an overview

J. D. Wood<sup>1\*</sup>, C. Giromini<sup>2</sup> and D. I. Givens<sup>3</sup>

<sup>1</sup>Bristol Veterinary School, University of Bristol, Bristol, United Kingdom, <sup>2</sup>Department of Veterinary  
Medicine and Animal Science, University of Milan, Milan, Italy, <sup>3</sup>Institute of Food, Nutrition and Health,  
University of Reading, Reading, United Kingdom

Consumption of animal-derived foods (ADFs), particularly red meat, is declining in high-income countries because of concerns over health and the effects on climate change but is increasing in low- and middle-income countries. As a group of foods, ADFs are high in good-quality protein and several key vitamins and minerals (notably vitamin B12, iron and zinc). There is evidence, though, that processed red meat poses risks of cardiovascular disease (CVD) and colorectal cancer and the same risks, although not so strong, are apparent for unprocessed red meat. Milk and milk products generally have a neutral disease risk and there is evidence of reduced risks of CVD and colorectal cancer. Similarly, white meat (chicken and fish) is not associated with disease risk whilst eggs have been linked with increased CVD risk because of their cholesterol content. The risks of chronic disease seem higher in high-income than in low- and middle-income countries, possibly due to different levels of consumption. Production of ADFs results in high greenhouse gas emissions per unit of output compared with plant proteins. Ruminant meat production has particularly high costs but wide variation between farms in different regions of the world suggests costs can be significantly lowered by changes to production systems. Reducing ADF consumption to benefit health and the environment has been proposed but in low-income countries, current levels of consumption of ADFs may be compatible with health and climate targets.

## KEYWORDS

red meat, white meat, fish, eggs, milk, milk products, global warming, cardiovascular disease

## 1 Introduction

Animal-derived foods (ADFs) (meat and meat products, milk and milk products, fish and seafood, and eggs) have been important constituents of the diets of people around the world for millions of years and are part of the culture of many ethnic groups. They provide high-quality protein and a range of nutrients important for the maintenance of health and



they contribute unique tastes and flavours to meals and dishes. However, since the 1950s, their consumption has been linked with the incidence of chronic diseases and more recently with climate change. In low- and middle-income countries, the production and consumption of ADFs have increased rapidly in recent years and are expected to increase further in the next 10 years. In high income countries consumption may have reached a peak and there are calls to reduce consumption for health and environmental reasons. Alternative forms of dietary protein based on plants and microbes are now widely available and others are emerging (e.g., cell-cultured meat and insects). There are therefore many questions surrounding the future of ADFs and this overview aims to summarise the current state of thinking.

## 2 Trends in consumption of ADFs

Although plants provide most (57%) of the protein in diets globally (Henchion et al., 2017), ADFs provide a high percentage of the dietary protein in many countries, for example 59% in the 19–64 age group in the UK (Public Health England, 2020). Of this, 34% is from meat and meat products, 13% from milk and milk products, 7% from fish and seafood and 5% from eggs. Individual countries vary in the relative contributions of the different ADFs, depending on historical and cultural factors (Auestad et al., 2015).

In the last 50 years (1961–2020), global production of ADFs has greatly increased: meat and meat products by 403% to 352 Mt, milk and milk products by 167% to 918 Mt, fish and seafood by 355% to 176 Mt and eggs by 513% to 92 Mt (FAO, 2021). Low- and middle-income countries, particularly in Asia, have shown the greatest growth, driven by population increases and per capita consumption, the latter explained by increasing incomes. There were wide variations in the growth of per capita consumption between countries and regions of the world (Table 1). Per capita consumption of all ADFs increased markedly in China, milk and milk products by 956% and meat by 1747%. Increases were much smaller in Europe and North America and consumption of milk fell

by 23% in the latter. Africa had the lowest levels of consumption and consumption of milk declined in the 50-year period. In China, consumption of all meat types increased, beef by 7388%. In Europe and North America, consumption of beef fell by 13% and 20%, respectively but levels were still higher than in China in 2020. In Africa, sheepmeat and beef consumption declined. Poultry showed the biggest increase among meat types in all regions and increased by 467% in the world as a whole.

According to the agricultural outlook published by OECD/FAO (2023), global meat production is expected to increase by a further 12% between 2022 and 2032, with most of the growth occurring in Asia. Poultry production will show the greatest growth globally (13%), poultry accounting for half of the additional meat production in the next 10 years. Pigmeat production will outstrip poultry production in China as the country recovers from the African Swine Fever outbreak in 2018. Beef production will show the least growth (9%). Meat consumption per capita is predicted to increase by 2% globally in the next 10 years with most of the growth occurring in low- and middle-income countries. Poultry will show the greatest increase and will provide 41% of protein from meat sources in 2032. The Outlook notes that concerns about some aspects of meat production (animal welfare, environmental costs and human health) is now global and is partly responsible for the switch from beef to poultry consumption in many countries, poultry having lower feed and environmental costs and white meat perceived as having less harmful effects on human health than red meats (see sections 4–6 in this review). These consumer concerns are causing moves towards veganism and vegetarianism in some countries. In UK, a recent poll by YouGov (2023) showed that 3% of adults now consider themselves vegan, 5% vegetarian and 71% meat-eaters. Consumers can now purchase a variety of non-meat protein foods including plant-based and microbial proteins and foods from non-traditional animal sources such as insects and cell-cultured meat (Frank et al., 2022).

World milk production is expected to grow by 15% between 2022 and 2032 (OECD/FAO, 2023). India is the largest milk-producing country and production will increase by 30% in this

TABLE 1 Consumption (kg/person/yr) of a. ADFs and b. Meat types, for World, Europe, China, North America and Africa in 1961 and 2020 (FAO, 2021).

	World		Europe		China		N. America		Africa	
	1961	2020	1961	2020	1961	2020	1961	2020	1961	2020
<b>a. ADF</b>										
Meat	22.92	42.26	47.24	75.82	3.35	61.89	74.24	100.72	13.32	16.46
Milk	75.04	70.19	171.2	182.3	2.37	25.02	220.80	169.13	29.96	27.22
Fish	8.96	20.25	13.85	21.77	4.33	40.33	11.33	18.28	4.57	9.58
Eggs	4.52	10.33	8.96	13.90	2.06	21.97	14.44	15.78	1.24	2.14
<b>b. Meat</b>										
Sheepmeat	1.91	1.96	3.61	1.65	0.15	3.80	1.78	0.64	2.58	2.35
Beef	9.32	8.98	15.58	13.54	0.09	6.74	34.38	27.38	6.91	5.15
Pigmeat	7.97	14.45	21.63	33.65	2.06	35.70	23.52	24.04	0.72	1.53
Poultry	2.86	16.21	4.61	25.29	0.95	15.13	13.42	47.93	1.36	6.21

period. Production in Europe and North America will remain static. Per capita consumption will increase by 7% globally, India having the highest per capita consumption at 52kg per year, most of which is liquid milk. Europe and North America consume more than half of their milk as processed products (butter and cheese) and the share of processed products is also increasing in other regions. As with meat, there is increasing availability of plant-based milk-like products.

Global fish production is expected to increase by 17% between 2022 and 2032 (OECD/FAO, 2023). Aquaculture will account for 54% of fish production in 2032, with production from capture fisheries not expected to increase. China continues to dominate world aquaculture production and will have a 56% share of global production in 2032. Per capita consumption of fish is expected to increase by 4% in the 10-year period with the greatest level of consumption (24.5 kg/year) occurring in Asia.

Global egg production is expected to increase by 12% between 2022 and 2032 (OECD/FAO, 2023) and by 2032, 76% of production will occur in low- and middle-income countries, 35% in China. Per capita consumption is expected to increase by 5% globally, with China having the highest level of consumption in 2032 (24.7 kg/year).

In conclusion, global production and consumption of all ADFs are expected to increase in the next 10 years, particularly in low- and middle-income countries where populations and incomes are increasing. There are downward trends in consumption in high-income countries, particularly for red meat, but per capita consumption levels are still relatively high.

### 3 Environmental effects of production of ADFs

The climate of the Earth is changing, with temperatures increasing and rainfall and weather events becoming more extreme (Henry et al., 2018). It is now recognised that the production of ADFs contributes significantly to climate change by increasing greenhouse gas emissions (GHGEs), the main cause of climate change and increasing pressure on other environment indicators such as land use, biodiversity loss, depletion of freshwater resources and pollution of aquatic and terrestrial ecosystems (Springmann et al., 2018; Scarborough et al., 2023). Production of ADFs in many parts of the world is negatively affected by climate change, for example production from ruminants in tropical and sub-tropical regions where people depend on livestock for income and nutrition (Henry et al., 2018).

It is estimated that globally the food chain from farm to retail is responsible for around 30% of anthropogenic GHGEs (Crippa et al., 2021; Scarborough et al., 2023), with meat, dairy, fish and eggs contributing about 56% of these emissions (Poore and Nemecek, 2018). The farm stage dominates the production of GHGEs, with post-farm gate activities, including processing, making negligible contributions in comparison. Estimates of GHGEs from the farm to retail stages per kg food product, based on data from 38,700 farms in 119 countries in Table 2 show that animal products are associated with much higher emissions than plant products, the lowest-impact

animal products typically exceeding those of vegetable substitutes (Poore and Nemecek, 2018). The biggest emissions are from ruminant production, with beef and cattle milk production estimated to account for 41% and 20% respectively of the livestock sector's emissions (Gerber et al., 2013). Beef production from dairy herds is associated with about 30% of the GHGEs of those from beef herds because the costs are shared between both meat and milk production. The main source of emissions (44% of livestock emissions) is methane from enteric fermentation and manure handling. Atmospheric amounts of methane have increased rapidly over the last decade and although methane remains in the atmosphere for a much shorter time than CO<sub>2</sub> it has approximately 30 times the climate-warming effect when measured over a 100-year period (UN, 2021).

ADFs are major sources of protein in the diet and when expressed per 100g protein, the difference in emission intensity between animals and plants, when expressed per kg, narrows but is still substantial (Table 2). It is argued that expressing GHGEs per 100g protein still overestimates emissions from ADFs compared with plant foods and the unit of comparison should allow for the ideal balance of amino acids in ADFs, their inclusion of all the essential amino acids and their higher digestibility (McAuliffe et al., 2023). Others have suggested that emissions from ruminants should take account of the other valuable nutrients provided in their products such as calcium and iodine in milk (Hobbs et al., 2020) and B vitamins, iron, selenium and zinc in meat (Lee et al., 2021).

The global analysis by Poore and Nemecek (2018) (Table 2) showed that among the 38,700 farms studied, there was wide variation in GHGEs. It was estimated that for beef production from beef herds, 25% of producers were responsible for 56% of GHGEs. There is therefore much scope for mitigation of emissions through changes in practices on farms. In ruminant production there is a strong correlation between productivity and emission intensity so the greatest potential for mitigation is in systems operating at low productivity in areas such as South Asia, South America and Africa (Gerber et al., 2013; Rivero et al., 2021). Better feeding, herd management, animal health and genetics can all improve productivity and reduce emission intensity. An important characteristic of ruminants is their ability to utilise grass-based (forage) diets although production from grain-based (concentrate) diets results in greater productivity and lower GHGEs per kg. Improvements are also possible through changes in feed constituents which reduce methane production (e.g., ionophores, plant bioactive compounds, condensed tannins and fatty acids), changes to manure handling and carbon sequestration in which land use change is reduced and depleted pastures are replenished. Gerber et al. (2013) concluded that because of the high current costs to the environment of ruminant production, even modest improvements in systems can yield substantial gains in emission intensities and food security. Rivero et al. (2021), using data from a global network of farms, showed that key changes in genetic and nutritional approaches can make important contributions to the sustainability of global ruminant livestock production.

Efforts to reduce GHGEs in the production of ADFs has mainly focussed on ruminants, especially beef, because of the evidence that emissions from this group are so high (Table 2). Pigs, poultry and

TABLE 2 Estimates of greenhouse gas emissions (kg CO<sub>2</sub> equivalents) from production to retail of some agricultural products.

Animals				Plants			
	10 <sup>th</sup> pc	Mean	90 <sup>th</sup> pc		10 <sup>th</sup> pc	Mean	90 <sup>th</sup> pc
<b>a. per kg product</b>							
Beef (beef herd)	40.4	99.5	209.9	Wheat	0.8	1.6	2.3
Beef (dairy herd)	17.9	33.3	50.9	Tomatoes	0.4	2.1	6.0
Pigmeat	7.4	12.3	22.3	Peas	0.6	1.0	1.7
Poultry meat	4.2	9.9	20.1	Bananas		0.9	
Milk	1.7	3.2	4.8	'Other vegetables'	0.2	0.5	1.0
Cheese	10.9	23.9	39.3	Potatoes	0.2	0.5	0.6
Farmed fish	5.7	13.6	26.5	Root vegetables	0.2	0.4	0.6
Eggs	2.9	4.7	8.4	Nuts	-3.7	0.4	3.8
<b>b. per 100g protein</b>							
Beef (beef herd)	20	50	105	Wheat	0.3	0.6	0.9
Beef (dairy herd)	9.1	17	26	Tomatoes	0.4	2.1	6.0
Pigmeat	4.6	7.6	14	Peas	0.3	0.4	0.8
Poultry meat	2.4	5.7	12	Bananas	0.6	0.9	1.2
Milk	1.7	3.2	4.8	'Other vegetables'	0.2	0.5	1.0
Cheese	4.9	11	18	Potatoes	0.2	0.6	0.9
Farmed fish	2.5	6.0	12	Root vegetables	0.2	0.4	0.6
Eggs	2.6	4.2	7.6	Nuts	-2.2	0.3	2.4

Results (mean, 10<sup>th</sup> and 90<sup>th</sup> percentiles) expressed in relation to a. kg retail product and b. 100g protein (Poore and Nemecek, 2018).

aquaculture are each responsible for about 7–10% of emissions from the livestock sector, mainly in the form of CO<sub>2</sub> (from the production, processing and transport of feed) and N<sub>2</sub>O (from fertilizers and manure) (Gerber et al., 2013; MacLeod et al., 2020). Mitigation in these sectors involves the adoption of better practices, including reducing land use change (e.g., in the production of cereals and soybeans) and improving efficiency (MacLeod et al., 2020; UN, 2021).

Springmann et al. (2018) modelled the effects of different mitigating influences on GHGEs from agriculture. The results showed that GHGEs could be reduced by 6% if food waste was halved, 10% if technological improvements were introduced on farms and by 29–56% if consumers changed their diets. The much lower environmental cost of vegetarian and vegan diets compared with meat-based diets was shown by Scarborough et al. (2023) in a UK study of 55,504 participants which linked food consumption and nutrient composition data with the environment indicators database of Poore and Nemecek (2018) (Table 2). The analysis accounted for variations in sourcing and production within each food group. The results for global warming potential (GWP), which accounts for emissions from CO<sub>2</sub>, N<sub>2</sub>O and methane are in Figure 1. They show that vegan diets had 24% of the GWP of the diets of high meat eaters (140g/d meat and meat products). The diets of low meat eaters (28.3g/d meat and meat products) had 52% of the GWP of those of high meat eaters. The emissions from the diets of low meat

eaters were only slightly greater than those from fish eaters (who also consumed 2g meat and meat products per day).

Examples of diets modified to reduce GHGEs are given in WHO/FAO (2003), USDA (2020) and Willett et al. (2019). Groups in several countries have established 'food-based dietary guidelines' which call for substantial reductions in the consumption of ADFs, particularly in ruminant products (Steenenson and Buttriss, 2021; Scarborough et al., 2023). Green et al. (2015) found in a modelling study that a reduction of 30% in GHGEs from UK diets was possible by reducing the contributions from some ADFs and switching between others. Reductions of more than 30% risked impairing nutritional value or required 'non-trivial' dietary shifts. Action at government level will be required to bring about these large changes in consumption and in UK, the Committee on Climate change has called for a 20% reduction in the consumption of beef, sheepmeat and dairy products by 2050 to help meet the UK's commitment to achieving 'net zero' (where emissions produced and removed from the atmosphere are in balance) by 2050 (CCC, 2020; Stewart et al., 2021).

Calls for reductions in the production and consumption of ADFs in high-income countries contrast with the projections that both production and consumption of ADFs in low- and middle-income countries will increase in the coming years as incomes and demand grow (OECD/FAO, 2023). There are also social considerations which suggest that strategies for dealing with

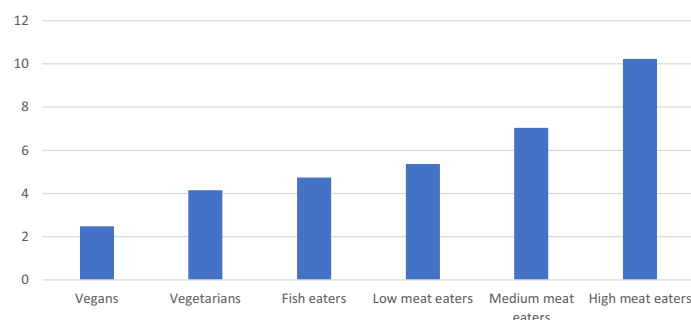


FIGURE 1

GHGEs (GWP<sub>100</sub> kg CO<sub>2</sub> equivalents/day) associated with the diets of vegans, vegetarians, fish eaters and low, medium and high meat eaters in UK. 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles were 2.09–3.36 for vegans and 7.04–15.95 for high meat eaters (Scarborough et al., 2023).

climate change will differ between countries. In some low- and middle-income countries, livestock are required for income, transport and draught power and their ownership increases social inclusiveness (Parlasca and Qaim, 2022). The plant foods available in these countries are deficient in key nutrients such as iron, zinc and vitamin B12 which are provided in meat, milk and fish (Adesogan et al., 2020). It is also probable that the low levels of production and consumption of ADFs in some of these countries results in emissions which are compatible with climate targets (Springmann et al., 2018). Scarborough et al. (2023) suggested that the UK could meet its emissions reduction targets if consumption of ADFs fell to a level above that currently consumed in low-income countries.

In all countries, production from ruminants often occurs in areas which are unsuitable for other forms of agriculture because of topography and soil type. Lee et al. (2021) showed that land use suitable for human-edible food production was much lower for ruminant production than for the production of pigmeat and chicken when expressed in relation to the nutrients produced. Ruminants can also utilise forages (e.g., hay and silages), crop residues (e.g., cereal straw) and food industry by-products (e.g., sugar beet pulp and brewers grains) which are not suitable for other types of animal production or indeed for human food. These benefits of ruminant production are often not accounted for when assessing the overall costs (Van Kernebeek et al., 2016).

It must also be recognised that the alternative forms of protein production suggested to replace production from ruminants and other ADFs (e.g., plant-based foods, microbial protein, cell-cultured meat and insects) are at a relatively early stage of development and have not been fully evaluated regarding their environmental costs and chemical/nutritional profiles (Henchion et al., 2017). Steenson and Buttriss (2021) concluded that the environmental benefits of some meat and milk alternatives have been overstated, for example by underestimating their energy, water and land use costs.

## 4 Nutrients in ADFs and daily intakes

The different types of ADFs contain nutrients important for the maintenance of health as shown in Tables 3–5. Many databases

exist and the data in the Tables 3–5 are from the UK database McCance and Widdowson's Composition of Foods (Public Health England, 2021). The foods shown are chosen to represent the range of ADFs: lean muscle from red (beef) and white (chicken) meat, liver from beef and chicken representative of organ meats, white (cod) and oily (mackerel) fish, chicken eggs and whole and semi-skimmed milk. The amounts per 100g are compared with the reference intake and 'significant amount' figures published by the European Food Safety Authority (EFSA) (EU, 2011) for the purposes of food labelling and making nutrient claims. All the foods are 'high in protein' (Table 3) because they contain more than 20% of the energy as protein, ranging from 22% in whole milk to 93% in cod. The UK rolling National Diet and Nutrition Survey (NDNS) (Public Health England, 2020) shows that ADFs contribute about 59% of dietary protein intake in men and women aged 19–64. The protein is of high nutritional value, having a favourable balance of amino acids, including the nine essential amino acids and has high bioavailability from the diet in contrast to plant proteins (McAuliffe et al., 2023).

Fat is a major source of energy in foods but over-consumption has been linked with obesity, coronary heart disease and some cancers (USDA, 2020). The samples of chicken muscle, chicken liver, cod and semi-skimmed milk in Table 3 are 'low in fat' (defined as <3g/100g for solids and <1.5g/100g for liquids). These same foods are 'low in saturated fat', saturated fat (SFA) being a risk factor for cardiovascular disease (CVD), the leading cause of mortality and morbidity worldwide (USDA, 2020), although the role of SFA in the aetiology of CVD is being increasingly challenged (Givens, 2023; Teicholz, 2023). The fat and SFA content of meat is greatly increased when adipose tissue is included in the food. For example, the sample of beef sausages listed in Public Health England (2021) has 19.5 g/100g fat and 7.6 g/100g SFA and is considered 'high in fat'. The NDNS survey results show that men and women aged 19–64 obtain 49% and 56% of their fat and SFA intake, respectively, from ADFs (22% of fat and 21% SFA from meat and meat products) (Public Health England, 2020). The definition of 'low energy' foods in EU (2011) is <170 kJ/100g so none of the ADFs meet this threshold. Neither can any of the ADFs be described as 'high in' MUFA or PUFA. The foods differ in the percentages of total fatty acids in the three main classes, beef muscle

TABLE 3 Macronutrient content (per 100g) of some ADFs (Public Health England, 2021).

	Meat		Liver <sup>c</sup>		Fish		Eggs <sup>f</sup>	Milk <sup>g</sup>	
	Beef <sup>a</sup>	Chicken <sup>b</sup>	Beef	Chicken	Cod <sup>d</sup>	Mackerel <sup>e</sup>		Whole	Semi-skimmed
Water (g)	71.9	75.1	72.0	75.8	81.6	61.9	76.8	87.6	89.4
Protein (g)	22.5	22.3	18.3	17.7	17.5	18.0	12.6	3.4	3.5
Fat (g)	4.3	2.1	3.4	2.3	0.6	17.9	9.0	3.6	1.7
Energy (kJ)	542	457	437	386	320	968	547	265	195
SFA (g) <sup>h</sup>	1.74	0.60	1.00	0.70	0.16	3.85	2.52	2.29	1.07
MUFA (g) <sup>i</sup>	1.87	1.00	0.60	0.50	0.14	6.69	3.44	0.96	0.39
PUFA (g) <sup>j</sup>	0.23	0.40	0.80	0.40	0.11	4.46	1.44	0.09	Tr
n-3 PUFA (g) <sup>k</sup>	0.07	NR	NR	0.11	0.08	4.05	0.13	0.02	0.01
Carbohydrates (g)	0	0	Tr	Tr	0	0	Tr	4.6	4.7

<sup>a</sup>Lean from 10 different joints.<sup>b</sup>Average of white and dark meat.<sup>c</sup>Average of 10 samples.<sup>d</sup>Flesh, average of 10 samples.<sup>e</sup>Flesh, average of 7 samples.<sup>f</sup>Chicken, whole, average of 12 samples.<sup>g</sup>Pasteurised, average of Summer and Winter milkings.<sup>h</sup>SFA saturated fatty acids.<sup>i</sup>MUFA monounsaturated fatty acids.<sup>j</sup>PUFA polyunsaturated fatty acids.<sup>k</sup>n-3 polyunsaturated fatty acids.

NR not recorded. Tr trace.

and milk (ruminant foods) having the highest percentages SFA and liver and fish the highest percentages of PUFA. Mackerel had the highest content of n-3 PUFA. About 60% of n-3 PUFA in mackerel are the long-chain fatty acids eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) (Strobel et al., 2012) so 100g mackerel

provides much more EPA+DHA than the 250mg/d recommended by EFSA (2017) or the 450mg/d recommended in UK (SACN, 2004) to benefit cardiovascular health. Most ADFs have little carbohydrate but both milk products contain intrinsic sugars – these do not contribute to ‘free sugar’ intake which is higher in most UK age

TABLE 4 Mineral content of some ADFs (Public Health England, 2021).

	Meat		Liver		Fish		Eggs	Milk	
	Beef	Chicken	Beef	Chicken	Cod	Mackerel		Whole	Semi-skimmed
Sodium (mg)	63	77	71	76	91	153	154	42	43
Potassium (mg)	<b>350</b>	<b>380</b>	<b>310</b>	260	<b>322</b>	<b>335</b>	145	157	156
Calcium (mg)	5	6	6	8	12	20	46	<b>120</b>	<b>120</b>
Magnesium (mg)	22	26	20	19	25	37	13	11	11
Phosphorus (mg)	<b>200</b>	<b>160</b>	<b>320</b>	<b>280</b>	<b>169</b>	<b>220</b>	<b>179</b>	96	94
Iron (mg)	<b>2.7</b>	0.7	<b>11.5</b>	<b>9.2</b>	0.10	0.98	1.72	0.02	0.02
Copper (mg)	0.03	0.03	<b>20.5</b>	0.5	0.02	0.08	0.05	Tr	Tr
Zinc (mg)	<b>4.1</b>	1.2	<b>14.2</b>	<b>3.7</b>	0.3	0.5	1.1	0.5	0.4
Selenium (µg)	7	<b>13</b>	<b>22</b>	NR	<b>23</b>	<b>42</b>	<b>23</b>	1	1
Chloride (mg)	51	95	85	<b>130</b>	<b>165</b>	<b>250</b>	<b>180</b>	89	87
Manganese (mg)	0.01	0.01	0.24	0.31	0.01	0.01	0.03	Tr	Tr
Iodine (µg)	10	7	NR	NR	<b>196</b>	<b>29</b>	<b>50</b>	<b>31</b>	<b>30</b>

Figures in bold show food is a ‘source’ of the mineral (EU, 2011).

Description of samples as Table 3.



TABLE 5 Vitamin content (per 100g) of some ADFs (Public Health England, 2021).

	Meat		Liver		Fish		Eggs	Milk	
	Beef	Chicken	Beef	Chicken	Cod	Mackerel		Whole	Semi-skimmed
B1 (thiamine) (mg)	0.10	0.14	<b>0.22</b>	<b>0.48</b>	0.06	<b>0.17</b>	0.08	0.03	0.03
B2 (riboflavin) (mg)	<b>0.21</b>	0.18	<b>2.52</b>	<b>2.16</b>	0.08	<b>0.30</b>	<b>0.50</b>	<b>0.23</b>	<b>0.24</b>
B3 (niacin) (mg)	<b>5.0</b>	<b>7.8</b>	<b>12.5</b>	<b>10.6</b>	2.3	<b>11.3</b>	0.10	0.20	0.10
B5 (pantothenic acid) (mg)	0.75	<b>1.16</b>	<b>8.4</b>	<b>6.1</b>	0.25	0.63	<b>1.35</b>	0.58	0.68
B6 (pyridoxine) (mg)	<b>0.53</b>	<b>0.38</b>	<b>0.48</b>	<b>0.82</b>	0.14	<b>0.40</b>	0.13	0.06	0.06
B7 (biotin) (μg)	1.0	2.0	<b>39.0</b>	<b>210.0</b>	1.3	5.8	<b>19.5</b>	2.5	3.0
B9 (folic acid) (μg)	19.0	19.0	<b>155</b>	<b>995</b>	7	1.0	<b>47</b>	8.0	9.0
B12 (cobalamin) (μg)	<b>2.0</b>	Tr	<b>68.0</b>	<b>35.0</b>	<b>1.5</b>	<b>8.8</b>	<b>2.7</b>	<b>0.9</b>	<b>0.9</b>
A (retinol) (μg)	Tr	11.0	<b>18800</b>	<b>9700</b>	2.0	54.0	<b>126</b>	36.0	19.0
C (ascorbic acid) (mg)	0	0	<b>21.0</b>	<b>28.0</b>	Tr	Tr	0	2.0	2.0
D (cholecalciferol) (μg)	0.5	0.1	0.3	0.2	Tr	<b>8.0</b>	<b>3.2</b>	Tr	Tr
E (α-tocopherol) (mg)	0.13	0.15	0.45	0.60	0.66	0.43	<b>1.29</b>	0.06	0.04

Figures in bold show food is a ‘source’ of the vitamin (EU, 2011).  
Description of samples as Table 3.

groups than the government recommendations (Public Health England, 2020).

Table 4 lists the major minerals in foods and their concentrations in ADFs. There is concern over high intakes of sodium from salt in the diet because this is a risk factor for high blood pressure and CVD (Micha et al., 2012). All the raw ADFs except mackerel and eggs can be described as ‘low in salt’ (< 120mg/100g, EU, 2011). However, the sodium content of foods in which salt is used for curing can greatly exceed this value, for example the sample of cured bacon listed in Public Health England (2021) has 1140mg sodium/100g. The NDNS results show that ADFs provide about 46% of sodium intake for UK men and women in the 19–64 age groups, 26% from meat and meat products (Public Health England, 2020). For the other minerals, low intakes are of greater concern and concentrations which exceed the ‘significant amount’ or ‘source’ level, defined as 15% of the reference intake per 100g, are shown in bold. Phosphorus is at ‘source’ levels in seven of the nine ADFs, potassium, selenium and iodine in five, iron and zinc in three and calcium in two. The NDNS survey results show that ADFs make important contributions to UK intakes of several minerals. For the 19–64 age group, meat and meat products provide 31% of zinc, 29% of selenium and 19% of iron intakes (Public Health England, 2020). Milk and milk products provide 34% of calcium and 32% of iodine intakes. Fish and fish products provide 16% of selenium and 10% of iodine. Intakes of some minerals are considerably below the Lower Reference Nutrient Intake (LRNI) level in several groups in the population, particularly in girls aged 11–18 in which 49% had intakes below the LRNI for iron, 47% for magnesium, 37% for potassium, 41% for selenium, 16% for zinc and 28% for iodine (Public Health England, 2020). It is probable that low intakes of ADFs are responsible for these shortfalls (Givens, 2018) and there is concern that this cohort will become more deficient if ADF intakes are reduced further.

Iron deficiency is a major public health concern in many countries, including UK, in which 9% of girls aged 11–18 have iron deficiency anaemia (Fairweather-Tait, 2023). The haem iron in meat is more bioavailable than the iron in vegetables in which phytates and polyphenols may inhibit absorption. Haem iron concentrations in meat differ between the species. Lombardi-Boccia et al. (2002) found values of 2.64, 2.25, 0.56 and 0.42 mg/100g in beef sirloin, lamb chop, pork chop and chicken leg, respectively.

Table 5 lists the major vitamins in foods and their concentrations in ADFs. The figures in bold indicate the ADF contains a ‘significant amount’ or is a ‘source’ of the vitamin (EU, 2011). As with the minerals, all the ADFs have important levels of some vitamins, with beef and chicken liver being highest in all except vitamins D and E. Intakes of organ meats such as liver have declined in UK and other countries but their high content of micronutrients is invaluable when nutrient density is important, for example in young children, especially in low-income countries with poor access to plant sources of protein and micronutrients (Miller et al., 2023). The NDNS survey results show that ADFs contribute 83% of cobalamin (vitamin B12) and 70% of vitamin D intakes in the 19–64 age groups in UK, more than 50% of riboflavin and niacin and more than 30% of vitamin A, thiamine, pyridoxine and vitamin E (Public Health England, 2020). The results show that intakes of some vitamins are below the LRNI, especially in girls aged 11–18 and women aged 19–64. For these groups, riboflavin intake is particularly low, with 12–21% of participants below the LRNI in girls and women.

Measurement of serum 25-hydroxyvitamin D showed that in 2016–2019 in UK, 19% of children aged 11–18, 16% of adults aged 19–64 and 13% of adults over 65 had levels below which there is a risk to musculoskeletal health (Public Health England, 2020). USDA (2020) reported that 90% of Americans do not consume

enough vitamin D. Again, low intakes of ADFs probably contributed to the UK shortfalls (Givens, 2018).

Animal-derived foods also contain many bioactive compounds present in small amounts that have a range of physiological and metabolic functions in the body which are not accounted for in standard nutritional studies. These bioactive compounds include creatine, taurine, carnitine, carnosine, choline,  $\alpha$ -lipoic acid, conjugated linoleic acid, glutathione, coenzyme Q10 and bioactive peptides (Park and Nam, 2015; Kulczynski et al., 2019). The properties of these compounds include antioxidant, lipid-lowering, antihypertensive, anti-inflammatory and immunomodulatory effects. Peptides derived from hydrolysis of proteins and studied mainly in milk include the angiotensin 1-converting enzyme (ACE) inhibitors which are antihypertensive (Park and Nam, 2015).

Studies have shown that in some low- to middle-income countries, ADFs provide essential nutrients that are not present in the plant foods available (Adesogan et al., 2020; Parlasca and Qaim, 2022). ADFs, which in general are nutrient-dense, play a vital role in the nutrition of children, especially in the complementary feeding period (6–23 months) when nutrient requirements are high and gastric capacity low (Ortenzi and Beal, 2021). In some parts of the world, where diets are inadequate in several key nutrients, including iron, zinc, folate, vitamin B12 and calcium, ADFs can address the nutritional gaps (Miller et al., 2023). In a meta-analysis of randomised control trials, Pimpin et al. (2019) found that animal protein supplementation during infancy and early childhood increased child weight and height-for-age and reduced the risk of stunting. Nutrient deficiencies in early life can also lead to poor cognitive development and brain-related disorders which can influence health in adult life, increasing the risks of CVD and type-2 diabetes (Adesogan et al., 2020).

## 5 Consumption of ADFs and chronic disease

Reports from some international organisations have stated that the diets commonly consumed in many developed countries are associated with increased risks from obesity, CVD, type-2 diabetes and some cancers (WCRF, 2018; Willett et al., 2019; USDA, 2020). These bodies advocate changes in dietary patterns that address the nutritional causes of disease in addition to the climate change costs of food production. In many of the dietary patterns suggested, there is an important place for some ADFs (poultry, fish, eggs and low-fat milk) but lower intakes of red meat (beef, sheepmeat and pigmeat), and particularly processed meat, are advocated. The most extreme proposals are those of the EAT-Lancet Commission (Willett et al., 2019) whose 'healthy reference diet' contains 14g/day red meat (there is also 29g chicken, 13g eggs and 28g fish). This contrasts with the 50.5g/day intake of red and processed meat currently consumed in the UK (Public Health England, 2020). The WCRF

(2018) report recommends 'consumers eat no more than moderate amounts of red meat and little, if any, processed meat' in 3 portions per week, amounting to 350–500g (50–71g/day).

The basis for these recommendations on health grounds is evidence from prospective cohort studies and meta-analyses of such studies showing that consumption of processed meat (red and white processed meat are usually not examined separately) is associated with mortality from CVD and all causes (Sinha et al., 2009; Rohrmann et al., 2013; Wang et al., 2016; Zhong et al., 2020; Iqbal et al., 2021). WCRF (2018) has concluded that processed meat is a convincing cause of colorectal cancer. Higher consumption of unprocessed red meat has been linked with CVD and all-cause mortality in some studies (Sinha et al., 2009; Zhong et al., 2020) but not others (Rohrmann et al., 2013; Iqbal et al., 2021). WCRF (2018) have concluded that red meat consumption is probably a cause of colorectal cancer but Lescinsky et al. (2022), noting high heterogeneity between studies, found a weak association between consumption of unprocessed red meat and colorectal cancer in their meta-analysis.

A wide range of meta-analyses of prospective studies indicate that consumption of milk and milk products has a neutral association with CVD risk overall, although some indicate a negative association with CVD, stroke in particular (summarised by Givens, 2023). In addition, there is increasing evidence that yoghurt consumption is associated with a reduced risk of type-2 diabetes (Gijssbers et al., 2016; Soedamah-Muthu and de Goede, 2018; Drouin-Chartier et al., 2019). The overall findings of a neutral or beneficial association of dairy foods with CVD from prospective cohort studies is counterintuitive to many, being contrary to the long-held hypothesis of the link between SFA consumption, LDL-cholesterol and atherosclerotic CVD. There are, however, a range of emerging factors in dairy foods which may explain this, some of which are independent of changes in blood lipids and some which moderate blood lipid effects (Givens, 2023). WCRF (2018) concluded that dairy consumption reduced the risk of colorectal cancer but indicated that there was limited-suggestive evidence that it increased the risk of prostate cancer.

No associations between poultry consumption and CVD or all-cause mortality have been found (Rohrmann et al., 2013; Abete et al., 2014; Zhong et al., 2020; Iqbal et al., 2021) and poultry consumption is not linked with colorectal cancer (WCRF, 2018). For fish consumption, Zhong et al. (2020) found no associations with CVD or all-cause mortality and Mohan et al. (2021) found a lower risk of CVD and overall mortality with a fish intake of 175g (2 servings) per week but only among people at risk of and having CVD, not in the general population. In a study of meat-eaters, fish-eaters and vegetarians, Key et al. (2014) found a lower risk of incident cancers in fish-eaters and vegetarians compared with meat-eaters. However, WCRF (2018), although noting limited evidence that fish consumption reduced the risks of liver and colorectal cancer, concluded that consumption of salted fish may increase the risk of nasopharyngeal cancer. Many studies have investigated the links between egg consumption, cholesterol consumption and the

risk of CVD with some showing no risk except in individuals with type-2 diabetes (Rong et al., 2013; Guo et al., 2018; Drouin-Chartier et al., 2020) and some showing increased risks (Song et al., 2016; Zhong et al., 2019; Zhao et al., 2022). Although it is generally agreed that there is only a weak link between dietary and serum cholesterol, high cholesterol intakes can lead to plaque formation and inflammation, increasing the risk of CVD (Zhao et al., 2022).

Huang et al. (2022) reported high relative risks from egg protein in a prospective cohort study of 416,000 men and women with a follow-up period of 16 years. These authors examined the effects of replacing 3% protein from several animal sources (red meat protein, white meat protein, dairy protein and egg protein) with plant protein. Replacing white meat protein did not affect the risk of mortality overall or from cancer or CVD. The biggest reductions in these risks were seen by replacing egg protein.

In contrast to diets containing animal protein, diets containing fruit, vegetables, whole grains, nuts and fibre have been shown to be protective against the risks of cardiometabolic disease outcomes (Huang et al., 2022; Miller et al., 2022). Shah and Iyengar (2022) in a literature review found that a vegetarian plant-based diet was associated with a lower cancer risk than a ketogenic diet based on meat, dairy, fish and eggs. The ketogenic diet had some positive outcomes such as a reduction in obesity, inflammation and insulin levels.

Zhang et al. (2021) noted that globally, the prevalence of dementia is increasing, especially in low- and middle-income countries where meat consumption is also increasing. These authors investigated associations between meat consumption and the risk of dementia in the UK Biobank cohort and found that higher processed meat consumption increased the risk of dementia but increased red meat consumption reduced the risk. Trends were non-significant for poultry and all-meat.

In conclusion, evidence from several sources shows that higher intakes of processed meat are associated with mortality from CVD, colorectal cancer and possibly dementia and supports the suggestion that consumption of processed meat should be at a low level. The evidence is less clear for red meat and Rohrmann et al. (2013), who showed no links between red meat consumption and CVD or cancer in 448,568 people across 10 European countries, contrasted European results with those in the US where meat intake is higher. Also, some US studies have included processed meat within the red meat category (Sinha et al., 2009; Huang et al., 2022). Iqbal et al. (2021) conducted their study in 21 low-, middle- and high-income countries and found that a high daily consumption of red meat (>37g vs 7g) was not associated with all-cause or CVD mortality. Hur et al. (2019) showed that a high proportion of the evidence linking processed and red meat intake with colorectal cancer was from Western countries and that there is no evidence of these associations in Asian countries, including Korea, where rates of colorectal cancer are high. Possible explanations for this discrepancy between countries could be genetic variation and/or differences in the daily amounts of red and processed meat consumed, which have been higher over a long period in Western countries.

Poultry and fish consumption are not linked with CVD or cancer risks and are seen as possible replacements for some processed red meat protein in the diet. The general conclusion is that milk and milk products do not impact on CVD and some studies point to a protective effect of dairy products against

colorectal cancer (WCRF, 2018). The data supports advice to maintain but not increase egg consumption but the risk of CVD mortality from extra egg consumption differed between country cohorts in the meta-analysis of Zhao et al. (2022). It was high in US cohorts (RR 1.08, 95% CI, 1.02-1.14), tended to be high in European cohorts (RR 1.05, 95% CI, 0.98-1.14) and was non-significant in Asian cohorts (RR 0.96, 95% CI, 0.87-1.06) (Zhao et al., 2022).

## 6 Constituents of ADFs and roles in disease

Several possible mechanisms underlying the effects of ADFs on chronic disease have been investigated. For processed meat, high concentrations of sodium, which increase blood pressure, could partly explain the higher risk of CVD (Micha et al., 2012). Nitrite/nitrate in cured meat can react with breakdown products of amino acids to form N-nitroso compounds which increase the risk of insulin resistance, CVD and cancer (Habermeyer et al., 2015). Haem iron catalyses the formation of N-nitroso compounds and increases their production in the gastro-intestinal tract (Sodring et al., 2022). Red meat consumption stimulates the production of N-nitroso compounds in the intestine but white meat, with a lower haem content, does not (Bingham et al., 2002). Both nitrite/nitrate and haem iron are pro-oxidants which can promote oxidative damage and inflammation in different organs (Etemadi et al., 2017). Another compound formed in the gut after the consumption of ADFs is trimethylamine N-oxide. Plasma concentrations of this choline metabolite have been shown to be positively associated with the risk of CVD and to have adverse effects on cholesterol metabolism and oxidative stress (Fretts et al., 2022).

The role of processed red meat in the development of colorectal cancer has been explained by the presence of many known mutagens including heterocyclic aromatic amines (HAA) and polycyclic aromatic hydrocarbons (PAH) produced during cooking (De Smet and Vossen, 2016). The N-nitroso compounds formed from haem iron in red meat are also carcinogenic. Hur et al. (2019) showed that the amounts and types of the N-nitroso compounds HAA and PAH depend on cooking methods and temperature and are sometimes found in other Korean foods at much higher levels than in processed meat. In a review, they found no evidence of correlations between the intakes of processed and red meat and the incidence of colorectal cancer in Asian studies.

Since the 1950s, long-chain (C12-C18) SFA in foods have been seen as risk factors for type-2 diabetes and CVD (WHO/FAO, 2003; USDA, 2020). Saturated fatty acids, particularly C14:0 and C16:0, raise total- and LDL-cholesterol levels in blood with a small HDL-raising effect. SFA increase coagulation, insulin resistance and inflammation, all of which increase the risk of type-2 diabetes and CVD (Calder, 2015). These effects are countered by PUFA and the correct balance of SFA to PUFA in the diet are considered important for cardiovascular health (Hooper et al., 2020).

Despite this evidence of the harmful effects of SFA, debate continues about their direct effects on CVD. Systematic reviews and meta-analyses of controlled trials have concluded there is no evidence to support the view that dietary SFA are associated with

CVD (Siri-Tarino et al., 2010; Chowdhury et al., 2014). Others have concluded that advice from governments to limit SFA intake is unwarranted (Astrup et al., 2021; Teicholz, 2023). However, this advice continues to be given. For example, current UK government advice is to limit SFA to 10% of total dietary energy from the current 13% (Public Health England, 2020).

There is evidence that the source of SFA is important in relation to the effects on CVD. For example, the prospective cohort studies of de Oliveira Otto et al. (2012) and Vissers et al. (2019) showed a positive association between CVD risk and SFA from meat but not with SFA from dairy. These conclusions are supported by results from the meta-analysis of prospective cohort studies by Bechthold et al. (2019). In support of these results, Forouhi et al. (2014) and Prada et al. (2021) showed that plasma concentrations of the odd-chain SFA 15:0 and 17:0, which are markers for dairy fat intake, had inverse associations with the risk of type-2 diabetes. Perna and Hewlings (2023) showed that CVD risk was low or neutral for dietary levels of short and medium-chain fatty acids (C4-C10), which are also at higher concentrations in milk than meat.

Givens (2018) noted that hypertension is a risk factor for CVD and that bioactive peptides from milk proteins have hypotensive effects. The high concentration of calcium in dairy products may also reduce CVD risk (Lorenzen and Astrup, 2011).

The consensus view until recently has been that dietary cholesterol is not a factor in blood cholesterol concentrations (USDA, 2020) but recent cohort studies have found that increased egg consumption (0.5-1 egg/day) with its extra cholesterol, significantly increases the risk of CVD mortality (Zhong et al., 2019; Zhao et al., 2022).

Fish have many constituents which impact positively on health including high quality protein, minerals and vitamins (Tables 3-5) (Zheng et al., 2012). Their high content of long-chain n-3 fatty acids is also important. These fatty acids benefit many CVD risk factors including blood triglyceride levels, blood pressure, heart rate, endothelial function and myocardial oxygen demand (Del Gobbo et al., 2016) and have recently been associated with reduced CVD incidence and mortality over 10- and 20-year follow-up periods (Critselis et al., 2023). Randomised clinical trials of fish oil supplements have found mixed effects on CVD events but a meta-analysis of 13 trials concluded that supplementation with marine algae was associated with lower CVD mortality (RR 0.93, 95% CI, 0.88-0.99) and total CVD (RR 0.97, 95% CI, 0.94-0.99) (Hu et al., 2019). It is of concern that farmed salmon, the main oily fish consumed in the UK and elsewhere, has been shown to contain considerably lower concentrations of EPA+DHA (1.2g/100g, Henriques et al., 2014) than the value of 2.5g/100g used by SACN (2004) to set the UK dietary guidelines which would result in an EPA+DHA intake of 450mg/day.

## 7 Concluding remarks

Animal-derived foods have made important contributions to the diets of consumers over many years and are widely enjoyed as components of a balanced diet. However, high levels of consumption, especially of meat, are now widely seen as a factor in climate change and increasing levels of chronic disease.

Ruminant meat production poses the greatest risks to the environment, from GHGEs, water use, land use and eutrophication of water courses, but wide variation in these indicators suggests average costs can be lowered. The greater use of marginal land and lower use of arable land for beef and sheepmeat production in many countries are mitigating factors. Milk production from ruminants is associated with lower environmental costs than meat production and crossbred beef production from dairy herds lowers costs compared with purebred beef production. The costs of pigmeat, chicken, fish and egg production are lower than those of beef and sheepmeat but still higher than plant-based alternative sources of protein.

In terms of chronic disease, meat production from ruminants, especially when processed, poses the greatest risks. It is not clear how processing increases the risks of CVD or colorectal cancer: nitrites/nitrates, salt and carcinogens introduced during cooking have been implicated. Processed meat from chicken is probably less damaging than that from red meat but red and white processed meats have not been studied separately in most studies. Meat products containing low levels of nitrites/nitrates, salt and fat are now widely available.

Milk and milk products are associated with low or negative risks of CVD and cancer compared with beef and sheepmeat. The high haem content of ruminant meats could explain part of the disease risk and this poses the question why pigmeat is included in most studies as a red meat. Apart from a low haem content, it shares other characteristics with chicken, including a similar nutrient profile and similar balance between SFA and PUFA (Wood, 2023). Penkert et al. (2021) noted that the separate effects of pigmeat on health have been examined in very few studies.

The disease risks associated with chicken and fish are low but we draw attention to the risk of CVD from high egg consumption, with its extra cholesterol. Chicken has had the greatest success among ADFs and is forecast to provide 41% of protein from meat sources globally by 2030.

The reductions in the consumption of red and processed meat called for in some reports to improve environmental and health outcomes are substantial. The EAT-Lancet Commission called for a greater than 50% reduction in the global consumption of red meat (Willett et al., 2019). Governments respond to such advice in different ways. The UK Government recommended consumption of 70g/day red and processed meat in the Eatwell Guide and present figures are around 50.5g/day (Stewart et al., 2021). The figure of 14g red meat per day included by Willett et al. (2019) in their 'healthy reference diet' would be hard to achieve. The assumption that red and processed meat will be replaced in diets by vegetables, fruit, beans and nuts (Willett et al., 2019) may also be problematic. Benefits to health and the environment would not occur if consumers switched to alternatives like ultra-processed foods, sales of which have recently increased (Srouf et al., 2019). The use of a 'ruminant meat tax' to limit consumption would be difficult politically and could result in unexpected costs (Lee et al., 2021).

Calls for lower levels of ADF consumption in high-income countries contrast with the increases in consumption predicted in low- and middle-income countries in the next 10 years. Some reports have shown lower risks of CVD and colorectal cancer associated with consumption of ADFs in these countries. This



may be due to lower levels of consumption of ADFs and as these increase the risks may increase.

This overview has outlined the current (2023–24) position of ADFs as foods in our diets and has described the challenges facing their production. This is a rapidly advancing story for society and the agricultural industry and we await further developments.

## Author contributions

JW: Writing – original draft. CG: Writing – original draft. DIG: Writing – original draft.

## Funding

The author(s) declare that no financial support was received for the research, authorship, and/or publication of this article.

## References

- Abete, I., Romaguera, D., Vieira, A. R., de Munain, A. L., and Norat, T. (2014). Association between total, processed, red and white meat consumption and all-cause, CVD and IHD mortality: a meta-analysis of cohort studies. *Br. J. Nutr.* 112, 762–775. doi: 10.1017/S000711451400124X
- Adesogan, A. T., Havelaar, A. H., McKune, S. L., Eilittä, M., and Dahl, G. E. (2020). Animal source foods: Sustainability problem or malnutrition and sustainability solution? Perspective matters. *Global Food Secur.* 25, 100325. doi: 10.1016/j.gfs.2019.100325
- Astrup, A., Teicholz, N., Magkos, F., Bier, D. M., Brenna, J. T., King, J. C., et al. (2021). Dietary saturated fats and health: Are the US guidelines evidence-based? *Nutrients* 13, 3305. doi: 10.3390/nu13103305
- Auestad, N., Hurley, J. S., Fulgoni, V. L., and Schweitzer, C. M. (2015). Contribution of food groups to energy and nutrient intakes in five developed countries. *Nutrients* 7, 4593–4618. doi: 10.3390/nu7064593
- Bechthold, A., Boeing, H., Schwedhelm, C., Hoffmann, G., Sven Knuppel, S., Iqbal, K., et al. (2019). Food groups and risk of coronary heart disease, stroke and heart failure: A systematic review and dose-response meta-analysis of prospective studies. *Crit. Rev. Food Sci. Nutr.* 59, 1071–1090. doi: 10.1080/10408398.2017.1392288
- Bingham, S. A., Hughes, R., and Cross, A. J. (2002). Effect of white versus red meat on endogenous N-nitrosation in the human colon and further evidence of a dose response. *J. Nutr.* 132, 3522S–3525S. doi: 10.1093/jn/132.11.3522S
- Calder, P. C. (2015). Functional roles of fatty acids and their effects on human health. *J. Parenteral Enteral Nutr.* 39, 18S–32S. doi: 10.1177/0148607115595980
- CCC (Committee on Climate Change) (2020) Land use: policies for a net zero UK. Available online at: <https://www.theccc.org.uk/publication/land-use-policies-for-a-net-zero-uk>.
- Chowdhury, R., Warnakula, S., Kunutsor, S., Crowe, F., Ward, H. A., Johnson, L., et al. (2014). Association of dietary, circulating, and supplement fatty acids with coronary risk. A systematic review and meta-analysis. *Ann. Internal Med.* 160, 398–406. doi: 10.7326/M13-1788
- Crippa, M., Solazzo, E., Guizzardi, D., Monforti-Ferrario, F., and Leip, A. (2021). Food systems are responsible for a third of global anthropogenic GHG emissions. *Nat. Food*. 2, 198–209. doi: 10.1038/s43016-021-00225-9
- Critselis, E., Tsiampalis, T., Damigou, E., Georgousopoulou, E., Barkas, F., Chrysoshoou, C., et al. (2023). High fish intake rich in n-3 polyunsaturated fatty acids reduces cardiovascular disease incidence in healthy adults: The ATTICA cohort study, (2002–2022). *Front. Physiol.* 14, 1158140. doi: 10.3389/fphys.2023.1158140
- Del Gobbo, L. C., Imamura, F., Aslibekyan, S., Marklund, M., Virtanen, J. K., Wennberg, M., et al. (2016).  $\omega$ -3 polyunsaturated fatty acid biomarkers and coronary heart disease. Pooling project of 19 cohort studies. *JAMA Internal Med.* 176, 1155–1166. doi: 10.1001/jamainternmed.2016.2925
- de Oliveira Otto, M. C., Mozaffarian, D., Kromhout, D., Bertoni, A. G., Sibley, C. T., Jacobs, D. R., et al. (2012). Dietary intake of saturated fat by food source and incident cardiovascular disease: the Multi-Ethnic Study of Atherosclerosis. *Am. J. Clin. Nutr.* 96, 397–404. doi: 10.3945/ajcn.112.037770
- De Smet, S., and Vossen, E. (2016). Meat: The balance between nutrition and health. *A review Meat Sci.* 120, 145–156. doi: 10.1016/j.meatsci.2016.04.008
- Drouin-Chartier, J. P., Chen, S., Li, Y., Schwab, A. L., Stampfer, M. J., Sacks, F. M., et al. (2020). Egg consumption and risk of cardiovascular disease: three large prospective US cohort studies, systematic review and updated meta-analysis. *BMJ* 368, m513. doi: 10.1136/bmj.m513
- Drouin-Chartier, J.-P., Li, Y., Korat, A. V. A., Ding, M., Lamarche, B., Manson, J. E., et al. (2019). Changes in dairy product consumption and risk of type 2 diabetes: results from 3 large prospective cohorts of US men and women. *Am. J. Clin. Nutr.* 110, 1201–1212. doi: 10.1093/ajcn/nqz180
- EFSA (European Food Standards Authority) (2017). *Dietary Reference Values for Nutrients. Summary Report* (Parma, Italy: EFSA Supporting Publication), 98. doi: 10.2903/sp.efsa.2017.e15121
- Etemadi, A., Sinha, R., Ward, M. H., Graubard, B. I., Inoue-Choi, M., Dawsey, S. M., et al. (2017). Mortality from different causes associated with meat, heme iron, nitrates, and nitrites in the NIH-AARP Diet and Health Study: population-based cohort study. *BMJ* 357, j1957. doi: 10.1136/bmj.j1957
- EU (European Union) (2011). Commission Regulation (EU) No. 1169/2011 of the European Parliament and of the Council of 25 October 2011 on the provision of food information to consumers. *Off. J. Eur. Union* 304, 18–63.
- Fairweather-Tait, S. (2023). The role of meat in iron nutrition of vulnerable groups of the UK population. *Front. Anim. Sci.* 4. doi: 10.3389/fanim.2023.1142252
- FAO (Food and Agriculture Organisation of the United Nations) (2021). Available online at: <http://www.fao.org/faostat/en/#data/FBS>.
- Forouhi, N. G., Koulman, A., Sharp, S. J., Imamura, F., Kroger, J., Schulze, M. B., et al. (2014). Differences in the protective association between individual plasma phospholipid saturated fatty acids and incident type 2 diabetes: the EPIC-InterAct case-cohort study. *Lancet Diabetes Endocrinol.* 2, 810–818. doi: 10.1016/S2213-8587(14)70146-9
- Frank, D., Oytam, Y., Hughes, J., McDonnell, C. K., and Bucklow, R. (2022). “Sensory perceptions and new consumer attitudes to meat,” in *New Aspects of Meat Quality*. Ed. P. P. Purslow (Woodhead Publishing Ltd, Cambridge), 853–886.
- Fretts, A. M., Hazen, S. L., Jensen, P., Budoff, M., Sitlani, C. M., Wang, M., et al. (2022). Association of trimethylamine N-oxide and metabolites with mortality in older adults. *JAMA Network Open* 5, e2213242. doi: 10.1001/jamanetworkopen.2022.13242
- Gerber, P. J., Steinfeld, H., Henderson, B., Mottet, A., Opio, C., Dijkman, J., et al. (2013). *Tackling climate change through livestock – A global assessment of emissions and mitigation opportunities* (Rome: Food and Agriculture Organization of the United Nations (FAO)).
- Gijsbers, L., Ding, E. L., Malik, V. S., de Goede, J., Geleijnse, J. M., and Soedamah-Muthu, S. S. (2016). Consumption of dairy foods and diabetes, incidence: a dose-response meta-analysis of observational studies. *Am. J. Clin. Nutr.* 103, 1111–1124. doi: 10.3945/ajcn.115.123216

## 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.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

## Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.



- Givens, D. I. (2018). Review: Dairy foods, red meat and processed meat in the diet: implications for health at key life stages. *Animal* 12, 1709–1721. doi: 10.1017/S1751731118000642
- Givens, D. I. (2023). Dairy foods and cardiometabolic diseases: an update and a reassessment of the impact of saturated fatty acids. *Proc. Nutr. Society* 82, 320–345. doi: 10.1017/S0029665123000083
- Green, R., Milner, J., Dangour, A. D., Haines, A., Chalabi, Z., Markandya, A., et al. (2015). The potential to reduce greenhouse gas emissions in the UK through healthy and realistic dietary change. *Climatic Change* 129, 253–265. doi: 10.1007/s10584-015-1329-y
- Guo, J., Hobbs, D. A., Cockcroft, J. R., Elwood, P. C., Pickering, J. E., Lovegrove, J. A., et al. (2018). Association between egg consumption and cardiovascular disease events, diabetes and all-cause mortality. *Eur. J. Nutr.* 57, 2943–2952. doi: 10.1007/s00394-017-1566-0
- Habermeyer, M., Roth, A., Guth, A., Diel, P., Engel, K.-H., Epe, B., et al. (2015). Nitrate and nitrite in the diet: how to assess their benefit and risk for human health. *Mol. Nutr. Food Res.* 59, 106–128. doi: 10.1002/mnfr.201400286
- Henchion, M., Hayes, M., Mullen, A. M., Fenelon, M., and Brijesh Tiwari, B. (2017). Future protein supply and demand: strategies and factors influencing a sustainable equilibrium. *Foods* 6, 53. doi: 10.3390/foods6070053
- Henriques, J., Dick, J. R., Tocher, D. R., and Bell, J. G. (2014). Nutritional quality of salmon products available from major retailers in the UK: content and composition of n-3 long-chain PUFA. *Br. J. Nutr.* 112, 964–975. doi: 10.1017/S0007114514001603
- Henry, B. K., Eckard, R. J., and Beauchemin, K. A. (2018). Review: Adaptation of ruminant livestock production systems to climate changes. *Animal* 12, s445–s456. doi: 10.1017/S1751731118001301
- Hobbs, D. A., Durrant, C., Elliott, J., Givens, D. I., and Lovegrove, J. A. (2020). Diets containing the highest levels of dairy products are associated with greater eutrophication potential but higher nutrient intakes and lower financial cost in the United Kingdom. *Eur. J. Nutr.* 59, 895–908. doi: 10.1007/s00394-019-01949-y
- Hooper, L., Martin, N., Jimoh, O. F., Kirk, C., Foster, E., and Abdelhamid, A. S. (2020). Reduction in saturated fat intake for cardiovascular disease. *Cochrane Database Systematic Rev.* (8), CD011737.
- Hu, Y., Hu, F. B., and Manson, J. E. (2019). Marine omega-3 supplementation and cardiovascular disease: an updated meta-analysis of 13 randomized control trials involving 127 477 participants. *J. Am. Heart Assoc.* 119, 013543. doi: 10.1161/JAHA.119.013543
- Huang, J., Liao, L. M., Weinstein, S. J., Sinha, R., Graubard, B. I., and Albanes, D. (2022). Association between plant and animal protein intake and overall and cause-specific mortality. *JAMA Internal Med.* 180, 1173–1184. doi: 10.1001/jamainternmed.2020.2790
- Hur, S. J., Jo, C., Yoon, Y., Jeong, J. Y., and Lee, K. T. (2019). Controversy on the correlation of red and processed meat consumption with colorectal cancer risk: an Asian perspective. *Crit. Rev. Food Sci. Nutr.* 59, 3526–3537. doi: 10.1080/10408398.2018.1495615
- Iqbal, R., Dehghan, M., Mente, A., Rangarajan, S., Wielgosz, A., Avezum, A., et al. (2021). Associations of unprocessed and processed meat intake with mortality and cardiovascular disease in 21 countries [Prospective Urban Rural Epidemiology (PURE) Study]: a prospective cohort study. *Am. J. Clin. Nutr.* 114, 1049–1058. doi: 10.1093/ajcn/nqaa448
- Key, T. J., Appleby, P. N., Crowe, F. L., Bradbury, K. E., Schmidt, J. A., and Travis, R. C. (2014). Cancer in British vegetarians: updated analyses of 4998 incident cancers in a cohort of 32,491 meat eaters 8612 fish eaters, 18,298 vegetarians, and 2246 vegans. *Am. J. Clin. Nutr.* 100, 378S–385S. doi: 10.3945/ajcn.113.071266
- Kulczynski, B., Sidor, A., and Gramza-Michałowska, A. (2019). Characteristics of selected antioxidative and bioactive compounds in meat and animal origin products. *Antioxidants* 8, 335. doi: 10.3390/antiox8090335
- Lee, M. R. F., Domingues, J. P., McAuliffe, G. A., Tichit, M., Accatino, F., and Takahashi, T. (2021). Nutrient provision capacity of alternative livestock farming systems per area of arable farmland required. *Sci. Rep.* 11, 14975. doi: 10.1038/s41598-021-93782-9
- Lescinsky, H., Afshin, A., Ashbaugh, C., Bisignano, C., Brauer, M., Ferrara, G., et al. (2022). Health effects associated with consumption of unprocessed red meat: a Burden of Proof study. *Nat. Med.* 28, 2075–2082. doi: 10.1038/s41591-022-01968-z
- Lombardi-Boccia, G., Martinez-Dominguez, B., and Aguzzi, A. (2002). Total heme and non-heme iron in raw and cooked meats. *J. Food Sci.* 67, 1738–1741.
- Lorenzen, J. K., and Astrup, A. (2011). Dairy calcium intake modifies responsiveness of fat metabolism and blood lipids to a high-fat diet. *Br. J. Nutr.* 105, 1823–1831. doi: 10.1017/S00071145110005581
- MacLeod, M. J., Hasan, M. R., Robb, D. H. F., and Rashid, M. M. U. (2020). Quantifying greenhouse gas emissions from global aquaculture. *Sci. Rep.* 10, 11679. doi: 10.1038/s41598-020-68231-8
- McAuliffe, G. A., Takahashi, T., Beal, T., Huppertz, T., Leroy, F., J. Buttriss, J., et al. (2023). Protein quality as a complementary functional unit in life cycle assessment (LCA). *Int. J. Life Cycle Assessment* 28, 146–155. doi: 10.1007/s11367-022-02123-z
- Micha, R., Michas, G., and Mozaffarian, D. (2012). Unprocessed red and processed meats and risk of coronary artery disease and type 2 diabetes – an updated review of the evidence. *Curr. Atheroscl. Rep.* 14, 515–524. doi: 10.1007/s11883-012-0282-8
- Miller, V., Micha, R., Choi, E., Karageorgou, D., Webb, P., and Mozaffarian, D. (2022). Evaluation of the quality of evidence of the association of foods and nutrients with cardiovascular disease and diabetes. A systematic review. *JAMA Network Open* 5, e2146705. doi: 10.1001/jamanetworkopen.2021.46705
- Miller, V., Webb, P., Cudhea, F., Zhang, J., Reedy, J., Shi, P., et al. (2023). Children's and adolescents' rising animal-source food intakes in 1990–2018 were impacted by age, region, parental education and urbanicity. *Nat. Food* 4, 305–319. doi: 10.1038/s43016-023-00731-y
- Mohan, D., Mente, A., Dehghan, M., Rangarajan, S., O'Donnell, M., Hu, W., et al. (2021). Associations of fish consumption with risk of cardiovascular disease and mortality among individuals with or without vascular disease from 58 Countries. *JAMA Internal Med.* 181, 631–649. doi: 10.1001/jamainternmed.2021.0036
- OECD-FAO (Organisation of Economic Cooperation and Development-Food and Agriculture Organisation of the United Nations) (2023). *Agricultural Outlook 2022-2032* (Paris: OECD Publishing).
- Ortenzi, F., and Beal, T. (2021). Priority micronutrient density of foods for complementary feeding of young children (6–23 months) in south and Southeast Asia. *Front. Nutr.* 8, 785227. doi: 10.3389/fnut.2021.785227
- Park, Y. W., and Nam, M. S. (2015). Bioactive peptides in milk and dairy products: a review. *Korean J. Food Sci. Anim. Resources* 35, 831–840. doi: 10.5851/kosfa.2015.35.6.831
- Parlasca, M. C., and Qaim, M. (2022). Meat consumption and sustainability. *Annu. Rev. Resource Economics* 14, 17–41. doi: 10.1146/annurev-resource-111820-032340
- Penkert, L. P., Ruogo, L., Huang, J., Gurcan, A., Chung, M., and Wallace, T. C. (2021). Pork consumption and its relationship to human nutrition and health: a scoping review. *Meat Muscle Biol.* 5, 1–22. doi: 10.22175/mmb.12953
- Perna, M., and Hewlings, S. (2023). Saturated fatty acid chain length and risk of cardiovascular disease: A systematic review. *Nutrients* 15, 30.
- Pimpin, L., Kranz, S., Liu, E., Shulkin, M., Karageorgou, D., Miller, V., et al. (2019). Effects of animal protein supplementation of mothers, preterm infants, and term infants on growth outcomes in childhood: a systematic review and meta-analysis of randomized trials. *Am. J. Clin. Nutr.* 110, 410–429. doi: 10.1093/ajcn/nqy348
- Poore, J., and Nemecek, T. (2018). Reducing food's environmental impacts through producers and consumers. *Science* 360, 987–992. doi: 10.1126/science.aag0216
- Prada, M., Wittenbecher, C., Eichelmann, F., Wernitz, A., Drouin-Chartier, J.-P., and Schulze, M. B. (2021). Association of the odd-chain fatty acid content in lipid groups with type 2 diabetes risk: A targeted analysis of lipidomics data in the EPIC-Potsdam cohort. *Clin. Nutr.* 40, 4988–4999. doi: 10.1016/j.clnu.2021.06.006
- Public Health England (2020). *National Diet and Nutrition Survey Rolling Programme Years 9 to 11 (2016/2017 to 2018/2019)* (London: Public Health England).
- Public Health England (2021). *McCance and Widdowson's The Composition of Foods. Integrated Dataset* (London: Public Health England).
- Rivero, M. J., Lopez-Villalobos, N., Evans, A., Berndt, A., Cartmill, A., Neal, A. L., et al. (2021). Key traits for ruminant livestock across diverse production systems in the context of climate change: perspectives from a global platform of research farms. *Reproduction Fertility Dev.* 33, 1–19. doi: 10.1071/RD20205
- Rohrmann, S., Overvad, K., Bueno-de-Mesquita, H. B., Jakobsen, M. U., Egeberg, R., Tjønneland, A., et al. (2013). Meat consumption and mortality – results from the European Prospective Investigation into Cancer and Nutrition. *BMC Med.* 11, 63–75. doi: 10.1186/1741-7015-11-63
- Rong, Y., Chen, L., Zhu, T., Song, Y., Yu, M., Shan, Z., et al. (2013). Egg consumption and risk of coronary heart disease and stroke: dose-response meta-analysis of prospective cohort studies. *BMJ* 346, e8539. doi: 10.1136/bmj.e8539
- SACN (Scientific Advisory Committee on Nutrition) (2004). *Advice on fish consumption: benefits and risks* (London: The Stationery Office).
- Scarborough, P., Clark, M., Cobiaci, L., Papier, K., Knuppel, A., Lynch, J., et al. (2023). Vegans, vegetarians, fish-eaters and meat-eaters in the UK show discrepant environmental impacts. *Nat. Food* 4, 565–574. doi: 10.1038/s43016-023-00795-w
- Shah, U. A., and Iyengar, N. M. (2022). Plant-based and ketogenic diets as diverging paths to address cancer. A Review. *JAMA Oncol.* 8, 1201–1208. doi: 10.1001/jamaoncol.2022.1769
- Sinha, R., Cross, A. J., Graubard, B. I., Leitzmann, M. F., and Schatzkin, A. (2009). Meat intake and mortality: A prospective study of over half a million people. *Arch. Intern. Med.* 169, 562–571. doi: 10.1001/archinternmed.2009.6
- Siri-Tarino, P. W., Sun, Q., Hu, F. B., and Krauss, R. M. (2010). Meta-analysis of prospective cohort studies evaluating the association of saturated fat with cardiovascular disease. *Am. J. Clin. Nutr.* 91, 535–546. doi: 10.3945/ajcn.2009.27725
- Sodring, M., Dragsted, L. O., Muller, M. H. B., Paulsen, J. E., Haug, A., and Egeland, B. (2022). “Meat and cancer evidence for and against,” in *New Aspects of Meat Quality*. Ed. P. P. Purslow (Woodhead Publishing Ltd, Cambridge), 579–607.
- Soedamah-Muthu, S. S., and de Goede, J. (2018). Dairy consumption and cardiometabolic diseases: systematic review and updated meta-analyses of prospective cohort studies. *Curr. Nutr. Rep.* 7, 171–182. doi: 10.1007/s13668-018-0253-y
- Song, M., Fung, T. T., Hu, F. B., Willett, W. C., Longo, V. D., Chan, A. T., et al. (2016). Association of animal and plant protein intake with all-cause and cause-specific mortality. *JAMA Internal Med.* 176, 1453–1463. doi: 10.1001/jamainternmed.2016.4182

- Springmann, M., Clark, M., Mason-D'Croz, D., Wiebe, K., Bodirsky, B. L., Lassale, L., et al. (2018). Options for keeping the food system within environmental limits. *Nature* 562, 519–525. doi: 10.1038/s41586-018-0594-0
- Srouf, B., Fezeu, L. K., Kesse-Guyot, E., Alles, B., Mejean, C., Andrianasolo, R. M., et al. (2019). Ultra-processed food intake and risk of cardiovascular disease: prospective cohort study (NutriNet-Santé). *BMJ* 365, 11451. doi: 10.1136/bmj.11451
- Stenson, S., and Buttriss, J. L. (2021). Healthier and more sustainable diets: What changes are needed in high-income countries? *Nutr. Bulletin* 46, 279–309. doi: 10.1111/mbu.12518
- Stewart, C., Piernas, C., Cook, B., and Jebb, S. A. (2021). Trends in UK meat consumption: analysis of data from years 1–11 (2008–09 to 2018–19) of the National Diet and Nutrition Survey rolling programme. *Lancet Planet Health* 5, e699–e708. doi: 10.1016/S2542-5196(21)00228-X
- Strobel, C., Jahreis, G., and Kuhnt, K. (2012). Survey of n-3 and n-6 polyunsaturated fatty acids in fish and fish products. *Lipids Health Disease* 11, 144–154. doi: 10.1186/1476-511X-11-144
- Teicholz, N. (2023). A short history of saturated fat: the making and unmaking of a scientific consensus. *Curr. Opin. Endocrinol. Diabetes Obes.* 30, 65–71. doi: 10.1097/MED.0000000000000791
- UN (United Nations Environment Programme and Climate and Clean Air Coalition) (2021). *Global Methane Assessment: Benefits and Costs of Mitigating Methane Emissions* (Nairobi: United Nations Environment Programme).
- USDA (United States Department of Agriculture) (2020). *Scientific Report of the 2020 Dietary Guidelines Advisory Committee*. U.S. Department of Agriculture (Washington, DC: Agricultural Research Service).
- Van Kernebeek, H. R. J., Oosting, S. J., Van Ittersum, M. K., Bikker, P., and De Boer, I. J. M. (2016). Saving land to feed a growing population: consequences for consumption of crop and livestock products. *Int. J. Life Cycle Assessment* 21, 677–687. doi: 10.1007/s11367-015-0923-6
- Vissers, L. E. T., Rijkse, J., Boer, J. M. A., Verschuren, W. M. M., van der Schouw, Y. T., and Sluijs, I. (2019). Fatty acids from dairy and meat and their association with risk of coronary heart disease. *Eur. J. Nutr.* 58, 2639–2647. doi: 10.1007/s00394-018-1811-1
- Wang, X., Lin, X., Ouyang, Y. Y., Liu, J., Zhao, G., Pan, A., et al. (2016). Red and processed meat consumption and mortality: dose-response meta-analysis of prospective cohort studies. *Public Health Nutr.* 19, 893–905. doi: 10.1017/S1368980015002062
- WCRF (World Cancer Research Fund). American Institute for Cancer Research (2018). *Diet, Nutrition, Physical Activity and Cancer* (London, UK: A Global Perspective. Continuous Update Project Expert Report. World Cancer Research Fund).
- WHO/FAO (World Health Organisation/Food and Agriculture Organisation of the United Nations) (2003). *Diet, nutrition and the prevention of chronic diseases: report of a joint WHO/FAO expert consultation* (Geneva: World Health Organisation).
- Willett, W., Rockström, J., Loken, B., Springmann, M., Lang, T., Vermeulen, S., et al. (2019). Food in the Anthropocene: the EAT–Lancet Commission on healthy diets from sustainable food systems. *Lancet* 393, 447–492. doi: 10.1016/S0140-6736(18)31788-4
- Wood, J. D. (2023). “Meat composition and nutritional value” in *Lawrie's Meat Science 9th edition*. Ed. F. Toldra (Cambridge: Woodhead Publishing Ltd), 665–685.
- YouGov (2023). *Dietary choices of Brits (eg vegetarian, flexitarian, meat-eater etc)* (London: YouGov poll. Biannual tracker. YouGov PLC).
- Zhang, H., Greenwood, D. C., Risch, H. A., Bunce, D., Hardie, L. J., and Cade, J. E. (2021). Meat consumption and risk of incident dementia: cohort study of 493,888 UK Biobank participants. *Am. J. Clin. Nutr.* 114, 175–184. doi: 10.1093/ajcn/nqab028
- Zhao, B., Gan, L., Graubard, B. I., Männistö, S., Albanes, D., and Huang, J. (2022). Associations of dietary cholesterol, serum cholesterol, and egg consumption with overall and cause-specific mortality: systematic review and updated meta-analysis. *Circulation* 145, 1506–1520. doi: 10.1161/CIRCULATIONAHA.121.057642
- Zheng, J., Huang, T., Yu, Y., Hu, X., Yang, B., and Li, D. (2012). Fish consumption and CHD mortality: an updated meta-analysis of seventeen cohort studies. *Public Health Nutr.* 15, 725–737. doi: 10.1017/S1368980011002254
- Zhong, V. W., Van Horn, L., Cornelis, M. C., Wilkins, J. T., Ning, H., Carnethon, M. R., et al. (2019). Associations of dietary cholesterol or egg consumption with incident cardiovascular disease and mortality. *JAMA* 321, 1081–1095. doi: 10.1001/jama.2019.1572
- Zhong, V. W., Van Horn, L., Greenland, P., Carnethon, M. R., Ning, H., Wilkins, J. T., et al. (2020). Associations of processed meat, unprocessed red meat, poultry, or fish intake with incident cardiovascular disease and all-cause mortality. *JAMA Internal Med.* 180, 503–512. doi: 10.1001/jamainternmed.2019.6969



## OPEN ACCESS

## EDITED BY

Ian Givens,  
University of Reading, United Kingdom

## REVIEWED BY

Nigel Scollan,  
Queen's University Belfast, United Kingdom  
Sandra Sofia Quinteiro Rodrigues,  
Centro de Investigação de Montanha (CIMO),  
Portugal

## \*CORRESPONDENCE

Eric N. Ponnampalam  
✉ eponnampalam@unimelb.edu.au  
Michelle Kearns  
✉ michelle.kearns@ucdconnect.ie  
Cletos Mapiye  
✉ cmapiye@sun.ac.za

RECEIVED 28 October 2023

ACCEPTED 02 February 2024

PUBLISHED 01 March 2024

## CITATION

Ponnampalam EN, Kearns M, Kiani A,  
Santhiravel S, Vahmani P, Prache S,  
Monahan FJ and Mapiye C (2024) Enrichment  
of ruminant meats with health enhancing  
fatty acids and antioxidants:  
feed-based effects on  
nutritional value and human health  
aspects – invited review.  
*Front. Anim. Sci.* 5:1329346.  
doi: 10.3389/fanim.2024.1329346

## COPYRIGHT

© 2024 Ponnampalam, Kearns, Kiani,  
Santhiravel, Vahmani, Prache, Monahan and  
Mapiye. This is an open-access article  
distributed under the terms of the [Creative  
Commons Attribution License \(CC BY\)](#). The  
use, distribution or reproduction in other  
forums is permitted, provided the original  
author(s) and the copyright owner(s) are  
credited and that the original publication in  
this journal is cited, in accordance with  
accepted academic practice. No use,  
distribution or reproduction is permitted  
which does not comply with these terms.

# Enrichment of ruminant meats with health enhancing fatty acids and antioxidants: feed-based effects on nutritional value and human health aspects – invited review

Eric N. Ponnampalam<sup>1,2\*</sup>, Michelle Kearns<sup>3\*</sup>, Ali Kiani<sup>4</sup>,  
Sarusha Santhiravel<sup>5</sup>, Payam Vahmani<sup>6</sup>, Sophie Prache<sup>7</sup>,  
Frank J. Monahan<sup>3</sup> and Cletos Mapiye<sup>8\*</sup>

<sup>1</sup>School of Agriculture, Food and Ecosystems Sciences, The University of Melbourne, Parkville, VIC, Australia, <sup>2</sup>Department of Jobs, Precincts and Regions, Agrifood Animal Production, Mill Park, VIC, Australia, <sup>3</sup>School of Agriculture and Food Science, University College Dublin, Dublin, Ireland, <sup>4</sup>Department of Animal Science, Lorestan University, Khorramabad, Iran, <sup>5</sup>Department of Biochemistry, Memorial University of Newfoundland, St. John's, NL, Canada, <sup>6</sup>Department of Animal Science, University of California, Davis, Davis, CA, United States, <sup>7</sup>INRAE, Université Clermont Auvergne Vetagro Sup, Unité Mixte de Recherche sur les Herbivores, St-Genès-Champanelle, France, <sup>8</sup>Department of Animal Sciences, Faculty of AgriSciences, Stellenbosch University, Matieland, South Africa

Optimising resource use efficiency in animal- agriculture-production systems is important for the economic, environmental, and social sustainability of food systems. Production of foods with increased health enhancing aspects can add value to the health and wellbeing of the population. However, enrichment of foods, especially meat with health enhancing fatty acids (HEFA) increases susceptibility to peroxidation, which adversely influences its shelf life, nutritional value and eating quality. The meat industry has been challenged to find sustainable strategies that enhance the fatty acid profile and antioxidant actions of meat while mitigating oxidative deterioration and spoilage. Currently, by-products or co-products from agricultural industries containing a balance of HEFA and antioxidant sources seem to be a sustainable strategy to overcome this challenge. However, HEFA and antioxidant enrichment processes are influenced by ruminal lipolysis and biohydrogenation, HEFA-antioxidant interactions in rumen ecosystems and muscle biofortification. A deep understanding of the performance of different agro-by-product-based HEFA and antioxidants and their application in current animal production systems is critical in developing HEFA-antioxidant co-supplementation strategies that would benefit modern consumers who desire nutritious, palatable, safe, healthy, affordable, and welfare friendly meat and processed meat products. The current review

presents the latest developments regarding discovery and application of novel sources of health beneficial agro-by-product-based HEFA and antioxidants currently used in the production of HEFA-antioxidant enriched ruminant meats and highlights future research perspectives.

#### KEYWORDS

red meat, dietary means, forages, phytonutrients, conjugated linoleic acid, omega-3 fatty acids, antioxidants, muscle fortification

## 1 Introduction

There are many breeds and genotypes within the ruminant animal species of sheep, goats and cattle around the world, each of them is adapted to the different environments they live in and the diets they consume. Ruminant animals obtain their nutrients from fresh forage materials of native rangelands or cultivated pastures, crop residues, cereal grains, preserved forages and agri-food by-products (Ponnampalam et al., 2022), and nutrition and feeding strategies play a major role in the wellness, productivity, and survival of animals. Numerous studies have investigated the effect of feeding systems and feed composition on the fat content, fatty acid (FA) composition and antioxidant status of meat in ruminants (Scollan et al., 2006; Chilliard et al., 2007; Noci et al., 2011; Chauhan et al., 2014; Berthelot and Gruffat, 2018; Vahmani et al., 2020). Dietary proteins, lipids and carbohydrates are vital for ruminant growth and development. Equally, vitamins, minerals and health enhancing fatty acids (HEFA) are crucial for animal health, well-being and product quality (Kaur et al., 2014; Ponnampalam et al., 2021a; Guo et al., 2023; Kearns et al., 2023b). The HEFA include the parent (precursors), their products (derivatives) as well as their biohydrogenation intermediates (BHI). These in turn include alpha-linolenic acid (ALA, C18:3n-3), eicosapentaenoic acid (EPA, C20:5n-3), docosapentaenoic acid (DPA, C22:5n-3), docosahexaenoic acid (DHA, C22:6n-3), linoleic acid (LA, C18:2n-6), rumenic acid (RA, cis(c)9, trans(t)11-18:2), and trans vaccenic acid (TVA, cis(c)9, trans(t)11-18:1). The economic return of animal production systems is largely dependent on the yield, quality, nutritional value and storage stability of the meat produced by the flock or herd.

Red meat, obtained from lamb/mutton, beef, and chevon, is rich in vital nutrients, including a high amount of highly digestible proteins, containing all essential amino acids to meet human requirements, B vitamins (mainly vitamin B12), zinc, iron, and selenium (Klurfeld, 2018). Red meat is one of the most important animal source foods in many countries all over the world. However, epidemiological data from meta-analyses shows that excessive consumption of red meat and processed meat can have deleterious effects, including an increased risk of colorectal cancer and premature death (Schwingshackl et al., 2017; WCRF et al., 2018), leading to recommendations to limit consumption to 500 g/week for red meat and 150 g/week for processed meat (Prache et al.,

2022a). North America, Europe and Oceania regions consume large quantities of red and white meat, African regions consume the least amount, and the Asia and Latin America regions consume moderate amounts. The per capita consumption per year of beef-veal, sheep meat (lamb and mutton), poultry meat and pork worldwide, and within major regions of the world is shown in Figure 1. As goat meat intake is very small in quantity around the world and mostly associated with some ethnic groups within countries, it was not shown. The per capita consumption of red meat around the world has increased from 10 to 20 kg of meat between 1961 and 2020 (Ritchie et al., 2019).

The mean consumption of unprocessed and processed red meat per person across countries varies due to affordability, availability, and preference. The low-fat content (of particular cuts) relevant to all meats has great importance due to the links found between meat FA consumption and prevalence of chronic disease (Bernstein et al., 2010; Abid et al., 2014). Table 1 below provides some information on consumption of beef-veal, sheep meat (lamb-mutton), poultry meat and pork from developed and developing countries around the world, expressed in retail weight.

Ruminant meat is a good source of HEFA. Linoleic acid and ALA are parent (precursor) fatty acids, which cannot be synthesised by the animal and human body and must be obtained from the diet (Kaur et al., 2014; Ponnampalam, 1999). These two FA are vital for the synthesis of their longer chain polyunsaturated fatty acid (PUFA) derivatives and their bioactive intermediates in the rumen and fortification in animal tissues (Ponnampalam et al., 2021b). In addition, ruminant meats contain nutrient antioxidants such as vitamins A, C and E, and the minerals copper, zinc and selenium (Bourre, 2011; Cabrera and Saadoun, 2014), which scavenge the free radicals and reactive oxygen species (ROS) in the cell, thereby mitigating oxidative stress and its consequences in the body (Zehiroglu and Ozturk Sarikaya, 2019). Both HEFA and antioxidants play a crucial role in the maintenance and/or enhancement of animal welfare, meat shelf life and sensory attributes and health of human beings (Scollan et al., 2006; Kurutas, 2015; Lauridsen, 2019; Ponnampalam et al., 2021a; Ponnampalam et al., 2022). Therefore, enriching ruminant meat, which is consumed by the majority of the world population, with HEFA and antioxidants could improve the nutritional value (i.e., health aspects), quality (i.e., sensory), and storage stability (i.e., shelf



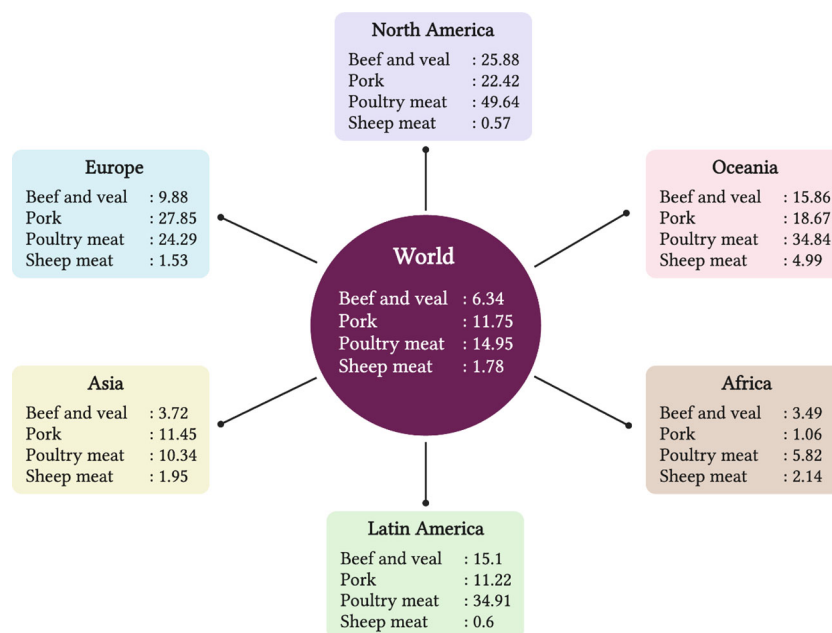


FIGURE 1

The per capita consumption (kg / year) of beef-veal, sheep meat (lamb and mutton), poultry and pork of world and major regions of world. Source: OECD/FAO (2021), OECD Agriculture statistics (database), <http://dx.doi.org/10.1787/agr-outl-dataen>.

life) of meat and eventually benefit the health of human beings as illustrated in Figure 2. This review aims to provide an update on aspects of various diets and feeding strategies contributing to the enrichment of HEFA and antioxidants in meat from sheep, goats and cattle, enabling improvement in the nutritional value, quality and health aspects of red meat that in turn may enhance health and well-being of humans upon consumption.

## 2 Feed-based enrichment of health enhancing fatty acid concentrations in red meat from sheep, goats and cattle

Meat from ruminant and monogastric animal species contributes important sources of nutrients from childhood to old age in many communities in developed and developing countries (FAO, 2011; Pereira and Vicente, 2013; FAO, 2017). Red meat from ruminants can offer balanced nutrient profiles and promote consumer health in many societies around the world (Pereira and Vicente, 2013), provided it is not consumed in excess (Prache et al., 2022a). Nutrient composition of meat is influenced by the type of diet that the animals consume. For example, feeding grain-based diets to ruminants increases intramuscular fat (i.e., marbling), omega(*n*)-6 FA concentrations and the *n*-6:*n*-3 ratio in meat (Aurousseau et al., 2004; Ponnampalam et al., 2017; Chikwanha et al., 2018, 2007; Berthelot and Gruffat, 2018; Gruffat et al., 2020; Clinquart et al., 2022; Davis et al., 2022). The latter effects are mainly due to variation in diet composition and nutrient availability of feeds affecting the ruminal biohydrogenation process, digestion and absorption of nutrients in the gastro-intestinal tract (GIT) of

the host animal and subsequent metabolism in the body, determining the availability of energy and nutrients for the synthesis of biochemical components in meat.

There are many reasons for the variation in HEFA concentrations in meat, mainly determined by the ruminal lipolysis and biohydrogenation process of microbial activity. Lipids/fats in the diet can be categorised as protected or unprotected, depending on their susceptibility to microbial degradation and biohydrogenation in the rumen. Dietary fats can be protected naturally (e.g., feeding whole oilseeds) or by chemical interventions (fat emulsification or encapsulation within proteins) to form calcium soaps or amides, which protect against rumen degradation. Protected fats are conditioned to limit their degradation in the rumen while unprotected fats are subjected to ruminal degradation, whereby PUFA are hydrogenated into SFA and free FAs as a result of ruminal lipolysis by microbes. Biohydrogenation is not comprehensive; a portion of unprotected fats may by-pass degradation in the rumen, thereby becoming available for absorption and deposition in muscle and other tissues.

Lipids are either consumed or synthesised *de novo* and it should be noted that the digestion and absorption of lipids (or fats) in ruminant and monogastric animals are not similar. This is due to their feeding nature and structure of digestive systems. Ruminant animals accustomed to consuming diets containing 1–4% fat, and lipid supplements fed to ruminants above 5–6% on a dry matter basis may cause negative effects on rumen microbial activity, affecting feed intake and animal productivity. With monogastric animals having a stomach as one organ for temporary storage of diet (fats) in the absence of rumen microbial activity, they can handle greater amounts of lipids in their diet and the fat deposition in meat resembles dietary lipid composition, while this is not the case for ruminants. More



TABLE 1 Per capita consumption (kg / year) of beef and veal, pork, poultry meat and sheep meat (lamb-mutton) from developed and developing countries around the world.

Countries	Per capita consumption of meat			
	Beef and veal	Pork	Poultry meat	Sheep meat
Argentina	35.55	11.51	40.45	0.96
Australia	23.51	23.93	45.77	6.94
Brazil	21.56	12.64	44.34	0.6
Canada	18.9	15.64	34.91	0.88
Chile	23.14	20.74	34.88	0.39
China	4.73	28.71	13.6	3.27
Colombia	9.67	9.33	31.03	0.02
Egypt	6.19	0.02	12.69	0.53
Ethiopia	2.5	0.01	0.49	1.98
European Union	10.41	33.18	23.91	1.31
India	0.58	0.18	2.38	0.52
Indonesia	2.01	0.68	12.61	0.45
Iran	4.7	0	22.98	3.54
Israel	25.08	0.99	63.84	1.52
Japan	7.29	16.65	17.73	0.16
Kazakhstan	21.8	5.71	22.91	7.95
Korea	12.08	30.35	20.08	0.37
Malaysia	5.1	5.63	44.05	0.89
Mexico	8.81	15.37	32.35	0.72
New Zealand	11.21	17.99	39.68	3.19
Nigeria	1.09	1.09	0.99	1.7
Norway	14.02	22.05	16.87	4.54
Pakistan	7.17	0	7.07	2.97
Paraguay	16.61	7.18	8.51	0.37
Peru	4.13	4.38	48.83	1.01
Philippines	2.33	10.66	14.05	0.27
Russian Federation	9.07	22.68	26.67	1.3
Saudi Arabia	4.2	0.31	37.22	4.53
South Africa	11.35	4.33	33.72	2.56
Switzerland	13.91	21.24	12.72	1.29
Thailand	1.13	9.46	7.24	0.03
Türkiye	7.54	0	17.38	1.19
Ukraine	4.72	13.84	21.19	0.19
United Kingdom	11.56	16.21	27.75	3.92
United States	26.67	23.2	51.33	0.53
Vietnam	5.14	31.42	15.2	0.19

Meat consumption expressed in retail weight. Source: OECD/FAO (2021), OECD Agriculture statistics (database), <http://dx.doi.org/10.1787/agr-outl-dataen>.

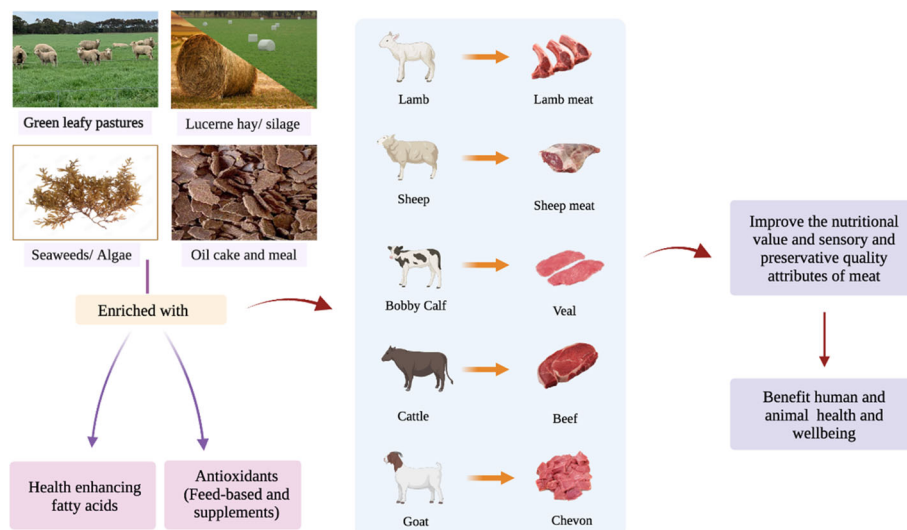


FIGURE 2

Schematic diagram showing pathways to enrich meat from ruminants with health enhancing FA and antioxidants delivering improved nutritional value and health aspects for consumers.

details on ruminal lipolysis, biohydrogenation and digestion process of dietary lipids can be found elsewhere (Swanson, 2019; Ponnampalam et al., 2021b).

## 2.1 Influence of diets on health enhancing fatty acids in lamb and mutton

Levels of HEFA in ruminant meat are largely dependent on the type of dietary fat consumed, the duration of feeding and ruminal biohydrogenation of PUFA. In this regard, a variety of nutritional strategies have been employed to increase HEFA deposition in sheep meat (i.e., lamb and mutton), which have been summarised in Table 2.

Meat from pasture-fed animals contains higher *n*-3 PUFA contents compared to grain-fed animals (Aurousseau et al., 2004; Nuernberg et al., 2005; Hajji et al., 2016, 2007; Berthelot and Gruffat, 2018; Gruffat et al., 2020), due to the naturally high levels of ALA in fresh pasture, a precursor for endogenous production of EPA, DPA and DHA (Ponnampalam et al., 2021b). It also contains a lower proportion of C16:0, which is pro-atherogenic (Berthelot and Gruffat, 2018). Grain supplementation at pasture diminishes these advantages, especially as the quantity of concentrate consumed increases (Montossi et al., 2013; Berthelot and Gruffat, 2018). Prolonged finishing periods on grain post-grazing diminishes *n*-3 PUFA accumulated in the meat, with lower ALA, EPA and DHA and their BHI such as CLAs (e.g., RA) and TVA levels observed in lamb meat (Aurousseau et al., 2007; Scerra et al., 2011). Conversely, there is a lack of data on the effect of the length of time an animal is finished on pasture pre-slaughter on the HEFA concentration in sheep meat. Pasture type can affect the HEFA composition of meat. Grazing lambs on legumes like lucerne and red clover (Fraser et al., 2004) or white clover (Lourenço et al., 2007) increased ALA levels in meat compared to lambs grazing grasses

like perennial ryegrass. Similarly, meat from lambs grazing chicory/arrow leaf clover had higher concentrations of *n*-3 PUFAs including ALA, EPA and DHA compared to lambs grazing brassica (De Brito et al., 2017). Lambs grazing botanically diverse pastures with phenol-rich plants produce meat richer in PUFA, ALA and LA than lambs grazing intensively managed pastures, with the concentration of these FA in the meat being linearly related to the phenolic concentration of the pasture (Willems et al., 2014). Plant secondary metabolites (polyphenol oxidase, flavonoids, tannins, essential oils and saponins) in legume and forb species can influence microbial biohydrogenation in the rumen, positively affecting beneficial *n*-3 PUFA and BHI outflow (Campidonico et al., 2016; Chikwanha et al., 2018; Frutos et al., 2020). Moreover, condensed tannins found in certain legumes can improve the lamb flavour by inhibiting the ruminal synthesis of skatole and indole, which are faecal-smelling compounds (Scollan et al., 2008; Girard et al., 2016; Rivaroli et al., 2019). Note here that sheep meat contains more HEFA than beef, due to lower ruminal biohydrogenation and a more selective eating behaviour of the animal (Prache et al., 2022b).

Generally, ruminants grazing fresh pasture consume higher amounts of *n*-3 PUFA compared to ruminants fed conserved forages (Ciftci et al., 2010) or total mixed ration (TMR) diets (Aurousseau et al., 2004, 2007; Berthelot and Gruffat, 2018; Gruffat et al., 2020). However, supplementation with *n*-3 PUFA rich oilseeds, marine- and plant-sourced oils and by-products have sometimes yielded more positive results. For example, addition of flaxseed to lamb diets resulted in increased contents of beneficial *n*-3 PUFA (i.e., ALA, EPA and DPA) in lamb and mutton (Noci et al., 2011; Ponnampalam et al., 2015; Urrutia et al., 2015; Berthelot and Gruffat, 2018). Diets supplemented with fish/algae oils increased long-chain *n*-3 PUFA levels such as EPA and DHA in lamb meat (Ponnampalam et al., 2016; Parvar et al., 2017), particularly when fed in an encapsulated form to protect against rumen

TABLE 2 Influence of diet on the health enhancing fatty acid composition (% of total fatty acids) of sheep meat.

Diet	Fatty acid (%)									Reference
	TVA	RA	LA	ALA	EPA	DPA	DHA	n-3	n-6	
Forage										
Grass-based permanent pasture	2.92	2.01	0.85	2.97	1.48	0.85	0.74	3.50	4.35	Rodríguez et al. (2020)
Chicory/plantain	2.40	1.98	0.76	3.59	1.91	0.92	0.99	4.12	5.04	
Perennial ryegrass pasture	2.92	1.46	–	1.39	–	–	–	2.40	5.88	Kliem et al. (2018)
Biodiverse pasture	2.40	1.30	–	1.66	–	–	–	2.70	6.74	
Botanically diverse	2.22	0.90	7.06	2.64	2.76	2.69	0.43	–	–	Lourenço et al. (2007)
Leguminosae-rich pasture	2.41	0.74	5.28	3.99	1.09	1.08	0.29	–	–	
Intensive ryegrass pasture	2.74	0.90	3.37	2.59	1.33	1.26	0.34	–	–	
Lucerne pasture	3.10	1.09	4.02	2.72	0.90	0.80	0.25	–	–	Fraser et al. (2004)
Red clover pasture	3.71	1.33	4.47	2.86	1.03	0.90	0.27	–	–	
Perennial ryegrass pasture	3.65	1.23	2.91	2.07	0.93	0.82	0.24	–	–	
Forage vs. Concentrate										
Concentrate + hay	–	0.21	4.30	0.29	0.28	0.63	0.21	1.41	6.94	Gruffat et al. (2020)
Alfalfa pasture	–	0.65	3.94	0.02	1.03	1.20	0.50	4.19	9.06	
Alfalfa pasture + sainfoin pellets	–	0.49	4.48	0.36	1.29	1.47	0.62	5.17	7.96	
Concentrate	–	0.42	3.82	0.44	0.18	0.46	0.80	0.99	5.37	Hajji et al. (2016)
Grass pasture	–	0.70	7.92	2.27	1.13	1.71	0.27	4.26	11.96	
Concentrate	0.42	0.59	12.55	0.51	0.38	–	0.28	1.77	22.24	Scerra et al. (2011)
Grass pasture	1.48	1.38	9.06	3.13	1.25	–	1.12	6.09	18.46	
Grass pasture	4.40	1.10	5.80	2.60	1.80	2.40	0.60	7.60	9.90	Aurousseau et al. (2007)
Grass pasture/short period on concentrate	4.70	1.00	5.70	1.70	1.30	1.80	0.50	5.30	9.10	
Grass pasture/long period on concentrate	2.00	0.90	5.70	1.20	1.20	1.50	0.50	4.80	9.50	
Concentrate	1.60	0.70	6.40	1.30	1.00	1.40	0.50	4.40	10.10	Nuernberg et al. (2005)
Concentrate	3.80	1.08	6.60	1.20	1.40	1.20	0.50	4.30	10.10	
Grass pasture	5.70	1.90	5.00	2.40	1.80	1.40	0.80	6.30	7.80	
Oil Supplementation										
TMR	–	–	7.26	0.45	0.48	0.29	0.32	1.54	8.94	Parvar et al. (2017)
TMR + 3% fish oil	–	–	9.22	0.82	1.94	0.9	1.78	5.54	10.91	
TMR + 3% canola oil	–	–	9.53	1.09	0.68	0.44	0.44	2.65	11.04	
TMR + 3% soybean oil	–	–	9.94	0.86	0.28	0.53	0.36	2.03	11.32	
TMR + 1.5% fish oil/1.5% canola oil	–	–	12.03	0.84	1.8	0.81	1.12	4.57	14.07	
TMR + 1.5% fish oil/1.5% soybean oil	–	–	10.52	0.82	0.72	0.8	0.78	3.11	12.16	
TMR + 1.5% soybean oil/1.5% canola oil	–	–	12.41	0.66	0.8	0.72	0.75	2.93	14.85	
Concentrate	3.79	0.26	8.79	0.53	0.19	0.42	0.12	1.43	13.38	Urrutia et al. (2015)
Concentrate + linseed	6.65	0.22	9.4	1.84	0.42	0.6	0.15	3.25	14.73	
Concentrate + chia seed	5.57	0.25	9.35	1.73	0.36	0.54	0.15	3.14	15.29	
Annual ryegrass hay/clover hay	–	–	2.94	1.35	0.69	0.55	0.30	–	–	Ponnampalam et al. (2015)
Annual ryegrass hay/clover hay + flaxseed	–	–	3.19	2.29	0.70	0.43	0.26	–	–	

(Continued)

TABLE 2 Continued

Diet	Fatty acid (%)									Reference
	TVA	RA	LA	ALA	EPA	DPA	DHA	<i>n</i> -3	<i>n</i> -6	
Oil Supplementation										
Annual ryegrass hay/clover hay + algae supplement	–	–	2.73	1.25	0.85	0.38	2.47	–	–	
Annual ryegrass hay/clover hay + flaxseed/algae supplement	–	–	2.84	1.61	0.67	0.32	1.93	–	–	
Concentrate	0.93	0.73	11.88	0.75	0.64	1.46	0.89	3.87	20.5	Nudda et al. (2015)
Concentrate + linseed	2.82	1.55	12.60	1.79	0.90	1.43	0.84	5.12	19.71	
Forage/concentrate + 3% palm oil	0.57	0.36	8.41	0.43	0.44	1.02	0.62	–	–	Gallardo et al. (2014)
Forage/concentrate + 3% olive oil	1.27	0.7	8.32	0.50	0.58	1.23	0.72	–	–	
Forage/concentrate + 3% fish oil	3.75	1.66	7.82	0.96	2.72	2.21	1.53	–	–	
Concentrate + rumen protected saturated fat	2.85	0.82	3.45	0.50	0.07	0.20	0.04	0.87	4.31	Noci et al. (2011)
Concentrate + camelina oil	4.61	0.95	2.86	1.27	0.11	0.20	0.05	1.75	3.70	
Concentrate + linseed oil	5.28	0.98	3.01	1.74	0.12	0.21	0.03	2.18	3.72	
By-products										
TMR	1.44	1.07	10.67	0.67	–	–	–	–	–	Bennato et al. (2023)
TMR + 10% grape pomace	2.32	1.22	11.97	0.61	–	–	–	–	–	
Concentrate	0.73	0.35	5.37	0.37	0.13	0.26	0.09	0.86	7.29	Natalello et al. (2019)
Concentrate + 20% pomegranate by-product	1.38	0.94	7.09	0.51	0.20	0.36	0.11	1.19	9.67	
Concentrate	0.67	0.18	10.48	0.26	0.16	0.40	0.10	–	–	Gómez-Cortés et al. (2019)
Concentrate + 50% camelina meal	1.26	0.28	8.99	0.25	0.15	0.38	0.14	–	–	
Concentrate + camelina meal/husks	3.59	0.79	11.12	0.34	0.13	0.39	0.11	–	–	
Concentrate	1.88	–	7.36	0.41	0.19	0.57	0.13	–	–	Asadollahi et al. (2017)
Concentrate + 7% roasted canola seed	2.02	–	9.77	0.64	0.23	0.65	0.19	–	–	
Concentrate + 36% sugar beet pulp	1.71	–	6.26	0.53	0.20	0.56	0.14	–	–	
Concentrate + 7% roasted canola seed + 36% sugar beet pulp	2.03	–	6.5	0.68	0.23	0.67	0.14	–	–	

TVA, trans-vaccenic acid; RA, rumenic acid; LA, linoleic acid; ALA, linolenic acid; EPA, eicosapentaenoic acid; DPA, docosapentaenoic acid; DHA, docosahexanoic acid; n-3, omega-3 fatty acids; n-6, omega-6 fatty acids.

TMR, total mixed ration.

biohydrogenation (Bessa et al., 2015). Supplementation of forage diets with *n*-6 rich oils (sunflower/soybean) has been shown to increase proportions of LA, RA and TVA, as well as other CLA isomers in lamb meat when compared to supplementation with *n*-3 PUFA rich oil sources (Chikwanha et al., 2018). Feeding lambs by-products such as grape/pomegranate pomace, soyabean hull and camelina meal, which are rich in antioxidants (polyphenols, flavonoids, anthocyanidins and tannins) led to enriched levels of ALA and total *n*-3 PUFA in meat (Gómez-Cortés et al., 2019; Natalello et al., 2019; Bennato et al., 2023). In summary, feeding pasture or high forage diets rich in *n*-3 PUFA leads to higher contents of health beneficial *n*-3 PUFA (ALA, EPA and DHA) and their BHI (RA and VA) in lamb meat. When high forage diets are fed along with *n*-6 PUFA rich sources, high concentrations of RA and VA are observed in meat, as *n*-6 rich dietary sources are more

effective at increasing RA and VA levels compared to *n*-3 rich dietary sources (Bessa et al., 2015; Chikwanha et al., 2018). Total mixed rations and grain-based diets may require the addition of a *n*-3 PUFA and forage sources to improve HEFA levels in sheep meat.

Meat from suckling lambs is widely consumed in southern Europe. In this case, lambs are considered as monogastric, and their meat FA profile reflects the feed-milk profile. Feeding ewes on good quality pastures (Joy et al., 2012), particularly biodiverse pastures containing various legume species (Cabiddu et al., 2005) has been shown to improve the HEFA content of meat from their lambs. The inclusion of *n*-3 PUFA rich oilseeds (Gallardo et al., 2015; Nudda et al., 2015) or marine oils (Gallardo et al., 2014) in ewe diets has also been shown to improve the HEFA content of lamb meat, but the inclusion of grape by-products did not significantly alter the HEFA content of lamb meat (Correddu et al., 2023).

## 2.2 Influence of diets on health enhancing fatty acids in beef and veal

The FA profile of veal and beef is largely influenced by diet, with forage finishing being the most practical strategy to increase the proportions of PUFAs, particularly *n*-3 PUFA and their BHIs (mostly RA and TVA), as previously reviewed by numerous authors (Mapiye et al., 2015; Vahmani et al., 2015; Berthelot and Gruffat, 2018). Therefore, only recent studies relating to the dietary manipulation of HEFA in beef have been included in Table 3.

The extent of these changes in beef is mainly dependent on the PUFA content of forage, in particular ALA, which is the predominant PUFA in most forage species (Dierking et al., 2010), and on finishing duration on these forages pre-slaughter (Noci et al., 2005). Noci et al. (2005) observed a linear increase in the *n*-3 PUFA content of beef up to 158 days of grazing. In general, fresh forages and pastures have higher contents of total lipids and total PUFA compared to conserved forages (i.e., silage and hay). This is mainly due to oxidative degradation of PUFA during haymaking and ensiling processes. In terms of species, legumes generally have higher contents of total FA, total PUFA and *n*-3 PUFAs, particularly ALA, compared to most grass species. However, grass offers greater levels of ALA than most cereal grains, which are the main sources of *n*-6 PUFA, mostly LA (Boufaïed et al., 2003). Consequently, beef from cattle grazing pastures containing white or red clover has higher proportions of *n*-3 PUFAs, along with a lower *n*-6:*n*-3 ratio (Lee et al., 2009; Berthelot and Gruffat, 2018; Moloney et al., 2018). Additionally, grazing steers on multispecies pasture consisting of different grasses, legumes and forbs resulted in beef with higher levels of LA, ALA and a higher *n*-6:*n*-3 ratio compared to beef from steers grazing perennial ryegrass (Kearns et al., 2023a). Given fresh forages and pastures contain higher concentrations of ALA, grazing is more effective in increasing *n*-3 PUFA and their respective BHIs while lowering the *n*-6:*n*-3 ratio in beef compared to feeding conserved forages and high-grain diets.

Conversely, LA is the predominant FA in grain-based diets which leads to increased *n*-6 PUFA contents, particularly LA, and higher *n*-6:*n*-3 ratios in grain-finished feedlot fed beef (Vahmani et al., 2015; Berthelot and Gruffat, 2018; Klopatek et al., 2022). Despite feedlot beef having a higher *n*-6:*n*-3 ratio (5:1 to 8:1) than forage-finished beef (1:1 to 3:1), the ratios are still lower than typical chicken and pork (15:1 to 19:1) (Dugan et al., 2015; Kim et al., 2020). In fact, consuming either forage or grain-finished beef may help to reduce the *n*-6:*n*-3 ratio in western diets which is currently estimated to be around 20:1 (DiNicolantonio and O'Keefe, 2021). In addition to forage-finishing strategies, attempts have been made to increase the amount of *n*-3 PUFAs in beef through supplementing diets with *n*-3 PUFA rich oils or oilseed meals (e.g., canola oil or canola meal). However, limited *n*-3 PUFA enrichments can be achieved using this approach because of extensive biohydrogenation of PUFA in the rumen (Vahmani et al., 2015) when compared with supplementing marine-based (algae) or chemically protected *n*-3 PUFA sources. Moreover, PUFA supplementation, particularly LA in forage diets often results in an increased tissue deposition of BHI, particularly TVA and RA, while supplementation in high-grain diets yields  $\text{t}10\text{-}18:1$  and  $\text{t}10,\text{c}12\text{-CLA}$  (Vahmani et al., 2020; Alves et al., 2021). Given recent studies have shown that ruminant-derived trans FAs such as  $\text{t}10\text{-}18:1$  (Vahmani et al., 2020) have similar adverse effects to that of industrial trans FAs (Verneque et al., 2022), it would be of importance to determine if the health value of beef enriched with *n*-3 PUFA is still maintained when different proportions of trans FAs are present.

## 2.3 Influence of diets on health enhancing fatty acids in chevon

Goat meat (i.e., chevon) has less fat than other red meat from ruminants (James and Berry, 1997), having about 50% less intramuscular fat (IMF) than beef and lamb with similar protein contents (Webb et al., 2005). In general, chevon contains higher

TABLE 3 Influence of diet on the health enhancing fatty acid composition (% of total fatty acids) of beef from ruminants.

Diet	Fatty acid (%)									Reference
	TVA	RA	LA	ALA	EPA	DPA	DHA	<i>n</i> -3	<i>n</i> -6	
Forage										
Perennial ryegrass pasture	–	–	3.64	0.82	0.52	1.02	–	2.77	5.58	Kearns et al. (2023a)
Perennial ryegrass/white clover pasture	–	–	4.33	1.12	0.65	1.20	–	3.40	6.54	
Multispecies pasture	–	–	5.91	1.56	0.66	1.25	–	3.93	8.47	
Rangeland pasture	2.08	0.63	3.97	1.52	0.89	0.95	–	3.52	6.02	Klopatek et al. (2022)
Rangeland pasture/irrigated pasture	2.44	0.58	2.48	1.09	0.41	0.63	–	2.24	3.71	
Perennial ryegrass/white clover pasture	–	0.46	2.11	1.13	0.58	0.93	–	2.92	3.19	Lee et al. (2021)
Permanent pasture	–	0.52	2.01	1.17	0.66	0.98	–	3.11	3.06	
Perennial ryegrass pasture	–	0.47	3.08	1.61	0.48	0.69	0.05	3.00	3.76	Moloney et al. (2018)
Perennial ryegrass/white clover pasture	–	0.58	2.51	1.23	0.48	0.61	0.06	2.52	3.15	

(Continued)



TABLE 3 Continued

Diet	Fatty acid (%)									Reference
	TVA	RA	LA	ALA	EPA	DPA	DHA	<i>n</i> -3	<i>n</i> -6	
Forage										
Grass silage	0.91	0.22	1.87	0.71	0.31	0.55	0.05	1.77	2.97	Lee et al. (2009)
Red clover silage	0.92	0.17	2.64	1.54	0.44	0.74	0.06	2.26	3.01	
0 days on perennial ryegrass	1.35	0.50	2.64	1.03	0.22	0.38	0.13	1.59	3.50	Noci et al. (2005)
40 days on perennial ryegrass	1.93	0.50	2.52	1.14	0.28	0.43	0.16	1.90	3.80	
90 days on perennial ryegrass	2.27	0.57	2.35	1.02	0.25	0.43	0.17	1.88	3.06	
158 days on perennial ryegrass	3.01	0.71	2.49	1.29	0.30	0.54	0.21	2.37	3.46	
Forage vs. Concentrate										
Silage + barley concentrate	–	0.18	4.07	0.61	0.20	0.36	0.02	1.21	5.35	Siphambili et al. (2022)
Silage + maize meal concentrate	–	0.21	5.37	0.72	0.33	0.55	0.06	1.69	7.13	
Silage + flaked meal concentrate	–	0.19	6.64	0.81	0.31	0.58	0.06	1.78	8.48	
Whole corn grain	–	0.21	5.67	0.22	0.17	0.40	0.09	0.92	8.15	Fruet et al. (2018)
Legume/grass pasture + whole corn gain supplementation	–	0.33	3.71	0.90	0.53	0.99	0.24	2.44	6.98	
Legume/grass pasture	–	0.41	4.22	1.59	0.66	1.21	0.10	3.60	6.79	
Concentrate	–	–	2.25	0.17	0.05	0.03	–	0.27	2.95	Hwang and Joo (2017)
Grass pasture	–	–	1.93	0.97	0.12	0.08	–	1.22	2.48	
Mixed pasture	3.58	0.64	2.59	1.17	0.54	0.85	0.09	2.65	3.46	Duckett et al. (2013)
Alfalfa pasture	3.32	0.61	2.85	1.32	0.60	0.91	0.10	2.92	3.79	
Pearl Millet pasture	3.56	0.70	2.27	1.06	0.49	0.76	0.07	2.39	3.08	
Concentrate	0.15	0.26	2.62	0.24	0.09	0.21	0.03	0.56	3.18	
Oil Supplementation										
Silage/concentrate	7.83	1.88	2.78	0.77	0.32	0.37	0.09	2.43	3.41	Moloney et al. (2022)
Silage/concentrate + sunflower/fish oil	8.34	2.14	2.65	0.74	0.34	0.37	0.10	2.43	3.28	
Barley based TMR + palmitic acid	–	0.42	3.42	0.46	0.10	0.36	0.06	0.98	4.46	Hennessy et al. (2021)
Barley based TMR + <i>n</i> -3 rumen protected supplement	–	0.56	4.07	0.53	1.60	0.77	0.55	3.45	4.95	
Grass hay + flaxseed	–	0.64	3.72	1.09	0.21	0.34	0.02	1.66	4.94	Mapiye et al. (2013)
Grass hay + sunflower seed	–	0.76	4.47	0.49	0.10	0.24	0.02	0.85	5.85	
Red clover silage + flaxseed	–	0.67	3.73	1.38	0.26	0.36	0.03	2.03	4.96	
Red clover silage + sunflower seed	–	0.79	5.17	0.39	0.10	0.23	0.02	0.74	6.89	
TMR	0.77	0.35	1.89	0.34	0.02	0.10	0.02	0.48	–	He et al. (2013)
TMR + 15% camelina meal	0.87	0.35	2.14	0.41	0.03	0.11	0.02	0.56	–	
TMR + 30% camelina meal	1.41	0.4	2.37	0.45	0.05	0.13	0.02	0.65	–	
Concentrate + rumen protected saturated fat	2.85	0.82	3.45	0.50	0.07	0.20	0.04	0.87	4.31	Noci et al. (2011)
Concentrate + camelina oil	4.61	0.95	2.86	1.27	0.11	0.20	0.05	1.75	3.70	
Concentrate + linseed oil	5.28	0.98	3.01	1.74	0.12	0.21	0.03	2.18	3.72	

TVA, trans-vaccenic acid; RA, rumenic acid; LA, linoleic acid; ALA, linolenic acid; EPA, eicosapentaenoic acid; DPA, docosapentaenoic acid; DHA, docosahexanoic acid; n-3, omega-3 fatty acids; n-6, omega-6 fatty acids.

TMR, total mixed ration.

ALA, EPA and DPA, but lower undesirable SFA (C14:0, C16:0, C16:1) and *n*-6:*n*-3 ratio compared with lamb and beef. Table 4 compares the fatty acid composition of chevon, lamb and beef determined from goat kids, lambs and calves, on % of total fatty acids.

Various factors affect the FA composition of goat meat, particularly the diet of the animal. Meat from goats grazing rangeland forages (Liotta et al., 2020) or high-forage diets supplemented with *n*-3 PUFA sources contain increased contents of *n*-3 PUFA and the BHIs than those raised intensively on high grain diets (Gagaoua et al., 2023). It has been reported that feeding goats with a grain diet containing threefold C18:1 compared to an alfalfa hay diet increased C18:1 in both IMF (i.e., marbling) and subcutaneous fat. Thus, when East African goats were supplemented with a grain diet (27% sunflower seed cake + 70% maize bran), the proportions of C18:1, TVA and LA in the omental fat increased compared to non-supplemented goats (Gagaoua et al., 2023). The increase in C18:1 in muscle or adipose tissues in response to higher grain levels in the diet could be due to the increase in the  $\Delta 9$  desaturase enzyme activities necessary for the conversion of C18:0 to C18:1, which can also be seen in sheep and cattle.

When goats are fed with oils rich in LA, it can bypass the rumen or is isomerised to RA, which can be bio-hydrogenated to TVA in the rumen increasing their deposition in the muscle tissues. Supplementing goat diets with canola or olive oils (e.g., oils rich in oleic acid) and sunflower or soybean oils (e.g., oils rich in LA) has mainly resulted in an increase in C18:1 and RA in the meat, respectively. On the other hand, supplementation of diets with oils rich in ALA can lead to an increase in the *n*-3 FA level in chevon. Related to this, the incorporation of 3% canola oil, a good source of ALA with a 2:1 ratio of *n*-6:*n*-3, into the goats' diet has enhanced ALA in the muscle, liver, and kidney fats (Karami et al., 2013). Studies report that supplementation of diets with oils can affect expression levels of genes associated with *de novo* FA synthesis in goats. A blend of linseed and palm oils (2:1) has reduced both rumen biohydrogenation of ALA and muscle oxidation of ALA in Cashmere goats. Diets supplemented with the blended oil, compared to linseed alone, have reduced the relative abundance of *Pseudobutyrvibrio*, a bacterial species that hydrogenate dietary ALA in the rumen, increasing *n*-3 PUFA, leading to a decrease in the *n*-6:*n*-3 FA ratio in goat meat. In this regard, a variety of nutritional strategies have been employed to

TABLE 4 Comparison of fatty acid composition (% of total fatty acids) and intramuscular fat (IMF, g per 100 g of meat) of muscle *longissimus dorsi* from goats (kids), lambs and calves.

Fatty acids	Goat kids	Lambs	Calves	SEM	P-value
Lauric acid (C12:0)	0.32	0.35	0.17	0.11	0.50
Myristic acid (C14:0)	1.77 <sup>b</sup>	2.62 <sup>ab</sup>	3.22 <sup>a</sup>	0.27	<0.01
Palmitic acid (C16:0)	20.0 <sup>b</sup>	23.5 <sup>a</sup>	26.0 <sup>a</sup>	0.78	<0.01
Unhealthy fatty acids (C14:0+C16:0+C16:1)	24.0 <sup>b</sup>	27.6 <sup>b</sup>	32.4 <sup>a</sup>	1.22	<0.01
Stearic acid (C18:0)	17.7	16.9	16.1	1.22	0.66
Saturated fatty acids (SFA)	41.4 <sup>b</sup>	46.2 <sup>a</sup>	47.4 <sup>a</sup>	1.35	0.02
Myristoleic acid (C14:1 <i>n</i> -9)	0.11 <sup>b</sup>	0.69 <sup>a</sup>	0.05 <sup>b</sup>	0.11	<0.01
Palmiteoleic (C16:1 <i>n</i> -9)	2.30 <sup>ab</sup>	1.51 <sup>b</sup>	3.10 <sup>a</sup>	0.40	0.05
Palmiteoleic (C17:1 <i>n</i> -9)	0.63	0.76	0.91	0.25	0.73
Oleic acid (C18:1 <i>n</i> -9)	39.8 <sup>a</sup>	39.8 <sup>a</sup>	35.1 <sup>b</sup>	1.38	0.01
Linoleic acid (LA; C18:2 <i>n</i> -6)	4.55	5.10	6.53	0.87	0.28
$\alpha$ -Linolenic acid (ALA; C18:3 <i>n</i> -3)	1.81 <sup>a</sup>	0.78 <sup>b</sup>	0.69 <sup>b</sup>	0.16	<0.01
Arachidonic acid (AA; C20:4 <i>n</i> -6)	2.04	1.82	1.63	0.44	0.81
Eicosapentaenoic acid (EPA; C20:5 <i>n</i> -3)	1.37 <sup>a</sup>	0.41 <sup>b</sup>	0.25 <sup>b</sup>	0.18	<0.01
Docosapentaenoic acid (DPA; C22:5 <i>n</i> -3)	1.44 <sup>a</sup>	0.49 <sup>b</sup>	0.56 <sup>b</sup>	0.19	<0.01
Docosahexaenoic acid (DHA; C22:6 <i>n</i> -3)	0.26	0.24	0.10	0.08	0.27
Sum of <i>n</i> -6 fatty acids	7.54	7.15	8.87	1.26	0.60
Sum of <i>n</i> -3 fatty acids	5.12 <sup>a</sup>	1.96 <sup>b</sup>	1.60 <sup>b</sup>	0.49	<0.01
PUFA/SFA ratio	0.33	0.21	0.24	0.04	0.20
<i>n</i> -6/ <i>n</i> -3 ratio	1.53 <sup>c</sup>	3.52 <sup>b</sup>	6.04 <sup>a</sup>	0.42	<0.01
Intramuscular fat content (g per 100 g meat)	2.6 <sup>b</sup>	3.9 <sup>a</sup>	2.7 <sup>b</sup>	0.37	<0.01

Source: Kiani et al. (2017); Values are average of 10 observations (*n* = 10); SEM, Standard error of means; PUFA, polyunsaturated fatty acids.

<sup>a,b,c</sup> mean values within a row with different superscript letters are significantly different (*P* < 0.05).

increase HEFA deposition in goat meat, which have been summarised in Table 5.

### 3 Feed-based enrichment of antioxidants in red meat from sheep, cattle and goats

It is known that diets rich in antioxidants offer better animal health (Ponnampalam et al., 2022), including resistance to heat stress and contribute to a reduction in deteriorative changes in meat quality post mortem by reducing radical formation within the cellular system and reducing the amount of oxidative damage in muscle tissues (Bekhit et al., 2013; Karre et al., 2013; Ponnampalam et al., 2022). Antioxidants reduce the occurrence of oxidative stress and infectious diseases in animals and humans (Lauridsen, 2019; Ponnampalam et al., 2022). Vitamin E (primarily  $\alpha$ -tocopherol) is considered an efficient antioxidant functioning compound in a hydrophobic environment. It has been proven from animal and human studies that vitamin E inhibits lipid peroxidation (Gruffat et al., 2020), and by scavenging lipid peroxy radicals, it prevents or delays the propagation of free radical-mediated chain reactions in the cellular systems. Antioxidants can act synergistically, for example,  $\alpha$ -tocopherol and  $\beta$ -carotene can act as an effective 'radical-scavenging mechanism' in biological membranes (Kurutas, 2015; Salami et al., 2016; Lauridsen et al., 2021). The inhibition of lipid peroxidation by a combination of the two fat-soluble antioxidants was shown to be greater than the sum of the individual inhibitions (Wrona et al., 2003). Figure 3 illustrates the mechanism of the effect of antioxidants on the quality of meat from ruminant animals (goat is taken as an example in the diagram). The antioxidant action of vitamin E and selenium have been proven in human and animal studies by their fortification in the tissues and defensive effects to reduce oxidation (Nozière et al., 2006). Carotenoids are also regarded as efficient  $O_2$  and ROS scavengers operating in cellular lipid bilayers. However, the action of other plant-based antioxidants, namely polyphenols (phenolic acids, tannins, flavonoids), has not been proven through their fortification in animal or human tissues. Flavonoids are thought to have a lower contribution to the direct antioxidative protection in animals and humans, due to their relatively poor absorption and difficulties with storage in animal tissues, even though they are potent scavengers of hydroxyl and superoxide radicals (Fiedor and Burda, 2014).

#### 3.1 Influence of diets on antioxidants in lamb and mutton

Modulating the FA profile of lamb and mutton to increase beneficial PUFAs increases susceptibility to lipid oxidation, which can negatively affect meat quality attributes. The presence of natural or supplemented antioxidants in the diet of ruminants can help to reduce oxidation and increase shelf-life (Prache et al., 2022b). Meat from pasture-fed sheep and lambs is characterised by having higher

muscle antioxidants levels (mainly  $\alpha$ -tocopherol) compared to those fed grains (Zervas and Tsiplakou, 2011; Gruffat et al., 2020), as fresh pasture is a rich source of antioxidants such as tocopherols, carotenoids and phenolic compounds (Prache et al., 2022b). However, variability between breeds in the metabolic fate of ingested carotenoids has been observed (Macari et al., 2017). The presence of different plant species within the pasture can also modulate antioxidant contents in meat, with higher  $\alpha$ -tocopherol concentrations reported in the meat of lambs grazing brassica and lucerne/phalaris compared to bladder clover (De Brito et al., 2017). Leguminous species are reported to contain lower levels of  $\alpha$ -tocopherol compared to grasses, which may explain higher lipid oxidation values in the meat of lambs grazing alfalfa versus perennial ryegrass (Fraser et al., 2004), however variable results have been reported (Hampel et al., 2021).

The antioxidant content of lamb meat declines with increased inclusion of senesced pasture and TMR in the diet (Ponnampalam et al., 2012, 2017), due to the lower levels of tocopherols, carotenoids and phenolic compounds available in these feed types (Moure et al., 2001). Supplementing feedstuffs containing natural antioxidants to increase concentrations in meat has yielded variable results (Falowo et al., 2014). Supplementing TMR diets with pomegranate silage (Kotsampasi et al., 2014), buckwheat silage (Keles et al., 2018) and increasing levels of *Acacia mearnsii* leaf-meal (Uushona et al., 2023) increased the antioxidant capacity and phenolic content of lamb meat. Inclusion of oat grain in senesced perennial ryegrass pasture lowered  $\alpha$ -tocopherol concentrations in lamb meat compared to senesced perennial lucerne pasture. A reduction in  $\alpha$ -tocopherol concentrations and increasing oxidation values have been reported in meat from lambs fed TMR supplemented with algae (Hopkins et al., 2014; Ponnampalam et al., 2016) and camelina hay/meal (Ponnampalam et al., 2021a). Overall, pasture grazing is the most advantageous way to increase the antioxidant content of sheep and lamb meat. Supplementation of senesced pasture and TMR diets with antioxidant rich by-products is important to sufficiently improve the antioxidant content of meat.

#### 3.2 Influence of diets on antioxidants in beef and veal

Use of dietary antioxidants is the most common strategy used to inhibit lipid, protein, and myoglobin oxidation in beef (Estévez, 2021; Petcu et al., 2023) and veal (Skřivanová et al., 2007; D'Agata et al., 2009). It has long been established that forage-based versus grain-based diets are highly endowed with diverse and potent antioxidants, which result in beef and veal with superior antioxidant and oxidative stability profiles (Descalzo and Sancho, 2008; Estévez, 2021). For illustrative purposes, feeding pasture versus grain diets can increase vitamin E content in beef up to 5.9  $\mu\text{g/g}$  of tissue exceeding the ideal concentration of 3.3–3.8  $\text{mg/g}$  tissue required to extend oxidative shelf life of beef (Liu et al., 1995; Descalzo and Sancho, 2008). However, the efficacy of these antioxidants in pasture-fed beef depends on dose and type of the antioxidant, plant species and maturity, seasonality, physical form,

TABLE 5 Influence of diet on the health enhancing fatty acid composition (% of total fatty acids) of meat from goats.

Diet	Fatty acids (%)									Reference
	TVA	RA	LA	ALA	EPA	DPA	DHA	n-3	n-6	
Forage vs. concentrate										
Rangeland pasture	–	0.13	–	–	–	–	–	0.12	0.18	Ryan et al. (2007)
Rangeland + 50% concentrate	–	0.15	–	–	–	–	–	0.05	0.21	
Rangeland + 70% concentrate	–	0.21	–	–	–	–	–	0.04	0.28	
Rangeland + 90% concentrate	–	0.36	–	–	–	–	–	0.00	0.02	
Oil supplementation										
Palm oil diet	–	–	0.54	1.39	1.12	–	0.86	4.17	8.71	Wang et al. (2020)
Linseed oil diet	–	–	0.64	1.52	1.22	–	1.04	4.69	9.65	
Mixed oil diet	–	–	0.51	1.71	1.51	–	1.25	5.44	8.91	
TMR	1.22	0.55	8.88	0.51	0.37	0.29	0.37	1.47	12.75	Abuelfatah et al. (2016)
TMR + 10% whole linseed	0.96	0.73	4.85	2.32	0.79	0.60	0.63	4.34	7.06	
TMR + 20% whole linseed	1.28	0.53	4.85	3.33	1.23	1.08	1.08	6.30	7.34	
TMR + canola oil	2.71	0.86	9.81	1.61	1.33	1.96	1.38	6.12	16.1	Karami et al. (2013)
TMR + palm oil	1.23	0.61	9.93	1.12	1.17	1.48	1.23	4.61	15.7	
TMR + palm oil	–	–	3.78	0.42	0.18	–	0.16	0.76	4.41	Najafi et al. (2012)
TMR + soybean oil	–	–	5.26	0.7	0.19	–	0.19	1.09	5.87	
TMR + fish oil	–	–	3.59	0.47	0.6	–	0.57	1.65	3.93	
By-products										
TMR	1.75	0.14	4.43	3.99	0.33	0.11	–	4.43	5.84	Semwogerere et al. (2023)
TMR + 5% hemp seed cake	3.12	0.18	4.84	5.38	0.44	0.15	–	5.92	6.78	
TMR + 10% hemp seed cake	3.79	0.19	4.9	6.08	0.52	0.19	–	6.79	7.33	
TMR	0.44	3.33	0.46	2.50	0.99	0.24	–	3.78	4.85	Kafle et al. (2021)
TMR + 25% peanut skin	0.37	3.48	0.42	2.72	0.96	0.24	–	3.92	4.93	
TMR + 50% peanut skin	0.38	3.73	0.49	2.80	0.88	0.24	–	3.92	5.22	
TMR + 75% peanut skin	0.36	3.42	0.41	2.33	0.99	0.24	–	3.56	4.89	
TMR	1.19	0.51	3.19	0.34	–	0.46	–	0.62	6.19	Martins Flores et al. (2021)
TMR + 50% grape pomace silage	1.51	0.49	4.89	0.37	–	0.30	–	0.62	8.15	
TMR + 50% grape pomace silage	2.33	0.68	5.71	0.41	–	0.21	–	0.62	10.63	
TMR + 50% grape pomace silage	4.17	1.03	7.03	0.43	–	0.24	–	0.79	13.99	
TMR	1.56	–	4.70	0.43	0.2	0.39	0.04	0.47	5.85	Pimentel et al. (2021)
TMR + 16 kg <i>Acacia mearnsii</i> extract	1.84	–	4.72	0.41	0.22	0.46	0.04	0.54	7.49	
TMR + 32 kg <i>Acacia mearnsii</i> extract	1.60	–	5.46	0.47	0.16	0.35	0.04	0.47	4.93	
TMR + 48 kg <i>Acacia mearnsii</i> extract	1.52	–	7.62	0.72	0.22	0.62	0.05	0.61	9.56	
TMR	0.47	–	12.36	0.6	0.39	0.56	0.41	1.95	18.32	Abubakr et al. (2015)
80% decanter cake	0.33	–	9.38	0.63	0.32	0.63	0.32	1.89	14.51	
80% palm kernel cake	0.40	–	9.14	0.61	0.32	0.58	0.36	1.89	14.16	
TMR + 5% palm oil	0.41	–	9.04	0.69	0.39	0.62	0.36	2.06	14.02	
TMR	–	–	8.01	1.06	0.33	–	–	1.39	11.8	Ahmed et al. (2015)

(Continued)

TABLE 5 Continued

Diet	Fatty acids (%)									Reference
	TVA	RA	LA	ALA	EPA	DPA	DHA	<i>n</i> -3	<i>n</i> -6	
By-products										
TMR + 0.5% green tea by-product	–	–	14.2	1.06	0.16	–	–	1.22	17.1	
TMR + 1% green tea by-product	–	–	13.1	1.03	0.29	–	–	1.32	17.5	
TMR + 2% green tea by-product	–	–	16.4	1.51	0.15	–	–	1.66	21.1	

TVA, trans-vaccenic acid; RA, rumenic acid; LA, linoleic acid; ALA, linolenic acid; EPA, eicosapentaenoic acid; DPA, docosapentaenoic acid; DHA, docosaehexanoic acid; n-3, omega-3 fatty acids; n-6, omega-6 fatty acids.  
TMR, total mixed ration.

duration of feeding, amount, and type of pro-oxidants (Ponnampalam et al., 2022; Kearns et al., 2023b).

Low-quality forages and high-grain diets can be supplemented with vitamin E to elevate levels in beef (Descalzo and Sancho, 2008; Petcu et al., 2023) and veal (D’Agata et al., 2009; Franco et al., 2012), subsequently minimizing oxidative deterioration. It has been suggested that vitamin E daily supplementation of 500 IU/head for 126 d or 1300 IU/head for 44 d could meet the ideal vitamin E levels in muscle required to enhance oxidative stability of beef (Liu et al., 1995; Suman et al., 2014). Apart from vitamin E, supplementation of organic selenium appears to somewhat increase oxidative capacity and stability of beef (Rossi et al., 2015; Huang et al., 2023) and veal (Skřivanová et al., 2007; Shabtay et al., 2008). In addition, supplementation of high-grain diets with polyphenolic extracts including flavonoids (Orzuna-Orzuna et al., 2023), a blend of alkaloids, saponins, and phenolic acids (De Zawadzki et al., 2017), resveratrol (Cui et al., 2023), ferulic acid (González-Ríos et al., 2016) and tannic acid (Tabke et al., 2017) enhances the antioxidant capacity and oxidative stability of beef. Similarly, supplementation of polyphenolic fruit by-products such as grape pomace in calves’ (Ianni et al., 2019) and steers’ (Tayengwa

et al., 2020) on high-grain diets increased the antioxidant capacity and oxidative stability of meat. Supplementing a blend of essential oils (Rivaroli et al., 2016; Ornaghi et al., 2020) and benzoic acid (Williams et al., 2022) slightly improved lipid stability without affecting colour shelf-life.

The effect of distiller’s grains on the oxidative capacity and lipid stability of beef varies from negative (Suman et al., 2014; De Mello et al., 2018) to neutral (Gill et al., 2008; Depenbusch et al., 2009) and positive (Bloomberg et al., 2011; Merayo et al., 2022) and, thus, merits further investigation. Interestingly, a blend of antioxidant sources tends to either have additive or synergistic effects. For example, a combination of vitamin E with polyphenolic extracts (Gobert et al., 2010; Delosièrè et al., 2020), essential oils (Fusaro et al., 2021) and distiller’s grains (Bloomberg et al., 2011) was more efficient in increasing antioxidant capacity and oxidative stability than the individual constituents, suggesting synergistic effects with vitamin E. However, high dietary levels of vitamin A suppress tissue deposition of vitamin E reducing antioxidant capacity and oxidative stability of beef (Daniel et al., 2009; Marti et al., 2011). Research should continue to explore synergistic effects of novel nutrient and non-nutrient antioxidants.

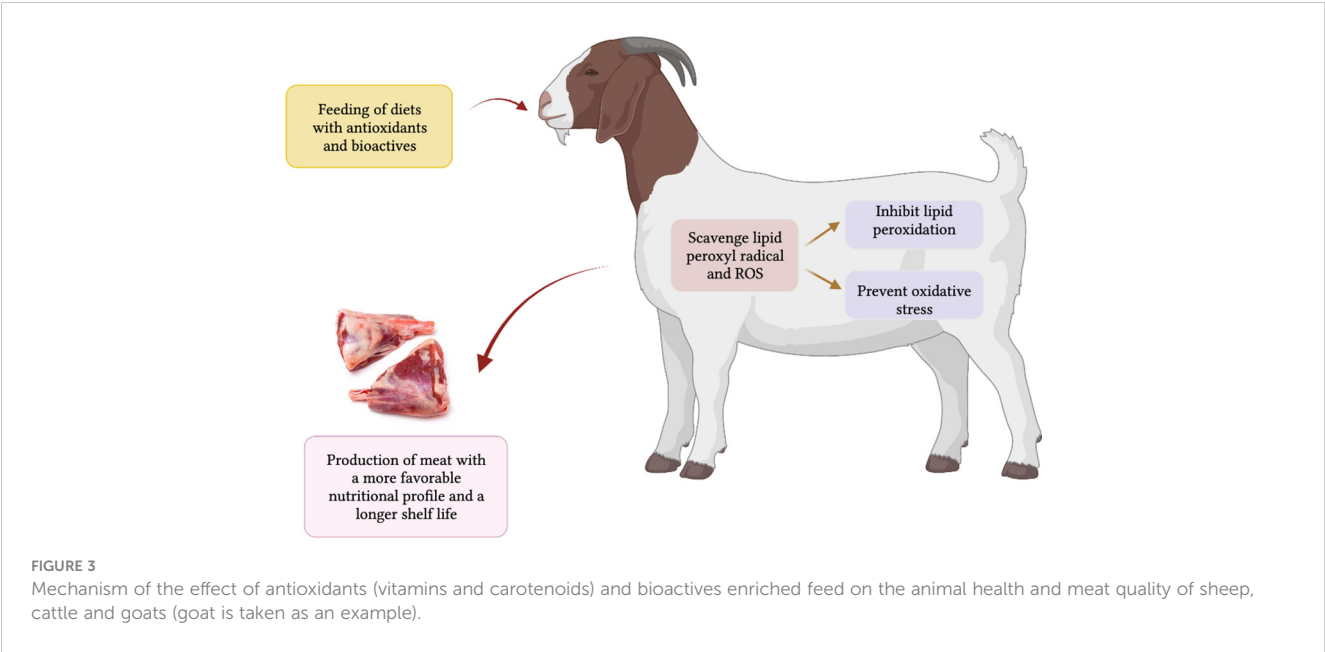


FIGURE 3  
Mechanism of the effect of antioxidants (vitamins and carotenoids) and bioactives enriched feed on the animal health and meat quality of sheep, cattle and goats (goat is taken as an example).



### 3.3 Influence of diets on antioxidants in chevon

Pasture-finished goats differ in colour attributes of meat ( $L^*$ ,  $a$ ,  $b$ , chroma and hue angle values) than goats finished on grain diets (Lee et al., 2008), the same for meat from sheep and cattle. Adding natural antioxidants (Vitamin E, Vitamin C, etc.) and polyphenols, as a nutritional strategy influences the colour stability of goat meat (Karami et al., 2011). For example, pomegranate seed pulp, a cheap source of polyphenols, has improved colour stability in chevon (Emami et al., 2015). Similarly, a dietary green tea by-product (20 g/kg dry matter) has improved the redness and yellowness values of goat meat (Ahmed et al., 2015).

It is noteworthy that supplementing the diet with a high content of  $n$ -3 PUFA might increase lipid oxidation and may raise concerns about the impairment of sensory attributes of chevon, similar to that observed with beef and lamb. The inclusion of high doses of  $n$ -3 PUFA has produced meat with unusual odours, unpleasant flavours, and a lower overall appreciation of kid meat (Moreno-Indias et al., 2012). A positive association between lipid oxidation and the content of  $n$ -3 PUFA in chevon has been reported (Abuelfatah et al., 2016). Intriguingly, liver and muscle (meat) fats from canola oil-fed kids contained fewer lipid oxidative substances compared to those from palm oil-supplemented kids (Karami et al., 2013). The latter study showed that canola oil effectively reduced lipid oxidation both in the blood and muscle tissue of goats. Furthermore, the concern about lipid oxidation of high-PUFA diets could be overcome by dietary supplementation of antioxidant polyphenols, a conclusion that is relevant to all ruminant species.

It has been reported that supplementation of diets containing polyphenols positively improved the FA profile and reduced lipid oxidation in chevon (Cimmino et al., 2018). Similarly, dietary green tea by-products (Ahmed et al., 2015) and extracts from olive mill water waste (Cimmino et al., 2018) reduced lipid oxidation in chevon. Overall, it seems that diets containing phenolic components are positive agents in reducing lipid oxidation in goat meat. These actions may be through synchronised effects with lipids such as unsaturated fatty acids and vitamins (such as vitamin E) at the GIT enterocyte level. However, the dietary biofortification of phytonutrients into tissues such as skeletal muscles is low due to lower rates of digestion and absorption; this is believed to be due to their action as antinutritional factors (causing toxicity to microbes) or binding agents with other nutrients (e.g., protein) leading to complex formation at the GIT level, resulting in reduced microbial degradation.

## 4 Future directions and gaps

The importance of HEFA and antioxidants is becoming increasingly important, particularly in relation to animal health, as well as the quality and nutritional value of meat, and ultimately human health and wellbeing. Also, there is an increasing trend towards the consumption of red meat compared with other white meats around the world, as global population and affluency increase

mainly from Asian and African regions. The social awareness of consumers relating to the quality of meat consumed, the nutrient content of meat that they select, and the health aspects of foods chosen is also expected to change in the coming years as world population become aware of healthy living (Ponnampalam and Holman, 2022). Therefore, addressing the enrichment of red meat with HEFA and antioxidants i.e., improving the nutritional value of meat, has gained much attention. The use of bioactive-rich (vitamins, HEFA, phenolic compounds, tannins, flavonoids) plant by-products for improving the nutritional quality attributes and shelf-life of the meat is under active investigation (Salami et al., 2019), but research is needed to evaluate their effects on other meat quality attributes and animal performance. A point of caution is meat safety, insofar as certain pathogenic agents in plants can be transferred to the meat (Prache et al., 2022a). Although several studies have investigated the effects of feed on the quality and nutritional values of meat, there is a lack of information on the absorption and bioavailability of particular feed-based antioxidants and FA, and their effect in animal- and human-tissues upon deposition. Some authors also point to the gap between food-scale studies and epidemiological studies (Prache et al., 2022a). There is a lack of data linking the FA profile of meat and its antioxidant content (and more generally the way it is produced), to the level of consumption and chronic diseases in humans. This requires a collective effort between research communities working in animal science, meat processing, consumer attitudes, human nutrition and epidemiology (Prache et al., 2022a).

Comparative studies on the consumption of red meat from ruminants versus white meat and their combinations as well as comparing with other sources of animal and plant proteins can provide valuable insights and knowledge into their potential effects on human health. However, this research aspect is lacking and not well proven by human intervention studies, relating it to long term consumption of red meat enriched with HEFA and antioxidants on blood lipid parameters, human health and wellbeing. This may be due to inadequate funding allocated by government bodies around the globe as it requires large funding and intense resources, as well as due to the ethical considerations, regulatory requirements, and recruitment challenges in enrolling adequate numbers of participants (observations) to validate data. Future studies should focus on not only investigating the absorption, bioaccessibility, and bioavailability of different antioxidants and FA through use of *in vitro* digestion models and *in vivo* animal studies, but also include human intervention studies undertaken with sound experimental designs covering appropriate replicates and number of observations, comparing the effects of red meat, white meat and other plant and animal protein sources (alone and/or in combination) in human health. Furthermore, animal and human cell lines should be treated (fortified) with plant-based antioxidants, for example phenolic acids or flavonoids, to study their real effects in animal and human tissues as they show antinutritional activities that may lead to lower digestion, absorption and biofortification. Such studies may provide an understanding of the impact of phytonutrients acting as a sole or additive components along with HEFA and other antioxidants (vitamin E, selenium) that are available in the meat to exert a beneficial effect on humans. This,

in turn, is key to gaining a deep insight into the mechanism of action of improving human health via enriching red meat with feed-based FA and antioxidants.

## 5 Conclusions

Regardless of ruminant species, high-quality pasture remains superior in producing meat enriched with HEFA, particularly *n*-3 PUFA and antioxidants, with some countries already utilising ‘grass-fed’ logos (see Salami et al., 2019; Davis et al., 2022). Low-quality forages and high grain diets require dietary supplementation with *n*-3 PUFA and antioxidants to raise their contents in meat and extend its shelf life. The importance of some dietary vitamins and minerals in the antioxidant actions and preservative aspects of PUFA in meat has been documented. A combination of nutrient antioxidants, mostly vitamin E and non-nutrient antioxidants, chiefly flavonoids, and carotenoids are speculated to synergistically stabilise high PUFA contents in ruminant meat. Nevertheless, the latter statement needs validation through well-designed *in vivo* studies undertaken in animal and human populations (with adequate replicates and numbers of observations) along with the quantification of flavonoids or carotenoids in circulatory systems and tissues such as skeletal muscles, and consequently their effects on human health. To this end, research should continue to explore effects of co-feeding of PUFA sources with different mixtures of novel nutrient and non-nutrient antioxidants on animal and human health as well as the underlying mechanisms.

## Author contributions

EP: Conceptualization, Writing – original draft, Writing – review & editing. MK: Writing – original draft, Writing – review & editing. AK: Writing – original draft, Writing – review & editing. SS: Writing – original draft, Writing – review & editing. PV: Writing – original draft, Writing – review & editing. SP: Writing – original draft, Writing – review & editing. FM: Writing – original

draft, Writing – review & editing. CM: Writing – original draft, Writing – review & editing.

## Funding

The author(s) declare that no financial support was received for the research, authorship, and/or publication of this article.

## Acknowledgments

The authors are grateful to the support of their corresponding organizations. The first author EP wishes to acknowledge Robyn D. Warner and Brian J. Leury of the University of Melbourne, Australia for their support and collaboration during his career. Their support allows EP to expand his research ideas and hypotheses using field- and laboratory-based investigations with fundamental and applied based research activities.

## 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.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

## Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

## References

- Abid, Z., Cross, A. J., and Sinha, R. (2014). Meat, dairy, and cancer. *Am. J. Clin. Nutr.* 100, 386S–393S. doi: 10.3945/ajcn.113.071597
- Abubakr, A., Alimon, A. R., Yaakub, H., Abdullah, N., and Ivan, M. (2015). Effect of feeding palm oil by-products based diets on muscle fatty acid composition in goats. *PLoS One* 10, e0119756–e0119756. doi: 10.1371/journal.pone.0119756
- Abuelfatah, K., Zuki, A. B. Z., Goh, Y. M., and Sazili, A. Q. (2016). Effects of enriching goat meat with *n*-3 polyunsaturated fatty acids on meat quality and stability. *Small Ruminant Res.* 136, 36–42. doi: 10.1016/j.smallrumres.2016.01.001
- Ahmed, S. T., Lee, J. W., Mun, H. S., and Yang, C. J. (2015). Effects of supplementation with green tea by-products on growth performance, meat quality, blood metabolites and immune cell proliferation in goats. *J. Anim. Physiol. Anim. Nutr.* 99, 1127–1137. doi: 10.1111/jpn.12279
- Alves, S. P., Vahmani, P., Mapiye, C., McAllister, T. A., Bessa, R. J. B., and Dugan, M. E. R. (2021). Trans-10 18:1 in ruminant meats: A review. *Lipids* 56, 539–562. doi: 10.1002/lipid.12324
- Asadollahi, S., Sari, M., Erafanmajd, N., Kiani, A., and Ponnampalam, E. N. (2017). Supplementation of sugar beet pulp and roasted canola seed in a concentrate diet altered carcass traits, muscle (longissimus dorsi) composition and meat sensory properties of arabian fattening lambs. *Small Ruminant Res.* 153, 95–102. doi: 10.1016/j.smallrumres.2017.05.012
- Aurousseau, B., Bauchart, D., Calichon, E., Micol, D., and Priolo, A. (2004). Effect of grass or concentrate feeding systems and rate of growth on triglyceride and phospholipid and their fatty acids in the M. longissimus thoracis of lambs. *Meat Sci.* 66, 531–541. doi: 10.1016/S0309-1740(03)00156-6
- Aurousseau, B., Bauchart, D., Faure, X., Galot, A. L., Prache, S., Micol, D., et al. (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 Sci.* 76, 241–252. doi: 10.1016/j.meatsci.2006.11.005
- Bekhit, A. E. D. A., Hopkins, D. L., Fahri, F. T., and Ponnampalam, E. N. (2013). Oxidative processes in muscle systems and fresh meat: Sources, markers, and remedies. *Compr. Rev. Food Sci. Food Saf.* 12, 565–597. doi: 10.1111/1541-4337.12027
- Bennato, F., Martino, C., Ianni, A., Giannone, C., and Martino, G. (2023). Dietary grape pomace supplementation in lambs affects the meat fatty acid composition, volatile profiles and oxidative stability. *Foods* 12, 1257. doi: 10.3390/foods12061257

- Bernstein, A. M., Sun, Q., Hu, F. B., Stampfer, M. J., Manson, J. E., and Willett, W. C. (2010). Major dietary protein sources and risk of coronary heart disease in women. *Circulation* 122, 876–883. doi: 10.1161/CIRCULATIONAHA.109.915165
- Berthelot, V., and Gruffat, D. (2018). “Fatty acid composition of muscle,” in *INRA Feeding System for Ruminants*. Eds. D. Sauvant, L. Delaby and P. Nozière (Academic Publishers, Wageningen, The Netherlands), 193–202.
- Bessa, R. J. B., Alves, S. P., and Santos-Silva, J. (2015). Constraints and potentials for the nutritional modulation of the fatty acid composition of ruminant meat. *Eur. J. Lipid Sci. Technol.* 117, 1325–1344. doi: 10.1002/ejlt.201400468
- Bloomberg, B. D., Hilton, G. G., Hanger, K. G., Richards, C. J., Morgan, J. B., and Vanoverbeke, D. L. (2011). Effects of vitamin E on color stability and palatability of strip loin steaks from cattle fed distillers grains. *J. Anim. Sci.* 89, 3769–3782. doi: 10.2527/jas.2011-3843
- Boufaïed, H., Chouinard, P. Y., Tremblay, G. F., Petit, H. V., Michaud, R., and Bélanger, G. (2003). Fatty acids in forages. I. Factors affecting concentrations. *Can. J. Anim. Sci.* 83, 501–511. doi: 10.4141/A02-098
- Bourre, J. M. (2011). Reintroducing beef in a balanced diet. *Bull. Académie Vétérinaire France* 164, 237–244. doi: 10.4267/2042/48092
- Cabiddu, A., Decandia, M., Addis, M., Piredda, G., Pirisi, A., and Molle, G. (2005). Managing mediterranean pastures in order to enhance the level of beneficial fatty acids in sheep milk. *Small Ruminant Res.* 59, 169–180. doi: 10.1016/j.smallrumres.2005.05.005
- Cabrera, M. C., and Saadoun, A. (2014). An overview of the nutritional value of beef and lamb meat from South America. *Meat Sci.* 98, 435–444. doi: 10.1016/j.meatsci.2014.06.033
- Campidonico, L., Toral, P. G., Priolo, A., Luciano, G., Valenti, B., Hervás, G., et al. (2016). Fatty acid composition of ruminal digesta and longissimus muscle from lambs fed silage mixtures including red clover, sainfoin, and timothy. *J. Anim. Sci.* 94, 1550–1560. doi: 10.2527/jas.2015-9922
- Chauhan, S. S., Celi, P., Ponnampalam, E. N., Leury, B. J., Liu, F., and Dunshea, F. R. (2014). Antioxidant dynamics in the live animal and implications for ruminant health and product (meat/milk) quality: role of vitamin E and selenium. *Anim. Production Sci.* 54, 1525–1536. doi: 10.1071/AN14334
- Chikwanha, O. C., Vahmani, P., Muchenje, V., Dugan, M. E. R., and Mapiye, C. (2018). Nutritional enhancement of sheep meat fatty acid profile for human health and wellbeing. *Food Res. Int.* 104, 25–38. doi: 10.1016/j.foodres.2017.05.005
- Chilliard, Y., Glasser, F., Ferlay, A., Bernard, L., Rouel, J., and Doreau, M. (2007). Diet, rumen biohydrogenation and nutritional quality of cow and goat milk fat. *Eur. J. Lipid Sci. Technol.* 109, 828–855. doi: 10.1002/ejlt.200700080
- Ciftci, M., Cerci, I. H., Kilinc, U., Yilmaz, O., Gurdogan, F., Seven, P. T., et al. (2010). Effects of alfalfa (fresh, silage, hay) on the fatty acid and conjugated linoleic acid amounts in lamb muscles and fats. *Rev. Médecine Vétérinaire* 161, 432–437.
- Cimmino, R., Barone, C. M. A., Claps, S., Varricchio, E., Rufrano, D., Caroprese, M., et al. (2018). Effects of dietary supplementation with polyphenols on meat quality in saanen goat kids. *BMC Veterinary Res.* 14, 181–181. doi: 10.1186/s12917-018-1513-1
- Clinquart, A., Ellies-Oury, M. P., Hocquette, J. F., Guillier, L., Santé-Lhoutellier, V., and Prache, S. (2022). Review: On-farm and processing factors affecting bovine carcass and meat quality. *Animal* 16, 100426–100426. doi: 10.1016/j.animal.2021.100426
- Correddu, F., Caratzu, M. F., Lunesu, M. F., Carta, S., Pulina, G., and Nudda, A. (2023). Grape, pomegranate, olive, and tomato by-products fed to dairy ruminants improve milk fatty acid profile without depressing milk production. *Foods* 12, 865. doi: 10.3390/foods12040865
- Cui, Y., Qi, J., Li, J., Zhang, Y., Yang, X., Xin, L., et al. (2023). Effects of dietary resveratrol supplementation in cattle on the anti-oxidative capacity and meat quality of beef steaks under high oxygen packaging. *Meat Sci.* 204, 109238. doi: 10.1016/j.meatsci.2023.109238
- D’Agata, M., Preziuso, G., Russo, C., and Gatta, D. (2009). Oxidation and antioxidant status: effects on shelf-life of meat from Limousine cattle fed with supplements of  $\alpha$ -tocopherol. *Ital. J. Anim. Sci.* 8, 405–415. doi: 10.4081/ijas.2009.405
- Daniel, M. J., Dikeman, M. E., Arnett, A. M., and Hunt, M. C. (2009). Effects of dietary vitamin A restriction during finishing on color display life, lipid oxidation, and sensory traits of longissimus and triceps brachii steaks from early and traditionally weaned steers. *Meat Sci.* 81, 15–21. doi: 10.1016/j.meatsci.2008.07.003
- Davis, H., Magistrali, A., Butler, G., and Stergiadis, S. (2022). Nutritional benefits from fatty acids in organic and grass-fed beef. *Foods* 11, 646. doi: 10.3390/foods11050646
- De Brito, G. F., Holman, B. W. B., McGrath, S. R., Friend, M. A., Van De Ven, R., and Hopkins, D. L. (2017). The effect of forage-types on the fatty acid profile, lipid and protein oxidation, and retail colour stability of muscles from White Dorper lambs. *Meat Sci.* 130, 81–90. doi: 10.1016/j.meatsci.2017.04.001
- Delosièrre, M., Durand, D., Bourguet, C., and Terlouw, E. C. (2020). Lipid oxidation, pre-slaughter animal stress and meat packaging: Can dietary supplementation of vitamin E and plant extracts come to the rescue? *Food Chem.* 309, 125668. doi: 10.1016/j.foodchem.2019.125668
- De Mello, A. S., Jenschke, B. E., Senaratne, L. S., Carr, T. P., Erickson, G. E., and Calkins, C. R. (2018). Effects of finishing diets containing wet distillers’ grains plus solubles on beef quality attributes and fatty acid profile. *Meat Sci.* 136, 16–22. doi: 10.1016/j.meatsci.2017.10.001
- Depenbusch, B. E., Coleman, C. M., Higgins, J. J., and Drouillard, J. S. (2009). Effects of increasing levels of dried corn distillers grains with solubles on growth performance, carcass characteristics, and meat quality of yearling heifers. *J. Anim. Sci.* 87, 2653–2663. doi: 10.2527/jas.2008-1496
- Descalzo, A. M., and Sancho, A. M. (2008). A review of natural antioxidants and their effects on oxidative status, odor and quality of fresh beef produced in Argentina. *Meat Sci.* 79, 423–436. doi: 10.1016/j.meatsci.2007.12.006
- De Zawadzki, A., Arrivetti, L. O. R., Vidal, M. P., Catai, J. R., Nassu, R. T., Tullio, R. R., et al. (2017). Mate extract as feed additive for improvement of beef quality. *Food Res. Int.* 99, 336–347. doi: 10.1016/j.foodres.2017.05.033
- Dierking, R. M., Kallenbach, R. L., and Grün, I. U. (2010). Effect of forage species on fatty acid content and performance of pasture-finished steers. *Meat Sci.* 85, 597–605. doi: 10.1016/j.meatsci.2010.03.010
- DiNicolaantonio, J. J., and O’Keefe, J. (2021). The importance of maintaining a low omega-6/omega-3 ratio for reducing the risk of autoimmune diseases, asthma, and allergies. *Missouri Med.* 118, 453–459.
- Duckett, S. K., Neel, J. P. S., Lewis, R. M., Fontenot, J. P., and Clapham, W. M. (2013). Effects of 553 forage species or concentrate finishing on animal performance, carcass and meat quality. *J. Anim. Sci.* 91, 1454–1467. doi: 10.2527/jas.2012-5914
- 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
- Emami, A., Nasri, M. H., Ganjkanlou, M., Zali, A., and Rashidi, L. (2015). Effects of dietary pomegranate seed pulp on oxidative stability of kid meat. *Meat Sci.* 104, 14–19. doi: 10.1016/j.meatsci.2015.01.016
- Estévez, M. (2021). Critical overview of the use of plant antioxidants in the meat industry: Opportunities, innovative applications and future perspectives. *Meat Sci.* 181, 108610. doi: 10.1016/j.meatsci.2021.108610
- Falowo, A. B., Fayemi, P. O., and Muchenje, V. (2014). Natural antioxidants against lipid-protein oxidative deterioration in meat and meat products: A review. *Food Res. Int.* 64, 171–181. doi: 10.1016/j.foodres.2014.06.022
- FAO (2011). *World livestock 2011 – Livestock in Food Security* (Rome: FAO).
- FAO (2017). *Driving Action Across the 2030 Agenda for Sustainable Development* (Rome, ITA). Available at: <http://www.fao.org/3/i7454en/i7454en.pdf>.
- Fiedor, J., and Burda, K. (2014). Potential role of carotenoids as antioxidants in human health and disease. *Nutrients* 6, 466–488. doi: 10.3390/nu6020466
- Franco, D., González, L., Bispo, E., Latorre, A., Moreno, T., Sineiro, J., et al. (2012). Effects of calf diet, antioxidants, packaging type and storage time on beef steak storage. *Meat Sci.* 90, 871–880. doi: 10.1016/j.meatsci.2011.10.008
- Fraser, M. D., Speijers, M. H. M., Theobald, V. J., Fychan, R., and Jones, R. (2004). Production performance and meat quality of grazing lambs finished on red clover, lucerne or perennial ryegrass swards. *Grass Forage Sci.* 59, 345–356. doi: 10.1111/j.1365-2494.2004.00436.x
- Fruet, A. P. B., Trombetta, F., Stefanello, F. S., Speroni, C. S., Donadel, J. Z., De Souza, A. N. M., et al. (2018). Effects of feeding legume-grass pasture and different concentrate levels on fatty acid profile, volatile compounds, and off-flavor of the M. longissimus thoracis. *Meat Sci.* 140, 112–118. doi: 10.1016/j.meatsci.2018.03.008
- Frutos, P., Hervás, G., Natalello, A., Luciano, G., Fondevila, M., Priolo, A., et al. (2020). Ability of tannins to modulate ruminal lipid metabolism and milk and meat fatty acid profiles. *Anim. Feed Sci. Technol.* 269, 114623. doi: 10.1016/j.anifeeds.2020.114623
- Fusaro, I., Cavallini, D., Giammarco, M., Manetta, A. C., Martuscelli, M., Mammi, L. M. E., et al. (2021). Oxidative status of Marchigiana beef enriched in n-3 fatty acids and vitamin E, treated with a blend of oregano and rosemary essential oils. *Front. Veterinary Sci.* 8. doi: 10.3389/fvets.2021.662079
- Gagaoua, M., Alessandrini, L., Das, A., Lamri, M., Bhattacharya, D., Kumar Nanda, P., et al. (2023). Intrinsic and extrinsic factors impacting fresh goat meat quality: an overview. *Meat Technol.* 64 (1), 20–40. doi: 10.18485/meattech.2023.64.1.3
- Gallardo, B., Gómez-Cortés, P., Mantecón, A. R., Juárez, M., Manso, T., and de la Fuente, M. A. (2014). Effects of olive and fish oil ca soaps in ewe diets on milk fat and muscle and subcutaneous tissue fatty-acid profiles of suckling lambs. *Anim. (Cambridge England)* 8, 1178–1190. doi: 10.1017/S1751731114000238
- Gallardo, B., Manca, M. G., Mantecón, A. R., Nudda, A., and Manso, T. (2015). Effects of linseed oil and natural or synthetic vitamin E supplementation in lactating ewes’ diets on meat fatty acid profile and lipid oxidation from their milk fed lambs. *Meat Sci.* 102, 79–89. doi: 10.1016/j.meatsci.2014.12.006
- Gill, R. K., Vanoverbeke, D. L., Depenbusch, B., Drouillard, J. S., and Dicostanzo, A. (2008). Impact of beef cattle diets containing corn or sorghum distillers grains on beef color, fatty acid profiles, and sensory attributes. *J. Anim. Sci.* 86, 923–935. doi: 10.2527/jas.2007-0244
- Girard, M., Dohme-Meier, F., Silacci, P., Ampuero Kragten, S., Kreuzer, M., and Bee, G. (2016). Forage legumes rich in condensed tannins may increase n-3 fatty acid levels and sensory quality of lamb meat: Forage legumes and sensory quality of lamb meat. *J. Sci. Food Agric.* 96, 1923–1933. doi: 10.1002/jsfa.7298
- Gobert, M., Gruffat, D., Habeau, M., Parafita, E., Bauchart, D., and Durand, D. (2010). Plant extracts combined with vitamin E in PUFA-rich diets of cull cows protect processed beef against lipid oxidation. *Meat Sci.* 85, 676–683. doi: 10.1016/j.meatsci.2010.03.024



- Gómez-Cortés, P., Galisteo, O. O., Ramírez, C. A., Blanco, F. P., de la Fuente, M. A., Sánchez, N. N., et al. (2019). Intramuscular fatty acid profile of feedlot lambs fed concentrates with alternative ingredients. *Anim. Production Sci.* 59, 914–920. doi: 10.1071/AN17885
- González-Ríos, H., Dávila-Ramírez, J. L., Peña-Ramos, E. A., Valenzuela-Melendres, M., Zamorano-García, L., Islava-Lagarda, T. Y., et al. (2016). Dietary supplementation of ferulic acid to steers under commercial feedlot feeding conditions improves meat quality and shelf life. *Anim. Feed Sci. Technol.* 222, 111–121. doi: 10.1016/j.anifeedsci.2016.10.011
- Gruffat, D., Durand, D., Rivaloli, D., Do Prado, I. N., and Prache, S. (2020). Comparison of muscle fatty acid composition and lipid stability in lambs stall-fed or pasture-fed alfalfa with or without sainfoin pellet supplementation. *Animal* 14, 1093–1101. doi: 10.1017/S1751731119002507
- Guo, Q., Li, T., Qu, Y., Liang, M., Ha, Y., Zhang, Y., et al. (2023). New research development on trans fatty acids in food: Biological effects, analytical methods, formation mechanism, and mitigating measures. *Prog. Lipid Res.* 89, 101199–101199. doi: 10.1016/j.plipres.2022.101199
- Hajji, H., Joy, M., Ripoll, G., Smeti, S., Mekki, I., Gahete, F. M., et al. (2016). Meat physicochemical properties, fatty acid profile, lipid oxidation and sensory characteristics from three North African lamb breeds, as influenced by concentrate or pasture finishing diets. *J. Food Composition Anal.* 48, 102–110. doi: 10.1016/j.jfca.2016.02.011
- Hampel, V. S., Poli, C. H. E. C., Joy, M., Tontini, J. F., DeVincenzi, T., Pardos, J. R. B., et al. (2021). Tropical grass and legume pastures may alter lamb meat physical and chemical characteristics. *Trop. Anim. Health Production* 53, 427–427. doi: 10.1007/s11250-021-02861-6
- He, M. L., Gibb, D., McKinnon, J. J., and McAllister, T. A. (2013). Effect of high dietary levels of canola meal on growth performance, carcass quality and meat fatty acid profiles of feedlot cattle. *Can. J. Anim. Sci.* 93, 269–280. doi: 10.4141/CJAS2012-090
- Hennessy, A. A., Kenny, D. A., Byrne, C. J., Childs, S., Ross, R. P., Devery, R., et al. (2021). Fatty acid concentration of plasma, muscle, adipose and liver from beef heifers fed an encapsulated n-3 polyunsaturated fatty acid supplement. *Anim. (Cambridge England)* 15, 100039–100039. doi: 10.1016/j.animal.2020.100039
- Hopkins, D. L., Clayton, E. H., Lamb, T. A., Van De Ven, R. J., Refshauge, G., Kerr, M. J., et al. (2014). The impact of supplementing lambs with algae on growth, meat traits and oxidative status. *Meat Sci.* 98, 135–141. doi: 10.1016/j.meatsci.2014.05.016
- Huang, Q., Wang, S., Yang, X., Han, X., Liu, Y., Khan, N. A., et al. (2023). Effects of organic and inorganic selenium on selenium bioavailability, growth performance, antioxidant status and meat quality of a local beef cattle in China. *Front. Veterinary Sci.* 10. doi: 10.3389/fvets.2023.1171751
- Hwang, Y., and Joo, S. (2017). Fatty acid profiles, meat quality, and sensory palatability of grain-fed and grass-fed beef from hanwoo, american, and Australian crossbred cattle. *Korean J. Food Sci. Anim. Resour.* 37, 153–161. doi: 10.5851/kosfa.2017.37.2.153
- Ianni, A., Luca, A. D., Martino, C., Bennato, F., Marone, E., Grotta, L., et al. (2019). Dietary supplementation of dried grape pomace increases the amount of linoleic acid in beef, reduces the lipid oxidation and modifies the volatile profile. *Anim. (Basel)* 9, 578. doi: 10.3390/ani9080578
- James, N. A., and Berry, B. W. (1997). Use of chevon in the development of low-fat meat products. *J. Anim. Sci.* 75, 571–577. doi: 10.2527/1997.752571x
- Joy, M., Ripoll, G., Molino, F., Dervishi, E., and Álvarez-Rodríguez, J. (2012). Influence of the type of forage supplied to ewes in pre- and post-partum periods on the meat fatty acids of suckling lambs. *Meat Sci.* 90, 775–782. doi: 10.1016/j.meatsci.2011.11.013
- Kafle, D., Lee, J. H., Min, B. R., and Kouakou, B. (2021). Carcass and meat quality of goats supplemented with tannin-rich peanut skin. *J. Agric. Food Res.* 5, 100159. doi: 10.1016/j.jafr.2021.100159
- Karami, M., Alimon, A. R., and Goh, Y. M. (2011). Effect of vitamin E, Andrographis paniculata and turmeric as dietary antioxidant supplementation on lipid and color stability of goat meat. *Small Ruminant Res.* 97, 67–71. doi: 10.1016/j.smallrumres.2011.02.005
- Karami, M., Ponnampalam, E. N., and Hopkins, D. L. (2013). The effect of palm oil or canola oil on feedlot performance, plasma and tissue fatty acid profile and meat quality in goats. *Meat Sci.* 94, 165–169. doi: 10.1016/j.meatsci.2013.02.004
- Karre, L., Lopez, K., and Getty, K. J. K. (2013). Natural antioxidants in meat and poultry products. *Meat Sci.* 94, 220–227. doi: 10.1016/j.meatsci.2013.01.007
- Kaur, N., Chugh, V., and Gupta, A. K. (2014). Essential fatty acids as functional components of foods – a review. *J. Food Sci. Technol.* 51, 2289–2303. doi: 10.1007/s13197-012-0677-0
- Kearns, M., Jacquier, J., Harrison, S. M., Cama-Moncunill, R., Boland, T. M., Sheridan, H., et al. (2023a). Effect of different botanically-diverse diets on the fatty acid profile, tocopherol content and oxidative stability of beef. *J. Sci. Food Agric.* 103, 4983–4992. doi: 10.1002/jsfa.12633
- Kearns, M., Ponnampalam, E. N., Jacquier, J. C., Grasso, S., Boland, T. M., Sheridan, H., et al. (2023b). Can botanically-diverse pastures positively impact the nutritional and antioxidant composition of ruminant meat? – Invited review. *Meat Sci.* 197, 109055–109055. doi: 10.1016/j.meatsci.2022.109055
- Keles, G., Kocaman, V., Ustundag, A. O., Zungur, A., and Ozdogan, M. (2018). Growth rate, carcass characteristics and meat quality of growing lambs fed buckwheat or maize silage. *Asian-Australasian J. Anim. Sci.* 31, 522–528. doi: 10.5713/ajas.17.0296
- Kiani, A., Gharoni, M. H., and Shariati, R. (2017). Comparison of the fatty acid composition of the longissimus dorsi muscle of kids, lambs and calves produced under Iranian transhumant production system. *Iranian J. Appl. Anim. Sci.* 7, 437–443.
- Kim, H. J., Kim, H. J., Jeon, J., Nam, K. C., Shim, K. S., Jung, J. H., et al. (2020). Comparison of the quality characteristics of chicken breast meat from conventional and animal welfare farms under refrigerated storage. *Poultry Sci.* 99, 1788–1796. doi: 10.1016/j.psj.2019.12.009
- Kliem, K. E., Thomson, A. L., Crompton, L. A., and Givens, D. I. (2018). Effect of selected plant species within biodiverse pasture on *in vitro* fatty acid biohydrogenation and tissue fatty acid composition of lamb. *Anim. (Cambridge England)* 12, 2415–2423. doi: 10.1017/S1751731118000265
- Klopatek, S. C., Xu, Y., Yang, X., Oltjen, J. W., and Vahmani, P. (2022). Effects of multiple grass- and grain-fed production systems on beef fatty acid contents and their consumer health implications. *ACS Food Sci. Technol.* 2, 712–721. doi: 10.1021/acsfodsctech.2c00021
- Klurfeld, D. M. (2018). What is the role of meat in a healthy diet? *Anim. Front.* 8, 5–10. doi: 10.1093/af/vfy009
- Kotsampasi, B., Christodoulou, V., Zotos, A., Liakopoulou-Kyriakides, M., Goulas, P., Petrotos, K., et al. (2014). Effects of dietary pomegranate byproduct silage supplementation on performance, carcass characteristics and meat quality of growing lambs. *Anim. Feed Sci. Technol.* 197, 92–102. doi: 10.1016/j.anifeedsci.2014.09.003
- Kurutas, E. B. (2015). The importance of antioxidants which play the role in cellular response against oxidative/nitrosative stress: Current state. *Nutr. J.* 15, 71–71. doi: 10.1186/s12937-016-0186-5
- Lauridsen, C. (2019). From oxidative stress to inflammation: Redox balance and immune system. *Poultry Sci.* 98, 4240–4246. doi: 10.3382/ps/pey407
- Lauridsen, C., Matte, J. J., Lessard, M., Celi, P., and Litta, G. (2021). Role of vitamins for gastro-intestinal functionality and health of pigs. *Anim. Feed Sci. Technol.* 273, 114823. doi: 10.1016/j.anifeedsci.2021.114823
- Lee, M. R. F., Evans, P. R., Nute, G. R., Richardson, R. I., and Scollan, N. D. (2009). A comparison between red clover silage and grass silage feeding on fatty acid composition, meat stability and sensory quality of the M. longissimus muscle of dairy cull cows. *Meat Sci.* 81, 738–744. doi: 10.1016/j.meatsci.2008.11.016
- Lee, J. H., Kouakou, B., and Kannan, G. (2008). Chemical composition and quality characteristics of chevon from goats fed three different post-weaning diets. *Small Ruminant Res.* 75, 177–184. doi: 10.1016/j.smallrumres.2007.10.003
- Lee, M. R. F., McAuliffe, G. A., Tweed, J. K. S., Griffith, B. A., Morgan, S. A., Rivero, M. J., et al. (2021). Nutritional value of suckler beef from temperate pasture systems. *Anim. (Cambridge England)* 15, 100257–100257. doi: 10.1016/j.animal.2021.100257
- Liotta, L., Chiofalo, V., Lo Presti, V., and Chiofalo, B. (2020). Effect of production system on growth performances and meat traits of suckling messinese goat kids. *Ital. J. Anim. Sci.* 19, 245–252. doi: 10.1080/1828051X.2020.1726832
- Liu, Q., Lanari, M. C., and Schaefer, D. M. (1995). A review of dietary vitamin E supplementation for improvement of beef quality. *J. Anim. Sci.* 73, 3131–3140. doi: 10.2527/1995.73103131x
- Lourenço, M., Van Ranst, G., De Smet, S., Raes, K., and Fievez, V. (2007). Effect of grazing pastures with different botanical composition by lambs on rumen fatty acid metabolism and fatty acid pattern of longissimus muscle and subcutaneous fat. *Anim. (Cambridge England)* 1, 537–545. doi: 10.1017/S1751731107000316
- Macari, S., Graulet, B., Andueza, D., and Prache, S. (2017). Nitrogen stable isotope and carotenoid pigments signatures in the meat as tools to trace back the diet: Comparison between two sheep breeds. *Small Ruminant Res.* 153, 107–113. doi: 10.1016/j.smallrumres.2017.05.013
- Mapiye, C., Aalhus, J. L., Turner, T. D., Rolland, D. C., Basarab, J. A., Baron, V. S., et al. (2013). Effects of feeding flaxseed or sunflower-seed in high-forage diets on beef production, quality and fatty acid composition. *Meat Sci.* 95, 98–109. doi: 10.1016/j.meatsci.2013.03.033
- Mapiye, C., Vahmani, P., Mlambo, V., Muchenje, V., Dzama, K., Hoffman, L. C., et al. (2015). The trans-octadecenoic fatty acid profile of beef: Implications for global food and nutrition security. *Food Res. Int.* 76, 992–1000. doi: 10.1016/j.foodres.2015.05.001
- Marti, S., Realini, C. E., Bach, A., Pérez-Juan, M., and DeVant, M. (2011). Effect of vitamin A restriction on performance and meat quality in finishing Holstein bulls and steers. *Meat Sci.* 89, 412–418. doi: 10.1016/j.meatsci.2011.05.003
- Martins Flores, D. R., da Fonseca, P., Franco, A., Schmitt, J., José Tonetto, C., Rosado Junior, A. G., et al. (2021). Lambs fed with increasing levels of grape pomace silage: Effects on meat quality. *Small Ruminant Res.* 195, 106234. doi: 10.1016/j.smallrumres.2020.106234
- Merayo, M., Rizzo, S. A., Rossetti, L., Pighin, D., and Grigioni, G. (2022). Effect of aging and retail display conditions on the color and oxidant/antioxidant status of beef from steers finished with DG-supplemented diets. *Foods* 11, 884. doi: 10.3390/foods11060884

- Moloney, A. P., McGettrick, S., Dunne, P. G., Shingfield, K. J., Richardson, R. I., Monahan, F. J., et al. (2022). Supplementation with Sunflower/Fish oil-containing concentrates in a grass-based beef production system: Influence on fatty acid composition, gene expression, lipid and colour stability and sensory characteristics of longissimus muscle. *Foods* 11, 4061. doi: 10.3390/foods11244061
- Moloney, A. P., O'Riordan, E. G., Schmidt, O., and Monahan, F. J. (2018). The fatty acid profile and stable isotope ratios of C and N of muscle from cattle that grazed grass or grass/clover pastures before slaughter and their discriminatory potential. *Irish J. Agric. Food Res.* 57, 84–94. doi: 10.1515/ijaf-2018-0009
- Montossi, F., Font-i-Furnols, M., del Campo, M., San Julián, R., Brito, G., and Sañudo, C. (2013). Sustainable sheep production and consumer preference trends: Compatibilities, contradictions, and unresolved dilemmas. *Meat Sci.* 95, 772–789. doi: 10.1016/j.meatsci.2013.04.048
- Moreno-Indias, I., Sanchez-Macias, D., Martinez-De La Puente, J., Morales-Dela Nuez, A., Hernandez-Castellano, L. E., Castro, N., et al. (2012). The effect of diet and DHA addition on the sensory quality of goat kid meat. *Meat Sci.* 90, 393–397. doi: 10.1016/j.meatsci.2011.08.004
- Moore, A., Cruz, J. M., Franco, D., Domínguez, J. M., Sineiro, J., José Núñez, M. A., et al. (2001). "Natural antioxidants from residual sources," in *Food Chemistry* (Elsevier Ltd, Oxford). doi: 10.1016/S0308-8146(00)00223-5
- Najafi, M. H., Zeinoaldini, S., Ganjkanlou, M., Mohammadi, H., Hopkins, D. L., and Ponnampalam, E. N. (2012). Performance, carcass traits, muscle fatty acid composition and meat sensory properties of male mahabadi goat kids fed palm oil, soybean oil or fish oil. *Meat Sci.* 92, 848–854. doi: 10.1016/j.meatsci.2012.07.012
- Natalello, A., Luciano, G., Morbidini, L., Valenti, B., Pauselli, M., Frutos, P., et al. (2019). Effect of feeding pomegranate byproduct on fatty acid composition of ruminal digesta, liver, and muscle in lambs. *J. Agric. Food Chem.* 67, 4472–4482. doi: 10.1021/acs.jafc.9b00307
- Noci, F., Monahan, F. J., French, P., and Moloney, A. P. (2005). Fatty acid composition of muscle fat and subcutaneous adipose tissue of pasture-fed beef heifers: Influence of the duration of grazing. *J. Anim. Sci.* 83, 1167–1178. doi: 10.2527/2005.8351167x
- Noci, F., Monahan, F. J., and Moloney, A. P. (2011). The fatty acid profile of muscle and adipose tissue of lambs fed camelina or linseed as oil or seeds. *Animal* 5, 134–147. doi: 10.1017/S1751731110001485
- Nozière, P., Graulet, B., Lucas, A., Martin, B., Grolier, P., and Doreau, M. (2006). Carotenoids for ruminants: From forages to dairy products. *Anim. Feed Sci. Technol.* 131, 418–450. doi: 10.1016/j.anifeedsci.2006.06.018
- Nudda, A., Battacone, G., Bee, G., Boe, R., Castaneres, N., Lovicu, M., et al. (2015). Effect of linseed supplementation of the gestation and lactation diets of dairy ewes on the growth performance and the intramuscular fatty acid composition of their lambs. *Anim. (Cambridge England)* 9, 800–809. doi: 10.1017/S175173111400305X
- Nuernberg, K., Nuernberg, G., Ender, K., Dannenberger, D., Schabbel, W., Grumbach, S., et al. (2005). Effect of grass vs. concentrate feeding on the fatty acid profile of different fat depots in lambs. *Eur. J. Lipid Sci. Technol.* 107, 737–745. doi: 10.1002/ejlt.200501141
- OECD/FAO (2021). "OECD-FAO agricultural outlook," in *OECD agriculture statistics (database)*. Paris: OECD Publishing. doi: 10.1787/agr-outl-dataen
- Ornaghi, M. G., Guerrero, A., Vital, A. C. P., De Souza, K. A., Passetti, R. A. C., Mottin, C., et al. (2020). Improvements in the quality of meat from beef cattle fed natural additives. *Meat Sci.* 163, 108059. doi: 10.1016/j.meatsci.2020.108059
- Orzuna-Orzuna, J. F., Dorantes-Iturbide, G., LarA-Bueno, A., Chay-Canul, A. J., Miranda-Romero, L. A., and Mendoza-Martinez, G. D. (2023). Meta-analysis of flavonoids use into beef and dairy cattle diet: Performance, antioxidant status, ruminal fermentation, meat quality, and milk composition. *Front. Veterinary Sci.* 10. doi: 10.3389/fvets.2023.1134925
- Parvar, R., Ghoorchi, T., and Shargh, M. S. (2017). Influence of dietary oils on performance, blood metabolites, purine derivatives, cellulase activity and muscle fatty acid composition in fattening lambs. *Small Ruminant Res.* 150, 22–29. doi: 10.1016/j.smallrumres.2017.03.004
- Pereira, P. M. d. C. C., and Vicente, A. F. d. R. B. (2013). Meat nutritional composition and nutritive role in the human diet. *Meat Sci.* 93, 586–592. doi: 10.1016/j.meatsci.2012.09.018
- Petcu, C. D., Mihai, O. D., Tăpăloagă, D., Gheorghe-Irimia, R. A., Pogurschi, E. N., Militaru, M., et al. (2023). Effects of plant-based antioxidants in animal diets and meat products: A Review. *Foods* 12, 1334. doi: 10.3390/foods12061334
- Pimentel, P. R. S., Pellegrini, C. B., Lanna, D. P. D., Brant, L. M. S., Ribeiro, C. V. D. M., Silva, T. M., et al. (2021). Effects of Acacia mearnsii extract as a condensed-tannin source on animal performance, carcass yield and meat quality in goats. *Anim. Feed Sci. Technol.* 271. doi: 10.1016/j.anifeedsci.2020.114733
- Ponnampalam, E. N., Burnett, V. F., Norng, S., Hopkins, D. L., Plozza, T., and Jacobs, J. L. (2016). Muscle antioxidant (vitamin E) and major fatty acid groups, lipid oxidation and retail colour of meat from lambs fed a roughage based diet with flaxseed or algae. *Meat Sci.* 111, 154–160. doi: 10.1016/j.meatsci.2015.09.007
- Ponnampalam, E. N., Burnett, V. F., Norng, S., Warner, R. D., and Jacobs, J. L. (2012). Vitamin e and fatty acid content of lamb meat from perennial pasture or annual pasture systems with supplements. *Anim. Production Sci.* 52, 255–262. doi: 10.1071/AN11054
- Ponnampalam, E. N. (1999). *Nutritional modification of muscle long chain omega-3 fatty acids in lamb: effects on growth and composition and quality of meat*. [master's thesis]. Melbourne, Australia: The University of Melbourne. 1999.
- Ponnampalam, E. N., Butler, K. L., Muir, S. K., Plozza, T. E., Kerr, M. G., Brown, W. G., et al. (2021a). Lipid oxidation and colour stability of lamb and yearling meat (Muscle longissimus lumborum) from sheep supplemented with camelina-based diets after short, medium, and long-term storage. *Antioxidants* 10, 1–19. doi: 10.3390/antiox10020166
- Ponnampalam, E. N., and Holman, B. W. B. (2022). "Sustainable animal production and meat processing," in *Lawrie's meat science textbook- edition 9*. Ed. F. Toldrá (Cambridge, United States: Elsevier Publisher of Scientific Books and Journals).
- Ponnampalam, E. N., Kiani, A., Santhiravel, S., Holman, B. W. B., Lauridsen, C., and Dunshea, F. R. (2022). The importance of dietary antioxidants on oxidative stress, meat and milk production, and their preservative aspects in farm animals: antioxidant action, animal health, and product quality-Invited Review. *Animals* 12, 3279. doi: 10.3390/ani12233279
- Ponnampalam, E. N., Lewandowski, P. A., Fahri, F. T., Burnett, V. F., Dunshea, F. R., Plozza, T., et al. (2015). Forms of n-3 (ALA, C18:3n-3 or DHA, C22:6n-3) Fatty Acids Affect Carcass Yield, Blood Lipids, Muscle n-3 Fatty Acids and Liver Gene Expression in Lambs. *Lipids* 50, 1133–1143. doi: 10.1007/s11745-015-4070-4
- Ponnampalam, E. N., Plozza, T., Kerr, M. G., Linden, N., Mitchell, M., Bekhit, A. E. D. A., et al. (2017). Interaction of diet and long ageing period on lipid oxidation and colour stability of lamb meat. *Meat Sci.* 129, 43–49. doi: 10.1016/j.meatsci.2017.02.008
- Ponnampalam, E. N., Sinclair, A. J., and Holman, B. W. B. (2021b). The sources, synthesis and biological actions of omega-3 and omega-6 fatty acids in red meat: An overview. *Foods* 10, 1358. doi: 10.3390/foods10061358
- Prache, S., Adamiec, C., Astruc, T., Baéza-Campone, E., Bouillot, P. E., Clinquart, A., et al. (2022a). Review: Quality of animal-source foods. *Animal* 16, 100376–100376. doi: 10.1016/j.animal.2021.100376
- Prache, S., Schreurs, N., and Guillier, L. (2022b). Review: Factors affecting sheep carcass and meat quality attributes. *Animal* 16, 100330–100330. doi: 10.1016/j.animal.2021.100330
- Ritchie, H., Rosado, P., and Roser, M. (2019). *Meat and dairy production*. Available at: <https://ourworldindata.org/meat-production>.
- Rivaroli, D. C., Guerrero, A., Velandia Valero, M., Zawadzki, F., Eiras, C. E., Campo, M. D. M., et al. (2016). Effect of essential oils on meat and fat qualities of crossbred young bulls finished in feedlots. *Meat Sci.* 121, 278–284. doi: 10.1016/j.meatsci.2016.06.017
- Rivaroli, D., Prunier, A., Meteau, K., do Prado, I. N., and 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. doi: 10.1017/S1751731118003543
- Rodriguez, R., Alomar, D., and Morales, R. (2020). Milk and meat fatty acids from sheep fed a plantain-chicory mixture or a grass-based permanent sward. *Anim. (Cambridge England)* 14, 1102–1109. doi: 10.1017/S1751731119002611
- Rossi, C. S., Compiani, R., Baldi, G., Bernardi, C. E. M., Muraro, M., Marden, J. P., et al. (2015). The effect of different selenium sources during the finishing phase on beef quality. *J. Anim. Feed Sci.* 24, 93–99. doi: 10.22358/jafs/65633/2015
- Ryan, S. M., Unruh, J. A., Corrigan, M. E., Drouillard, J. S., and Seyfert, M. (2007). Effects of concentrate level on carcass traits of Boer crossbred goats. *Small Ruminant Res.* 73, 67–76. doi: 10.1016/j.smallrumres.2006.11.004
- Salami, S. A., Guinguina, A., Agboola, J. O., Omede, A. A., Agbonlahor, E. M., and Tayyab, U. (2016). Review: In vivo and postmortem effects of feed antioxidants in livestock: A review of the implications on authorization of antioxidant feed additives. *Anim. (Cambridge England)* 10, 1375–1390. doi: 10.1017/S1751731115002967
- Salami, S. A., Luciano, G., O'Grady, M. N., Biondi, L., Newbold, C. J., Kerry, J. P., et al. (2019). Sustainability of feeding plant by-products: A review of the implications for ruminant meat production. *Anim. Feed Sci. Technol.* 251, 37–55. doi: 10.1016/j.anifeedsci.2019.02.006
- Scerra, M., Luciano, G., Caparra, P., Foti, F., Cilione, C., Giorgi, A., et al. (2011). Influence of stall finishing duration of Italian Merino lambs raised on pasture on intramuscular fatty acid composition. *Meat Sci.* 89, 238–242. doi: 10.1016/j.meatsci.2011.04.012
- Schwingshackl, L., Schwedhelm, C., Hoffmann, G., Lampousi, A., Knüppel, S., Iqbal, K., et al. (2017). Food groups and risk of all-cause mortality: A systematic review and meta-analysis of prospective studies. *The American J. Clin. Nutr.* 105, 1462–1473. doi: 10.3945/ajcn.117.153148
- Scollan, N. D., Dannenberger, D., Schreurs, N. M., Lane, G. A., Tavendale, M. H., Barry, T. N., et al. (2008). Pastoral flavour in meat products from ruminants fed fresh forages and its amelioration by forage condensed tannins. *Anim. Feed Sci. Technol.* 146, 193–221. doi: 10.1016/j.anifeedsci.2008.03.002
- Scollan, N., Hocquette, J.-F. O., Nuernberg, K., Dannenberger, D., Richardson, I., and Moloney, A. (2006). Innovations in beef production systems that enhance the nutritional and health value of beef lipids and their relationship with meat quality. *Meat Sci.* 74, 17–33. doi: 10.1016/j.meatsci.2006.05.002
- Semwogerere, F., Chikwanha, O. C., Katiyatiya, C. L. F., Marufu, M. C., and Mapiye, C. (2023). Health value and keeping quality of chevon from goats fed finisher diets containing hemp (*Cannabis sativa* L.) seed cake. *Meat Sci.* 198, 109114–109114. doi: 10.1016/j.meatsci.2023.109114



- Shabtay, A., Eitam, H., Tadmor, Y., Orlov, A., Meir, A., Weinberg, P., et al. (2008). Nutritive and antioxidative potential of fresh and stored pomegranate industrial byproduct as a novel beef cattle feed. *J. Agric. Food Chem.* 56, 10063–10070. doi: 10.1021/jf8016095
- Siphambili, S., Moloney, A. P., O'riordan, E. G., Mcgee, M., Harrison, S. M., and Monahan, F. J. (2022). Partial substitution of barley with maize meal or flaked meal in bovine diets: Effects on fatty acid and  $\alpha$ -tocopherol concentration and the oxidative stability of beef under simulated retail display. *Anim. Production Sci.* 62, 182–190. doi: 10.1071/AN20627
- Skřivanová, E., Marounek, M., De Smet, S., and Raes, K. (2007). Influence of dietary selenium and vitamin E on quality of veal. *Meat Sci.* 76, 495–500. doi: 10.1016/j.meatsci.2007.01.003
- Suman, S. P., Hunt, M. C., Nair, M. N., and Rentfrow, G. (2014). Improving beef color stability: practical strategies and underlying mechanisms. *Meat Sci.* 98, 490–504. doi: 10.1016/j.meatsci.2014.06.032
- Swanson, K. C. (2019). "Small intestinal anatomy, physiology, and digestion in ruminants," in *Reference Module in Food Science* (Elsevier, Amsterdam, The Netherlands).
- Tabke, M. C., Sarturi, J. O., Galyean, M. L., Trojan, S. J., Brooks, J. C., Johnson, B. J., et al. (2017). Effects of tannic acid on growth performance, carcass characteristics, digestibility, nitrogen volatilization, and meat lipid oxidation of steers fed steam-flaked corn-based finishing diets. *J. Anim. Sci.* 95, 5124–5136. doi: 10.2527/jas2017.1464
- Tayengwa, T., Chikwanha, O. C., Gouws, P., Dugan, M. E. R., Mutsvangwa, T., and Mapiye, C. (2020). Dietary citrus pulp and grape pomace as potential natural preservatives for extending beef shelf life. *Meat Sci.* 162, 108029. doi: 10.1016/j.meatsci.2019.108029
- Urrutia, O., Soret, B., Insausti, K., Mendizabal, J. A., Purroy, A., and Arana, A. (2015). The effects of linseed or chia seed dietary supplementation on adipose tissue development, fatty acid composition, and lipogenic gene expression in lambs. *Small Ruminant Res.* 123, 204–211. doi: 10.1016/j.smallrumres.2014.12.008
- Uushona, T., Chikwanha, O. C., Katiyatiya, C. L. F., Strydom, P. E., and Mapiye, C. (2023). Fatty acid and oxidative shelf-life profiles of meat from lambs fed finisher diets containing *Acacia mearnsii* leaf-meal. *Meat Sci.* 201, 109190–109190. doi: 10.1016/j.meatsci.2023.109190
- Vahmani, P., Mapiye, C., Prieto, N., Rolland, D. C., McAllister, T. A., Aalhus, J. L., et al. (2015). The scope for manipulating the polyunsaturated fatty acid content of beef: A review. *J. Anim. Sci. Biotechnol.* 6, 29–29. doi: 10.1186/s40104-015-0026-z
- Vahmani, P., Ponnampalam, E. N., Kraft, J., Mapiye, C., Bermingham, E. N., Watkins, P. J., et al. (2020). Bioactivity and health effects of ruminant meat lipids. Invited Review. *Meat Sci.* 165, 108114–108114. doi: 10.1016/j.meatsci.2020.108114
- Verneque, B. J. F., MaChado, A. M., De Abreu Silva, L., Lopes, A. C. S., and Duarte, C. K. (2022). Ruminant and industrial trans-fatty acids consumption and cardiometabolic risk markers: A systematic review. *Crit. Rev. Food Sci. Nutr.* 62, 2050–2060. doi: 10.1080/10408398.2020.1836471
- Wang, X., Martin, G. B., Wen, Q., Liu, S., Li, Y., Shi, B., et al. (2020). Palm oil protects  $\alpha$ -linolenic acid from rumen biohydrogenation and muscle oxidation in cashmere goat kids. *J. Anim. Sci. Biotechnol.* 11, 100–100. doi: 10.1186/s40104-020-00502-w
- WCRF, AICR and CUP Expert report (2018). *Meat, fish and dairy products and the risk of cancer* (London, UK: WCRF International).
- Webb, E. C., Casey, N. H., and Simela, L. (2005). Goat meat quality. *Small Ruminant Res.* 60, 153–166. doi: 10.1016/j.smallrumres.2005.06.009
- Willems, H., Kreuzer, M., and Leiber, F. (2014). Alpha-linolenic and linoleic acid in meat and adipose tissue of grazing lambs differ among alpine pasture types with contrasting plant species and phenolic compound composition. *Small Ruminant Res.* 116, 153–164. doi: 10.1016/j.smallrumres.2013.11.002
- Williams, M. S., Mandell, I. B., Wood, K. M., and Bohrer, B. M. (2022). The effects of feeding benzoic acid and/or active dry yeast (*Saccharomyces cerevisiae*) on fatty acid composition, sensory attributes, and retail shelf-life of beef longissimus thoracis. *Trans. Anim. Sci.* 7, 161. doi: 10.1093/tas/txac161
- Wrona, M., Korytowski, W., Różanowska, M., Sarna, T., and Truscott, T. G. (2003). Cooperation of antioxidants in protection against photosensitized oxidation. *Free Radical Biol. Med.* 35, 1319–1329. doi: 10.1016/j.freeradbiomed.2003.07.005
- Zehiroglu, C., and Ozturk Sarikaya, S. B. (2019). The importance of antioxidants and place in today's scientific and technological studies. *J. Food Sci. Technol.* 56, 4757–4774. doi: 10.1007/s13197-019-03952-x
- Zervas, G., and Tsiplakou, E. (2011). The effect of feeding systems on the characteristics of products from small ruminants. *Small Ruminant Res.* 101, 140–149. doi: 10.1016/j.smallrumres.2011.09.034



## OPEN ACCESS

## EDITED BY

Jeff Wood,  
University of Bristol, United Kingdom

## REVIEWED BY

Susan Fairweather-Tait,  
University of East Anglia, United Kingdom  
Davide Lanzoni,  
University of Milan, Italy

## \*CORRESPONDENCE

Egil Prestløkken  
✉ egil.prestlokken@nmbu.no

<sup>†</sup>These authors share senior authorship

RECEIVED 30 April 2024

ACCEPTED 27 August 2024

PUBLISHED 14 October 2024

## CITATION

Egelandsdal B, Grabez-Ågren V, Mydland LT,  
Haug A and Prestløkken E (2024) Animal  
breeding and feeding tools may close  
human nutrition gaps.  
*Front. Anim. Sci.* 5:1426044.  
doi: 10.3389/fanim.2024.1426044

## COPYRIGHT

© 2024 Egelandsdal, Grabez-Ågren, Mydland,  
Haug and Prestløkken. This is an open-access  
article distributed under the terms of the  
[Creative Commons Attribution License \(CC BY\)](#).  
The use, distribution or reproduction in other  
forums is permitted, provided the original  
author(s) and the copyright owner(s) are  
credited and that the original publication in  
this journal is cited, in accordance with  
accepted academic practice. No use,  
distribution or reproduction is permitted  
which does not comply with these terms.

# Animal breeding and feeding tools may close human nutrition gaps

Bjørge Egelandsdal<sup>1</sup>, Vladana Grabez-Ågren<sup>1</sup>,  
Liv Torunn Mydland<sup>2</sup>, Anna Haug<sup>2†</sup> and Egil Prestløkken<sup>2\*†</sup>

<sup>1</sup>Faculty of Chemistry, Biotechnology and Food Science, Norwegian University of Life Sciences, Ås, Norway, <sup>2</sup>Faculty of Biosciences, Norwegian University of Life Sciences, Ås, Norway

The last century has witnessed many innovations in agriculture and food technologies that have ensured the production of sufficient quantities of good hygienic food. Animal scientists have contributed substantially to efficient breeding and feeding practices by adapting animals for faster growth and improving feed efficiency and utilization. Breeding goals and feeding recommendations have been proposed with a primary focus on profitability to promote significant changes in the macronutrient content, i.e., animal body protein and fat reduction. However, improving the nutritional quality of meat was not included in the profit assessment. Increasing the lean meat fraction is consistent with the goal of public dietary guidelines for human nutrition proposed in 1980, emphasizing the importance of reducing the consumption of animal fat, particularly saturated fat. The application of breeding and feeding tools to modify and improve the fatty acid composition has been partly implemented in pigs and broiler chickens to supplement the dietary recommendations for humans. The health benefits of lean “red meat” have been questioned in recent years, with dietary guidelines and upper limits being introduced for human intake. Animal breeding indirectly reduces the total and heme iron (the redness generator) content in meat, due to covariation with priority breeding goals. Two micronutrients play important roles in the human diet and are derived largely from meat (selenium) and milk (iodine) if the amount provided and absorbed is sufficient and predictable. The iodine content can be highly dependent on the use of novel (more sustainable) feeds. The micronutrients discussed in this study (Fe, Se, I, and vitamin D) highlight opportunities for the utilization of breeding and feeding knowledge to adjust their levels to procure meat with a high nutrient density. The gaps in micronutrient levels in humans must be addressed by navigating within approved animal feeding levels. Animal scientists must recognize the nutritional impact of breeding and feeding and advertise them. In addition, human nutritionists must acknowledge the existing and potential changes in animal production to meet the dietary guidelines. Sustainable food production within the “One Health” concept can only be achieved through cooperation.

## KEYWORDS

livestock, breeding, feeding, nutritional guidelines, meat, milk

# 1 Introduction

Selective breeding has been practiced since the 18th century to improve carcass quality and meat production; however, significant changes have been reported in this practice since 1960 (Siegel, 2014; Knap and Wang, 2012). Larger carcasses, more milk, meat production with less fat, and improved feed efficiency have remained the focus of animal selection. Breeding and efficient feed utilization have yielded more animal products in recent years, sparring debates on the health and well-being of the animals (Tixier-Boichard, 2018). Access to greater amounts of food through efficient agricultural practices, innovative food technologies, and improved nutrition have facilitated the increase in population from a few million during the hunter-gathering period to eight billion at present.

The rapid growth in the production of farmed animals in the 1970s has increased the focus on sustainability. Revising agricultural practices to facilitate the incorporation of more plant-based food in the human diet, reducing the consumption of meat, and use more non-edible and novel resources as feed was an important approach of the sustainability period (1970–present).

Awareness regarding the importance of food and nutrition has increased over the last century. The period from 1950 to 1970 is important in the human nutrition timeline due to the increased focus on protein malnutrition as a major global challenge (Mozaffarian et al., 2018). Food energy surpluses (fat- and starch-rich products) were prevalent in many industrialized countries in the 1980s. Nutritional guidelines have warned against the high intake of animal fat since the late 1970s, with extensive studies being

conducted on this topic. Reducing the intake of lean “red meat” has been recommended by nutritional guidelines, with an upper level (UL) provided from around 2015.

Micronutrient deficiency (hidden hunger) is a global challenge that has persisted for centuries. However, the combination of hidden hunger and energy surplus is a more recent challenge. The situation has been associated with a greater availability of energy rich and nutrient poor industrial foods. Although not a pressing topic at present, micronutrient dilution of raw materials may be a future challenge. Thus, in addition to increasing meat healthiness and nutrient density, improving the efficiency and use of more sustainable or novel feeds is also important.

This article reflects on the measures taken in the domain of animal breeding and feeding guidelines over the past 100 years through international and Norwegian/Nordic loops. Guidelines have been formulated for the nutritional requirements of human beings. Thus, the role of food categories (such as meat and grains) in the human diet was also surveyed in this study. The changes in the fat and Fe levels represent historical changes in animal breeding practices. The Se and I levels represent the dominant choice of animal feeding practices. Changes in the production and feeding practices lead to changes in vitamin D levels. Thus, detailed summaries of fat, a macronutrient, and these four micronutrients (Fe, Se, I, and vitamin D) have been provided in this article. Finally, measures to maintain the nutrient-dense nature of animal products, which may provide health benefits, have also been proposed.

## 2 Changes in meat and milk composition through efficient breeding and feeding in the last century

### 2.1 Advances in improving the quality of carcass and meat composition through breeding in the last century

The inheritance of genes was described by the Austrian monk Gregor Mendel in 1860. Sewall Wright, along with Ronald Fisher and John B.S. Haldane, established the theory behind breeding in populations (Larson, 2006) as the basis for selecting animals to maximize genetic gain for certain traits in a population in the 1920s. A model for applied animal breeding was established based on these theories (Lush, 1931), with breeding programs increasing animal production and efficiency over the next few decades (Figure 1). Traits that increase the growth rate and lean meat deposition have been favored in the domain of meat production as they improve feed efficiency and enable the production of more meat per kilogram of feed consumed. The implementation of these breeding programs has yielded successful outcomes in all species, particularly in poultry.

To the best of our knowledge, the nutritional quality of meat has not been considered an economically valuable trait; thus, it is not

**Abbreviations:** AA, Arachidonic acid; AC, After Christ; ADG, Average Daily Gain; AI, Adequate Intake; ALA,  $\alpha$ -Linolenic acid; ARC, Agricultural Research Council; BC, Before Christ; CVD, Cardiovascular disease; DGA, Dietary Guidelines for Americans; DM, Dry Matter; DHA, Docosahexaenoic acid; DPA, Docosapentaenoic acid; DRI, Dietary reference intake; E%, Energy percentage, i.e., percentage of total energy intake; EC, European Commission; EFSA, European Food Safety Authority; EPA, Eicosapentaenoic acid; EU, European Union; FA, Fatty acid; FAO, Food and Agriculture Organization; FCR, Feed Conversion Ratio; Fe, Iron; GPx, Glutathione peroxidase; HDL-C, High density lipoprotein cholesterol; HeFe, Heme iron; HHS, Department of Health and Human services; I, Iodine; IDA, Iron deficiency anemia; LDL, Low density lipoprotein; LA, Linoleic acid; LTL, Longissimus thoracis et lumborum; M-HDL-P, Number of medium HDL particles; MUFA, Monounsaturated fatty acids; NASEM, The National Academies of Sciences, Engineering, and Medicine in US; N-HeFe, Non-heme iron; NNR, Nordic Nutrition Recommendations; NRC, The National Research Council in US; PRI, Population Reference Intake; PUFA, Polyunsaturated fatty acids; RDA, Recommended daily allowances; RDI, Recommended Daily Intake; Rem-C, Remaining cholesterol; RI, Recommended intake; RS, Recommended supply; Se, Selenium; SFA, Saturated fatty acids; S-LDL-P, Number of small LDL particles; TF, Total fat; TFe, Total iron; TG, Triglycerides; TMR, Total mixed ration; UL, Upper limit; UN, United Nations; UV, Ultraviolet; UVB, Ultraviolet B; US, United States; USDA, United States Department of Agriculture; VitD, Vitamin D; VLDL-TG, Very low density – triglycerides; WHO, World Health Organization; Ø, Mean diameter.

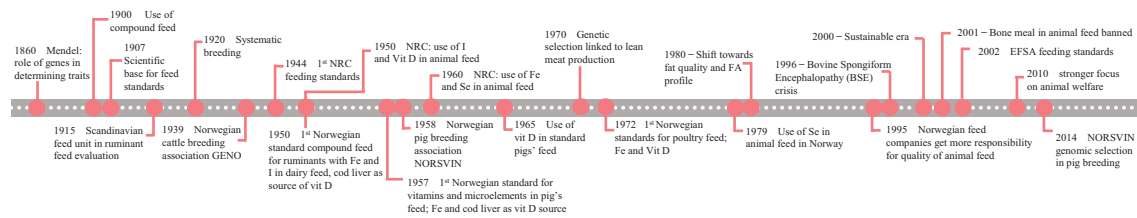


FIGURE 1

Overview of the historical development in animal genetic and dietary changes. Impact of breeding programs and the development of knowledge regarding animal health and feed efficiency on use and guidelines at USA (National Research Council, NRC) and Norwegian levels with a focus on four micronutrients (Fe, Se, I, and vitamin D).

acknowledged in breeding programs. Leaner meat is considered favorable economically and nutritionally. However, breeding techniques to facilitate faster growth and the production of leaner meat have changed genetic characteristics and favored an increase in the prevalence of larger glycolytic muscle cells over smaller oxidative muscle cells in broiler chickens. This reduces the inclusion of Fe and Se in muscle cells (Thiruvenkadan et al., 2019). Similarly, realizing that the pig is sufficiently lean has increased the focus on dressing percentage, meat quality, reproduction, and animal health without considering the changes in nutritional quality occurring over time. The benefits of consuming pork meat have increased. However, the amount of unsaturated fatty acids in pork has not been adequately acknowledged. The subsequent sections will discuss this point.

## 2.2 Advances in feeding standards and recommendations in the last century

The first feed standard was introduced by the German scientist Thaer (1754–1828) in 1810, who compared potential feedstuffs with meadow hay (Coffey et al., 2016). Weende analysis (“the proximate analysis”) of main nutrients, along with the pioneering work conducted by Wolff, Armsby, Kellner, and others on the digestibility and energetic contribution, have facilitated the formulation of basic principles for feed evaluation in the second half of the 19th century. These guidelines continued to be used over 150 years later (Weisbjerg et al., 2010). The National Research Council (NRC) set forth the first edition of its recommendations in 1944 in the USA (Figure 1). The NRC recommendations remain the global standard for all domestic animals, including pets and fish. However, the EU recommendations set forth by the European Food Safety Authority (EFSA) in 2002 are followed in Norway (Figure 1). The EU recommendations have defined risks and proposed upper limits (UL) for human food and animal feed, including health and welfare. Thus, this organization influences the achievements in sustainability. Notably, the influence of some nutrients on product quality has been defined in the One Health concept (Mackenzie and Jeggo, 2011) in Europe. For instance, I and Se have been incorporated in animal feed to ensure the minimum or maximum transfer of these elements into human food in accordance with these recommendations.

### 2.3 Alteration of animal carcass and meat and milk composition through breeding and feeding

Mozaffarian et al. (2018) stated that “relatively few rigorous evaluations have been conducted on the potential long-term health consequences of modern shifts in agricultural practices (breeding, feeding, and food processing)”. This section discusses the variability in the total fat (TF) composition in the carcass, its derived fatty acid (FA) content, and the four micronutrients that play important roles in maintaining human health.

### 2.3.1 Total fat and fatty acids in meat

Energy deficiency was more prevalent among humans in previous decades. Consequently, the TF content was considered more important than the quantity of lean meat and quality of fat. However, the increased focus on incorporating high-quality protein in the human diet and increasing awareness regarding the health benefits of certain FAs, along with the strong focus on feed utilization and production costs in terms of quantity and quality, especially pig fat, have changed dramatically since 1950. This reduction has been attributed to the efficient breeding and selection of animals using progeny testing, with an emphasis on the traits linked to the growth rate and feed conversion ratio (FCR), such as carcass dissection, backfat measurements, and body composition determined via computed tomography (CT). The Food and Agriculture Organization/World Health Organization (FAO/WHO) has acknowledged the large changes in TA and FA composition via genetics, feeding, and trimming techniques (FAO, 2010). However, the overarching relevance of transitioning to the consumption of healthier meat is underexplored.

Genetic changes in the quantity and quality of fat have been achieved via long-term shifts. Genotyping, which has replaced progeny testing, has enabled a significant improvement in the speed of genetic gain over the past 20–30 years. Emerging genetic technologies may reduce the time required to achieve quality improvement. The short-term shifts, independent of the “permanent” genetic changes, can be traced back to feeding. The FA composition of monogastric animals is easily affected by feeding as the body fat reflects the FA composition of the feed. As such, substantial knowledge exists for designing the quality of monogastric meat according to potential demands. Section 4

TABLE 1 Aspects related to animal feed dietary sources and animal recommendations of intake or supply through feed for four micronutrients.

Items	Main dietary sources animals	Source	Animal species			
			Dairy cattle	Growing cattle	Growing pigs	Chicken
Iron	Inorganic salts such as ferrous sulfate, blood meal, meat and bone meal, and soil	NRC EU Norway FKF	1 mg/kg milk <sup>1</sup> 450 mg/kg feed <sup>5</sup> 50 mg/kg DM <sup>9</sup> 0 <sup>10</sup>	50 mg/kg DM <sup>2</sup> 450 mg/kg feed <sup>7</sup> 50 mg/kg DM <sup>9</sup> 0 <sup>10</sup>	60 mg/kg feed <sup>3</sup> 750 mg/kg feed <sup>5</sup> 80 mg/kg feed <sup>11</sup> 160 mg/kg feed <sup>10</sup>	80 mg/kg feed <sup>4</sup> 450 mg/kg feed <sup>5</sup> 20 mg/kg <sup>12</sup> 150 mg/kg feed <sup>10</sup>
Selenium	Inorganic salts like Na selenite or selenate, organic components such as Se-yeast and fish meal	NRC EU Norway FKF	0.3 mg/kg DM <sup>1</sup> 0.5 mg/kg feed <sup>6</sup> 0.2 mg/kg DM <sup>9</sup> 0.4 mg/kg feed <sup>10</sup>	0.1 mg/kg DM <sup>2</sup> 0.5 mg/kg feed <sup>6</sup> 0.1 mg/kg DM <sup>9</sup> 0.4 mg/kg feed <sup>10</sup>	0.1 mg/kg feed <sup>3</sup> 0.5 mg/kg feed <sup>6</sup> 0.2 mg/kg feed <sup>11</sup> 0.4 mg/kg feed <sup>10</sup>	0.15 mg/kg feed <sup>4</sup> 0.5 mg/kg feed <sup>6</sup> 0.3 mg/kg feed <sup>12</sup> 0.4 mg/kg feed <sup>10</sup>
Iodine	Inorganic Ca iodate, Na- or K iodine, fish meal, and seaweeds	NRC EU Norway FKF	0.5–1.0 mg/kg DM <sup>1</sup> 5.0 mg/kg feed <sup>7</sup> 1.0 mg/kg DM <sup>9</sup> 5.0 mg/kg feed <sup>10</sup>	0.5 mg/kg DM <sup>2</sup> 10 mg/kg feed <sup>7</sup> 0.5 mg/kg DM <sup>9</sup> 5.0 mg/kg feed <sup>10</sup>	0.14 mg/kg feed <sup>3</sup> 10 mg/kg feed <sup>7</sup> 0.30 mg/kg feed <sup>11</sup> 0.65 mg/kg feed <sup>10</sup>	0.35 mg/kg feed <sup>4</sup> 10 mg/kg feed <sup>7</sup> 1.25 mg/kg feed <sup>12</sup> 1.5 mg/kg feed <sup>10</sup>
Vit D	Synthetic Vitamin D <sub>3</sub> (cholecalciferol), cod-liver oil, sun dried hay	NRC EU Norway FKF	1.00 µg/kg BW <sup>1</sup> 100 µg/kg DM <sup>8</sup> 0.75 µg/kg BW <sup>9</sup> 50 µg/kg feed <sup>10</sup>	7.5 µg/kg DM <sup>2</sup> 100 µg/kg feed <sup>8</sup> 0.25 µg/kg BW <sup>9</sup> 50 µg/kg feed <sup>10</sup>	3.75 µg/kg feed <sup>3</sup> 50 µg/kg feed <sup>8</sup> 10 µg/kg feed <sup>11</sup> 30 µg/kg feed <sup>10</sup>	7.5 µg/kg feed <sup>4</sup> 125 µg/kg feed <sup>8</sup> 110 µg/kg DM <sup>12</sup> 110 µg/kg feed <sup>10</sup>

Values with reference to various sources are given as recommended intake (NRC), maximum content allowed (all EU figures), Norwegian recommendations (Norway), and “common” Norwegian practice (FKF) (at dry matter [DM]; 12% water kg feed; or body weight [BW]).

<sup>1</sup>(NASEM, 2021); <sup>2</sup>(NASEM, 2016); <sup>3</sup>(NRC, 2012); <sup>4</sup>(NRC, 1994); <sup>5</sup>(EC, 2017); <sup>6</sup>(EC, 2020); <sup>7</sup>(EC, 2015); <sup>8</sup>(EC, 2019); <sup>9</sup>(Volden, 2011); <sup>10</sup>(FKF, 2024); <sup>11</sup>(Tybirk et al., 2023); <sup>12</sup>(Svihus, 2016).

highlights examples related to the influence of breeding and feeding on the TF and FA composition of meat in monogastric animals.

2.3.2 Content of selected micronutrients in meat and milk

Micronutrients are not the primary targets in breeding programs, and genetic changes are the consequence of correlations with traits in breeding indexes. However, breeding and feeding techniques have differential effects on the micronutrient content in meat. Selected essential micronutrients, such as Fe, Se, I, and vitamin D, in feeding protocols within a historical framework for dairy cows, beef cattle, fattening pigs, and broilers have been considered in this study to illustrate this. Table 1 summarizes the main dietary sources and feeding recommendations provided in Europe, the USA (NRC), and Norway/Nordic countries.

2.3.2.1 Iron

The role of dietary Fe in the prevention of Fe deficiency in young animals has been known since the early 1930s (Blaxter et al., 1957), and animal feed has been supplemented with Fe for more than a century. Commonly used Fe sources have poor bioavailability; consequently, Fe is supplemented in excess to achieve adequate intake (AI). However, Fe is efficiently recycled in the body, and tissue growth is the main factor affecting the requirement for Fe. The fifth revised edition of the NRC for poultry (NRC, 1966) recommended supplementing the feed for starter chickens (0–8 weeks) with 40 mg Fe/kg; however, this was increased to 80 mg/kg in the 1971 revision (NRC, 1971b). The 1979 edition (NRC, 1979) recommended supplementing the feed for growing pigs (20–120 kg BW) with 40–60 mg Fe/kg. The 1971 revision recommended supplementing the feed for all types of dairy cattle with 100 mg Fe/kg; however, this was reduced to 50 mg Fe/kg in 1978 (NRC, 1978). The current recommendations set forth by the

NRC and EFSA reflect these figures (Table 1). The NRC recommendations compensate for the expected milk loss (1 mg/kg milk) in adult dairy cows only (NASEM, 2021).

The addition of Fe to ruminant, pig, and chicken feeds was mandated in Norway when feeding standards were introduced in 1950, 1957, and 1972, respectively (Homb, 1979) (Figure 1). Presently, ruminant feed is not usually supplemented with Fe as Fe intake from natural sources is considered sufficient. However, pig and poultry feeds are supplemented with 160 and 150 mg Fe/kg, respectively (FKF, 2024) (Table 1). This amount is twice that recommended by the NRC, but is well within the maximum content recommended in the EU. Although the upper tolerable limit is high, it is normally not a source of concern in animal feeding. Blood meal and meat and bone meal are rich in Fe; however, they are not commonly used in the feeds for farm animals due to disease risks.

2.3.2.2 Selenium

Selenium is a scarce trace element. The Se content in plants reflects the Se content in the soil. Feed ingredients cultivated in the central plains of the USA and Canada are usually rich in Se. In contrast, the soil and thus plants in most European regions, including the Nordic region, are low in Se content. Selenium was recognized as an essential element in the late 1950s. The NRC has recommended supplementation of Se from the mid-1960s; however, supplementation of poultry and pig feed and later ruminant feed was first approved by the FDA in 1974 (Brummer et al., 2014). Se content in the range of 0.03–0.05 mg/kg feed is considered “marginal” in the UK (ARC, 1980). Notably, 0.1 mg Se/kg was required for the optimal activity of glutathione peroxidase (GPx) in milk-fed lamb, which corresponded with NRC recommendations for dairy cattle (NRC, 1971a, 1978).



The NRC currently recommends increasing the Se content to 0.3 mg Se/kg dry matter (DM) feed for dairy cattle (Table 1). The NRC recommends supplementing pig and poultry feed with 0.10 and 0.15 mg Se/kg DM; in contrast, the EU has limited the Se content to  $\leq 0.5$  mg/kg feed for all species (Table 1). Inorganic supplements are used most commonly; however, interest in organic supplements, such as Se-yeast, has been increasing in recent years, and they facilitate more efficient transfer into meat (Malbe et al., 1995; Ortman and Pehrson, 1999; Cruickshank et al., 2021). Thus, the maximum Se content was limited to 0.2 mg/kg feed when using organic supplements (EFSA, 2021). The NRC and EFSA list the upper tolerable level as 5 mg Se/kg feed.

The addition of 0.1 mg Se/kg feed in all animal feed was mandated in 1979 in Norway (Figure 1). The concentration was then increased to 0.2 mg/kg feed. However, 0.40–0.45 mg Se/kg is added to all compound feeds (Table 1) at present such that the upper 0.5 mg/kg feed limit is not exceeded. Fish meal is a good natural source of Se in animal feed. However, Se can also be supplied orally as boluses or tablets before slaughter to increase the Se content in the meat.

### 2.3.2.3 Iodine

Iodine is present in saltwater oceans and is at relatively high levels in fish meal. The I content in plants and soil diminishes as the distance from the sea increases. Animal feeds are supplemented with I in the form of iodide or iodate; notably, iodate which is more resistant to volatilization. The important role played by I in the proper functioning of the thyroid gland in vertebrates and humans has been reported since the early 1900s. The “Proceedings of the Iowa Academy of Science”, (Evvard and Culbertson, 1924) described I as “a Factor in Feeding Young Growing Swine,” citing several articles published between 1913 and 1924 indicating the requirement for I in animal diets. According to ARC (1980), Mitchell and McClure (1937) estimated requirements of non-lactating cows in the range of 0.03–0.07 mg/kg DM feed. The NRC set forth the first recommendations for I in chicken (0.20 mg/kg feed) and swine (0.22 mg/kg feed) feed in 1954 and 1953, respectively. The NRC recommended supplementing the feed of dairy cattle with 0.76 mg I/kg feed in 1958. However, the Norwegian ministry of Agriculture has recommended supplementation with I in dairy cattle through feed to prevent goiter in humans since 1951, considering the efficient transfer of I from feed to milk (Breirem and Homb, 1958). This recommendation corresponded to approximately 0.5 mg I/kg feed.

Current recommendations for the supplementation of I in animal feed can be classified as additions for the biofortification of milk and AI to meet the requirements of the animal. To meet the requirements of the animal, I is supplemented at 0.15–1.0 mg I/kg feed, with the highest level being supplied for goitrogenic diets (Table 1). Up to 5 mg I/kg feed can be used for the biofortification of milk; however, the upper recommended limit is 2 mg I/kg feed (EFSA, 2013). Concerns have been raised regarding an excessively high content of I in cow milk, which is not suitable for infants. The upper recommended intake is based on public health issues also in the USA, with the intake being set to 50 mg I/day in dairy cows by

the NASEM (2021). This limit corresponds to the recommended limit of 2 mg I/kg feed in the diet of high-yielding cows (EFSA, 2013). Supplementation with up to 10 mg I/kg feed is permitted in the feed of growing cattle, pigs, and chickens in the EU (Table 1).

### 2.3.2.4 Vitamin D

Vitamin D<sub>3</sub> is formed in the skin of most mammals in sunlight through the ultraviolet (UV) lighting of 7-dehydrocholesterol. The introduction of synthetic vitamin D in the 1950s and 1960s has led to cod liver oil and sun-cured hay being replaced as the main sources of vitamin D in animal feeds. The NRC has recommended the intake of vitamin D since its inception (1944) based on publications from the 1930s providing the understanding that Ca and P play essential roles in the normal development of the skeletal system. Initially, the feeds for chicken and pigs (20–120 kg) were supplemented with 2.2 and 5.0 µg vitamin D/kg, respectively (NRC, 1953, 1954). In 1950, the NRC recommended supplementation with 0.17 µg vitamin D/kg live animal body weight (BW) in beef cattle. In contrast, the NRC (1958) recommended supplementation with 0.050–0.075 µg vitamin D/kg BW for young heifers, whereas no recommendation was proposed for lactating cows. In UK, the ARC (1980) defined the requirement of vitamin D as 0.10 and 0.25 µg/kg BW in growing cattle and lactating cows, respectively. Current recommendations for AI of vitamin D vary across different species of animals, ranging from 30 to 125 µg/kg DM feed (Table 1), which are considerably higher than the early recommendations. The upper tolerable levels are high. Vitamin D levels of up to 1,000 µg/kg feed can be tolerated for shorter periods (EFSA, 2014), which is much higher than the present recommendations.

## 2.4 Sustainability and leaving traditional feeds

The strong focus on animal value chain sustainability-related matters in Europe (Figure 1) began in 1996 due to the bovine spongiform encephalopathy (BSE) crisis and the ban on the inclusion of mammalian meat and bone meal in animal feed in 2001 (Coffey et al., 2016). In addition, the increase in global population has led to an increased demand for protein, thereby increasing the requirement for water and land. Furthermore, achieving sustainable feed and food security, along with animal health and welfare, has become a key objective in Europe due to the reliance on soy imports and concerns about greenhouse gas emissions. The use of alternative protein sources, such as micro- and macro-algae, insects, single-cell proteins, and fermented products will facilitate animal food production in a sustainable manner (Makkar, 2018). Alternatives comprising plant matrices with high nutritional profiles and low environmental impacts (like hemp) have attracted further interest in recent years. The potential of novel or alternative feed sources (ingredients, additives, and functional ingredients) to facilitate the production of sustainable livestock is evaluated based on feed efficiency, environmental impact, and economic value (Halmemies-Beauchet-Filleau et al., 2018). However, the development of a strategy for sustainable livestock production is complex and includes accompanying risks,

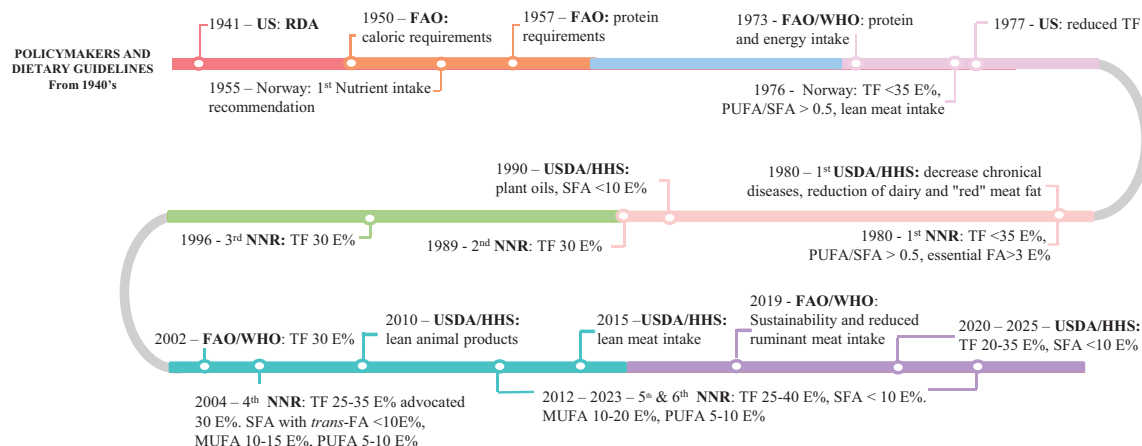


FIGURE 2

Overview of the development of human dietary guidelines at the global (WHO/FAO) and national (USA and Norway) levels with a focus on macronutrients (protein, fat, FA, and cholesterol). USDA/HHS, Dietary guidelines for Americans; NNR, Nordic Nutrient Recommendations; RDA, Recommended Dietary Allowances; TF, Total fat content; FA, Fatty acids; SFA, Saturated fatty acids; MUFA, Monounsaturated fatty acids; PUFA, Polyunsaturated fatty acids; E%, Energy percentage, i.e., percentage of total energy intake.

which are possibly reflected in the safety and nutritional value of animal products. The quality of meat and milk and the effects of manipulating their nutritional value using novel breeding tools remain to be elucidated. Furthermore, evidence supporting the changes in meat and milk composition induced by changes in feed composition and dietary treatments remains to be clarified. Therefore, characterizing the effects of alternative feed sources on the nutritive value of livestock is necessary. Section 4.4 exemplifies this through the renewed interest in using seaweed in animal diets.

### 3 The initiation and timelines of dietary guidelines for humans

The period during and after the Second World War emphasized the requirement for nutritional guidelines (Figures 2, 3). These guidelines were proposed officially in the late 1970s. Joint reports by the UN FAO/WHO often consider selected nutrients for nationwide assessment. The first relevant joint report focused on protein and energy intake (FAO/WHO,

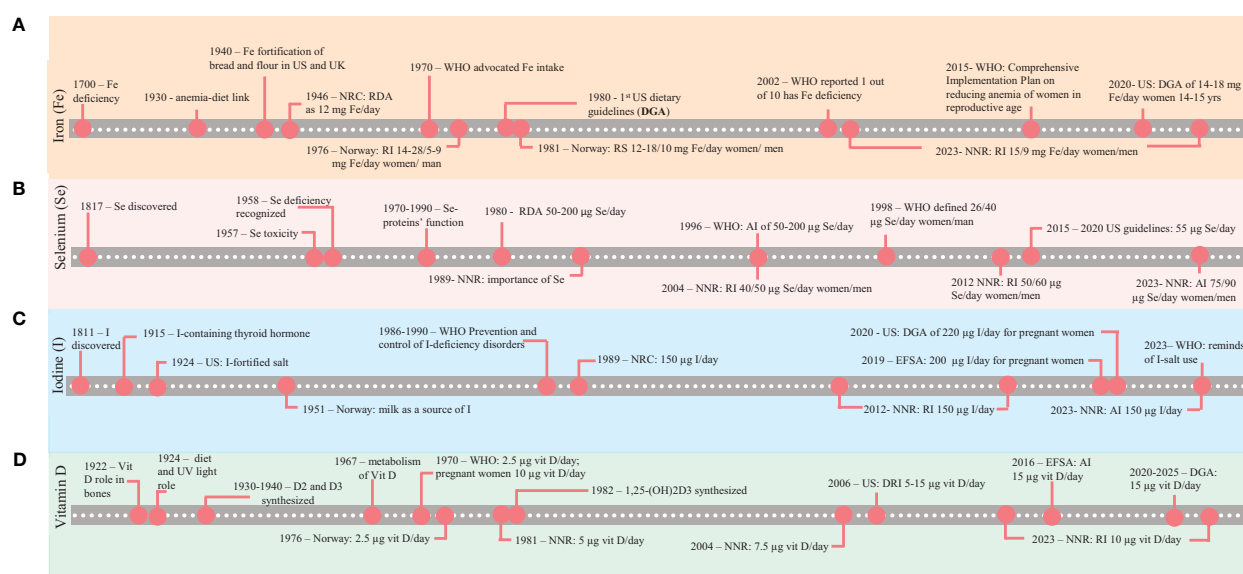


FIGURE 3

Timeline of the discovery and guidelines for four selected micronutrients, (A) Fe, (B) Se, (C) I, and (D) vitamin D, in the human diet (1800–2023) at global (WHO/FAO) and national (USA and Norway) levels. NRC, National Research Council; NNR, Nordic Nutrient Recommendations; RDA, Recommended Dietary Allowances; RI, recommended intake; RS, Recommended supply; AI, adequate intake; DRI, Dietary reference intake.

1973). However, the FAO released reports on energy and protein requirements in 1950 (FAO, 1950) and 1958 (FAO, 1958). The first dietary guidelines (DGA) were released in 1980 (thereafter at 5-year intervals) in the USA. The first Nordic Nutrition Recommendations (NNR) were published in 1980 (thereafter at approximately 8-year intervals). The initiative to develop a joint NNR was based on local nutritional advice supported by Report No. 32 released in 1975 (Norwegian Parliament, 1975). The FAO/WHO releases joint reports on specific macronutrients and micronutrients; in contrast, individual countries or regions provide more comprehensive guidelines. Most dietary recommendations are similar and focus on nutrients, products, or raw materials. The focus on reducing the intake of saturated fat, salt, and sugar is clear. However, the Brazilian guidelines, set forth in 2015, introduced the concept of ultra-processed foods and a new classification system for such foods (Ministry of Health Brazil, 2015) to discourage the high intake of nutrient-poor foods that can contribute to lifestyle-related diseases (Dicken and Batterham, 2022). Established in 2002, the EFSA advises the EU on food safety and nutrition in the complete (plant and animals) food chain (EFSA, 2024b).

The following section describes the guidelines for animal fats (TF and FA) and the fate of the four selected micronutrients playing essential roles in meat nutrition in the past 60 years. The term “meat” does not encompass processed meat products unless stated otherwise.

## 3.1 Animal fats

### 3.1.1 Total fat

A political report published in the USA in 1977 (McGovern, 1977) recommended reducing the intake of TF and cholesterol (Figure 2). Subsequent guidelines (USDA/HHS, 1980) have reflected the requirement for maintaining energy balance (preventing obesity) and reducing the intake of refined sugar, TF, cholesterol, saturated fatty acids (SFAs), added salt, and animal fat. The FAO/WHO (2002) recommends limiting the maximum intake of TF to 30 E%. The FAO (2010) has reported that the total E% is not an issue at present; however, the quality of fat must be maintained.

The first Nordic recommendations (NNR issues of 1980, 1989, and 1996) sought to reduce the intake of TF and increase the intake of carbohydrates and fiber (Figure 2). In addition, the consumption of lean meat was also supported. The subsequent recommendations proposed by the NNR recommended the intake of TF first to be 30 E% and then 40 E%. The UL was possibly set to 40 E% as starches *per se* are not healthy (WCRF, 2023) and should not replace fat or protein to a great extent.

### 3.1.2 Fat categories and fatty acid composition

The USDA/HHS (1990) recommends SFAs of <10 E% (Figure 2). These guidelines also recommend the intake of dietary plant oils and limiting the intake of land-based animal fats. The USDA/HHS (2005) has published specifications regarding the

intake of essential FAs. The DGA 2020 recommended limiting the intake of linoleic acid (LA) and  $\alpha$ -linolenic acid ALA at 12(17) g/100 g and 1.1(1.6) g/100 g for women and men (age group 19–50), respectively. The SFA recommendations have not changed over time (USDA/HHS, 2020; Astrup et al., 2020).

A report on diet and chronic diseases published by the FAO/WHO (2002) identified myristic acid (C14:0) and palmitic acid (C16:0) as convincing/probable factors promoting CVD. However, ALA, LA, and oleic acid have exhibited opposite trends. The FAO/WHO published a report on sustainable healthy diets (FAO/WHO, 2019) and expressed that monounsaturated fatty acids (MUFA) are an important component of unsaturated fat.

It is recommended in Norway that the polyunsaturated fatty acid (PUFA):SFA ratio be maintained at >0.5 (Norwegian Parliament, 1975). The NNR reports (NNR, 1989, 1996) focus on the quality of fat. The subsequent reports (NNR, 2004, 2012, 2023) have recommended ranges for SFAs, MUFAs, and PUFAs for the population aged  $\geq 2$  years. The sum of MUFAs and PUFAs should constitute at least two-thirds of the total FA intake in the diet. The NNR (2004) have provided detailed recommendations for SFAs <10 E%, *trans*-FA <1 E%, and with 1 E% from n-3 PUFA. Specific recommendations for LA and ALA have been set as >3 E% and >0.5 E% from ALA (NNR, 2004). The NNR reports published from 2012 to 2023 have made recommendations for n-3 PUFA, LA, and ALA. The recommendations for the intake of PUFAs is maintaining an n-6:n-3 ratio of 5; however, the evidence is insufficient (FAO, 2010; NNR, 2023).

The increase in the number of constraints with time, despite no success in reaching SFAs <10 E% in Norway (Directory of Health, 2023), the USA (Biing-Hwan et al., 2023) and the EU countries (EC, 2023), must be noted.

## 3.2 Lean meat

Figure 2 presents the transition from supporting the consumption of lean meat to specific restrictions (FAO/WHO, 2019; NNR, 2023) due to the reported negative effects of “red meat” on human health (WCRF, 2024) and the environment. Notably, proper local calculations of the environmental effects are often missing. Nevertheless, “white meat” is now a replacement in many parts of the world, and global poultry meat production has increased from <10 Mt in the early 1960s to almost 150 Mt and 40% of the total meat produced in 2023 (FAO, 2023). Limited documentation exists regarding the significant differences in the protein quality ranking of different meats.

## 3.3 The development of guidelines for some micronutrients needed in the human diet

Figure 3 presents the development of guidelines for micronutrients by the WHO, the USA, and the Nordic region. Section 4 summarizes human deficiencies in detail.

TABLE 2 Contribution (%) of various food categories in the human diet to selected macronutrients and micronutrients in which animal food (meat and milk) could be relevant.

Nutrients	Main functions	Main deficiency symptoms/signs	Contribution in diet (%): min - max values		
			US	EU countries	Nordic/ Norway
Iron	Hemoglobin in blood and myoglobin in muscles	Anemia, fatigue, and pallor	Grain 45*,1 Meat 20 <sup>1</sup> Veg. 8 <sup>1</sup> Dietary supplements 8 <sup>1</sup>	Grain 26 <sup>2</sup> –38* <sup>3</sup> Meat 14–29 <sup>2</sup> Veg. 12 <sup>4</sup> –39 <sup>2</sup>	Grain 26 <sup>2</sup> –43*,6/37 <sup>7</sup> Meat 20 <sup>5</sup> –25 <sup>6</sup> /20 <sup>7</sup> Veg. 13 <sup>5,6</sup> –22 <sup>8</sup> /13 <sup>7</sup>
Selenium	Antioxidant through glutathione peroxidase (GPx)	Higher mortality risk, muscle weakness, and fatigue	Meat 37 <sup>1</sup> Grain 34 <sup>1</sup> Egg 7 <sup>1</sup> Dietary supplements 7 <sup>1</sup>	Meat 24** <sup>4</sup> –34 <sup>9</sup> Grain 7 <sup>4</sup> –27 <sup>3</sup> Dairy 16** <sup>4</sup> Fish 12 <sup>9</sup> –15 <sup>3</sup>	Meat 21 <sup>10</sup> –33 <sup>6</sup> /20 <sup>11</sup> Cereals 6 <sup>10</sup> –22 <sup>6</sup> /29 <sup>11</sup> Dairy 15 <sup>10</sup> –22 <sup>6</sup> /13 <sup>11</sup> Fish 15 <sup>10</sup> –20 <sup>8</sup> /15 <sup>11</sup>
Iodine	Thyroid hormones T3 and T4	Goiter, thyroid dysfunction, cretinism, and pregnancy issues	Dairy 50 <sup>12</sup> Eggs 16 <sup>12</sup>	Dairy 12–53 <sup>13</sup> Grain 2–53 <sup>13</sup> Fish 4–32 <sup>13</sup>	Fish 7–47/21 <sup>13</sup> Dairy 30–37/36 <sup>13</sup> Grain 4–23/6 <sup>13</sup>
Vit D	Ca metabolism, bone growth, immunity systems	Ricket, osteomalacia, and reduced immunity	Fortified foods (Dairy, cereals a.o.) 66 <sup>14</sup> Natural diet 19 <sup>14</sup> Dietary supplements 15 <sup>14</sup>	Fish/shell 8–68 <sup>15</sup> Fat spreads 20–36*,15 Meat 10–31 <sup>15</sup>	Fish 21–57 <sup>16</sup> /40 <sup>7</sup> Fat spreads 14–35*,16/30 <sup>7</sup> Dairy 5–23*,16 Egg 17 <sup>7</sup>

\*Fortified products included; \*\* Substitutes included. Data were obtained from adults (>18 years). Sexes were averaged. <sup>1</sup> (Yan et al., 2024); <sup>2</sup> (Hallberg and Rossander-Hulthen, 1989); <sup>3</sup> (Roberts et al., 2018); <sup>4</sup> (RIVM, 2024); <sup>5</sup> (Gunnarsdóttir et al., 2010–2011); <sup>6</sup> (Helldán et al., 2013); <sup>7</sup> (Totland et al., 2012); <sup>8</sup> (Pedersen et al., 2015); <sup>9</sup> (Buffini et al., 2023); <sup>10</sup> (Amcoff et al., 2012); <sup>11</sup> (Haug et al., 2022); <sup>12</sup> (Lee et al., 2016); <sup>13</sup> (Bath et al., 2022); <sup>14</sup> (Newman et al., 2019); <sup>15</sup> (Spiro and Buttriss, 2014); <sup>16</sup> (Itkonen et al., 2021) (reference 11 has poor population representativity).

Table 2 highlights the primary deficiency symptoms and the dietary importance of micronutrients across various food categories.

3.3.1 Iron

Iron deficiency was first recognized as a health issue in the 17th century (Guggenheim, 1995) (Figure 3A). The presence of Fe in blood was recognized in 1825; however, the role of Fe in the diet was then still a speculation (Poskitt, 2003). Table 2 outlines the primary functions of Fe in humans. The FAO/WHO (1970) recommended the intake of iron according to the percentage of animal foods in the diet. The PRI for menstruating women was set as 14, 19, and 28 mg Fe/day, depending on the intake of animal-based food. The recommendations for women (15–50 years) have since been set to approximately 15 mg Fe/day (USDA/HHS, 2020; NNR, 2023). Fe deficiency in vulnerable groups persists as a challenge, as indicated by the WHO (WHO, 2002, 2009; McGuire, 2015). Ferrari et al. (2011) reported Fe sufficiency (serum ferritin levels of >15 µg/L) in 71.7% of girls aged 12.5–14.99 years in 10 European cities. This finding suggests that Fe deficiency (see Section 4) may be detected in subsamples of the population in the coming decades even in developed countries, possibly amplified by gastrointestinal disorders (Pasricha and Moir-Meyer, 2023) or nutrient dilution (Marles, 2017). The UL for human adults has been set to 45 (NASEM, 2006) and 40 mg Fe/day as a “safe level of intake” (a more conservative UL) (EFSA, 2024a).

The FAO/WHO recognized that heme Fe (HeFe) has higher bioavailability than inorganic Fe in 1970 (FAO/WHO, 1970). Meat contains factors that increase human Fe absorption from plant-based foods (Consalez et al., 2022; Nair and Augustine, 2018; Fairweather-

Tait, 2023). However, this factor may be less noticeable when considered for all types of diets (Consalez et al., 2022).

3.3.2 Selenium

Figure 3B presents the Se requirements in human nutrition. Table 2 presents the main symptoms of Se deficiency and its function. The WHO emphasized the lack of knowledge about Se requirements in the human diet (WHO, 1996). The initial recommendations for Se intake were imprecise (NRC, 1989; WHO, 1996; FAO/WHO, 2004).

Selenium intake is suboptimal in many locations in Europe (Stoffaneller and Morse, 2015). A 50% increase in the intake was recommended from 2012 to 2023 in the Nordic region (NNR, 1996, 2012, 2023). The UL for Se intake is 255 µg Se/day (EFSA, 2023). Approximately 70–80% of Se is absorbed depending on the food item (Alexander and Olsen, 2023). C-bound Se (organic Se) is absorbed better than inorganic Se.

3.3.3 Iodine

Fortification of salt with I was commenced in 1924 (Figure 3C) to tackle I deficiency (Andersson et al., 2012), and this is still the main strategy recommended by the WHO (2014). Although the WHO aimed to eliminate I deficiency by the year 2000 (WHO, 1986a, 1990), two billion individuals (WHO, 2007), including citizens in several European countries (Ittermann et al., 2020), are still at risk of developing I deficiency.

The recommended AI of I has been set to 150 and 200 µg/day in adults and pregnant women, respectively (NNR, 2023). The AI recommended by the NNRs is consistent with those recommended



in the EU and USA (USDA/HHS, 2020), whereas the NNRs set forth in 2023 recommend a slightly lower AI for pregnant women (200 µg I/day vs. 220 µg I/day). The UL for adults is set at 600 µg I/day (NNR, 2023). Inorganic I (iodides, I<sup>-</sup>), like table salt, is easily absorbed from the diet (Jahreis et al., 2001) and is the dominant form of I in milk (80–93% of total iodine) (van der Reijden et al., 2019).

### 3.3.4 Vitamin D

A link between sunlight (UV) and health was established between 1890 and 1930 (Figure 3D). Diet was then identified to have a similar function as the sun for the human body, and the vitamins D<sub>2</sub> and D<sub>3</sub> were identified as relevant (Jones, 2022). The bioactivity of the different vitamins D<sub>2</sub>, D<sub>3</sub>, 25-(OH)D<sub>3</sub>, and 1,25-(OH)<sub>2</sub>D<sub>3</sub>, are as follows: 1,25-(OH)<sub>2</sub>D<sub>3</sub> > 25-(OH)D<sub>3</sub> > D<sub>3</sub> = D<sub>2</sub> (Blunt et al., 1968). The relative bioactivity of 25-(OH)D<sub>3</sub> compared with those of D<sub>3</sub> and D<sub>2</sub> has been debated (Tripkovic et al., 2017; Cashman et al., 2012; Durrant et al., 2022).

Figure 3D presents the gradual increase in recommendations for vitamin D intake (FAO/WHO, 1970; EFSA, 2016; USDA/HHS, 2020; NNR, 2023) and the UL for vitamin D is set to 100 µg/day. EFSA (2016) has set the suitable blood target value as 50 nmol/L for all population groups.

### 3.3.5 Balance in micronutrients

Nutritional guidelines recommend assessing dietary patterns (USDA/HHS, 2020) as an additional measure to determine the intake of single nutrients. However, these guidelines should encompass micronutrient ratios (Kelly et al., 2018), provided that the ratio of these micronutrients is significant. Two ratios (vitamin D/Fe and I/Se) were deemed important in this article. Most observational studies have confirmed the presence of a positive relationship between Fe and vitamin D intake (Azizi-Soleiman et al., 2016). An imbalance between the intakes of I and Se may lead to cancer of the thyroid and exocrine organs and glands, e.g. stomach, breast, and prostate (Dijk-Brouwer et al., 2022). A high I:Se ratio indicated a potential harmful effect in rats (Hotz et al., 1997).

## 4 Changes in carcass, meat, and milk composition: maintaining food healthiness and sustainability through breeding and feeding

### 4.1 Case 1 – Improvement in the quality and quantity of fats from monogastric animals

#### 4.1.1 Total fat

Dietary animal fats have garnered significant attention. Pork fat is the most ingested type of animal fat in some countries (World Population Review, 2024); thus, clarifying its health benefits is important. The reduction in backfat thickness in pigs has been a breeding goal in Norway since the mid-1950s (Figure 4). This goal aims to transform pigs into lean and feed-efficient animals. The dramatic change in backfat thickness can be attributed to the demand for increased production efficiency. However, this is consistent with the nutritional debate that emerged later regarding the requirement for more protein and less animal fat. Breeding techniques have increased the amount of meat from approximately 40% to 60% of carcass weight (Figure 4; Supplementary Table 1), with the backfat thickness declining from 34 mm to 5 mm (Figure 4B). The reduction in backfat thickness, on average, was approximately 13 kg of adipose tissue per slaughtered pig. The TF content was estimated based on the supplied pig carcasses (devoid of head and front paws) and the Norwegian human population in 1953 (3.429 million individuals, 4.82 kg of pork fat per capita/year consumed) and 2020 (5.379 million individuals, 4.25 kg pork fat per capita per year, wholesale numbers). Notably, Norway is not involved in the major export or import of pork meat (<0.02% import in 2021). The TF content in the muscles of chickens may have declined over time due to extensive breeding (Zotte et al., 2019).

#### 4.1.2 Fatty acid composition of pork

The changes in the fat composition of pork observed in previous studies can be attributed to genetic factors or animal feed. In addition to the reduction in backfat thickness in pigs facilitated

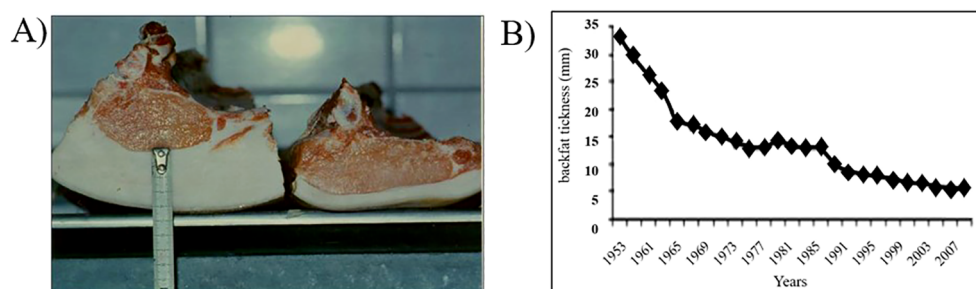


FIGURE 4

The impact of Norwegian pig breeding programs on carcass traits. (A) Illustrations of backfat thickness between 1953 (left) and 1980 (right). Source: Originally published in "Studies on a two trait selection experiment in pigs. III. Correlated responses in daily feed intake, feed conversion and carcass traits", O. Vangen, *Acta Agriculturae Scandinavica B*, 1980, 29, 337–345 (Vangen, 1980), reprinted by permission of the publisher (Taylor & Francis Ltd, <http://www.tandfonline.com>). (B) The decrease in backfat thickness. Source: Originally published in *Genetic analyses of meat, fat and carcass quality traits measured by rapid methods*, E. Gjerlaug-Enger, Philosophiae Doctor (PhD) Thesis No. 13, Norwegian University of Life Sciences (NMBU), Ås, Norway (Gjerlaug-Enger, 2011), reprinted by permission of the author.



TABLE 3 Changes of fatty acid classes in meat of Norwegian Landrace through breeding goals.

Year	Iodine value (g/100 fat)	SFA <sup>1</sup> % of total FA	MUFA	PUFA
1960 <sup>a</sup>	53.4	45.3	43.3	10.4
1987 <sup>b</sup>	n.a.	41.8	47.4	10.2
1990 <sup>a</sup>	61.9	38.5	45.9	14.4
2021 <sup>c</sup>	n.a.	33.9	47.9	15.3 + 2.8 <sup>d</sup>
2022 <sup>a</sup>	67.6	34.0	47.6	17.0

<sup>1</sup> FA, Fatty acid; SFA, Saturated fatty acid; MUFA, Monounsaturated fatty acid; PUFA, Polyunsaturated fatty acid.  
<sup>a</sup> Data received from Norsvin; <sup>b</sup> high-fat pork mince (Landsforeningen for Kostholdog Helse, 1988); <sup>c</sup> NMBU data; <sup>d</sup> unidentified FA content. For further details, see [Supplementary Information](#).

by selective breeding, important changes have also been observed in the FA composition. The SFA content in pork fat has declined, whereas the PUFA content has increased (Table 3), making pork fat a potentially important source of PUFA for humans. The intake of SFAs via pork has decreased by 33% per capita from 1960 to the present. In addition to the genetic changes, the FA composition of meat from monogastric animals, such as pigs, is strongly influenced by the dietary FA composition.

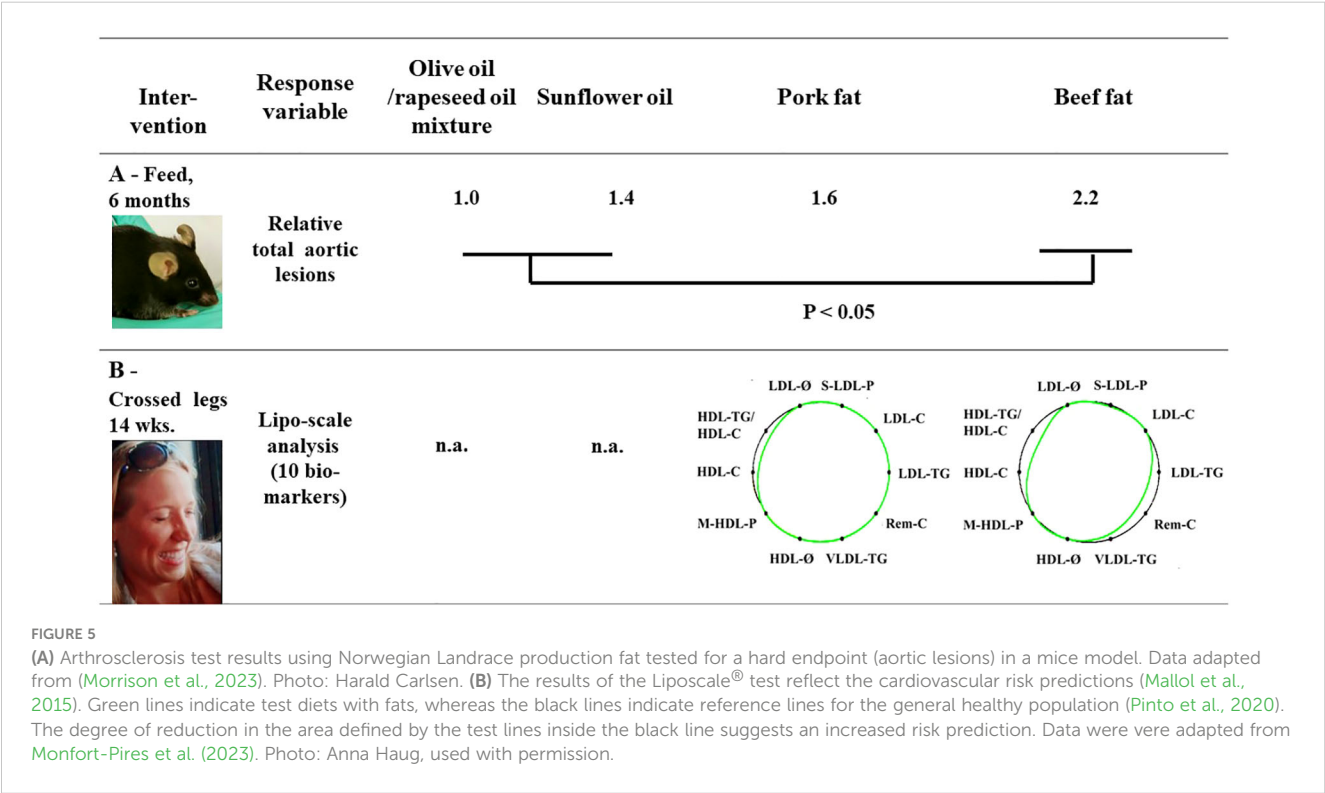
The pork fat ingested at present is consistent with the updated (NNR, 2023) recommendation for a minimum dietary intake of the MUFA+PUFA fraction (two-thirds of the TF content; Table 3). Various effective strategies can be applied to improve the composition of FA to increase the (long chain) n-3 PUFA content.

Studies investigating whether the changes in animal fat composition significantly affect human health are scarce. However, assessing the changes in fat from monogastric animals (chicken and pork) and the accompanying changes in human health

over time is difficult due to the lack of time-correct samples. A comparison of the present composition of animal fat with assumed healthier oils (e.g., rapeseed and olive oils) in terms of health benefits using a mouse model (Figure 5) revealed that the health benefits of pork fat are closer to those of some oils than beef fat. This has led to questions regarding whether the grouping of pork in the “red meat” group based on fat quality is appropriate. Data from the human intervention (Liposcale<sup>®</sup> data, Figure 5) show that the intake of pork fat is more beneficial than the intake of beef fat. Thus, the ranking supports the mouse model experiment.

4.1.3 Fatty acid composition of chicken

Chicken is an important source of unsaturated FA, such as n-6 FA, in countries wherein the intake of chicken is twice the intake of pork, and the intake of beef is limited. The SFA content in chicken fat is lower than that in pork fat. The n-6 fatty acid levels are significantly higher than the n-3 fatty acid levels in commercial chicken meat. The ratio of



9.5 (The Norwegian Food Safety Authority, 2016–2017a) is approximately two times higher than the ratio based on the recommended intakes of n-6 and n-3 fatty acids in the NNR (NNR, 2023). However, the n-6:n-3 ratio can be improved by implementing feeding programs with an additional focus on reducing the content of inflammatory arachidonic acid (AA).

Haug et al. (2012a) produced two types of chicken meats via feeding. The first type was obtained by feeding the chicken a commercial feed-like concentrate containing 4% soybean oil (SO). The second type was obtained by feeding the chicken a feed in which the SO was replaced with 2% rapeseed oil + 2% linseed oil (RLO). The content of n-3 PUFAs in the RLO feed is 3.4 times higher. The n-6:n-3 ratio in the RLO feed is 1.75, compared with the n-6:n-3 ratio of 9.8 in the SO feed. The n-3 PUFA content of the breast meat of chickens fed RLO was 2.7 times higher than that of the SO meat, and the n-6:n-3 ratios were 1.57 and 6.5 in the RLO- and SO-fed chickens, respectively (Haug et al., 2012a). A human intervention involving the ingestion of approximately 160 g of the two chicken meats daily for 4 weeks was carried out (Haug et al., 2012a). Consumption of RLO chicken resulted in an increase in the content of EPA+DHA in the blood of participants who had a low EPA+DHA% in serum phospholipids (<4.6%) before the intervention. Thus, a simple change in chicken feed can have beneficial effects on the amount of EPA (increased) and AA: EPA ratio (reduced) in the serum phospholipids in humans.

Improvement in the FA composition of meat can be achieved by modifying the diet of these animals; however, the sustainability demand at present is for the inclusion of locally produced oils (including neighboring countries) in feed. The direct use of oils in the human food chain may present challenges. However, the focus on formulating feed for farmed animals that does not involve using fields suitable for farming plant crops for humans has increased in recent years.

## 4.2 Case 2 – The effect of genetics and production systems on iron content in meat

### 4.2.1 The reduction of Fe content in muscle through efficient breeding and reduced physical activity

The Fe content in the meat acquired from all production animals has decreased over the previous 80–100 years. Selective breeding has reduced the requirement for Fe and myoglobin (Mb) in muscle cells (see Sections 2 and 3). Extensive breeding may diminish the “normal” function of mitochondria (Zhang et al., 2023; Suliga et al., 2022). Reduced physical activity (increased use of indoor housing) can reduce the requirement for Mb as an oxygen reservoir in cells. Newcom et al. (2004) reported that approximately one-third of the variation in pork muscle Mb can be attributed to different genetic factors. This finding indicates the genetic potential for variation. Apple et al. (2007) tested 50, 100, or 150 ppm of Fe from Availa-Fe (Fe with amino acid complex) and revealed the absence of any significant differences in the Japanese color score, HeFe level, or total He level in slaughtered animals. Thus, the Fe content in pig meat cannot be easily altered by feeding. Similar

results have been reported in chickens. Although outdoor production is expected to yield redder meat, it is not always found (Olsson and Pickova, 2005).

The Fe content in indigenous chickens in Kenya (Chepkemai et al., 2017) is 2.16 mg Fe/100 g of whole chickens. Red Jungle fowl thighs contain approximately 2.6 mg Fe/100 g meat (Callforlife, 2024). The ancient Polverari chicken (known since 1400–1500) contains 1.62 mg HeFe/100 g thigh (Pellattiero et al., 2020), indicating that the TFe is at least 2.1 mg/100 g (RIVM, 2023a). Whole chicken and thighs may contain 0.8 mg Fe/100 g at present (RIVM, 2023b). In Norway (The Norwegian Food Safety Authority, 2023a; 2016–2017b), skinned raw chicken and thighs contain 0.5 mg Fe/100 g and 0.7 mg Fe/100 g, respectively. Thus, although it is difficult to obtain accurate Fe data to facilitate the comparison of ancient and present chicken breeds, the Fe content in chicken meat has decreased significantly through breeding, presumably by 70–75%.

The *longissimus thoracis et lumborum* (LTL) of pigs contain 0.8 mg Fe/100 g (The Norwegian Food Safety Authority, 2023b). Similarly, pork fillet contains 0.4 mg Fe/100 g (RIVM, 2023c). Minced pork meat, which represents a larger part of the carcass, contains 0.8 mg Fe/100 g (The Norwegian Food Safety Authority, 2023c) to 0.9 mg Fe/100 g (RIVM, 2023d). The *musculus serratus anterior* of wild boar, a presumed oxidative muscle, contains 4.0–5.6 mg Fe/100 g (Skobrák et al., 2011). Compared with the commercially available pork meat, an 18–41% reduction in Fe content was reported by the authors. A Polish study reported that Fe content in domestic pigs was 60% lower than that in wild boars (Babicz and Kasprzyk, 2019).

The Fe content in beef has also exhibited a declining trend. Sambugaro et al. (2023) reported that the Fe content in the LTLs of endangered cattle breeds and dominant well-bred Norwegian Red Cattle was 2.73 mg Fe/100 g and 2.09 mg Fe/100 g, respectively, indicating a reduction of approximately 23%. Fairweather-Tait (2023) provided a more detailed description of the HeFe and HeFe/TFe content in meat. Notably, a lesser decline in the Fe content in the meat was observed in animals subjected to lesser breeding.

### 4.2.2 Breeding affects heme iron reduction in the muscle

Few food composition databases provide the HeFe data for muscle-based foods. Thus, assessing the changes in the HeFe: TFe ratio is difficult. Pellattiero et al. (2020) revealed that compared with those in ancient slow-breeding animals, present-day commercially available chickens had 70.4% and 69.7% lesser HeFe content in the breast and thigh muscles, respectively. The HeFe content in commercially available chickens is 33% of the TFe (RIVM, 2023e).

Changes in the Fe content of pork meat sourced from wild boars have been observed. Kasprzyk et al. (2019) reported the presence of Mb in wild boars of different weights (45–90 kg), with 1.64–4.5 mg HeFe/100 g being detected in the LTL. However, the data reported for TFe in wild boars vary substantially, thereby hindering the precise calculation of the HeFe: TFe ratio. Sampels et al. (2023) reported the color variables of whiteness and redness that are expected to correlate with Mb content in the *M. triceps brachii* muscle. Whiteness increased from 31.3 in wild boar meat to 47.2 in commercially

available pig meat, whereas redness decreased from 15.4 to 2.4 (Minolta data). Whiteness values >60 in commercially available pigs indicate a muscle defect. The HeFe : TFe ratio in pork mince was reported as 0.55 (RIVM, 2023d). Cross et al. (2012) reported that the HeFe level was <67% of the TFe level in the chuck part of beef in the USA. The HeFe level in beef mince accounts for approximately 80% of the TFe, according to RIVM (2023f), indicating a different breeding strategy than that used for pork and chicken. Thus, as shown in Section 4.2.1, the decline in heme content over time in beef is expected to be lower than that in chicken or pork.

#### 4.2.3 A human intervention elucidating the effect of the decline in iron content through animal breeding and feeding dilution

An insufficient amount of absorbable Fe remains the primary cause of Fe deficiency in women in most countries (Pasricha and Moir-Meyer, 2023). The average daily Fe intake in the Nordic and Baltic Countries ranges from 9.4–14.5 mg Fe/day according to the NNR (2023), with the lowest intake being observed among women in Iceland and the highest intake being observed among men in Latvia (Lemming and Pitsi, 2022). The average daily Fe intake of women in the Nordic and Baltic regions was below the recommended intake in all countries (Lemming and Pitsi, 2022).

A relatively recent peer-reviewed publication from the USA (Sun and Weaver, 2021) measured the serum Fe levels, hemoglobin levels, red cell distribution width and mean size, Fe intake, and diseases contracted from 1999 to 2018. A significant decline in Fe intake and hemoglobin levels was observed in this study. Notably, the Fe content in most food products (62.2%), including meat, fruits, and vegetables, was less in 2018 than that in 1999. The Fe content in meat declined to 80–86% of the value in 1999 during the period from 1999–2015, whereas the Fe content in turkey meat declined to 61% of the value in 1999 (Datasource: USDA Nutrient Database). The decline in dietary Fe intake observed in the USA could be related to the decline in the Fe content of food products due to more intensive agriculture and a shift in dietary patterns (Sun and Weaver, 2021). The findings of the study by Yan et al. (2024) support this conclusion. A recent commentary paper questioned the reliability of the estimated decline in Fe intake in the USA; however, this study acknowledged the presence of groups vulnerable to Fe deficiency (Engle-Stone et al., 2022). Fairweather-Tait (2023) summarized human interventions related to HeFe and TFe absorption and indicated that the absorption efficiency also depends on the degree of deficiency. An increase in Fe intake through the consumption of meat has been reported in Norway (up by 3% from 1959 to 2022) (See [Supplementary Material](#)).

### 4.3 Case 3 – The selenium content in meat is affected by breeding and feeding

Approximately one billion individuals are affected by Se deficiency globally (Jones et al., 2017); however, the symptoms of Se deficiency in humans remain unclear (Table 2). Studies from the USA and Europe (Alexander and Olsen, 2023) have defined Se

deficiency as plasma/serum Se values <100 µg/L. The intake of Se was below the AI recommended for the Nordic region (NNR, 2023) (Figure 3) in >80% of the participants in an intervention study (Haug et al., 2022). The average daily intake (ADI) of Se in the Nordic and Baltic countries ranges from 20–88 µg Se/day, with the lowest intake being observed among women in Lithuania and the highest intake being observed among men in Finland (Lemming and Pitsi, 2022). Thus, large parts of the Nordic and Baltic populations are below the AI of 75 and 90 µg Se/day recommended for women and men, respectively (NNR, 2023). The dietary sources of Se may change over time (nutrient dilution) and vary across different years depending on the import pattern of food. A Polish study revealed that cereals provide less amounts of Se over time (Zbigniew, 2002). Thus, the consumption of meat products may be more effective in combating Se deficiency than the consumption of cereals (Zbigniew, 2002). The results shown in Table 2 confirm these findings.

#### 4.3.1 Factors affecting the selenium content in meat during recent decades

The Se concentration in the soil is the key determinant of Se concentration in meat. For instance, the Se content in meat sourced from the USA may be higher than that in meat sourced from a European country with suboptimal levels of Se in the soil. The study conducted by Zhang et al. (1993) revealed that ground beef, pork, and chicken sourced from Texas contained 19.0 µg Se/100 g, 27.0 µg Se/100 g, and 13.0 µg Se/100 g, respectively. In contrast, beef, pork, and chicken sourced from France contained 6.0 µg Se/100 g, 8.0 µg Se/100 g, and 5.0 µg Se/100 g, respectively.

According to the Cicual database in France, raw chicken meat contains 12.4 µg Se/100 g (Cicual, 2020). The Se content in beef and pork meat in the USA (USDA/FDC, 2003) is higher than that in some European countries (e.g., Norway), whereas that of other countries is closer to the USA (e.g., Finland). The implementation of a biofortification program using Se (as selenate) as a fertilizer in Finland since 1985 has led to an increase in the Se content in food crops, livestock, and the human population, with the Se levels in human serum doubling over the subsequent 5-year period (Hartikainen, 2005). However, providing a general conclusion regarding the temporal changes in the Se content of meat is difficult. Selective breeding to decrease the number of oxidative muscle cells may have reduced the requirement for Se (Wesolowski et al., 2022) in the muscle. Feed supplementation increases the Se content in the muscles; however, the magnitude achieved via recommended feeding and that achieved via breeding remains unclear.

#### 4.3.2 Selenium content in meat assessed in a human intervention

An intervention study revealed that the intake of 55, 135, or 215 µg Se/day via Se-enriched meat significantly increased the plasma Se levels (van der Torre et al., 1991). Haug et al. (2018; 2022) reported a human intervention wherein 0.5 mg yeast-Se + 0.2 mg Selenite Se/kg of feed was fed to Norwegian Red bulls (control group was fed 0.2 mg Selenite Se/kg feed only). The raw meat (LTL) sourced from the control and experimental groups contained 11.7 and 15.2 µg Se/100

g, respectively. Commercially available LTL in Norway contains, on average, 7.8 µg Se/100 g (Egelandsdal et al., 2020). Biofortification of beef with Se ensures that meat is a source of Se, even in accordance with the updated NNR (2023) recommendations. A high amount of meat was consumed by young women for a short duration in a human intervention study (Haug et al., 2022). This study revealed that the consumption of Se-fortified beef increased the serum Se levels in young women that had less than 85 µg Se/L serum. Se uptake was surprisingly efficient, consistent with the WHO recommendations (WHO 1986b). Thus, muscle is an important organ for the storage of Se (50% of the Se content in the body), and optimizing the Se content in meat to meet specific consumer needs is possible (Oster et al., 1988).

Chicken feed supplemented with Se-rich yeast (0.5 and 0.84 mg Se/kg feed) increased the Se content from 28 to 39 µg Se/100 g in the chicken thigh muscle (Haug et al., 2007a). The higher concentration is similar to the Se content in wild fish (Haug et al., 2007b). In addition, the Se content in pork can be increased by adding organic Se to the feed (Gjerlaug-Enger et al., 2015), but an increase in the plasma Se levels in a human intervention with Se-enriched pork meat yielded unclear results (Bugel et al., 2004).

#### 4.4 Case 4 – Iodine in milk and meat seen through the loop of ruminant diets

Iodine is commonly added to dairy feed at 3–4-fold higher levels than the requirement of the animal in many countries, including Norway, to increase the I content in milk. Dairy products are a major source of I in Mediterranean and Western diets (Table 2; Niero et al., 2023). However, unlike milk, I is not transferred efficiently to the muscles. Consequently, the I content in animal feed for dairy and meat production should vary, as indicated by Meyer et al. (2008). The average daily intake of I in the Nordic and the Baltic countries ranges from 25–268 µg/day, with the lowest intake being observed in women in Lithuania and the highest intake being observed in men in Denmark (Lemming and Pitsi, 2022). The most recent update from the Iodine Global Network (IGN) lists Norway among the countries with insufficient I intake among school-age children (SAC) (IGN, 2022). This is supported by studies showing I deficiency among young and pregnant women (Henjum et al., 2018; Nystrom et al., 2016) indicating the risk of low I intake in certain population groups of the population. The present

Norwegian inclusion of 5 µg I/g in one type of table salt is having a minor dietary relevance.

##### 4.4.1 Iodine content in milk is affected by feeding but varies over time and by season

The I content in the feed is the major factor influencing the I content in the milk. However, goitrogenic components, such as thiocyanates originating from glucosinolates in cruciferous plants (e.g., *Brassica rapa*), inhibit the transfer of I from the feed to milk. Iodine is transferred from the blood into cells via the sodium iodine symporter (NIS). Thiocyanate acts as a competitive inhibitor in NIS. Information regarding the influence of breeding on NIS or the genetic effect on the I content in milk is unknown; nevertheless, the I content in milk can be efficiently manipulated through feeding.

The variation in the I content in milk over the years is a source of concern. Table 4 summarizes the I content in the summer and winter milk in Norway between 1971 and 2013. The I content in milk decreased dramatically from 231 µg/kg in the winter of 2000 (Dahl et al., 2003) to 122 µg/kg in the winter of 2008 in Norway (Haug et al., 2012a) (Table 4). However, the rate of inclusion of I in the diet remained unchanged. The reduction in the I content in milk can be attributed to the increased inclusion of rapeseed products in the dairy cattle diets (Trøan, 2017). Rapeseed products contain glucosinolates, which result in a 30–70% reduction in the I content in milk even at extremely low levels (Trøan et al., 2015). Notably, the I content in milk increased between 2008 and 2012/13 despite the increased use of rapeseed products in feed (Table 4). This increase was achieved by increasing the dietary inclusion of I from 2 to 5 mg/kg in pelleted compound feed mixtures, corresponding to an increase from approximately 0.8 to 2.0 mg/kg DM in the total ration.

The I content in milk varies seasonally. This reduction in I content in milk during summer could be attributed to the lower concentrate intake, given that I is supplemented through concentrate. However, data from the Norwegian Dairy Recording System from 2011 to 2016 indicated a minor reduction in the intake of the concentrate during summer compared with that in winter. Iodine-containing teat dips are not used commonly (Whist et al., 2007), thus the reduction cannot be attributed to them. The presence of goitrogenic substances in pasture and fresh grass compared with silage could result in a reduction in the I content in milk. Although not well-documented, these substances suppress the transfer of I from feed to milk (Trøan, 2017). Nevertheless, these findings indicate that the I content in the feed should be elevated during summer.

##### 4.4.2 Seaweed as a re-vitalized and iodine rich ingredient in ruminant diets

Seaweed has been used as animal feed in coastal areas for hundreds of years. It was mainly offered along with fish offal as an emergency feed during winter. Isaachsen and Al. (1917) conducted the first experiment on dried seaweed in dairy cow diets (Ringen, 1939) at our university. The palatability and energy value were low; thus, seaweed was not included in quantitative animal feed. Increased focus on sustainable feed systems has garnered attention to the use of seaweed in diet. In addition, seaweed has been identified as a promising mineral source in ruminant diets that

TABLE 4 Variations of iodine content in Norwegian milk due to time and season.

Season/ year	Iodine content (µg I/kg) <sup>1</sup>			
	1972/1973	2000	2008	2012/2013
Summer	66 ± 8.5	93 ± 17	92 ± 34	128 ± 92
Winter	122 ± 15	231 ± 34	122 ± 40	212 ± 78

<sup>1</sup> Average iodine content (± STD) in studied milk from 1971/1972 (Renaa and Staveland, 1974), 2000 (Dahl et al., 2003), 2008 (Haug et al., 2012b), and 2012/2013, (Trøan et al., 2015) (adapted from (Trøan, 2017)).



positively affects the I content in milk and meat and enhances the physicochemical properties of meat (Grabež et al., 2022, 2023a; Makkar et al., 2016; Newton et al., 2021; Grabež et al., 2023b).

The incorporation of seaweeds in animal diets presents several possibilities and challenges. Compared with that in grazing animals (117 µg I/L milk), supplementation with *Ascophyllum nodosum* (113 g/day, corresponding to 0.6% in DM) resulted in a significant increase in the I content in milk (480 µg I/L milk) in cows (Antaya et al., 2019). Furthermore, an increase in the inclusion levels of *A. nodosum* (57 g/d, 113 g/d, and 170 g/d, corresponding to 0.3, 0.6, and 1.0% in DM, respectively) in the diets of dairy cow, had a direct effect on I content in milk (602 µg I/L milk, 1,014 µg I/L milk, and 1369 µg I/L milk) (Antaya et al., 2015). Comparable results were reported by Newton et al. (2023), who demonstrated high I content in milk (1,886 µg I/L milk) when the diet of Holstein cows was supplemented with 330 g (corresponding to 1.3% in DM) *A. nodosum* daily. Thus, seaweed can biofortify milk with I; however, it is also associated with a risk of the excessive addition of seaweed or the addition of seaweed with excessively high I content, rendering the I content in milk excessive, especially for infants. The transfer of I to milk may be counterbalanced by the simultaneous supplementation of the feed with rapeseed products. To the best of our knowledge, the potential effect in a combination of seaweed and goitrogenic feedstuffs remains underexplored.

A recent experiment conducted at our university farm comprised feeding dairy cows in peak lactation (on average 50 days in milk) a total mixed ration (TMR) comprising grass silage and concentrate (65:35 ratio on DM basis) or a TMR including 1% DM of *S. latissima* over a 4-week period. Feeding 1% seaweed (corresponding to 220–240 g/day) to dairy cows resulted in a higher feed intake and milk yield (Ueland, 2022). Furthermore, the I content was 6.6 times higher in milk. A potential risk of including high amounts of *S. latissima* in the feed of dairy animals is the transfer of As, Pb, Cd, and other heavy metals (Sharma et al., 2018). The findings of Ueland (2022) indicate that <1% of the total As content was transferred to milk.

In addition to the use of seaweed in dairy cow diets, the effect of including *S. latissima* in the diets of finishing lamb and bulls on the I content in meat was also examined (Grabež et al., 2022, 2023b). The inclusion of *S. latissima* at 2.5% and 5% on a DM basis (105.5 and 204.6 mg I/kg DM feed, respectively) compared with standard feed (5.4 mg I/kg DM feed) in lamb feed increased the I content in lamb meat by 26-fold and 37-fold, respectively, compared with conventionally indoor fed lambs (2.3 µg I/100 g of meat); an intake of 100 g would represent only 1.5% of the recommended AI. Seaweed supplementation could increase this level to 40–59% of the AI (Grabež et al., 2023a), making it another relevant source of I. In another study, 0.8% blanched *S. latissima* (on DM basis) was added to the feed of finishing bulls as the maximum inclusion level to comply with present law regarding I and As content in ruminant feed. The addition of blanched *S. latissima* induced a five-fold increase in the I content in meat. Thus, the use of seaweed as an I source in animal feed is feasible. Furthermore, it could be a promising strategy for producing I-rich meat and meat products. However, the level of its inclusion depends on the choice of seaweed species and the characterization of their mineral composition (Cabrita et al., 2016).

#### 4.4.3 I level in milk assessed in human intervention studies

Few studies have investigated the bioavailability of I from various dietary sources. Organically bound I, such as iodophores (complexed I) and protein-bound I, reduce the bioavailability of I. Nevertheless, Dydykin et al. (2019) reported that iodotyrosine and iodocasein are superior to iodized salt as external additives in meat products in the prevention of I deficiency in children. However, studies assessing the bioavailability of dietary I directly from meat and meat products are scarce.

### 4.5 Case 5 – The effect of genetics and production systems on the vitamin D content in meat

The vitamin D levels and intake of each species varies depending on the geographical location. Vitamin D deficiency in humans is often defined as blood values of <30 nmol/L for 25-(OH) D<sub>3</sub>, with a suitable target value of 50 nmol/L for all population groups (EFSA, 2016). This deficiency has been recorded in many countries (Palacios and Gonzalez, 2014). The average daily vitamin D intake in the Nordic and Baltic countries is <10 µg/day, except in Finland (Lemming and Pitsi, 2022). Muscle foods are presently considered vitamin-D-deficient food.

#### 4.5.1 Increasing the low vitamin D content in the muscles via breeding, feed, and UVB light

Vitamin D influences mitochondrial function; thus, breeding glycolytic cells will reduce the requirement for vitamin D (Dzik and Kaczor, 2019). Burild et al. (2016) reported that the total vitamin D content in red pork muscles, independent of the type of vitamin used in feed (max 50 µg 25-(OH)D<sub>3</sub> or D<sub>3</sub>/kg feed), was higher. This may reflect the higher intramuscular fat content in red muscles (Burild et al., 2016). Feeds supplemented with 25-(OH)D<sub>3</sub> would be more favorable than those supplemented with D<sub>3</sub> if the aim is to increase the total vitamin D content in lean meat (<20% fat). The total vitamin D content varies depending on breeding, feeding, and possibly body mass composition (degree of fatness); the latter has been observed in humans to influence serum 25-(OH)D levels (Kim and Cho, 2019).

A decline in the vitamin D content in meat was also observed when animals were raised indoors without any UV light facility and vitamin D<sub>3</sub> content in the feed was low. Outdoor activity (sunlight exposure) may increase vitamin D levels more than feeding (Madson et al., 2012). UVB can increase the vitamin D<sub>3</sub> content in pork and poultry (Rosbotham et al., 2022). Schutkowski et al. (2013) reported a vitamin D<sub>3</sub> content of 0.5 µg D<sub>3</sub>/100 g in hen legs following the application of UVB illumination through four daily intervals. The 25-(OH)D<sub>3</sub> level also increased, resulting in the effective vitamin D concentration increasing to 1.5 µg/100 g (Jakobsen, 2007) pending the bioactivity factor used for 25-(OH) D<sub>3</sub>. The use of UV light in pigs for 6 min/day for 10 weeks can result in a significant increase in the D<sub>3</sub> level relative to the level recommended by the EFSA in animal feed (Neill et al., 2021,



2023). However, the application of UVB light requires further research (Rana and Campbell, 2021).

#### 4.5.2 Content of 25-(OH)D<sub>3</sub> in meat assessed in a human intervention

A higher 25-(OH)D<sub>3</sub> content has been observed in beef, with levels of 0.16 µg/100 g being observed in meat (raised indoor) available commercially in the Norwegian market (minced beef) (Egelandsdal et al., 2020). Haug et al. (2018) reported an increase in the 25-(OH)D<sub>3</sub> content in minced beef from 0.10 µg/100 g meat to 0.29 µg/100 g when the feed was supplemented with 0.025 g D<sub>3</sub>/kg feed and 0.1 g D<sub>3</sub>/kg feed, respectively. The increase in the 25-(OH)D<sub>3</sub> content through the EFSA-recommended feed level may not seem large. However, the consumption of beef increased the blood 25-(OH)D<sub>3</sub> levels of the intervention participants that had 25-(OH)D<sub>3</sub> levels < 30 nmol/l (Haug et al., 2022). Nutrient-optimized beef can improve the blood levels of participants with low to normal 25-(OH)D<sub>3</sub>. However, the meat was examined in a high-dose-short-time intervention in the study (Haug et al., 2022). Further studies using lower doses and long-term administration must be conducted to verify whether vitamin D optimized meat improves the blood base values of individuals with 25-(OH)D<sub>3</sub> levels <50 nmol/L.

#### 4.6 Ratio of the selected micronutrients

The intake ratios for vitamin D/Fe (range 1.18–0.4) and I/Se (range 4.93–0.97) have been reported for the Nordic and Baltic regions (Lemming and Pitsi, 2022; See [Supplementary Material, Figure 2](#) and [Table 2](#) for vitamin D/Fe and I/Se). Although reference blood values are lacking for ratios, extreme ratios may pose an additional burden on the total intake of these micronutrients.

### 5 Critical views on human and animal nutritional guidelines in the context of improvements in milk and meat healthiness

Europe and the USA have produced enough food to ensure adequate caloric and macronutrient supply since the 1960s (Roser et al., 2023). Obesity (WHO, 2022) and hidden hunger have been included in the agenda. Nevertheless, higher-income consumers consuming fewer but higher-quality foods remains a prevailing trend (Hocquette et al., 2024; Liu et al., 2023).

#### 5.1 The animal breeding and feeding timeline advanced faster than human nutrition guidelines: case fat

Fat limited in or devoid of essential FA and micronutrients is only an energy source. Therefore, the initial focus of the meat value chain is to decrease the ratio of fat to lean meat in animals to improve profitability and human health. However, whether further advancements in fat reduction in pigs, chickens, or turkeys should be continued is debated due to the physiological limitations of the

animal. Furthermore, it is unclear whether the focus should be directed toward FA composition and animal health.

An increase in the MUFA and PUFA content is achievable in pork meat via feeding and breeding (Gjerlaug-Enger et al., 2011; van Son et al., 2017). Clear incitements for continuing the improvements have not been proposed, partly due to the challenges in the meat production value chain (e.g., lipid oxidation and soft fat), a lack of recognition from human dietary guideline generators, increased feed and raw food material costs, and constraints on animal feed.

#### 5.2 Breeding achievements: case Fe

The drivers of the increased production of high-quality protein for humans via breeding have not focused on the Fe content in meat. In theory, the losses in Fe with breeding could be compensated for by a higher intake of meat (and organs) from beef in vulnerable groups. However, the consumption of beef is considered to increase the risk of developing chronic diseases (FAO, 2023), which limits intake. Increasing the intake of chicken and turkey may place meat in a category that it is no longer a good source of Fe (i.e., ≥15% of daily intake). Reversing the present breeding choice would increase production costs per kilogram of meat. Thus, increased feed supplementation may be required if high-yield grains/plants with lower mineral accumulation (“the dilution effect”) are used (Marles, 2017).

Few countries record HeFe data in their databases to an extent relevant for epidemiological modeling, bearing in mind that animal breeding is mostly local. Heme, carrying Fe, was in 2015 (WCRF, 2015), but not clearly in 2024 (WCRF, 2024), suggested to be causal for colon cancer. Aglago et al. (2023) reported a negative association between heme and colon cancer only in men.

The genetic changes in cattle, pork, and poultry vary, and the breeding goals for cattle may depend on dairy needs, e.g., if dual-purpose cattle are the focus. Thus, it is questionable that we use only two groups (“red or white” meat) and link these to chronic diseases nationwide. The levels of HeFe and SFAs, two assumed causal predictors implicated in lifestyle diseases, have clearly decreased in pork and chicken over the years. Our Supplementary data suggest that women favor meat with a reduced iron content (for example, chicken) that is less likely to prevent Fe deficiency even when their meat intake is increased.

#### 5.3 Should we aim for nutrient richer or poorer meat: case Se and vitamin D

The Se and vitamin D content in meat may be negatively influenced by breeding choices. However, the existing literature on this topic is not detailed. The approach used here involves the supplementation of the feed with Se. Biofortification will be a necessary step in many parts of the world (Christophersen et al., 2013) to ensure adequate Se intake. This could yield animal products that are beneficial for human health and livestock (Haug et al., 2007b). Thus, focusing on the Se levels in meat and other

animal products is important, but the Se content in the feed must be adjusted to obtain an optimal Se content in the products.

The EFSA reported that consumers are unlikely to exceed the UL for Se, except for regular users of supplements (pills) containing high doses of Se or regular users of high-Se foods, such as Brazil nuts (Turck et al., 2023). Supplementing the feed up to the UL of animals, along with intensive end feeding, can increase the Se or vitamin D content of meat.

Increasing the 25-(OH)D<sub>3</sub> content beyond 0.5 µg 25-(OH)D<sub>3</sub>/100 g meat is challenging (Schmid and Walther, 2013); however, even this low level has a high utility in individuals with low vitamin D levels. The preceding sections have discussed the possibilities for increasing the vitamin D content in meat via feeding and technologies. However, further studies must be conducted on increasing the vitamin D levels in lean meat as many individuals have a low vitamin D/Fe ratio. Meat producers should aim to maximize and stabilize vitamin D levels. This is especially relevant in regions where animals are mostly reared indoors.

Nutrient-based criteria (such as proteins, MUFAs, vitamin B, and Zn) must be used by the meat industry to distinguish meat products from refined foods containing mostly fat or sugar and practically no essential nutrients, such as Se or vitamin D. Meat should supply nutrients missing from the diet at the highest level possible while being sustainable. Improving meat production beyond the present solutions is not necessarily costly (Haug et al., 2018). Selenium also accumulates in organs, such as the liver, that are not consumed commonly. The reintroduction of organs into the human food chain appears sustainable, given the global scarcity of Se.

## 5.4 Human iodine demand may necessitate dairy cattle

Milk and dairy products will continue to be the prime sources of I in the foreseeable future in Norway and many other countries (Bath et al., 2022). Increasing the I content in the feed remains the most efficient way of increasing I content in milk. NASEM (2021) recognizes this role in animal feeding and recommends increasing the levels of I in the ration (from 0.5 to 1.0 mg/kg DM) when using goitrogenic diets. Although the key is to ensure sufficient I content to facilitate thyroxine synthesis in cows, this increase indirectly preserves the I content in milk. Recommendations for achieving the optimal I content in milk remain to be established in Norway. However, considerable knowledge regarding milk production within the preset I range has been accumulated. Trøan et al. (2015) presented a model ensuring that the I content in milk was within certain limits. The I content in milk was related to the dietary I intake and the proportion of rapeseed products in the diet. Such models should be implemented to address the variations in the I content in milk due to the presence of goitrogenic components in the feed. This also plays an important role in facilitating sustainability, as rapeseed products contain sustainable, cost-efficient, and high-quality feed protein. The inclusion of I in the Norwegian compound feed for dairy cows has been set to 5 mg I/kg based on an agreement between the Norwegian feed and dairy

industries aiming to declare I content in drinking milk. However, a UL of 5 mg I/kg may not be sufficient to stabilize the I content in milk for declaration. Alternatively, a combination of seaweed and goitrogenic feedstuffs can be used to reduce the level of I in milk.

The transfer of I to meat is not as efficient as that to milk; however, the amount of I in the feed beyond the present UL will increase the I content in meat to a level that makes meat a relevant source of I. In addition, the transfer of I from the feed to meat (and organs) differs among animal species. Implementation of this knowledge would necessitate the adjustment of present practices and regulations regarding the I level permitted in feed rations, depending on which animal to feed and the intended use.

## 6 Conclusion

More research must be conducted to address the present situation regarding meat. The animal-to-meat value chain must explore the use of their tools, with a stronger focus on meat healthiness. However, human nutrition guidelines are not updated at a sufficient rate in relation to the advances made in livestock research and production. Livestock research is particularly relevant in an era in which the demand for sustainability can accelerate the development of new feed and genetic solutions. Closer collaboration between the entire animal value chain, human nutritionists, and feed and food authorities will aid in addressing the complexity of healthiness and sustainability. The fat case used here would have been developed more efficiently and received more positive publicity through such a collaboration.

The following can be concluded from this article:

- There is an urgent need to terminate the concept of “red meat.” Redness is related to the content of myoglobin-containing heme, which can be measured and adjusted via animal breeding and production. The names of the animal species investigated must be used to accelerate the identification of components associated with an increased risk of colon cancer. This approach will aid in determining how emerging animal science tools can be used to produce healthier meat.
- Regarding sustainability, national accounting must be performed to confirm that an optimal intake of Se can be maintained via the intake of meat (and organs).
- The vitamin D content in meat should be maximized within legislative frames.
- Feeding legislation must be developed to stabilize sustainable I levels in cattle milk, the most important dietary source of I.
- The UL values of feed should be used to improve the nutrient density of meat while maintaining animal health and welfare.
- The nutrient density of meat must be maintained and improved. Consuming less but higher-quality meat should be a beneficial choice in the long run, especially for consumers vulnerable to hidden hunger.

## Ethics statement

Written informed consent was obtained from the individual(s), and minor(s)' legal guardian/next of kin, for the publication of any potentially identifiable images or data included in this article.

## Author contributions

BE: Conceptualization, Writing – original draft, Data curation, Formal analysis, Methodology, Project administration, Writing – review & editing. VG-Å: Conceptualization, Project administration, Writing – original draft, Writing – review & editing. LM: Resources, Writing – original draft, Writing – review & editing. AH: Data curation, Formal analysis, Methodology, Validation, Writing – original draft, Writing – review & editing. EP: Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Writing – original draft, Writing – review & editing.

## Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. EP and LM are employed by NMBU (University), BE and AH have state pensions. VG-Å was funded by Foods of Norway, Research Project (Research Council of Norway; grant no. 237841/030).

## Acknowledgments

We thank Eli Gjerlaug-Enger (Norsvin) and Morten Røe (Animalia) for providing historical slaughter data and Gisken

Trøan for providing valuable input regarding iodine and milk. We also thank Professor Emeritus Odd Vangen for providing historical information and data related to pork breeding. We also thank University lector Elin Bjørge Løken for explaining the Norwegian Food Survey data acquired before 1980. We would like to thank Editage ([www.editage.com](http://www.editage.com)) for English language editing.

## 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.

## Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fanim.2024.1426044/full#supplementary-material>

## References

- Aglago, E. K., Cross, A. J., Riboli, E., Fedirko, V., Hughes, D. J., Fournier, A., et al. (2023). Dietary intake of total, heme and non-heme iron and the risk of colorectal cancer in a European prospective cohort study. *Br. J. Cancer* 128, 1529–1540. doi: 10.1038/s41416-023-02164-7
- Alexander, J., and Olsen, A. K. (2023). Selenium - a scoping review for Nordic nutrition recommendations 2023. *Food Nutr. Res.* 67, 1–7. doi: 10.29219/fnr.v67.10320
- Amcoff, E., Edberg, A., Barbieri, H. E., Lindroos, A. K., Nölsén, C., Pearson, M., et al. (2012). "Riksmaten – vuxna 2010–11, Livsmedels- och näringsintag bland vuxna i Sverige," in *Livsmedelsdataenheten, Livsmedelsverket* (Swedish). (ed.). Uppsala: Livsmedelsverket (Swedish Food Agency).
- Andersson, M., Karumbunathan, V., and Zimmermann, M. B. (2012). Global iodine status in 2011 and trends over the past decade. *J. Nutr.* 142, 744–750. doi: 10.3945/jn.111.149393
- Antaya, N. T., Ghelichkhan, M., Pereira, A. B. D., Soder, K. J., and Brito, A. F. (2019). Production, milk iodine, and nutrient utilization in Jersey cows supplemented with the brown seaweed *Ascophyllum nodosum* (kelp meal) during the grazing season. *J. Dairy Sci.* 102, 8040–8058. doi: 10.3168/jds.2019-16478
- Antaya, N. T., Soder, K. J., Kraft, J., Whitehouse, N. L., Guindon, N. E., Erickson, P. S., et al. (2015). Incremental amounts of *Ascophyllum nodosum* meal do not improve animal performance but do increase milk iodine output in early lactation dairy cows fed high-forage diets. *J. Dairy Sci.* 98, 1991–2004. doi: 10.3168/jds.2014-8851
- Apple, J. K., Wallis-Phelps, W. A., Maxwell, C. V., Rakes, L. K., Sawyer, J. T., Hutchison, S., et al. (2007). Effect of supplemental iron on finishing swine performance, carcass characteristics, and pork quality during retail display. *J. Anim. Sci.* 85, 737–745. doi: 10.2527/jas.2006-231
- ARC. (1980). *The nutrient requirements of ruminant livestock*. Technical review. 2nd ed (Agric. Res. Coun. by the Commonwealth Agricultural Bureaux: UK). Available at: <https://openlibrary.org/books>.
- Astrup, A., Magkos, F., Bier, D. M., Brenna, J. T., De Oliveira Otto, M. C., Hill, J. O., et al. (2020). Saturated fats and health: A reassessment and proposal for food-based recommendations: JACC State-of-the-Art Review. *J. Am. Coll. Cardiol.* 76, 844–857. doi: 10.1016/j.jacc.2020.05.077
- Azizi-Soleiman, F., Vafa, M., Abiri, B., and Safavi, M. (2016). Effects of iron on vitamin D metabolism: A systematic review. *Int. J. Prev. Med.* 7, 126–132. doi: 10.4103/2008-7802.195212
- Babicz, M., and Kasprzyk, A. (2019). Comparative analysis of the mineral composition in the meat of wild boar and domestic pig. *Ital. J. Anim. Sci.* 18, 1013–1020. doi: 10.1080/1828051x.2019.1610337
- Bath, S. C., Verkaik-Kloosterman, J., Sabatier, M., Ter Borg, S., Eilander, A., Hora, K., et al. (2022). A systematic review of iodine intake in children, adults, and pregnant women in Europe-comparison against dietary recommendations and evaluation of dietary iodine sources. *Nutr. Rev.* 80, 2154–2177. doi: 10.1093/nutrit/nuac032
- Biing-Hwan, L., Guthrie, J., and Smith, T. (2023/2023). *Dietary quality by food source and demographics in the United States 1977–2018* (U.S.: Department of Agriculture. United States Department of Agriculture), EIB–249. Available at: <https://www.ers.usda.gov/webdocs/publications/105956/eib-249.pdf?v=4454.8>. ERS, ed.
- Blaxter, K. L., Sharman, G. A., and MacDonald, A. M. (1957). Iron-deficiency anaemia in calves. *Br. J. Nutr.* 11, 234–246. doi: 10.1079/bjn19570043
- Blunt, J. W., Deluca, H. F., and Schnoes, H. K. (1968). 25-hydroxycholecalciferol. A biologically active metabolite of vitamin D3. *Biochemistry* 7, 3317–3322. doi: 10.1021/bi00850a001

- Breirem, K., and Homb, T. (1958). *Mineral-tilskudd til melkekyr* (Norwegian: Landbrukshøyskolens institutt for husdyrernæring og føringslære, Ås).
- Brummer, F. A., Pirelli, G. J., and Hal, J. A. (2014). *Selenium supplementation Strategies for livestock in Oregon. Oregon State: Extension Service*. Available online at: <https://extension.oregonstate.edu/sites/default/files/documents/em9094.pdf#EM%209094%20%20%20E2%80%A2%20%20June%202014> (Accessed 03.04.2024).
- Buffini, M., Nugent, A. P., Walton, J., Flynn, A., and McNulty, B. A. (2023). Selenium intakes in the Irish adult population. *J. Nutr. Sci.* 12, 1–10. doi: 10.1017/jns.2023.23
- Bugel, S., Sandstrom, B., and Skibsted, L. H. (2004). Pork meat: a good source of selenium? *J. Trace Elem. Med. Biol.* 17, 307–311. doi: 10.1016/S0946-672X(04)80033-6
- Burild, A., Lauridsen, C., Faqir, N., Sommer, H. M., and Jakobsen, J. (2016). Vitamin D3 and 25-hydroxyvitamin D3 in pork and their relationship to vitamin D status in pigs. *J. Nutr. Sci.* 5, e3. doi: 10.1017/jns.2015.28
- Cabrita, A. R. J., Maia, M. R. G., Oliveira, H. M., Sousa-Pinto, I., Almeida, A. A., Pinto, E., et al. (2016). Tracing seaweeds as mineral sources for farm-animals. *J. App. Phycol.* 28, 3135–3150. doi: 10.1007/s10811-016-0839-y
- Callforlife. (2024). *Jungle fowl, thigh nutrition facts* (Calorie and nutrient database Callforlife). Available online at: <https://www.callforlife.com/calories/jungle-fowl-thigh> (Accessed 05.01.2024).
- Cashman, K. D., Seamans, K. M., Lucey, A. J., Stocklin, E., Weber, P., Kiely, M., et al. (2012). Relative effectiveness of oral 25-hydroxyvitamin D3 and vitamin D3 in raising wintertime serum 25-hydroxyvitamin D in older adults. *Am. J. Clin. Nutr.* 95, 1350–1356. doi: 10.3945/ajcn.111.031427
- Chepkemai, M. W., M. J., Sila, D., Oyier, P., Malaki, P., Ndiema, E., et al. (2017). Physical characteristics and nutritional composition of meat and eggs of five poultry species in Kenya. *Livest. Res. Rural Dev.* 29. Available at: <http://www.lrrd.org/lrrd29/8/somm29153.html>.
- Christophersen, O. A., Lyons, G., Haug, A., and Steinnes, E. (2013). "Selenium," in *heavy metals in soils*. Ed. B. J. Alloway Whiteknights, Reading, UK: Springer University of Reading, 429–463. doi: 10.1007/978-94-007-4470-7\_16
- Ciqual. (2020). *French Food Composition database. Chicken, meat, raw. Selenium 2009*. Available online at: <https://ciqual.anses.fr/#/aliments/36003/chicken-meat-raw> (Accessed 25.02.2024).
- Coffey, D., Dawson, K., Ferket, P., and Connolly, A. (2016). Review of the feed industry from a historical perspective and implications for its future. *J. Appl. Anim. Nutr.* 4, 3. doi: 10.1017/jan.2015.11
- Consalez, F., Ahern, M., Andersen, P., and Kjellevold, M. (2022). The effect of the meat factor in animal-source foods on micronutrient absorption: A scoping review. *Adv. Nutr.* 13, 2305–2315. doi: 10.1093/advances/nmac089
- Cross, A. J., Harnly, J. M., Ferrucci, L. M., Risch, A., Mayne, S. T., and Sinha, R. (2012). Developing a heme iron database for meats according to meat type, cooking method and doneness level. *Food Nutr. Sci.* 3, 905–913. doi: 10.4236/fns.2012.37120
- Cruikshank, K. M., Hately, B., Gehman, A. M., Koenig, K. M., Ribeiro, E. S., and Steele, M. A. (2021). Effect of supplementary selenium source on dairy cow performance, Antioxidant Status, and apparent absorption and retention. *J. Anim. Sci.* 99, 80–80. doi: 10.1093/jas/skab235.145
- Dahl, L., Opsahl, J. A., Meltzer, H. M., and Julshamn, K. (2003). Iodine concentration in Norwegian milk and dairy products. *Br. J. Nutr.* 90, 679–685. doi: 10.1079/bjn2003921
- Dicken, S. J., and Batterham, R. L. (2022). Ultra-processed food: a global problem requiring a global solution. *Lancet Diabetes Endocrinol.* 10, 691–694. doi: 10.1016/S2213-8587(22)00248-0
- Dijk-Brouwer, D. A. J., Muskiet, F. A. J., Verheesen, R. H., Schaafsma, G., Schaafsma, A., and Geurts, J. M. W. (2022). Thyroidal and extrathyroidal requirements for iodine and selenium: A combined evolutionary and (patho) physiological approach. *Nutrients* 14, 1–29. doi: 10.3390/nu14193886
- Directory of Health. (2023). *Utviklingen i norsk kosthold* (Norwegian). Available online at: [www.helsedirektoratet.no/rapporter/utviklingen-i-norsk-kosthold](http://www.helsedirektoratet.no/rapporter/utviklingen-i-norsk-kosthold) (Accessed 18.04.2024).
- Durrant, L. R., Bucca, G., Hesketh, A., Moller-Levet, C., Tripkovic, L., Wu, H., et al. (2022). Vitamins D<sub>2</sub> and D<sub>3</sub> have overlapping but different effects on the human immune system revealed through analysis of the blood transcriptome. *Front. Immunol.* 13, e790444. doi: 10.3389/fimmu.2022.790444
- Dydykin, A. S., Aslanova, M. A., Derevitskaya, O.K., and Soldatova, N. E. (2019). Effectiveness of using iodine-containing additives in meat products for child nutrition. *IOP Conf. Ser.: Earth Environ. Sci.* 333, 012060. doi: 10.1088/1755-1315/333/1/012060
- Dzik, K. P., and Kaczor, J. J. (2019). Mechanisms of vitamin D on skeletal muscle function: oxidative stress, energy metabolism and anabolic state. *Eur. J. Appl. Physiol.* 119, 825–839. doi: 10.1007/s00421-019-04104-x
- EC. (2015). Commission implementing regulation (EU) 2015/861 of 3 June 2015 concerning the authorisation of potassium iodide, calcium iodate anhydrous and coated granulated calcium iodate anhydrous as feed additives for all animal species. *OJEU. C/2015/3628*. Available online at: <https://eur-lex.europa.eu/legal-content>. (Accessed: April 24, 2024).
- EC. (2017). Corrigendum to Commission Implementing Regulation (EU) 2017/2330 of 14 December 2017 concerning the authorisation of Iron(II) carbonate, Iron(III) chloride hexahydrate, Iron(II) sulphate monohydrate, Iron(II) sulphate heptahydrate, Iron(II) fumarate, Iron(II) chelate of amino acids hydrate, Iron(II) chelate of protein hydrolysates and Iron(II) chelate of glycine hydrate as feed additives for all animal species and of Iron dextran as feed additive for piglets and amending Regulations (EC) No 1334/2003 and (EC) No 479/2006. *OJEU. L 351/203*. Available online at: <https://eur-lex.europa.eu/legal-content>. (Accessed: April 24, 2024).
- EC. (2019). Commission Implementing Regulation (EU) 2019/49 of 4 January 2019 concerning the authorisation of sodium selenite, coated granulated sodium selenite and zinc-L-selenomethionine as feed additives for all animal species. *OJEU. L 10/2*. Available online at: <https://eur-lex.europa.eu/legal-content>. (Accessed: April 24, 2024).
- EC. (2020). Commission implementing regulation (EU) 2020/377 of 5 March 2020 concerning the authorisation of sodium selenate as a feed additive for ruminants. *OJEU. C/2020/1234*. Available online at: <https://eur-lex.europa.eu/legal-content>. (Accessed: April 24, 2024).
- EC. (2023). Saturated fat intake across the EU, Norway and the United Kingdom. Available online at: [https://knowledge4policy.ec.europa.eu/health-promotion-knowledge-gateway/dietary-fats-5b\\_en](https://knowledge4policy.ec.europa.eu/health-promotion-knowledge-gateway/dietary-fats-5b_en). (Accessed: Sept 11, 2024)
- EFSA. (2013). Scientific Opinion on the safety and efficacy of iodine compounds (E2) as feed additives for all species: calcium iodate anhydrous and potassium iodide, based on a dossier submitted by HELM AG. *EFSA J.* 11, e3101. doi: 10.2903/j.efsa.2013.3101
- EFSA. (2014). Scientific Opinion on the Safety and efficacy of vitamin D3 (cholecalciferol) as a feed additive for all animal species or categories based on a dossier submitted by Lohmann Animal Health GmbH. Available online at: <https://efsa.onlinelibrary.wiley.com/doi/pdf/10.2903/j.efsa.2014.3568>.
- EFSA. (2016). Dietary reference values for vitamin D. *EFSA J.* 14, e04547. doi: 10.2903/j.efsa.2016.4547
- EFSA. (2021). Panel on Additives and Products or Substances used in Animal Feed (FEEDAP), Bampidis V, Azimonti G, Bastos ML, Christensen H, Dusemund B, et al. Safety and efficacy of the feed additive consisting of selenium-enriched yeast (*Saccharomyces cerevisiae* CNCM I-3060) for all animal species (Alltech Ireland). *EFSA J.* 19, e06979. doi: 10.2903/j.efsa.2021.6979
- EFSA. (2023). Panel on Nutrition, Novel Foods and Food Allergens (NDA). (Turck D, et al.) Scientific opinion on the tolerable upper intake level for selenium. *EFSA J.* 21, e07704. doi: 10.2903/j.efsa.2023.7704
- EFSA. (2024a). Draft scientific opinion on the tolerable upper intake level for iron. Available online at: <https://connect.efsa.europa.eu/RM/s/publicconsultation2/a0ITk000000A0f57pc0835> (Accessed 29.05.2024).
- EFSA. (2024b). EFSA: science, safe food, sustainability. Available online at: <https://www.efsa.europa.eu/en> (Accessed 18.04.2024).
- Egelandsdal, B., Oostindjer, M., Hovland, E. M., Okholm, B., Saarem, K., Bjerke, F., et al. (2020). Identifying labelling and marketing advantages of nutrients in minced beef meat: A case study. *Meat Sci.* 159, e107920. doi: 10.1016/j.meatsci.2019.107920
- Engle-Stone, R., Haile, D., and Luo, H. (2022). We pose some uncertainties in the analysis of national trends in iron intake and risk of deficiency, but support the need for addressing iron deficiency among vulnerable groups in the United States. *J. Nutr.* 152, 639–640. doi: 10.1093/jn/nxab360
- Evvard, J. M., and Culbertson, C. C. (1924). Iodine, a factor in feeding young growing swine. *Proc. Iowa Acad. Sci.* 31, 309–317. Available at: <https://scholarworks.uni.edu/pias/vol31/iss1/89>.
- Fairweather-Tait, S. (2023). The role of meat in iron nutrition of vulnerable groups of the UK population. *Front. Anim. Sci.* 4, e1142252. doi: 10.3389/fanim.2023.1142252
- FAO. (1950). Calorie requirements: report of the Committee of Calorie Requirements. Sept. 1949. *FAO Nutr. Stud.* 5, 1–97. Available at: <https://www.fao.org/nutrition/requirements/archive/en/>.
- FAO. (1958). Protein requirements: report of the FAO Committee Oct. 1955. *FAO Nutr. Ser.* 16, 1–118. Available at: <https://www.fao.org/nutrition/requirements/archive/en/>.
- FAO. (2010). *Fats and fatty acids in human nutrition* (Rome: FAO Food Nutri. pap 91 Food and Agriculture Organization of the United Nations, FAO).
- FAO. (2023). *Meat Market Review: Emerging trends and outlook 2023* (Rome: Food and Agriculture Organization of the United Nations, Rome, Italy). Available at: <https://www.fao.org/3/cc9074en/cc9074en.pdf>.
- FAO/WHO. (1970). Requirements of ascorbic acid, vitamin D, vitamin B12, folate and iron. *WHO Techn. Rep. Ser.* 452, 1–76.
- FAO/WHO. (1973). Energy and protein requirements. *WHO Tech. Rep.Ser.* 552, 329–332. doi: 10.1002/food.19740180314
- FAO/WHO. (2002). Diet, nutrition and the prevention of chronic diseases. *WHO Tech. Rep. Ser.* 916, 1–149.
- FAO/WHO. (2004). *Human vitamin and mineral requirements (with 1998 expert consultation)* (Geneva: FAO/WHO NFS team).
- FAO/WHO. (2019). *Sustainable healthy diets- guiding principles* (Rome: Food and Agriculture Organization of the United Nations/WORLD HEALTH ORGANIZATION, Rome, Italy). Available at: <https://iris.who.int>.
- Ferrari, M., Mistura, L., Patterson, E., Sjöström, M., Diaz, L. E., Stehle, P., et al. (2011). Evaluation of iron status in European adolescents through biochemical iron indicators: the HELENA Study. *Eur. J. Clin. Nutr.* 65, 340–349. doi: 10.1038/ejcn.2010.279
- FKF. (2024). Felleskjøpet Fôrutvikling: Iron in ruminant feed. Email to: [egil.prestlokken@nmbu.no](mailto:egil.prestlokken@nmbu.no).



- Gjerlaug-Enger, E. (2011). *Genetic analyses of meat, fat and carcass quality traits measured by rapid methods*. Philosophiae Doctor (PhD) Thesis No. 13, Norwegian University of Life Sciences (NMBU), Ås, Norway.
- Gjerlaug-Enger, E., Aass, L., Odegard, J., Kongsro, J., and Vangen, O. (2011). Genetic parameters of fat quality in pigs measured by near-infrared spectroscopy. *Animal* 5, 1495–1505. doi: 10.1017/S1751731111000528
- Gjerlaug-Enger, E., Haug, A., Gaarder, M., Ljøkel, K., Stenseth, R. S., Sigfridson, K., et al. (2015). Pig feeds rich in rapeseed products and organic selenium increased omega-3 fatty acids and selenium in pork meat and backfat. *Food Sci. Nutr.* 3, 120–128. doi: 10.1002/fsn3.182
- Grabež, V., Coll-Brasas, E., Fulladosa, E., Hallenstvedt, E., Haseth, T. T., Overland, M., et al. (2022). Seaweed inclusion in finishing lamb diet promotes changes in micronutrient content and flavour-Related compounds of raw meat and dry-Cured leg (Fenalår). *Foods* 11, e1043. doi: 10.3390/foods11071043
- Grabež, V., Devle, H., Kidane, A., Mydland, L. T., Overland, M., Ottestad, S., et al. (2023a). Sugar Kelp (*Saccharina latissima*) Seaweed added to a growing-finishing lamb diet has a positive effect on quality traits and on mineral content of meat. *Foods* 12, e2131. doi: 10.3390/foods12112131
- Grabež, V., Mydland, L. T., Papoutsis, D., Øverland, M., and Egelandsdal, B. (2023b). Effect of low-dose blanched *Saccharina latissima* in finishing bulls' diets on carcass and meat quality traits. *Front. Anim. Sci.* 4, e1233244. doi: 10.3389/fanim.2023.1233244
- Guggenheim, K. Y. (1995). Chlorosis: the rise and disappearance of a nutritional disease. *J. Nutr.* 125, 1822–1825. doi: 10.1093/jn/125.7.1822
- Gunnarsdóttir, S., Guðmannsdóttir, R., Þorgeirsdóttir, H., Torfadóttir, J. E., Steingrimsdóttir, L., Tryggvadóttir, E. A., et al. (2010–2011). *Hvað borða Íslendingar? Könnun á mataræði Íslendinga 2019–2021 (In Icelandic)* (Reykjavik: Directorate of Health).
- Hallberg, L., and Rossander-Hulthen, L. (1989). Prevalence of iron deficiency in European countries and attempts to analyze possible causes of differences. *Bibl. Nutr. Dieta* 44, 94–105. doi: 10.1159/000417305
- Halmemies-Beauchet-Filleau, A., Rinne, M., Lamminen, M., Mapato, C., Ampapon, T., Wanapat, M., et al. (2018). Review: Alternative and novel feeds for ruminants: nutritive value, product quality and environmental aspects. *Animal* 12, 295–309. doi: 10.1017/S1751731118002252
- Hartikainen, H. (2005). Biogeochemistry of selenium and its impact on food chain quality and human health. *J. Trace Elem. Med. Biol.* 18, 309–318. doi: 10.1016/j.jtemb.2005.02.009
- Haug, A., Eich-Greatorex, S., Bernhoft, A., Wold, J. P., Hetland, H., Christophersen, O. A., et al. (2007a). Effect of dietary selenium and omega-3 fatty acids on muscle composition and quality in broilers. *Lipids Health Dis.* 6, 29–37. doi: 10.1186/1476-511X-6-29
- Haug, A., Graham, R. D., Christophersen, O. A., and Lyons, G. H. (2007b). How to use the world's scarce selenium resources efficiently to increase the selenium concentration in food. *Microb. Ecol. Health Dis.* 19, 209–228. doi: 10.1080/08910600701698986
- Haug, A., Nyquist, N. F., Mosti, T. J., Andersen, M., and Hostmark, A. T. (2012a). Increased EPA levels in serum phospholipids of humans after four weeks daily ingestion of one portion chicken fed linseed and rapeseed oil. *Lipids Health Dis.* 11, e104. doi: 10.1186/1476-511X-11-104
- Haug, A., Taugbol, O., Prestlokken, E., Govasmark, E., Salbu, B., Schei, I., et al. (2012b). Iodine concentration in Norwegian milk has declined in the last decade. *Acta Agric. Scand. Section A -Anim. Sci.* 62, 127–134. doi: 10.1080/09064702.2012.754932
- Haug, A., Vermeer, C., Ruud, L., Monfort-Pires, M., Grabež, V., and Egelandsdal, B. (2022). Nutrient-optimized beef enhances blood levels of vitamin D and selenium among young women. *Foods* 11, e631. doi: 10.3390/foods11050631
- Haug, A., Vhile, S. G., Berg, J., Hove, K., and Egelandsdal, B. (2018). Feeding potentially health promoting nutrients to finishing bulls changes meat composition and allow for product health claims. *Meat Sci.* 145, 46–468. doi: 10.1016/j.meatsci.2018.07.015
- Helldán, A., Raulio, S., Kosola, M., Tapanainen, H., Ovaskainen, M.-L., and Virtanen, S. (2013). *The National FINDIET 2012 Survey* (Tampere, Finland: Juvenes Print - Suomen Yliopistopaino Oy). Available at: <https://urn.fi/URN>.
- Henjum, S., Aakre, I., Lilleengen, A. M., Garnweidner-Holme, L., Borthne, S., Pajalic, Z., et al. (2018). Suboptimal iodine status among pregnant women in the Oslo area, Norway. *Nutrients* 10, e280. doi: 10.3390/nu10030280
- Hocquette, J.-F., Chriki, S., Fournier, D., and Ellies-Oury, M.-P. (2024). Review: Will “cultured meat” transform our food system towards more sustainability? *Animal* [In Press]. doi: 10.1016/j.animal.2024.101145
- Homb, T. (1979). *Grain and other concentrates in Norwegian animal production (In Norwegian)* (Steinkjer, Norway: Statens Kornforetning).
- Hotz, C. S., Fitzpatrick, D. W., Trick, K. D., and L'abbe, M. R. (1997). Dietary iodine and selenium interact to affect thyroid hormone metabolism of rats. *J. Nutr.* 127, 1214–1218. doi: 10.1093/jn/127.6.1214
- IGN. (2022). *Global scorecard of iodine nutrition in 2022 in the general population based on school-age children (SAC)* (Ottawa, Canada: IGN). Available online at: [https://ign.org/app/uploads/2024/01/Scorecard\\_2023\\_References\\_July-2023\\_Final.pdf](https://ign.org/app/uploads/2024/01/Scorecard_2023_References_July-2023_Final.pdf) (Accessed 01.11.2024).
- Isaachsen, H., and Al, E. (1917). *Forsøk med tørket tang til melkefê. (In Norwegian)* (Ås: NMBU).
- Itkonen, S. T., Andersen, R., Bjørk, A. K., Brugard Konde, A., Eneroth, H., Erkkola, M., et al. (2021). Vitamin D status and current policies to achieve adequate vitamin D intake in the Nordic countries. *Scand. J. Public Health* 49, 616–627. doi: 10.1177/1403494819896878
- Ittermann, T., Albrecht, D., Arohonka, P., Bilek, R., De Castro, J. J., Dahl, L., et al. (2020). Standardized map of iodine status in Europe. *Thyroid* 30, 1346–1354. doi: 10.1089/thy.2019.0353
- Jahreis, G., Hausmann, W., Kiessling, G., Franke, K., and Leiterer, M. (2001). Bioavailability of iodine from normal diets rich in dairy products—results of balance studies in women. *Exp. Clin. Endocrinol. Diabetes* 109, 163–167. doi: 10.1055/s-2001-14840
- Jakobsen, J. (2007). Bioavailability and bioactivity of vitamin D3 active compounds – Which potency should be used for 25-hydroxyvitamin D3? *Int. Congr. Ser.* 1297, 133–142. doi: 10.1016/j.ics.2006.08.026
- Jones, G. (2022). 100 years of vitamin D: Historical aspects of vitamin D. *Endocr. Connect.* 11, e210594. doi: 10.1530/EC-21-0594
- Jones, G. D., Droz, B., Greve, P., Gottschalk, P., Poffet, D., McGrath, S. P., et al. (2017). Selenium deficiency risk predicted to increase under future climate change. *Proc. Natl. Acad. Sci. U.S.A.* 114, 2848–2853. doi: 10.1073/pnas.1611576114
- Kasprzyk, A., Stadnik, J., and Stasiak, D. (2019). Technological and nutritional properties of meat from female wild boars (*Sus scrofa scrofa* L.) of different carcass weights. *Arch. Anim. Breed* 62, 597–604. doi: 10.5194/aab-62-597-2019
- Kelly, O. J., Gilman, J. C., and Ilich, J. Z. (2018). Utilizing dietary micronutrient ratios in nutritional research may be more informative than focusing on single nutrients. *Nutrients* 11, e282. doi: 10.3390/nu10010107
- Kim, Y.-A., and Cho, Y. J. (2019). The association between visceral fat, subcutaneous fat and serum 25-hydroxyvitamin D3 levels. *Obes. Med.* 13, 29–33. doi: 10.1016/j.jobmed.2018.12.005
- Knap, P. W., and Wang, L. (2012). “Pig breeding for improved feed efficiency,” in *Feed efficiency in swine*. Ed. J. F. Patience (Wageningen Academic Press Publishers, Wageningen), 167–181.
- Landsforeningen for Kosthold og Helse. (1988). *Statens ernæringsråds matvaretabell, vedlegg 2: Fettsyreinnhold i matvarer, product 3.148 (In Norwegian)* (Oslo: Statens ernæringsråd).
- Larson, E. J. (2006). *Evolution: The remarkable history of a scientific theory* (Modern Library Chronicles) (New York, USA: Random House Publishing Group), 221–243.
- Lee, K. W., Shin, D., Cho, M. S., and Song, W. O. (2016). Food group intakes as determinants of iodine status among US adult population. *Nutrients* 8, 1–13. doi: 10.3390/nu8060325
- Lemming, E. W., and Pitsi, T. (2022). The Nordic Nutrition Recommendations 2022 - food consumption and nutrient intake in the adult population of the Nordic and Baltic countries. *Food Nutr. Res.* 66, e8572. doi: 10.29219/fnr.v66.8572
- Liu, J., Almeida, J. M., Rampado, N., Panea, B., Hocquette, E., Chriki, S., et al. (2023). Perception of cultured “meat” by Italian, Portuguese and Spanish consumers. *Front. Nutr.* 10, e1043618. doi: 10.3389/fnut.2023.1043618
- Lush, J. L. (1931). The number of daughters necessary to prove a sire. *J. Dairy Sci.* 14, 209–220. doi: 10.3168/jds.00022-0302(31)93466-8
- Mackenzie, J. S., and Jeggo, M. H. (2011). 1st international one health congress. *EcoHealth*, 2011 1–2. doi: 10.1007/s10393-011-0676-z
- Madson, D. M., Ensley, S. M., Gauger, P. C., Schwartz, K. J., Stevenson, G. W., Cooper, V. L., et al. (2012). Rickets: case series and diagnostic review of hypovitaminosis D in swine. *J. Vet. Diagn. Invest.* 24, 1137–1144. doi: 10.1177/1040638712461487
- Makkar, H. P. S. (2018). Review: Feed demand landscape and implications of food-not feed strategy for food security and climate change. *Animal* 12, 1744–1754. doi: 10.1017/S175173111700324X
- Makkar, H. P. S., Tran, G., Heuzé, V., Giger-Reverdin, S., Lessire, M., Lebas, F., et al. (2016). Seaweeds for livestock diets: A review. *Anim. Feed Sci. Technol.* 212, 1–17. doi: 10.1016/j.anifeedsci.2015.09.018
- Malbe, M., Klaassen, M., Fang, W., Myllys, V., Vikerpuur, M., Nyholm, K., et al. (1995). Comparisons of selenite and selenium yeast feed supplements on Se-incorporation, mastitis and leucocyte function in Se-deficient dairy cows. *Zentralbl. Veterinarmed.* 42, 111–121. doi: 10.1111/j.1439-0442.1995.tb00362.x
- Mallol, R., Amigo, N., Rodriguez, M. A., Heras, M., Vinaixa, M., Plana, N., et al. (2015). Liposcale: a novel advanced lipoprotein test based on 2D diffusion-ordered 1H NMR spectroscopy. *J. Lipid Res.* 56, 737–746. doi: 10.1194/jlr.D050120
- Marles, R. J. (2017). Mineral nutrient composition of vegetables, fruits and grains: The context of reports of apparent historical declines. *J. Food Compos. Anal.* 56, 93–103. doi: 10.1016/j.jfca.2016.11.012
- McGovern, G. (1977). *Nutrition and human needs, dietary goals for the United States: US Senate Select Committee* (Washington DC, USA: US Government Printing Office).
- McGuire, S. (2015). Comprehensive implementation plan on maternal, infant, and young child nutrition. WHO, Geneva, Switzerland 2014. *Adv. Nutr.* 6, 134–135. doi: 10.3945/an.114.007781



- Meyer, U., Weigel, K., Schöne, F., Leiterer, M., and Flachowsky, G. (2008). Effect of dietary iodine on growth and iodine status of growing fattening bulls. *Livest. Sci.* 115, 219–225. doi: 10.1016/j.livsci.2007.07.013
- Ministry of Health Brazil. (2015). *Dietary guidelines for the Brazilian population*. Available online at: [https://bvsms.saude.gov.br/bvs/publicacoes/dietary\\_guidelines\\_Brazilian\\_population.pdf](https://bvsms.saude.gov.br/bvs/publicacoes/dietary_guidelines_Brazilian_population.pdf). (Accessed: Sept 11, 2024)
- Mitchell, H. H., and McClure, F. J. (1937). Mineral nutrition of farm animals, Committee on Animal Nutrition, Division of Biology and Agriculture, National Research Council. *Bull. Natl. Res. Coun.* 99, 1937. Available at: <https://www.cabidigitallibrary.org/doi/full/10.5555/19371404117>.
- Monfort-Pires, M., Lamichhane, S., Alonso, C., Egelandsdal, B., Oresic, M., Jordahl, V. O., et al. (2023). Classification of common food lipid sources regarding healthiness using advanced lipidomics: A four-Arm crossover study. *Int. J. Mol. Sci.* 24, e4941. doi: 10.3390/ijms24054941
- Morrison, M. C., Egelandsdal, B., Harvei, S., Rocha, S. D. C., Pieterman, E. J., Kleemann, R., et al. (2023). Differential effects of plant and animal fats on obesity-induced dyslipidemia and atherosclerosis in Ldlr<sup>-/-</sup> Leiden mice. *FASEB J.* 37, e23096. doi: 10.1096/fj.202300585R
- Mozaffarian, D., Rosenberg, I., and Uauy, R. (2018). History of modern nutrition science-implications for current research, dietary guidelines, and food policy. *BMJ* 361, k2392. doi: 10.1136/bmj.k2392
- Nair, K. M., and Augustine, L. F. (2018). Food synergies for improving bioavailability of micronutrients from plant foods. *Food Chem.* 238, 180–185. doi: 10.1016/j.foodchem.2016.09.115
- NASEM. (2006). *Institute of Medicine of National Academies, Dietary eference intakes: The essential guide to nutrient requirements* (Washington, DC: The National Academies Press).
- NASEM. (2016). *Nutrient requirements of beef cattle. 8th rev. ed* (Washington, DC: The National Academies Press).
- NASEM. (2021). *Nutrient requirements of dairy cattle* (Washington, DC: The National Academic Press).
- Neill, H. R., Gill, C. I. R., McDonald, E. J., McMurray, R., McRoberts, W. C., Loy, R., et al. (2023). Improving vitamin D content in pork meat by UVB biofortification. *Meat Sci.* 199, e109115. doi: 10.1016/j.meatsci.2023.109115
- Neill, H. R., Gill, C. I. R., McDonald, E. J., McRoberts, W. C., Rosbotham, E. J., Boland, R., et al. (2021). Improving vitamin D content in pork meat by UV bio-enrichment. *Proc. Nutr. Soc.* 80:E140. doi: 10.1017/s0029665121002639.
- Newcom, D. W., Stalder, K. J., Baas, T. J., Goodwin, R. N., Parrish, F. C., and Wiegand, B. R. (2004). Breed differences and genetic parameters of myoglobin concentration in porcine longissimus muscle. *J. Anim. Sci.* 82, 2264–2268. doi: 10.2527/2004.8282264x
- Newman, J. C., Malek, A. M., Hunt, K. J., and Marriott, B. P. (2019). Nutrients in the US Diet: Naturally occurring or enriched/fortified food and beverage sources, plus dietary supplements: NHANES 2009–2012. *J. Nutr.* 149, 1404–1412. doi: 10.1093/jn/nxz066
- Newton, E. E., Petursdottir, A. H., Rikharethsson, G., Beaumont, C., Desnica, N., Giannakopoulou, K., et al. (2021). Effect of dietary seaweed supplementation in cows on milk macrominerals, Trace elements and heavy metal concentrations. *Foods* 10, e1526. doi: 10.3390/foods10071526
- Newton, E. E., Theodoridou, K., Terre, M., Huws, S., Ray, P., Reynolds, C. K., et al. (2023). Effect of dietary seaweed (*Ascophyllum nodosum*) supplementation on milk mineral concentrations, transfer efficiency, and hematological parameters in lactating Holstein cows. *J. Dairy Sci.* 106, 6880–6893. doi: 10.3168/jds.2022-23074
- Niero, G., Visentin, G., Censi, S., Righi, F., Manuelian, C. L., Formigoni, A., et al. (2023). Invited review: Iodine level in dairy products-A feed-to-fork overview. *J. Dairy Sci.* 106, 2213–2229. doi: 10.3168/jds.2022-22599
- NNR. (1989). *Nordic Nutrient Recommendations 1989*. Available online at: <https://www.norden.org/en/nordic-council-ministers>.
- NNR. (1996). *Nordic Nutrition Recommendations 1996* (Sandström, B. et al.). *Scand. J. Nutr.* 40, 161–165.
- NNR. (2004). *Nordic Nutrition Recommendations 2004. Integrating nutrition and physical activity*, Copenhagen 2004, Scanprint AS, Århus. (Oslo, Norway: Sosial og helsedirektoratet IS-1219) (Accessed: Sept 11, 2024)
- NNR. (2012). *Nordic Nutrition Recommendations 2012. Integrating nutrition and physical activity*. Available online at: <https://norden.diva-portal.org/smash/get/diva2:704251/FULLTEXT01.pdf>. (Accessed: Sept 11, 2024).
- NNR. (2023). *Nordic Nutrition Recommendations 2023 -Integrating Environmental Aspects*. (Blomhoff, R. et al.). Available online at: <https://pub.norden.org/nord2023-003/nord2023-003.pdf>.
- Norwegian Parliament. (1975). *Om norsk ernærings- og matforsyningspolitikk, (1975-1976)*. Report 32. (In Norwegian) (Oslo, Norway: Ministry of Agriculture). Available at: [https://www.stortinget.no/no/Saker-og-publikasjoner/Stortingsforhandlinger/Lesevisning?p=1975-76&paid=3&wid=d&psid=DIVL97&pgid=d\\_0095](https://www.stortinget.no/no/Saker-og-publikasjoner/Stortingsforhandlinger/Lesevisning?p=1975-76&paid=3&wid=d&psid=DIVL97&pgid=d_0095).
- NRC. (1953). “Recommended nutrient allowances for swine,” in *Recommended nutrient allowances for domestic animals, 2nd rev. ed* (National Research Council (U.S., Washington DC).
- NRC. (1954). *Nutrient requirements for poultry* (Washington DC: The National Academies Press). doi: 10.17226/21448. 3rd rev. National Research Council (U.S.).
- NRC. (1958). *Nutrient Requirements of Dairy Cattle. 2nd rev. ed* (Washington DC: The National Academies Press).
- NRC. (1966). *Nutrient Requirements of Poultry. 5th rev. ed* (Washington DC: The National Academies Press).
- NRC. (1971a). *Nutrient Requirements of Dairy Cattle. 4th rev. ed* (Washington DC: The National Academies Press).
- NRC. (1971b). *Nutrient Requirements of Poultry. 6th rev. ed* (Washington DC: The National Academies Press).
- NRC. (1978). *Nutrient Requirements of Dairy Cattle. 5th rev. ed* (Washington DC: The National Academies Press).
- NRC. (1979). *Nutrient Requirements of Swine. 8th rev. ed* (Washington DC: The National Academies Press).
- NRC. (1989). *Recommended Dietary Allowances. 10th ed* (Washington DC: National Academies Press).
- NRC. (1994). *Nutrient Requirements of Poultry. 9th rev. ed* (Washington DC: The National Academies Press).
- NRC. (2012). *Nutrient Requirements of Swine. 11th rev. ed* (Washington DC: National Academies Press).
- Nystrom, H. F., Brantsaeter, A. L., Erlund, I., Gunnarsdottir, I., Hulthen, L., Laurberg, P., et al. (2016). Iodine status in the Nordic countries - past and present. *Food Nutr. Res.* 60, e31969. doi: 10.3402/fnr.v60.31969
- Olsson, V., and Pickova, J. (2005). The influence of production systems on meat quality, with emphasis on pork. *Ambio* 34, 338–343. doi: 10.1639/0044-7447(2005)034[0338:tiopsol]2.0.co;2
- Ortman, K., and Pehrson, B. (1999). Effect of selenate as a feed supplement to dairy cows in comparison to selenite and selenium yeast. *J. Anim. Sci.* 77, 3365–3370. doi: 10.2527/1999.77123365x
- Oster, O., Schmiedel, G., and Prellwitz, W. (1988). The organ distribution of selenium in German adults. *Biol. Trace Elem. Res.* 15, 23–45. doi: 10.1007/BF02990125
- Palacios, C., and Gonzalez, L. (2014). Is vitamin D deficiency a major global public health problem? *J. Steroid Biochem. Mol. Biol.* 144 Pt A, 138–145. doi: 10.1016/j.jsbmb.2013.11.003
- Pasricha, S. R., and Moir-Meyer, G. (2023). Measuring the global burden of anaemia. *Lancet Haematol.* 10, e696. doi: 10.1016/S2352-3026(23)00171-0
- Pedersen, A. N., Christensen, T., Matthiessen, J., Knudsen, V. K., Rosenlund-Sørensen, M., Biloft-Jensen, A., et al. (2015). *Danskernes kostvaner 2011-2013 (In Danish)*. Ed. D. F. A. F. Ernæring (Albertslund: DTU National Food Institute (English)).
- Pellattiero, E., Tasoniero, G., Cullere, M., Gleeson, E., Baldan, G., Contiero, B., et al. (2020). Are meat quality traits and sensory attributes in favor of slow-growing chickens? *Anim. (Basel)* 10, e960. doi: 10.3390/ani10060960
- Pinto, X., Masana, L., Civeira, F., Real, J., Ibarretxe, D., Candas, B., et al. (2020). Consensus document of an expert group from the Spanish Society of Arteriosclerosis (SEA) on the clinical use of nuclear magnetic resonance to assess lipoprotein metabolism (Liposcale(R)). *Clin. Investig. Arterioscler.* 32, 219–229. doi: 10.1016/j.arteri.2020.04.004
- Poskitt, E. M. (2003). Early history of iron deficiency. *Br. J. Haematol.* 122, 554–562. doi: 10.1046/j.1365-2141.2003.04529.x
- Rana, M. S., and Campbell, D. L. M. (2021). Application of ultraviolet light for poultry production: A review of impacts on behavior, physiology, and production. *Front. Anim. Sci.* 2, e699262. doi: 10.3389/fanim.2021.699262
- Rena, T., and Staveland, K. (1974). Undersøkelse av innholdet av jod i melk fra forskjellige steder i Norge i 12-måneders-perioden juli 1971-juni 1972. (In Norwegian). *Tidssk. norske Lægeforening* 94, 990–993.
- Ring, J. (1939). *The feed value of seaweed meal (In Norwegian)* (Norges landbrukskøyskole, Ås: Føringforsøkene).
- RIVM. (2023a). *Dutch Food Composition Database*. Available online at: <https://www.rivm.nl/en/dutch-food-composition-database> (Accessed 07.08.2024).
- RIVM. (2023b). *Dutch Food Composition Database- Chicken w skin raw NEVO code 108*. Available online at: <https://nevo-online.rivm.nl/Home/En> (Accessed 07.08.2024).
- RIVM. (2023c). *Dutch Food Composition Database-Pork fillet raw. Nevo Code 1418*. Available online at: <https://nevo-online.rivm.nl/Home/En> (Accessed 07.08.2024).
- RIVM. (2023d). *Dutch Food Composition Database-Minced pork raw. Nevo code 1421. 08*. Available online at: <https://nevo-online.rivm.nl/Home/En> (Accessed 07.08.2024).
- RIVM. (2023e). *Dutch Food Composition Database-Mince chicken raw Nevo code 3139. 08*. Available online at: <https://nevo-online.rivm.nl/Home/En> (Accessed 07.08.2024).
- RIVM. (2023f). *Dutch Food Composition Database-Minced beef raw Nevo code 1405. 08*. Available online at: <https://nevo-online.rivm.nl/Home/En> (Accessed 07.08.2024).
- RIVM. (2024). *DNFCS 2019-2021: Mean contribution of food sources to intake of nutrients*. Available online at: <https://statline.rivm.nl/#/RIVM/nl/dataset/50122NED/table?ts=1718976020313> (Accessed 07.08.2024).
- Roberts, C., Steer, T., Maplethorpe, N., Cox, L., Meadows, S., Nicholson, S., et al. (2018). *National diet and nutrition survey, results from years 7 and 8 (combined) of the*

Rolling Programme, (2014/2015 to 2015/2016) (London: Public Health England Road). Agency, P. H. E. A. F. S. (ed.).

Rosbotham, E. J., Gill, C. I. R., McDonald, E. J., McRoberts, W. C., Rainey, N., Loy, R., et al. (2022). "Enhanced vitamin D content of chicken by UVB bio-enrichment does not influence sensory evaluation," in *Irish Section Conference 2022, 15–17 June 2022, Proc. Nutr. Soc.-Impact of nutrition science to human health: past perspectives and future directions*, Vol. 81. Cambridge, UK: Cambridge University Press. doi: 10.1017/s0029665122001835

Roser, M., Ritchie, H., and Rosado, P. (2023). *Food supply-Our world in data*. Available online at: <https://ourworldindata.org/food-supply> (Accessed 01.07.2024).

Sambugaro, N., Egelandsdal, B., Grabez, V., Røe, M., Zotte, A. D., Therkildsen, M., et al. (2023). "Identifying possible market advantages of meat from native endangered cattle," in *69th International Congress of Meat Science and Technology*, Padua, Italy: 69th International Congress of Meat Science and Technology, Aug 20, 2023 to Aug 25, 2023. (Helsinki, Finland: DigiCoMST, leader Eero Puolanne Viikki).

Sampels, S., Jonsson, M., Sandgren, M., Karlsson, A., and Segerkvist, K. A. (2023). Sustainable delicacy: variation in quality and sensory aspects in wild boar (*Sus scrofa*). Meat and comparison to pork meat-A case study. *Foods* 12, e1664. doi: 10.3390/foods12081644

Schmid, A., and Walther, B. (2013). Natural vitamin D content in animal products. *Adv. Nutr.* 4, 453–462. doi: 10.3945/an.113.003780

Schutkowski, A., Kramer, J., Kluge, H., Hirsch, F., Krombholz, A., Theumer, T., et al. (2013). UVB exposure of farm animals: study on a food-based strategy to bridge the gap between current vitamin D intakes and dietary targets. *PLoS One* 8, e69418. doi: 10.1371/journal.pone.0069418

Sharma, S., Neves, L., Funderud, J., Mydland, L. T., Øverland, M., and Horn, S. J. (2018). Seasonal and depth variations in the chemical composition of cultivated *Saccharina latissima*. *Algal Res.* 32, 107–112. doi: 10.1016/j.algal.2018.03.012

Siegel, P. B. (2014). Evolution of the modern broiler and feed efficiency. *Annu. Rev. Anim. Biosci.* 2, 375–385. doi: 10.1146/annurev-animal-022513-114132

Skobrák, E. B., Bodnár, K., Jónas, E. M., Gundel, J., and Javor, A. (2011). The comparison analysis of the main chemical composition parameters of wild boar meat and pork. *J. Anim. Sci. Biotech.* 44, 105–112.

Spiro, A., and Buttriss, J. L. (2014). Vitamin D: An overview of vitamin D status and intake in Europe. *Nutr. Bull.* 39, 322–350. doi: 10.1111/nbu.12108

Stoffaneller, R., and Morse, N. L. (2015). A review of dietary selenium intake and selenium status in Europe and the Middle East. *Nutrients* 7, 1494–1537. doi: 10.3390/nu7031494

Suliga, P., Abie, S. M., Egelandsdal, B., Alvsøe, O., Johnny, A., Kathiresan, P., et al. (2022). Beyond standard PSE testing: An exploratory study of bioimpedance as a marker for ham defects. *Meat Sci.* 194, 1–9. doi: 10.1016/j.meatsci.2022.108980

Sun, H., and Weaver, C. M. (2021). Decreased iron intake parallels rising iron deficiency anemia and related mortality rates in the US Population. *J. Nutr.* 151, 1947–1955. doi: 10.1093/jn/nxab064

Svihus, B. (2016). "Før og næringsbehov (In Norwegian)," in *Fjørfeboka*. Ed. M. F. Bagly (Fagbokforlaget, Bergen), 79–114.

The Norwegian Food Safety Authority. (2016–2017a). *Matvaretabellen, Chicken, without skin, raw, code 140*. Available online at: <https://www.matvaretabellen.no> (Accessed 07.08.2024).

The Norwegian Food Safety Authority. (2016–2017b). *Matvaretabellen, Chicken, thigh (leg without drumstick), without skin, raw, Code 224b*. Available online at: <https://www.matvaretabellen.no> (Accessed 07.08.2024).

The Norwegian Food Safety Authority. (2023a). *Food Composition Table, Chicken, with skin, raw, 2020, code 140*. Available online at: <https://www.matvaretabellen.no> (Accessed 07.08.2024).

The Norwegian Food Safety Authority. (2023b). *Food Composition Table, Pork, striploin, raw, 2023 Code 332*. Available online at: <https://www.matvaretabellen.no> (Accessed 07.08.2024).

The Norwegian Food Safety Authority. (2023c). *Food Composition Table, Pork, minced meat, 9 % fat, raw, 2023. Code 332*. Available online at: <https://www.matvaretabellen.no> (Accessed 07.08.2024).

Thiruvankadan, A. K., Prabakaran, R., and Panneerselvam, S. (2019). Broiler breeding strategies over the decades: an overview. *World's Poult. Sci. J.* 67, 309–336. doi: 10.1017/s004393391000328

Tixier-Boichard, M. (2018). "Are there limits to selection in poultry? Alternative production and local breeds," in *LVI Symposium Científico de Avicultura, Asociación Española de Ciencia Avícola - American European Community Association - Wildlife Preservation Society of Australia*. Spain: (WPSA-AECA) World's Poultry Science Association La Asociación Española de Ciencia Avícola Valladolid.

Totland, T. H., Melnæs, B. K., Lundberg-Hallén, N., Helland-Kigen, K. M., Lund-Blix, N. A., Myhre, J. B., et al. (2012). National dietary survey among men and women aged 18–70 years 2010–11. (Norkost 3 landsomfattende kostholdsundersøkelse blant menn og kvinner i Norge i alderen 18–70 år, 2010–2011.). (Oslo, Norway: Norwegian Directorate of Health). pp. 1–70.

Trippkovic, L., Wilson, L. R., and Lanham-New, S. A. (2017). Vitamin D<sub>2</sub> vs. vitamin D<sub>3</sub>: They are not one and the same. *Nutr. Bull.* 42, 331–337. doi: 10.1111/nbu.12293

Trøan, G. (2017). Effect of feeding rapeseed products differing in glucosinolate concentration on iodine concentration in cow milk. *Philosophiae Doctor (PhD) Thesis* No. 14, Norwegian University of Life Sciences (NMBU). Ås Norway.

Trøan, G., Dahl, L., Meltzer, H. M., Abel, M. H., Indahl, U. G., Haug, A., et al. (2015). A model to secure a stable iodine concentration in milk. *Food Nutr. Res.* 59, e29829. doi: 10.3402/fnr.v59.29829

Turck, D., Bohn, T., Castenmiller, J., de Henauw, S., Hirsch-Ernst, K. I., Knutsen, H. K., et al. (2023). Scientific opinion on the tolerable upper intake level for selenium. *EFSA J* 21, e07704. doi: 10.2903/j.efsa.2023.7704

Tyrbirk, P., Sloth, N. M., and Blaabjerg, K. (2023). *Normer for næringsstoffer (In Danish)* (Aarhus Denmark (In Danish: SEGES Innovation). Available online at: <https://svineproduksjon.dk> (Accessed 10.01.2024).

Ueland, M. (2022). *Saccharina latissima* in rations for dairy cows; effects on feed intake, milk yield and chemical composition of the milk. Master thesis. (Norwegian University of Life Sciences, Ås, Norway). pp. 1–62. Available at: <https://hdl.handle.net/11250/3039209>

USDA/FDC. (2003). *FoodData Central. Beef ground FDC ID 174030 Pork ground PDC ID 167902. 2002 (beef) and 1992 (pork)*. Available online at: <https://fdc.nal.usda.gov>. (Accessed: Sept 11, 2024).

USDA/HHS. (1980). *Dietary guidelines for Americans 1980*. Available online at: <https://www.dietaryguidelines.gov/about-dietary-guidelines>. (Accessed: Sept 11, 2024).

USDA/HHS. (1990). *Dietary guidelines for Americans 1990*. Available online at: <https://www.dietaryguidelines.gov/sites>. (Accessed: Sept 11, 2024).

USDA/HHS. (2005). *Dietary guidelines for Americans 2005*. Available online at: <https://www.dietaryguidelines.gov/about-dietary-guidelines>. (Accessed: Sept 11, 2024).

USDA/HHS. (2020). *Dietary guidelines for Americans 2020–2025*. Available online at: <https://www.dietaryguidelines.gov/about-dietary-guidelines>. (Accessed: Sept 11, 2024).

van der Reijden, O. L., Galetti, V., Burki, S., Zeder, C., Krzystek, A., Haldimann, M., et al. (2019). Iodine bioavailability from cow milk: a randomized, crossover balance study in healthy iodine-replete adults. *Am. J. Clin. Nutr.* 110, 102–110. doi: 10.1093/ajcn/nqz092

van der Torre, H. W., Van Dokkum, W., Schaafsma, G., Wedel, M., and Ockhuizen, T. (1991). Effect of various levels of selenium in wheat and meat on blood Se status indices and on Se balance in Dutch men. *Br. J. Nutr.* 65, 69–80. doi: 10.1079/bjn19910067

van Son, M., Enger, E. G., Grove, H., Ros-Freixedes, R., Kent, M. P., Lien, S., et al. (2017). Genome-wide association study confirm major QTL for backfat fatty acid composition on SSC14 in Duroc pigs. *BMC Genom.* 18, e369. doi: 10.1186/s12864-017-3752-0

Vangen, O. (1980). Studies on a two trait selection experiment in pigs. III. Correlated responses in daily feed intake, feed conversion and carcass traits. *Acta Agric. Scand.* 29, 337–345.

Volden, H. (2011). *NorFor – The Nordic feed evaluation system to ruminants* (Wageningen: Wageningen Academic Press Publishers).

WCRF. (2015). *Red meat and bowel cancer risk – how strong is the evidence?* Available online at: <https://www.wcrf.org/red-meat-and-bowel-cancer-risk-how-strong-is-the-evidence/> (Accessed 01.07. 2024).

WCRF. (2023). *Diet activity and cancer*. Available online at: <https://www.wcrf.org/diet-activity-and-cancer/risk-factors/> (Accessed 10.01. 2024).

WCRF. (2024). *Red and processed meat and cancer risk - Preventing cancer*. Available online at: <https://www.wcrf-uk.org/preventing-cancer/what-can-increase-your-risk-of-cancer/red-and-processed-meat-and-cancer-risk/> (Accessed 18.04. 2024).

Weisbjerg, M. R., Rinne, R., Spörndly, A., Ekern, O., and Harstad, M. (2010). The history of feed evaluation for ruminants, with special emphasis on the Nordic countries, in *1st Nordic Feed Sci. Conf*, Uppsala, Sweden: Swedish University of Agricultural Sciences, 20–23 June 2010. Available at: <https://jukuri.luke.fi/handle/10024/477010>.

Wesolowski, L. T., Semanchik, P. L., and White-Springer, S. H. (2022). Beyond antioxidants: Selenium and skeletal muscle mitochondria. *Front. Vet. Sci.* 9, e1011159. doi: 10.3389/fvets.2022.1011159

Whist, A. C., Østerås, O., and Solverød, L. (2007). *Staphylococcus aureus* and *Streptococcus dysgalactiae* in Norwegian herds after introduction of selective dry cow therapy and teat dipping. *J. Dairy Res.* 74, 1–8. doi: 10.1017/S0022029906002135

WHO. (1986a). "Prevention and control of iodine deficiency disorders," in *Thirty-ninth world health assembly, Agenda item 29*, 16th May. (Geneva, Switzerland: World Health Organization)

WHO. (1986b). *Environmental Health Criteria 58: Selenium* (Geneva: International Programme on Chemical Safety). Available at: <http://www.inchem.org/>.

WHO. (1990). *Prev WHO, 1986b). Environmental Health Criteria 58: Selenium* (Geneva: International Programme on Chemical Safety). Available at: <http://www.inchem.org/>, ention and control of iodine deficiency disorders. Forty-third world health assembly. Agenda item 17, 14th May.

WHO. (1996). *Trace elements in human nutrition and health* (Geneva Belgium). (Geneva, Switzerland: World Health Organization) (ed.).

WHO. (2002). *World Health Report: Reducing risks, Promoting Healthy Life* (Geneva, Switzerland: World Health Organization). Available at: [World health report: 2002 \(who.int\)](http://www.who.int).

WHO. (2007). *Assessment of iodine deficiency disorders and monitoring their elimination: a guide for programme managers. 3rd ed* (Geneva, Switzerland: World Health Organization Nutrition and Food Safety (NFS) Team).

- WHO. (2009). *Global health risks: mortality and burden of disease attributable to selected major risks* (Geneva: World Health Organization).
- WHO. (2014). *World Health Organization. Guideline: fortification of foodgrade salt with iodine for the prevention and control of iodine deficiency disorders*. (Geneva, Switzerland: World Health Organization).
- WHO. (2022). *European regional obesity report. Regional Office for Europe* (Copenhagen: World Health Organization).
- World Population Review. (2024). *Pork consumption by country*. Available online at: <https://worldpopulationreview.com/> (Accessed 01.16.2024).
- Yan, X., Wang, X., Zhang, J., Ming, Z., Zhang, C., Ma, P., et al. (2024). National trends in nine key minerals intake (quantity and source) among U.S. adults 1999 to March 2020. *Nutr. J.* 23, 1–13. doi: 10.1186/s12937-024-00950-4
- Zbigniew, M. (2002). Cereal products as a source of selenium in Polish food rations. (In Polish. *Rocz. Panstw. Zakl. Hig.* 53, 377–383.
- Zhang, X., Shi, B., and Spallholz, J. E. (1993). The selenium content of selected meats, seafoods, and vegetables from Lubbock, Texas. *Biol. Trace Elem. Res.* 39, 161–169. doi: 10.1007/BF02783186
- Zhang, X., Xing, T., Li, J., Zhang, L., and Gao, F. (2023). Mitochondrial dysfunction and calcium dyshomeostasis in the pectoralis major muscle of broiler chickens with wooden breast myopathy. *Poult. Sci.* 102, 1–11. doi: 10.1016/j.psj.2023.102872
- Zotte, A. D., Tasoniero, G., Baldan, G., and Cullere, M. (2019). Meat quality of male and female Italian Padovana and Polverara slow-growing chicken breeds. *Ital. J. Anim. Sci.* 18, 398–404. doi: 10.1080/1828051x.2018.1530963



## OPEN ACCESS

## EDITED BY

Carlotta Giromini,  
University of Milan, Italy

## REVIEWED BY

John Malcolm Gowdy,  
Rensselaer Polytechnic Institute, United States  
Kiriaki M. Keramitsoglou,  
Democritus University of Thrace, Greece

## \*CORRESPONDENCE

Sungtae Eun  
✉ steun99@gmail.com

RECEIVED 23 August 2024

ACCEPTED 06 December 2024

PUBLISHED 20 December 2024

## CITATION

Eun S (2024) Change of dietary patterns on CO<sub>2</sub> emissions under the African swine fever in South Korea. *Front. Clim.* 6:1485355. doi: 10.3389/fclim.2024.1485355

## COPYRIGHT

© 2024 Eun. This is an open-access article distributed under the terms of the [Creative Commons Attribution License \(CC BY\)](#). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.

# Change of dietary patterns on CO<sub>2</sub> emissions under the African swine fever in South Korea

Sungtae Eun\*

Research Fellow of Jeonbuk State Institute, Jeonju-si, Jeollabuk-do, Republic of Korea

African swine fever (ASF) occurred in Gyeonggi of South Korea in 2019 and there were 21 reported cases in domestic swine farms. South Korea is the one of top countries for pork consumption, and half of the 2.9 million tons of meat consumed in 2022 were pork. Outbreaks from animal products have a severe impact on the shift of diet and the change in dietary patterns of consumers shape climate change. Moreover, animal products account for 18% of worldwide GHG emissions which is more than industry (16%), transportation (13.5%), and energy usage (13%). This study is the first study to analyze the regional impact of animal products associated with climate change in South Korea. The objective of this study is to analyze the regional effect of dietary shifts on per capita CO<sub>2</sub> emissions from household consumption in South Korea. Synthetic Control Method (SCM) is employed to analyze the impact of ASF on the change of per capita CO<sub>2</sub> emissions from household consumption by shifting the nutritional patterns in South Korea. The dependent variable is per capita CO<sub>2</sub> emissions from household consumption, and the type of event is an epizootic disease. The event period is between 2010 and 2021 (pre-intervention: 2010–2018 and post-intervention: 2019–2021). By establishing synthetic Gyeonggi from the optimal synthetic control unit, the trajectories present how dietary shifts have influenced per capita CO<sub>2</sub> emissions from household consumption in a positive direction after ASF. ASF caused consumer dietary shifts from pork to other types of meat. This divergence between Gyeonggi and synthetic Gyeonggi indicates that there is an impact influencing per capita CO<sub>2</sub> emissions from household consumption after ASF. Performing an SCM analysis with the treated (Gyeonggi) and control (thirteen municipalities) units, the study found that the two trajectory lines (Gyeonggi and synthetic Gyeonggi) were similar before diverging after the introduction of ASF. The gaps also indicate the impact of the shift in dietary patterns on per capita CO<sub>2</sub> emissions from household consumption.

**JEL classification:** C31, Q54.

## KEYWORDS

African swine fever, meat consumption per capita, per capita CO<sub>2</sub> emissions, change of dietary patterns, synthetic control method (SCM)

## 1 Introduction

Pork is the most-consumed meat in the world, and it has an expanding and highly competitive global market (USDA, 2023).<sup>1</sup> South Korea is among the top countries for pork consumption; in 2022, around 2.9 million tons of meat were consumed, and half of that meat was pork [Korea Meat Trade Association (KMTA), 2024]. Pork consumption in South Korea has rapidly grown

<sup>1</sup> Pork is the most widely eaten meat in the world (36%) followed by poultry (33%), beef (24%), and goat (5%) (USDA, 2023).



since the early 2000s, and the demand for pork is still highly imbalanced due to Korean consumers' unique preferences for specific cuts of meat (Shi, 2021). Consumers in South Korea have a unique consumption pattern and a strong preference for high-fat cuts such as belly and Boston butt (Choe et al., 2015). Table 1 indicates that in 2019, per capita beef and poultry consumption increased by 7.6% and 6.6%, respectively, while per capita pork consumption decreased by 1.2%. Per capita pork consumption is increasing by an annual average of 2.4%.

High feed and energy costs restrict South Korea's domestic pork production, so the total swine supply is expected to decline due to high production costs. Compound feed prices during the first 11 months of 2022 increased by 22% over the same period in 2021 (Ban, 2023). In agriculture, overuse of resources has increased greenhouse gas (GHG) emissions, causing serious environmental consequences such as climate change, and global warming. Animal products, such as red meat, dairy, and eggs, account for 18% of worldwide GHG emissions, more than industry (16%), transportation (13.5%), and energy usage (13%) (Jeong et al., 2023). Considering that over one-third of GHG emissions originate from the food system, livestock meat production plays a large part in the industry (Sugimoto et al., 2020; Liu et al., 2023). Growing demand for meat products causes the release of more GHG emissions into the atmosphere.<sup>2</sup>

Rogissart et al. (2019) found that the dietary patterns of consumers shape climate change. Nutritional patterns normally comprise 10%–30% of CO<sub>2</sub> emissions from households, and animal-based products have a larger impact on GHG emissions than plant-based products (Center for Sustainable Systems, University of Michigan, 2022; Afrouzi et al., 2023). In 2019, African swine fever (ASF)<sup>3</sup> occurred in Gyeonggi of South Korea in Figure 1; there were twenty-one reported cases in domestic swine farms and over 2,600 cases in wild boar (Cho et al., 2022). Loss of livestock, decreased market value, food insecurity, environmental impacts, and efforts to respond to animal diseases come at considerable costs to livelihoods and both public and private sector interests (Weaver and Habib, 2020).

The presence of ASF in China and Southeast Asia indicates the importance of animal diseases to economics, and epizootic diseases highlight the associated economic and human costs and the potential costs of other animal disease outbreaks in the future. Table 2 indicates the cost of living<sup>4</sup> of consumer goods in Gyeonggi, South Korea. In 2019, the indexes of beef and poultry increased by 3.4% and 1.2%, respectively, while pork decreased by 4.1% after the outbreak of ASF in Figure 2.

TABLE 1 Food consumption per capita in South Korea (kg/person).

Year	Beef	Pork	Poultry	Fish
2011	13.5	30.5	16.1	59.7
2012	13.2	32.3	16.0	56.4
2013	13.6	32.9	16.1	52.3
2014	14.6	33.5	18.1	55.4
2015	14.7	35.9	18.9	56.4
2016	14.5	37.0	19.3	54.9
2017	15.3	37.7	18.8	56.7
2018	15.8	40.6	19.7	56.8
2019	17.0	40.1	21.0	54.7
2020	16.7	38.0	22.5	54.7
2021	20.5	38.3	22.2	55.6

Source: Food and Agriculture Organization of the United Nations (2023).



This study is limited to an analysis of dietary patterns for various foods, making regional data collection difficult. However, this paper is the first study to analyze the regional impact associated with climate change in South Korea. The objective of this study is to analyze the regional effect of dietary shifts on per capita CO<sub>2</sub> emissions from household consumption in South Korea. By applying the synthetic control method (SCM), this study shows how ASF has affected dietary changes, causing an increase in per capita CO<sub>2</sub> emissions. The food industry causes GHG emissions, and shifts in dietary practices influence the environment and human health (Aleksandrowicz et al., 2016).

<sup>2</sup> Each kilogram of beef product produces 99.48 kgCO<sub>2</sub>eq, while poultry and pig products produce 9.87 and 12.31 kgCO<sub>2</sub>eq, respectively (STATISTA (2024)).

<sup>3</sup> ASF is a highly contagious disease in domestic pigs [World Organization for Animal Health (WOAH), 2023], and it causes tremendous socioeconomic damage.

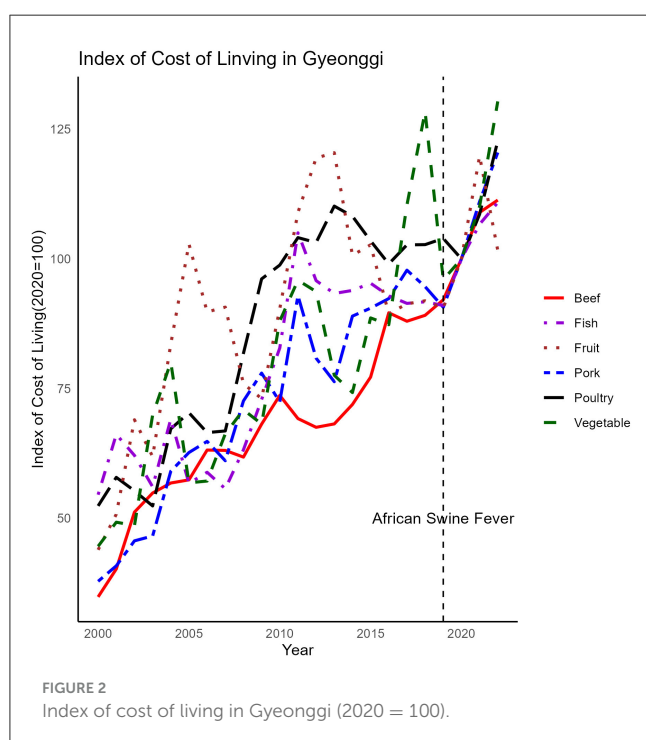
<sup>4</sup> Cost of living is calculated periodically in nearly representative baskets of consumer goods.



TABLE 2 Index of cost of living in Gyeonggi (2020 = 100).

Year	Beef	Pork	Poultry	Fish	Fruit	Vegetable
2011	69.2	92.9	104.1	105.0	108.9	95.9
2012	67.5	80.9	103.1	95.8	119.4	93.7
2013	68.2	76.3	110.2	93.3	120.5	77.6
2014	71.9	89.0	108.2	93.9	100.7	74.2
2015	77.2	90.5	103.5	95.3	102.7	88.6
2016	89.6	92.3	99.0	92.9	89.4	87.3
2017	88.0	97.8	102.7	91.4	91.3	110.4
2018	89.1	94.6	102.7	91.7	91.9	128.4
2019	92.1	90.7	103.9	91.0	90.5	96.0
2020	100.0	100.0	100.0	100.0	100.0	100.0
2021	109.0	120.5	108.6	106.7	119.8	110.1

Source: Korea Statistical Information Service (KOSIS) (2024).



## 2 Method and data

This study applies the Synthetic Control Method (SCM)<sup>5</sup> to analyze the impact of ASF on the change of per capita CO<sub>2</sub> emissions from household consumption by shifting the nutritional patterns in South Korea. SCM is a particularly useful analysis tool for case studies with relatively small sample data in comparison to other methods. Constructing the donor pool is a critical step for getting an acceptable estimate and two outcomes derive from

<sup>5</sup> The Synthetic Control Method (SCM) has been employed to estimate the impact of an intervention on various research interests: terrorism (Abadie and Gardeazabal, 2003), political action (Bohn et al., 2014), local construction (Ando, 2015), and disasters (Wang et al., 2013).

SCM. The synthetic control unit relies on the analogous factors between the predictor's estimates of the exposed and unexposed units (Bouttell et al., 2018). The weighted average of the control unit from the SCM is needed to make it feasible and similar to the treated unit (Abadie et al., 2010).

Assume that observable units  $i = 1, \dots, J$  and time  $t = 1, \dots, T_0, T_0 + 1, \dots, T$ , without the loss of generality, the treated (exposed to the event) unit is  $i = 1$ , and the control units (unexposed to the event) are  $i = 2, \dots, J$ ; the pre-event period is  $t = 1, \dots, T_0$ , and the post-event period is  $t = T_0 + 1, \dots, T$  (Abadie et al., 2010). Let  $Y_{it}^N$  be the outcome with no event, and  $Y_{it}^I$  be the outcome with an event at time  $t$  and unit  $i$ .<sup>6</sup>  $D_{it}$  be an indicator that indicates the value 1 if unit  $i$  experienced the event at time  $t$  and the value 0 otherwise; the impact of the event is assessed by the subtraction  $Y_{it}^I$  from  $Y_{it}^N$  in Equation 1 that is,  $\alpha_{it} = Y_{it}^I - Y_{it}^N$  in the post-event period in Equation 2.

$$Y_{it}^I = Y_{it}^N + \alpha_{it} \cdot D_{it} \quad (1)$$

$$\alpha_{it} = Y_{it}^I - Y_{it}^N \quad (2)$$

The optimal synthetic control unit is constructed from four vectors ( $X_0$ ,  $X_1$ ,  $Z_0$ , and  $Z_1$ ) with two weights ( $W$  and  $V$ ). The  $X_0$  and  $Z_0$  indicate the predictor's and outcome's values of the control unit, and  $X_1$  and  $Z_1$  indicate the predictor's and outcome's values of the treated unit. Then, two weights  $W$  present the minimized distance between the predictors and each control unit's weight in Equation 3, and  $V$  present the minimized distance between the outcomes of treated and control unit in the pre-event period in Equation 4. From a minimized MSPE<sup>7</sup> of the outcomes of treated/control units, the outer optimization is derived. The optimization provides asymptotically unbiased estimates of the treated unit (Abadie et al., 2010). Therefore, the optimal weight ( $W_j^*$ ) is estimated from four vectors showing the impact of the event in Equation 5.

$$W^* = \underset{W}{\operatorname{argmin}} \sqrt{(X_1 - X_0 W)' V (X_1 - X_0 W)} \quad (3)$$

$$V^* = \underset{V}{\operatorname{argmin}} (Z_1 - Z_0 W^* (V))' (Z_1 - Z_0 W^* (V)) \quad (4)$$

$$\hat{\alpha}_{it} = Y_{it}^I - \sum_{j=2}^{J+1} W_j^* \cdot Y_{jt} \quad (5)$$

In this study, the dependent variable is per capita CO<sub>2</sub> emissions from household consumption, and the type of event is an epizootic disease. The event period is between 2010 and 2021 (pre-intervention: 2010–2018 and post-intervention: 2019–2021).

The treated unit, Gyeonggi, and the selected 13 municipalities in South Korea which are not exposed to ASF in 2019 are included. The predictors from 14 municipalities are employment ratio, gross regional domestic product (GRDP) per capita, economic growth rate, and cost of living index (beef, pork, poultry, and fish) in Table 3.

<sup>6</sup> The superscript  $N$  above  $Y$  indicates the outcome is not exposed to the event, and the superscript  $I$  above  $Y$  indicates the outcome is exposed to the event.

<sup>7</sup> MSPE stands for mean squared prediction error that presents the difference between the fitted and the true value.

TABLE 3 Variables description.

Variables	Description
Dependent variable	Per capita CO <sub>2</sub> emissions from household consumption (2010–2021)
Treated region	Gyeonggi in South Korea
Control units (Donor pool)	13 municipalities in South Korea
Predictors <sup>a</sup>	<ul style="list-style-type: none"><li>• Cost of living index (Poultry, Beef, Pig, and Fish)</li><li>• Employment ratio (Male and Female)<sup>a</sup></li><li>• Gross regional domestic product<sup>b</sup></li><li>• Economic growth rate<sup>c</sup></li></ul>
Intervention year	Year of the African Swine Fever occurred (Year of 2019)

Source: KOSIS, Korea Statistical Information Service; GIR, Greenhouse gas Inventory and Research center; GDD, Gyeonggi Data Dream.

<sup>a</sup>Employment of ratio of each municipality in South Korea.

<sup>b</sup>Gross regional domestic product (GRDP) measures the size of region's economy.

<sup>c</sup>Economic growth rate is measured annually of each municipality in South Korea.

### 3 Result

This study describes the per capita CO<sub>2</sub> emissions from household consumption as a dependent variable, and ten independent variables are taken to create the synthetic control unit. The estimates of predictors in the pre-intervention period are presented in Table 4, which shows the similarity between Gyeonggi and synthetic Gyeonggi.<sup>8</sup>

In Table 5, the weights/regression weights of every municipality for creating the synthetic control unit are stated.<sup>9</sup> The numbers in parentheses indicate the optimum synthetic unit for construction, such as Jeju (36.1%), Seoul (34.1%), Gyeongbuk (22.0%), and Ulsan (5.5%). This implies that the mix of weighted municipalities provides the optimal synthetic control unit in the pre-event period. The regression weights of the unexposed units also deliver a synthetic control unit.<sup>10</sup>

By establishing synthetic Gyeonggi from the optimal synthetic control unit, Figures 3, 4 present how dietary shifts have influenced per capita CO<sub>2</sub> emissions from household consumption in a positive direction after ASF. Figure 3 presents the comparison of per capita CO<sub>2</sub> emissions between Gyeonggi and synthetic Gyeonggi between 2010 and 2021.

That trajectory of per capita CO<sub>2</sub> emissions of synthetic Gyeonggi closely follows Gyeonggi's per capita CO<sub>2</sub> emissions in the pre-intervention period. However, in 2019, the per capita CO<sub>2</sub> emissions of Gyeonggi and synthetic Gyeonggi diverged in different directions. ASF caused consumer dietary shifts from pork to other types of meat. This divergence between Gyeonggi and synthetic

8 There are variables indicating a not-quite resemblance between Gyeonggi and synthetic Gyeonggi. This is because Gyeonggi's consumption is moderate relative to the regions in the control unit, which means there is no linear combination of regions that implies that synthetic Gyeonggi is not perfectly reproduced (Chelwa et al., 2015).

9 The results are from R, and the codes are modified by Becker et al. (2016).

10 The regression weights are not restricted to lie between zero and one, allowing extrapolation. The synthetic control method makes explicit the contribution of each comparison unit to the counterfactual of interest (Abadie et al., 2012).

TABLE 4 Characteristics in the pre-intervention.

		Gyeonggi	Synthetic Gyeonggi
Per capita CO <sub>2</sub> emissions from household consumption (kgCO <sub>2</sub> eq/person) <sup>a</sup>		65.61	65.82
Cost of living index (2020 = 100) <sup>b</sup>	Beef	75.67	76.10
	Pork	85.52	84.96
	Poultry	103.70	100.96
	Fish	93.81	92.87
	Fruit	102.93	85.56
	Vegetable	89.46	87.37
Employment ratio (%)	Male	73.19	72.76
	Female	48.43	53.95
Per capita gross regional domestic product (million KRW) <sup>c</sup>		33.80	37.63
Economic growth rate (%) <sup>d</sup>		5.70	2.60

Source: Estimated by SCM.

<sup>a</sup>CO<sub>2</sub> emission from household consumption (tons/person), average between 2010 and 2018.

<sup>b</sup>Cost of living index measures relative cost of living over regions and measures differences in the price of goods and services, average between 2000 and 2018.

<sup>c</sup>GRDP measures the size of a region's economy, average between 2000 and 2018.

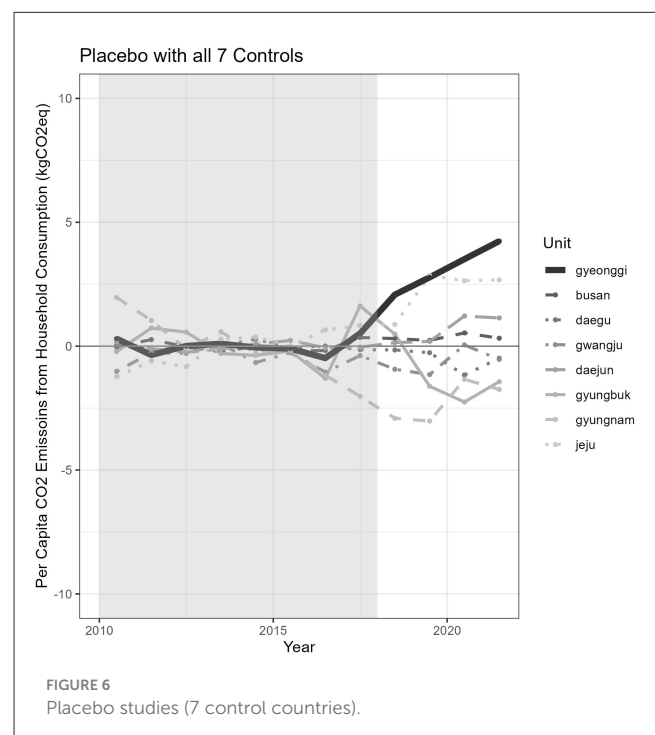
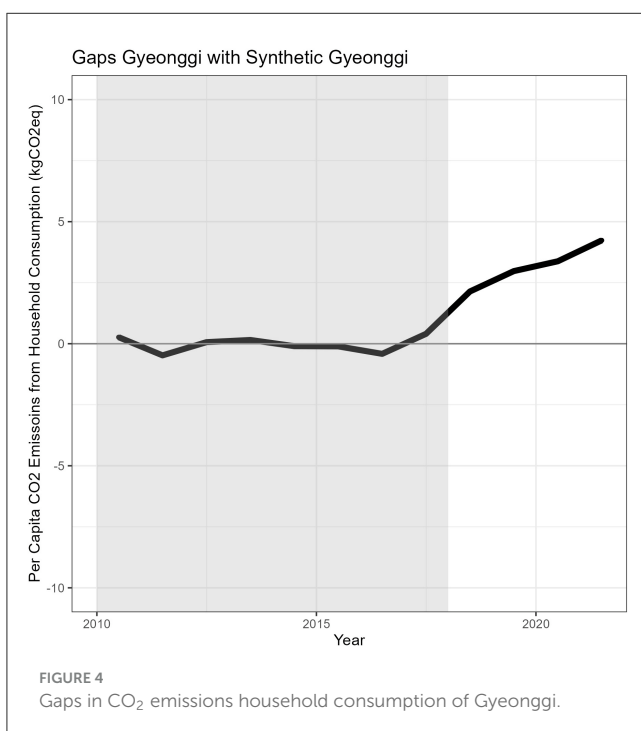
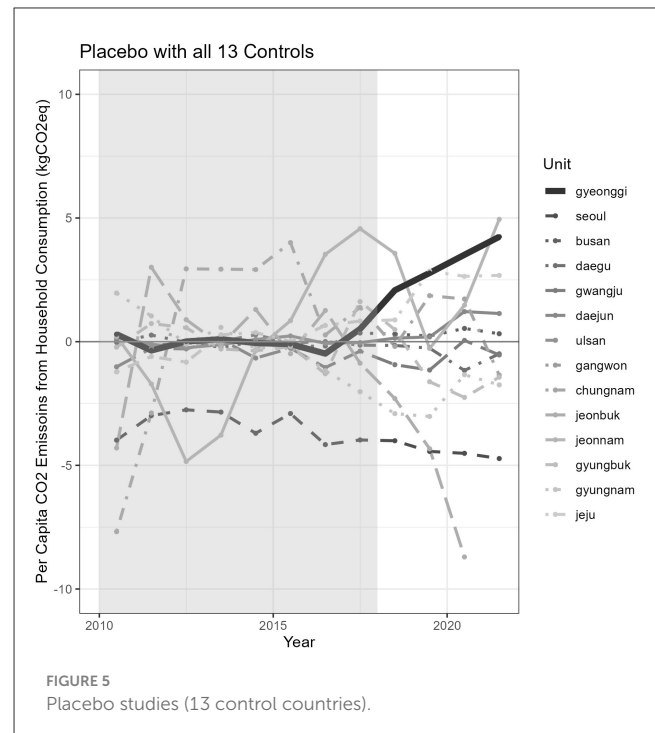
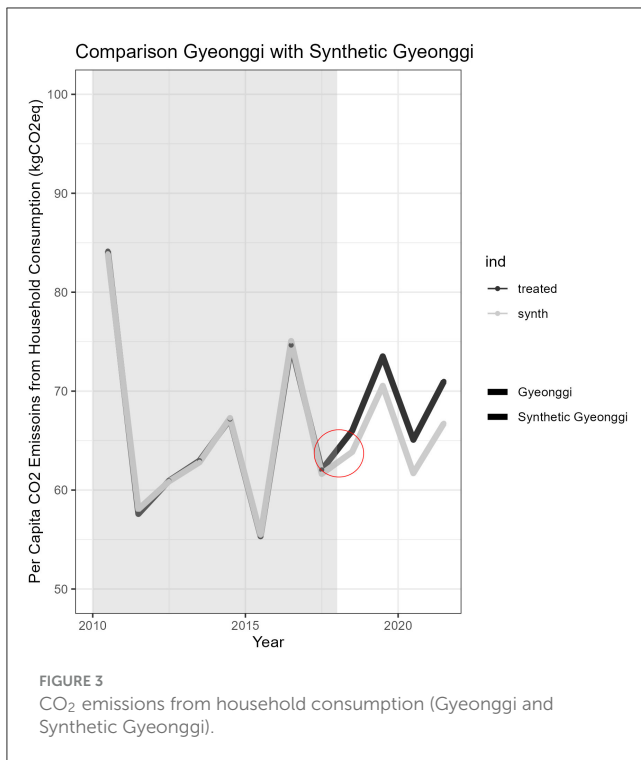
<sup>d</sup>Economic growth rate measures a region's economic growth, average between 2000 and 2018.

TABLE 5 Weight for each control unit.

Country	Synthetic control	Regression weight
Seoul	0.341	−0.81
Busan	0.001	1.56
Daegu	0.002	−0.21
Gwangju	0.000	0.16
Daejun	0.016	0.53
Ulsan	0.055	−0.30
Gangwon	0.000	−0.96
Chungnam	0.000	1.45
Geonbuk	0.000	−1.23
Geonnam	0.000	0.34
Gyeongbuk	0.220	−1.19
Gyeongnam	0.004	1.32
Jeju	0.361	0.35

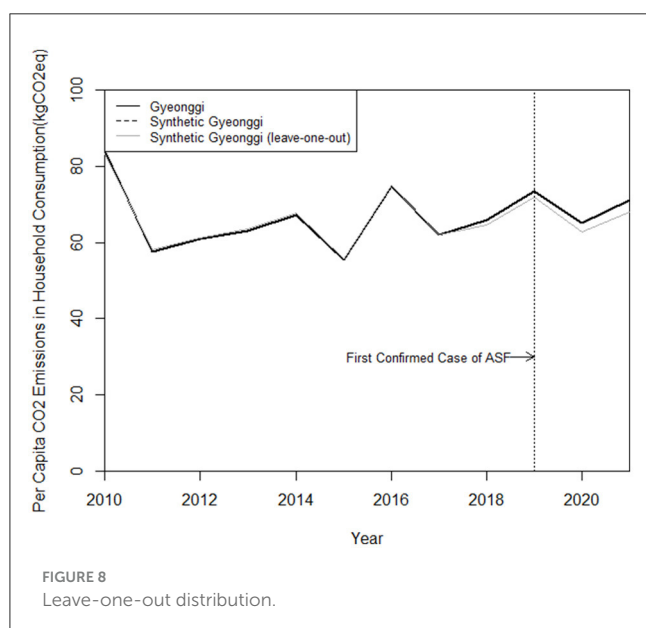
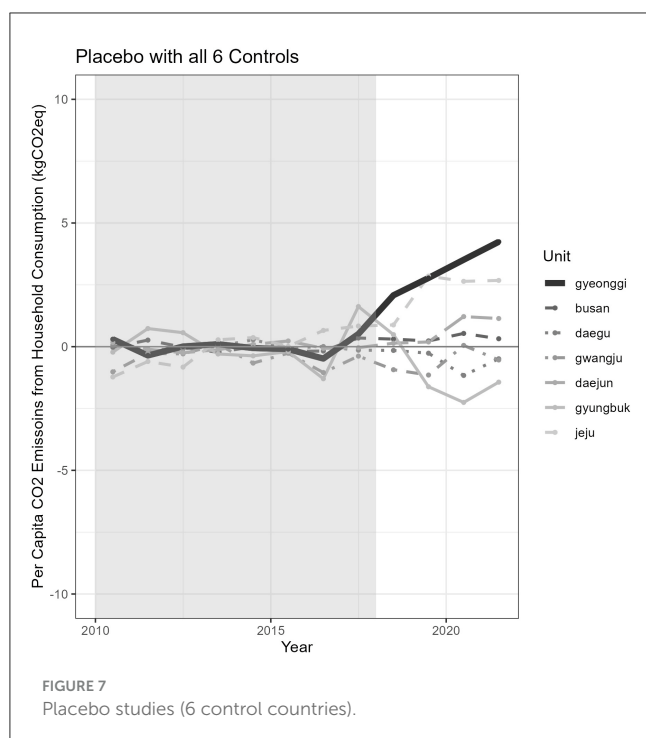
Source: Estimated by SCM.

Gyeonggi clearly indicates that there is an impact influencing per capita CO<sub>2</sub> emissions from household consumption after ASF. Figure 4 presents the gaps in the per capita CO<sub>2</sub> emissions between Gyeonggi and synthetic Gyeonggi. While the difference in the pre-intervention period is within ±1%, a divergence emerged after the introduction of ASF.



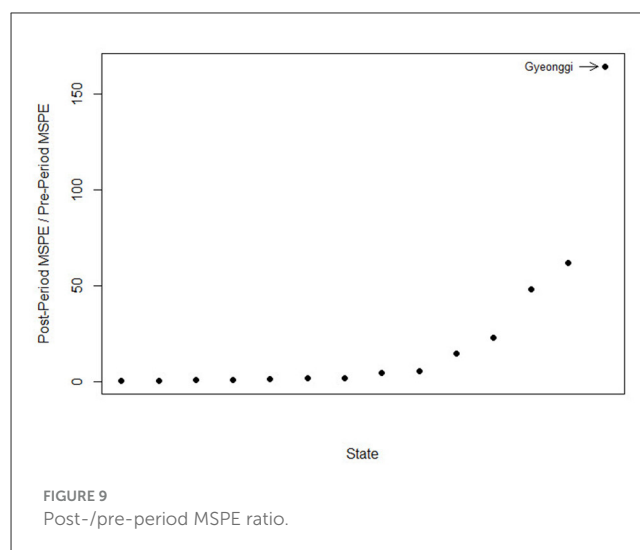
Placebo studies were performed by applying the SCM to support the statistical significance of ASF. The significance of the event is not established if there are gaps indicating a distinct magnitude between the tested and synthetic tested units (Abadie and Gardeazabal, 2003). For all thirteen municipalities in the control unit, placebo tests were conducted (Figures 5–7). For per capita CO<sub>2</sub> emissions, the study presents a good

fit, and other studies present the worst fit if it brings out the distant MSPE. Figure 6 presents the placebo studies, excluding municipalities showing an MSPE 20 times higher than that of the exposed unit (Gyeonggi). Six municipalities, including Seoul, are excluded, and there are still considerable deviations from zero. Figure 7 presents the exclusion of municipalities with 10 times higher MSPE, and one municipality was discarded. After exclusion through placebo studies (Figures 6, 7), there



were six unaffected units left. Thus, this study finds that the random permutation possibility of the event is  $1/6 = 0.166$ , representing an 84% statistical significance for the study.<sup>11</sup>

<sup>11</sup> The statistical inference presents the statistical significance of the proximity of the synthetic control unit to the treated unit. After excluding ten times higher MSPE than Gyeonggi, Figure 8 provides six unaffected units. The proximity of the synthetic control unit to the treated unit has a probability of  $1/6$  (0.166) and shows 84% significance of proximity.



The leave-one-out in Figure 8 was performed next to estimate the sensitivity of the results, and the test was applied to give positive weights to the municipalities. The analysis used an optimal  $W^*$  to minimize the distance between Gyeonggi and synthetic Gyeonggi in the pre-event span (Abadie et al., 2012). The gray lines of synthetic Gyeonggi with one of the six municipalities left out are recreated, and they are close to one another. The gaps between actual Gyeonggi and the six gray lines indicate that the study is robust to the exclusion of any particular municipality (Gong and Rao, 2016). The ratio of the post- to pre-event span MSPE of all 14 municipalities (one treated and 13 control units) is presented in Figure 9.

The MSPE ratio of Gyeonggi stands out, and the post-ASF MSPE is 164.53 times that of the pre-ASF MSPE. The second-highest MSPE ratio is 61.74 in Daejun, indicating that the ratio of Gyeonggi is 266% larger than that of the Daejun. The probability of having such a large ratio as Gyeonggi is  $1/13 = 0.076$  (7.6%) when any municipality randomly experiences ASF. Table 6 provides the ratio of post- to pre-ASF MSPE and RMSPE (root mean squared prediction error).<sup>12</sup> Empirically, by estimating MSPE/RMSPE, the study can assess goodness of fit. MSPE/RMSPE ratios showing the highest values indicate an impact from ASF. The two exhibit ratios of Gyeonggi are far from the rest of the municipalities. Therefore, there is a substantial event influencing the per capita CO<sub>2</sub> emissions from household consumption.

## 4 Conclusion and discussion

Dietary practices can be affected by various factors such as socioeconomic status, demographics, culture, and lifestyle (Czarnocinska et al., 2020; Hassan et al., 2020), and the health of dietary patterns are linked to environmental sustainability (Grosso et al., 2020). Animal-based foods require higher energy use and cause more GHG emissions than plant-based foods (Scarborough

<sup>12</sup> RMSPE is the rooted value of MEPE.

TABLE 6 MSPE/RMSPE ratio (post- to pre-intervention).

Region	MSPE ratio (post/pre)	RMSPE ratio (post/pre)	Region	MSPE ratio (post/pre)	RMSPE ratio (post/pre)
Gyeonggi	164.53	12.83	Seoul	1.78	1.34
Daejun	61.75	7.86	Gyungnam	1.78	1.34
Daegu	47.85	6.92	Jeonnam	1.42	1.19
Jeonbuk	22.62	4.76	Ulsan	0.93	0.96
Jeju	14.59	3.82	Gwangju	0.55	0.74
Gyungbuk	5.21	2.28	Gangwon	0.39	0.63
Busan	4.22	2.05	Chungnam	0.17	0.42

Source: Estimated by MSCMT.

et al., 2014). This is what motivated this study to determine the relationship between per capita CO<sub>2</sub> emissions and shifts in dietary patterns. In 2019, the swine farms in Gyeonggi in South Korea lost economic animals and consumers had to alter their dietary patterns. When an epizootic disease occurs in a country, the industries related to production and consumption are influenced by the event. Therefore, this study analyzed changes in dietary patterns after the ASF outbreak in South Korea, influencing the per capita CO<sub>2</sub> emissions from household consumption.

To analyze the relationship between dietary patterns and per capita CO<sub>2</sub> emissions, the synthetic control method (SCM) is employed. In particular, the analysis focused on regional municipalities that provide little data. The SCM is widely used to estimate the impact of an event such as terrorism, political action, economic development plan, and natural disasters. There are studies (Aleksandrowicz et al., 2016; Geibel and Freund, 2023) analyzing the changes in dietary patterns and their impact on the emissions of greenhouse gas emissions, but they focus on the production side. However, this study concentrates on the consumption side, and how the consumers react to an external event such as an epizootic disease.

By performing an SCM analysis with the treated (Gyeonggi) and control (13 municipalities) units, the study found that the two trajectory lines (Gyeonggi and synthetic Gyeonggi) were similar before diverging after the introduction of ASF. The gaps also indicate the impact of the shift in dietary patterns on per capita CO<sub>2</sub> emissions from household consumption. These two decisive figures indicate the effects of an epizootic disease, and the critical point of applying the SCM is to establish a synthetic control unit. How the Gyeonggi and synthetic Gyeonggi are similar is provided in the previous section such as per capita CO<sub>2</sub> emissions, cost of living indices, and economic factors.

The SCM is an effective method for analyzing limited samples, but it causes statistical problems for sensitivity and robustness. Therefore, the critical part of performing the analysis is selecting predictors that indicate the similarities between the treated and control units. Placebo studies, a post- to pre-MSPE ratio, and a leave-one-out were performed to support the statistical inferences. The figures present evidence that the trajectory divergences result from shifts in consumer dietary patterns. This study is the first to analyze at the level of municipalities, presenting the relationship between dietary pattern shifts and per capita CO<sub>2</sub> emissions from household consumption after ASF.

The relationship between the shifts in dietary patterns and per capita CO<sub>2</sub> emissions is proven through the evidence supporting the statistical inferences. However, the collection of predictors of municipalities in South Korea for analysis was limited. Climate change is one of the biggest concerns this planet has, and it affects the living. Upon analyzing the relationship between the change in dietary patterns and per capita CO<sub>2</sub> emissions, the outcomes of this study are meaningful. When an unexpected epizootic disease occurs in a country, the authority tries to recover the losses of farms and stabilize a disequilibrium in consumption. By building a synthetic control unit, policymakers, farmers, and even consumers can expect how much an epizootic disease causes damage.

## Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: Korean Statistical Information Service.

## Author contributions

SE: Writing – original draft, Writing – review & editing.

## Funding

The author(s) declare that no financial support was received for the research, authorship, and/or publication of this article.

## Conflict of interest

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

## Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated



organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or

claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

## References

- Abadie, A., Diamond, A., and Hainmueller, J. (2010). Synthetic control methods for comparative case studies: estimating the effect of California's tobacco control program. *J. Am. Stat. Assoc.* 105, 493–505. doi: 10.1198/jasa.2009.ap08746
- Abadie, A., Diamond, A., and Hainmueller, J. (2012). Synth: an R package for synthetic control methods in comparative case studies. *J. Stat. Softw.* 42, 1–17. doi: 10.18637/jss.v042.i13
- Abadie, A., and Gardeazabal, J. (2003). The economic costs of conflict: a case study of the Basque country. *Am. Econ. Rev.* 93, 113–132. doi: 10.1257/00028280321455188
- Afrouzi, H. N., Ahmed, J., Siddique, B. M., Khairuddin, N., and Hassan, A. (2023). A comprehensive review on carbon footprint of regular diet and ways to improving lowered emissions. *Results Eng.* 18:101054. doi: 10.1016/j.rineng.2023.101054
- Aleksandrowicz, L., Green, R., Joy, E. J., Smith, P., and Haines, A. (2016). The impacts of dietary change on greenhouse gas emissions, land use, water use, and health: a systematic review. *PLoS ONE* 11:e0165797. doi: 10.1371/journal.pone.0165797
- Ando, M. (2015). Dreams of urbanization: Quantitative case studies on the local impacts of nuclear power facilities using the synthetic control method. *J. Urban Econ.* 85, 68–85. doi: 10.1016/j.jue.2014.10.005
- Ban, Y. K. (2023). *Livestock and Product Semi-annual (South Korea)*. USDA Foreign Agricultural Service.
- Becker, M., Klößner, S., and Pfeifer, G. (2016). *Cross-Validating Synthetic Controls*. MPRA Paper No. 83679.
- Bohn, S., Lofstrom, M., and Raphael, S. (2014). Did the 2007 legal Arizona workers act reduce the state's unauthorized immigrant population? *Rev. Econ. Stat.* 96, 258–269. doi: 10.1162/REST\_a\_00429
- Bouttell, J., Craig, P., Lewsey, J., Robinson, M., and Popham, F. (2018). Synthetic control methodology as a tool for evaluating population-level health interventions. *J. Epidemiol. Commun. Health* 72, 673–678. doi: 10.1136/jech-2017-210106
- Center for Sustainable Systems, University of Michigan (2022). *Carbon Footprint Factsheet*. Pub. No. CSS09-05.
- Chelwa, G., Walbeek, C., and Blecher, E. (2015). "Evaluating South Africa's tobacco control initiative: a synthetic control approach," in *ERSA Working Paper: Economic Research Southern Africa*.
- Cho, K. H., Hong, S. K., Jang, M. K., Ryu, J. H., Kim, H. J., Lee, Y. R., et al. (2022). Comparison of the virulence of Korean African swine fever isolates from pig farms during 2019–2021. *Viruses* 14:2512. doi: 10.3390/v14112512
- Choe, J. H., Yang, H. S., Lee, S. H., and Go, G. W. (2015). Characteristics of pork belly consumption in South Korea and their health implication. *J. Animal Sci. Technol.* 57, 1–7. doi: 10.1186/s40781-015-0057-1
- Czarnocinska, J., Wadolowska, L., Lonnie, M., Kowalkowska, J., Jezewska-Zychowicz, M., and Babicz-Zielinska, E. (2020). Regional and socioeconomic variations in dietary patterns in a representative sample of young polish females: a cross-sectional study (GEBaHealth project). *Nutr. J.* 19:26. doi: 10.1186/s12937-020-00546-8
- Food and Agriculture Organization of the United Nations (2023). *Food Balance*. Available at: <https://www.fao.org/faostat/en/#data/FBS>
- Geibel, I., and Freund, F. (2023). The effects of dietary changes in Europe on greenhouse gas emissions and agricultural incomes in Ireland and Denmark. *Environ. Res. Lett.* 18:124026. doi: 10.1088/1748-9326/ad0681
- Gong, X., and Rao, M. (2016). The economic impact of prolonged political instability: a case study of Fiji. *Policy Stud.* 37, 370–386. doi: 10.1080/01442872.2016.1157856
- Grosso, G., Fresán, U., Bes-Rastrollo, M., Marventano, S., and Galvano, F. (2020). Environmental impact of dietary choices: role of the Mediterranean and other dietary patterns in an Italian cohort. *Int. J. Environ. Res. Public Health* 17:1468. doi: 10.3390/ijerph17051468
- Hassan, F., Kalsoom, S., Sheikh, N. H., and Humayun, A. (2020). Factors affecting food consumption patterns and dietary practices of adolescent girls: an explanatory sequential mixed method study. *Ann. King Edward Med. Univ.* 26, 9–18. doi: 10.21649/akemu.v26i1
- Jeong, D., Kim, Y. S., Cho, S., and Hwang, I. (2023). A case study of CO2 emissions from beef and pork production in South Korea. *J. Animal Sci. Technol.* 65:427. doi: 10.5187/jast.2022.e109
- Korea Meat Trade Association (KMTA) (2024). *Meat Consumption*. Available at: [http://www.kmta.or.kr/kr/data/stats\\_spend.php](http://www.kmta.or.kr/kr/data/stats_spend.php)
- Korea Statistical Information Service (KOSIS) (2024). Available at: <https://kosis.kr/index/index.do>
- Liu, T. C., Wu, Y. C., and Chau, C. F. (2023). An overview of carbon emission mitigation in the food industry: efforts, challenges, and opportunities. *Processes* 11:1993. doi: 10.3390/pr11071993
- Rogissart, L., Fouchet, C., and Bellassen, V. (2019). *Estimating greenhouse gas emissions from food consumption: methods and results*. Doctoral dissertation, Inconnu.
- Scarborough, P., Appleby, P. N., Mizdrak, A., Briggs, A. D., Travis, R. C., Bradbury, K. E., et al. (2014). Dietary greenhouse gas emissions of meat-eaters, fish-eaters, vegetarians and vegans in the UK. *Clim. Change* 125, 179–192. doi: 10.1007/s10584-014-1169-1
- Shi, P. (2021). *Source Differentiated Pork Import Demand for South Korea: Implications to Canadian Exports*. University of Alberta.
- STATISTA (2024). *Average Greenhouse Gas Emissions Per Kilograms of Major Food Products Worldwide*. Available at: <https://www.statista.com/statistics/1201677/greenhouse-gas-emissions-of-major-food-products/#?text=Food%20emissions%20vary%20greatly%20depending,les%20than%2010%20kg%20CO2eq>
- Sugimoto, M., Murakami, K., Fujiwara, A., Asakura, K., Masayasu, S., and Sasaki, S. (2020). Association between diet-related greenhouse gas emissions and nutrient intake adequacy among Japanese adults. *PLoS ONE* 15:e0240803. doi: 10.1371/journal.pone.0240803
- USDA (2023). *Livestock, Dairy, and Poultry Outlook: October 2023*. Economic Research Service. LDP-M-352.
- Wang, Y. -D., Byrne, J., Kurdgelashvili, L., Brehm, C., Saul, K. M., Kramer, G., et al. (2013). *International Energy Policy in the Aftermath of the Fukushima Nuclear Disaster: An Analysis of Energy Policies of the U.S., U.K., Germany, France, Japan, China and Korea*. Center for Energy and Environment Policy; University of Delaware.
- Weaver, T. R. D., and Habib, N. (2020). *Evaluating losses associated with African swine fever in the People's Republic of China and Neighboring Countries*. ADB East Asia Working Paper Series. No. 27. doi: 10.22617/WPS200263-2
- World Organization for Animal Health (WOAH) (2023). Available at: <https://www.woah.org/en/home/>

# Frontiers in Animal Science

Understanding the use and management of  
animals for food production

A multidisciplinary journal that advances our  
understanding of food and livestock production,  
while safeguarding animal welfare and  
environmental sustainability.

## Discover the latest Research Topics

[See more →](#)

### Frontiers

Avenue du Tribunal-Fédéral 34  
1005 Lausanne, Switzerland  
[frontiersin.org](https://frontiersin.org)

### Contact us

+41 (0)21 510 17 00  
[frontiersin.org/about/contact](https://frontiersin.org/about/contact)



### Frontiers in Animal Science

