



Deposition and enrichment of carotenoids in livestock products: An overview

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ABSTRACT

A wide range of research has illustrated that carotenoids play a key role in human health through their versatile beneficial biological functions. Traditionally, the majority dietary sources of carotenoids for humans are obtained from vegetables and fruits, however, the contribution of animal-derived foods has attracted more interest in recent years. Livestock products such as eggs, meat, and milk have been considered as the appropriate and unique carriers for the deposition of carotenoids. In addition, with the enrichment of carotenoids, the nutritional quality of these animal-origin foods would be improved as well as the economic value. Here, we offer an overview covering aspects including the physicochemical properties of carotenoids, the situation of carotenoids fortified in livestock products, and the pathways that lead to the deposition of carotenoids in livestock products. The summary of these important nutrients in livestock products will provide references for animal husbandry and human health.

1. Introduction

Carotenoids are a class of widespread isoprenoid compounds biosynthesized mainly by photosynthetic organisms such as plants, cyanobacteria and algae, while some fungi and bacteria as well as certain invertebrate animals also have this ability (Meléndez-Martínez et al., 2022; Rodríguez-Concepción et al., 2018). In addition to pigmentation and provitamin A activity (α -carotene, β -carotene and β -cryptoxanthin are the main representatives), carotenoids have been proposed to confer many other functions, such as anti-oxidant, anti-inflammatory, photoprotective, and stimulation of gap junctional communication (De Souza Mesquita et al., 2021; Junji, 2023; Saini et al., 2020; Stahl & Sies, 2012; Tanumihardjo, 2012). On this basis, many studies have shown that carotenoids play a positive role in the prevention or treatment of various diseases (Bohn, 2019; Cooper, 2004; Milani et al., 2017). Therefore, sufficient intake of these nutritional components is vital for the maintenance of human body health. Nowadays, despite plant-derived food including fruit and vegetables still being the main dietary sources of

carotenoids in the human diet, nevertheless, livestock products should not be overlooked as an excellent strategy to ingest carotenoids (Meléndez-Martínez et al., 2022; Meléndez-Martínez, 2019). In particular, fortification and enrichment of edible eggs with carotenoids have been proposed for a long time (Surai & Sparks, 2001), and more and more consumers have accepted and are interested in these functional foods. Meanwhile, with the widely application of carotenoids in animal husbandry, the research about the deposition of carotenoids in meat, milk and other livestock products such as some animal offal (liver) has gradually increased. It should note that aquatic animals are also rich in certain important carotenoids, especially some fish and shellfish, and the review of Tan et al. provided a detailed demonstration about this topic (Tan et al., 2022). However, there is no doubt that the production and consumption of livestock products are much higher than those of aquatic products all over the world (Scanes, 2018; Edwards et al., 2019). Hence, it is necessary to give more attention about the deposition and enrichment of carotenoids in livestock products, which will make a great significance for human rational diet.

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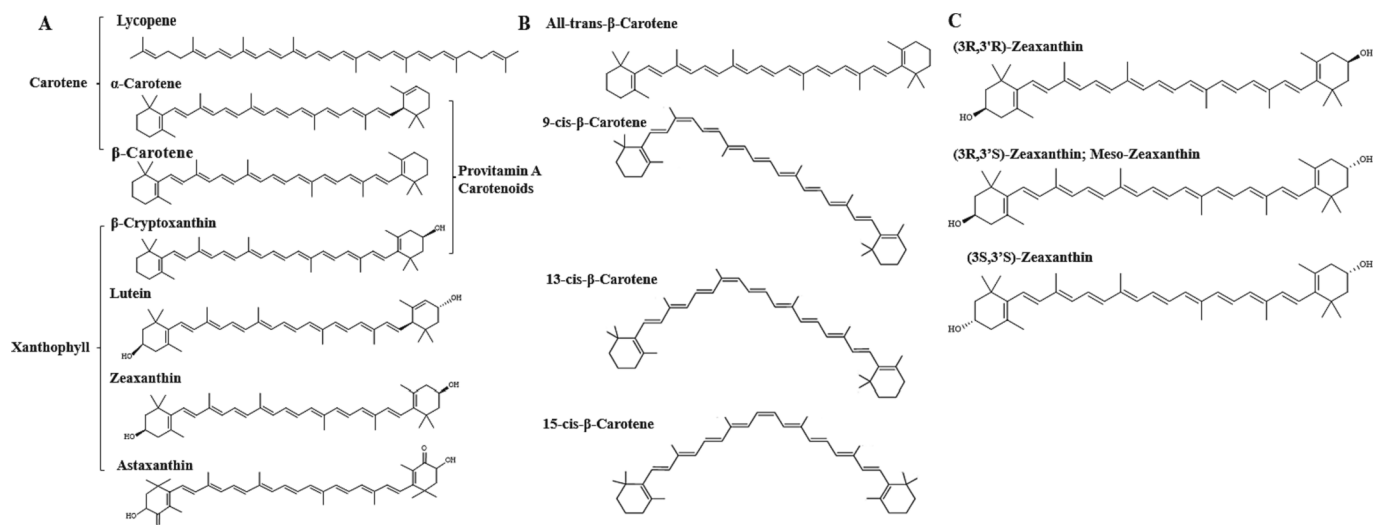


Fig. 1. Chemical structures of various carotenoids. A, Major carotenoids(*all-trans* configuration) in livestock products. B, Different geometrical isomers of β -carotene. C, Optical isomers of zeaxanthin.

Like humans, poultry and livestock are incapable of synthesizing carotenoids *in vivo*. The deposition of carotenoids in animals body is through the uptake of these compounds in diet, hence feed is an important factor that affects the carotenoid levels in the livestock products (Álvarez et al., 2015; Meléndez-Martínez, Esquivel, & Rodríguez-Amaya, 2023). Specifically, carotenoids need to be released from the feed, solubilized into digestive juice, and form mixed micelles, then absorbed by enterocytes, after a series of metabolic reactions, transferred to the blood and finally accumulated in target tissues and organs (Álvarez et al., 2015; Geng et al., 2022). Moreover, the metabolic pathway of uptake of carotenoids by humans is very similar to the above process, whether the carotenoids are derived from plant food or animal food. However, it is worth noting that carotenoid bioavailability from livestock products is generally considered to be high (Schweiggert & Carle, 2017), this further suggests that livestock products are an important vehicle for these bioactive compounds. For instance, Chung et al. conducted an intervention study with a crossover design to compare the bioavailability of lutein in four different dietary sources. The results showed that the lutein bioavailability from eggs was higher than that from other sources such as lutein supplements, lutein ester supplements, and spinach under the equivalent intake dose. (Chung et al., 2004). The study of Morifuji et al. in a randomized crossover trial demonstrated that the co-ingestion of β -carotene and fermented milk resulted in a significant increase in the absorption of this carotenoid in both humans and rats (Morifuji et al., 2020). Some studies have pointed out that dietary lipid intake can improve carotenoid absorption by several mechanisms, where the unique fat composition in livestock products may be the reason for promoting the stability and bioavailability of carotenoids (Conboy Stephenson, Ross, & Stanton, 2021; Desmarchelier & Borel, 2017).

In general, maize, alfalfa and other feedstuff contain a certain amount of carotenoids, but the species and contents are limited and hard to meet the needs to produce carotenoid nutrient-fortified livestock products. Therefore, many strategies have been developed to increase the amount of carotenoids in the diet of livestock and poultry. Among them, the most direct method is dietary supplementation with carotenoid additives in the diet. The production, encapsulation and application of some carotenoid additives, such as β -carotene, lutein, canthaxanthin, and astaxanthin, is now relatively mature. Carotenoids as feed additives can either be obtained through chemical synthesis, extracted from natural sources, and produced by microorganisms (Langi et al., 2018). Comparatively speaking, the microbial production of carotenoids has received more attention in recent years owing to its being

natural, efficient, low-cost, and environmental-friendly (Mussagy et al., 2021). Currently, β -carotene is produced mainly in the microalgae *Dunaliella salina* and the fungus *Blakeslea trispora* (Zhang, 2018). The microalgae *Haematococcus pluvialis* is considered as the best source of natural astaxanthin. To date, with the application of genetic modification of natural microbial system, the production of astaxanthin and other carotenoids in the microalgal species has been further improved (Zhu et al., 2023). Meanwhile, metabolic engineering strategies on *Escherichia coli* has also been widely developed to achieve the heterologous production of many carotenoid additives, such as lycopene, β -carotene, astaxanthin and zeaxanthin (Mussagy, Winterburn, Santos-Ebinuma, & Pereira, 2019; Zhu et al., 2023). In addition to the use of feed additives, fruit and vegetable by-products are other sources of carotenoids in the feeding of poultry and livestock. Processing by-products from orange, carrot, and tomato has been applied in animal diet, which contains several carotenoids including α -carotene, β -carotene, lutein, zeaxanthin, β -cryptoxanthin, and not only realized the further utilization of by-products but also improved the level of carotenoids in the animal's body (Akdemir et al., 2012; Seidavi et al., 2020; Titcomb et al., 2019; Xue, Li, & Pan, 2013). Furthermore, based on metabolic engineering, a breed of high-carotenoid biofortified maize has been achieved, these kinds of crops have been used as feed to supplement carotenoids for animals (especially poultry). Liu et al. modified the carotenoids biosynthesis pathway in maize seed to generate astaxanthin-rich maize, subsequently the astaxanthin-rich maize was fed to laying hens and successfully produced astaxanthin-fortified eggs (Liu et al., 2021). Another study has shown that high-carotenoid maize, compared with common maize, had no adverse effects on poultry health, but could significantly improve the amount of several carotenoids in chickens' livers and pigmentation effect in muscle after supplementing it in the diet (Díaz-Gómez et al., 2017). With the progress of technology, it is more convenient to supplement carotenoids in the diet of poultry and livestock while the cost is becoming reduced, which laid a foundation for the development of carotenoid-fortified livestock products.

In this review, we introduce several kinds of key carotenoids and describe their characteristics. Then, several current scientific studies of the deposition and enrichment of different carotenoids in animal-derived foods are listed. Moreover, we briefly summarize the metabolism and bioconversion of carotenoids in animal's body. This work will help people systematically understand the deposition and enrichment of carotenoids in livestock products, and the specific process.

Table 1
The deposition and enrichment of different carotenoids in livestock products.

Carotenoid	Specie	Product	Dietary Source	Supplemental Level	Duration	Deposition Amount	Reference
Lycopene	Laying Hens	Eggs	Tomato oleoresins (containing 15 % lycopene)	100, 200, 300 mg/kg lycopene in feed (adding tomato oleoresins into diet)	21 days	1.58, 1.67, 1.71 µg/g yolk (no detected in control group)	(Honda et al., 2019)
Lycopene	Laying Hens	Eggs	Tomato powder (containing 6 % lycopene)	300 and 600 mg/kg lycopene in feed (adding tomato powders into diet)	90 days	6.53 and 8.05 µg/g yolk (no detected in control group)	(Akdemir et al., 2012)
Lycopene	Laying Hens	Eggs	Commercial additive product	20 mg/kg lycopene in feed	90 days	2.40 µg/g yolk (no detected in control group)	(Orhan et al., 2021)
Lycopene	Laying Hens	Eggs	Commercial additive product	10 and 20 mg/kg lycopene in feed	28 days	0.80 and 0.88 µg/g yolk (no detected in control group)	(An et al., 2019)
Lycopene	Pigs	Meat	Commercial additive product	20 mg/kg lycopene in feed	28 days	about 6–8 µg/g belly meat ^d (no detected in control group)	(An et al., 2019)
Lycopene	Chickens	Liver	Commercial additive product	75 mg/kg lycopene in feed	36 days	2.82 µg/g liver DM ^b (0.27 µg/g in control group)	(Englmaierová et al., 2011)
Lycopene	Chickens	Liver	Commercial additive product	10 and 20 mg/kg lycopene in feed	28 days	1.67 and 3.69 µg/g liver (no detected in control group)	(Lee et al., 2016)
α-Carotene	Laying Hens	Eggs	Purple haze carrots (chopped into 5–10 mm pieces)	4.63 mg/day α-carotene per hen (70 g/day carrot for per hen ^c)	28 days	1.29 µg/g yolk (0.01 µg/g in control group)	(Hammershøj et al., 2010)
β-Carotene	Laying Hens	Eggs	Purple haze carrots (chopped into 5–10 mm pieces)	7.88 mg/day β-carotene per hen (70 g/day carrot for per hen ^d)	28 days	3.39 µg/g yolk (0.03 µg/g in control group)	(Hammershøj et al., 2010)
β-Carotene	Laying Hens	Eggs	Commercial additive product	15, 30, 60, 120 mg/kg β-carotene in feed	49 days	1.04, 2.60, 5.97, 13.48 µg/g yolk (no detected in control group)	(Miao et al., 2023)
β-Carotene	Laying Hens	Eggs	Commercial additive product	5, 10, 20, 40 mg/kg β-carotene in feed	21 days	1.81, 2.68, 5.19, 4.81 µg/g yolk (0.14 µg/g in control group)	(Jiang et al., 1994)
β-Carotene	Laying Hens	Eggs	Engineered high-carotenoid biofortified maize	3.18 mg/kg β-carotene in freeze-dried feed (biofortified maize account for 62 % in feed)	20 days	0.45 µg/g yolk (0.05 µg/g in control group)	(Moreno et al., 2020)
β-Carotene	Steers	Meat	Commercial additive product	750 mg/day of β-carotene for per steer	28 days	0.154 µg/g M. semimembranosus (0.023 µg/g in control group)	(Muramoto et al., 2003)
β-Carotene	Steers	Meat	Commercial additive product	5.5, 27.5, 137.5 mg/kg β-carotene in feed	Unspecified ^e	0.202, 0.969, 0.985 µg/g longissimus muscle (0.115 µg/g in control group)	(Condron et al., 2014)
β-Carotene	Steers	Meat	Commercial additive product	600, 1200, 1800 mg/day of β-carotene for per steer	90 days	0.19, 0.28, 0.33 µg/g muscle (0.18 µg/g in control group)	(Jin et al., 2015)
β-Carotene	Cows	Colostrum	Commercial additive product	800 mg/day of β-carotene for per cow	21 days	1.49 µg/mL milk (0.65 µg/mL in control group)	(Prom et al., 2022)
β-Carotene	Laying Hens	Liver	Commercial additive product	15, 30, 60, 120 mg/kg β-carotene in feed	49 days	1.67, 2.30, 7.97, 16.90 µg/g liver (no detected in control group)	(Miao et al., 2023)
β-Carotene	Pigs	Liver	Commercial additive product	10 mg/kg β-carotene in feed	98 days	0.49 µg/g liver (no detected in control group)	(Schweigert et al., 2001)
β-Carotene	Steers	Liver	Commercial additive product	5.5, 27.5, 137.5 mg/kg β-carotene in feed	Unspecified ^e	0.531, 1.207, 2.225 µg/g liver (0.578 µg/g in control group)	(Condron et al., 2014)
β-Carotene	Steers	Liver	Commercial additive product	600, 1200, 1800 mg/day of β-carotene for per steer	90 days	7.43, 8.39, 9.32 µg/g liver (2.52 µg/g in control group)	(Jin et al., 2015)
α-Cryptoxanthin	Laying Hens	Eggs	Engineered high-carotenoid biofortified maize	5.38 mg/kg α-cryptoxanthin in freeze-dried feed	20 days	13.93 µg/g yolk (0.03 µg/g in control group)	(Moreno et al., 2020)

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Table 1 (continued)

Carotenoid	Specie	Product	Dietary Source	Supplemental Level	Duration	Deposition Amount	Reference
				(biofortified maize account for 62 % in feed)			
β -Cryptoxanthin	Laying Hens	Eggs	Engineered high-carotenoid biofortified maize	3.12 mg/kg β -cryptoxanthin in feed (biofortified maize account for 60 % in feed)	40 days	4.88 μ g/g yolk (1.07 μ g/g in control group) ^f	(Heying et al., 2014)
β -Cryptoxanthin	Laying Hens	Eggs	β -Cryptoxanthin biofortified maize	2.60 mg/kg β -cryptoxanthin in feed (biofortified maize account for 60 % in feed)	20 days	2.32 μ g/g yolk (0.30 μ g/g in control group)	(Liu et al., 2012)
β -Cryptoxanthin	Laying Hens	Eggs	Engineered high-carotenoid biofortified maize	3.29 mg/kg β -cryptoxanthin in freeze-dried feed (biofortified maize account for 62 % in feed)	20 days	2.64 μ g/g yolk (0.08 μ g/g in control group)	(Moreno et al., 2020)
β -Cryptoxanthin	Chickens	Liver	Engineered high-carotenoid biofortified maize	2.09 mg/kg β -cryptoxanthin in freeze-dried feed (biofortified maize account for 58 % in feed)	27 days	7.42 μ g/g liver (no detected in control group)	(Díaz-Gómez et al., 2017)
β -Cryptoxanthin	Laying Hens	Liver	Engineered high-carotenoid biofortified maize	3.12 mg/kg β -cryptoxanthin in feed (biofortified maize account for 60 % in feed)	40 days	about 3.04 μ g/g liver (about 0.28 μ g/g in control group) ^g	(Heying et al., 2014)
Lutein	Laying Hens	Eggs	Red carrot leaves	Red carrot leaves account for 0.4 % in feed	28 days	3.37 μ g/g yolk (2.04 μ g/g in control group)	(Titcomb et al., 2019)
Lutein	Laying Hens	Eggs	Marigold powder	Marigold powder account for 0.05 % in feed	28 days	5.30 μ g/g yolk (2.04 μ g/g in control group)	(Titcomb et al., 2019)
Lutein	Laying Hens	Eggs	Mixture of marigold flower meal and spinach meal ^h	11.1, 14.6, 17.5 g/kg mixture in feed	14 days	81.0, 84.0, 109.0 μ g/g yolk DM (11.2 μ g/g in control group)	(Sünder et al., 2022)
Lutein	Laying Hens	Eggs	Marigolds flower extract	2.36, 3.85, 4.86, 9.01, 9.52 mg/kg lutein in feed (adding 150,350,550,750,950 mg/kg marigold flower extract in feed)	70 days	18.56, 29.11, 30.27, 30.80, 36.33 μ g/g yolk DM (12.34 μ g/g in control group)	(Skrivan et al., 2016)
Lutein	Laying Hens	Eggs	Microalgae powder	4.441 mg/kg lutein in feed (adding 3.2 % dried <i>D. tertiolecta mp3</i> powder. in feed)	21 days	38.9 μ g/g belly yolk (10.4 μ g/g control group)	(Kim & Shin, 2022)
Lutein	Quails	Eggs	Marigolds extract	10.56 mg/kg lutein in feed (marigold extract account for 0.2 % in feed)	23 days	31.14 μ g/g yolk (1.65 μ g/g in control group)	(Karadas et al., 2006)
Lutein	Cows	Bovine Milk	Marigolds extract (containing 2 % lutein)	2, 3, 4 g/day of lutein for per cow (adding marigolds extractive into diet)	84 days	7.0, 12.0, 15.0 μ g/L milk (5.9 μ g/L in control group)	(Xu et al., 2014)
Lutein	Cows	Bovine Milk	Marigolds extractive (containing 2 % lutein)	4 g/day of lutein for per cow (adding marigolds extractive into diet)	56 days	10.25 μ g/L milk (6.45 μ g/L in control group)	(Wang et al., 2018)
Zeaxanthin	Laying Hens	Eggs	Mixture of marigold flower meal and spinach meal ⁱ	11.1, 14.6, 17.5 g/kg mixture in feed	14 days	14.3, 14.4, 14.4 μ g/g yolk DM (5.5 μ g/g in control group)	(Sünder et al., 2022)
Zeaxanthin	Laying Hens	Eggs	Heterotrophic <i>Chlorella</i>	10 and 20 g/kg dry <i>Chlorella</i> biomass in feed	54 days	10.44 and 15.94 μ g/g yolk (7.09 μ g/g in control group)	(Kotrbaček et al., 2013)
Zeaxanthin	Laying Hens	Eggs	Engineered high-carotenoid biofortified maize	12.14 mg/kg zeaxanthin in freeze-dried feed (biofortified maize account for 62 % in feed)	20 days	29.89 μ g/g yolk (0.60 μ g/g in control group)	(Moreno et al., 2020)
Zeaxanthin	Laying Hens	Eggs	Marigolds flower extract	1.55, 2.46, 3.42, 6.55, 7.16 mg/kg zeaxanthin in feed(adding 150, 350, 550, 750, 950 mg/kg marigold flower extract in feed)	70 days	10.27, 14.93, 18.92, 20.81, 25.59 μ g/g yolk DM (5.92 μ g/g in control group)	(Skrivan et al., 2016)
Zeaxanthin	Laying Hens	Eggs	Microalgae powder	7.071 mg/kg lutein in feed (adding 3.2 % dried <i>D. tertiolecta mp3</i> powder. in feed)	21 days	26.0 μ g/g belly yolk (9.9 μ g/g control group)	(Kim and Shin, 2022)
Zeaxanthin	Chickens	Liver	Engineered high-carotenoid biofortified maize	10.33 mg/kg zeaxanthin in freeze-dried feed (biofortified maize account for 58 % in feed)	35 days	7.19 μ g/g freeze-dried liver (1.30 μ g/g in control group)	(Díaz-Gómez et al., 2017)
Meso-Zeaxanthin	Chickens	Meat	Oil containing meso-zeaxanthin diacetate	70 mg/kg meso-zeaxanthin in feed (adding oil into diet)	56 days	about 0.02 μ g/g in muscle ⁷ (no detected in control group)	(Phelan et al., 2018)

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Table 1 (continued)

Carotenoid	Specie	Product	Dietary Source	Supplemental Level	Duration	Deposition Amount	Reference
Astaxanthin	Laying Hens	Eggs	Commercial additive product	42 mg/kg astaxanthin in feed	28 days	21.77 µg/g yolk (no detected in control group)	(Wang et al., 2022)
Astaxanthin	Laying Hens	Eggs	Commercial additive product	7.1, 14.2, 21.3, 42.6 mg/kg astaxanthin in feed	56 days	2.43, 6.65, 10.67, 22.13 µg/g yolk (no detected in control group)	(Dansou et al., 2021)
Astaxanthin	Laying Hens	Eggs	Commercial additive product	15, 30, 45, 60 mg/kg astaxanthin in feed	84 days	15.9, 31.9, 38.2, 64.3 µg/g yolk (no detected in control group)	(He et al., 2023)
Astaxanthin	Laying Hens	Eggs	Commercial additive product	10, 20, 40, 80 mg/kg astaxanthin in feed	21 days	13.2, 15.8, 15.7, 36.2 µg/g yolk (no detected in control group)	(Magnuson et al., 2018)
Astaxanthin	Laying Hens	Eggs	Commercial additive product	25, 50, 100 mg/kg astaxanthin in feed	42 days	12.87, 21.06, 44.20 µg/g yolk (no detected in control group)	(Gao et al., 2020)
Astaxanthin	Laying Hens	Eggs	Astaxanthin biofortified maize	24.32 mg/kg astaxanthin in feed	28 days	14.15 µg/g yolk (no detected in control group)	(Liu et al., 2021)
Astaxanthin	Chickens	Meat	Commercial additive product	15 and 30 mg/kg astaxanthin in feed	21 days	0.17, 0.20 µg/g pectoralis major (no detected in control group)	(Akiba et al., 2001)
Astaxanthin	Chickens	Liver	Commercial additive product	15 and 30 mg/kg astaxanthin in feed	21 days	0.85, 1.14 µg/g liver (no detected in control group)	(Akiba et al., 2001)
Astaxanthin	Laying Hens	Liver	Commercial additive product	10, 20, 40, 80 mg/kg astaxanthin in feed	42 days	3.39, 3.50, 4.92, 5.78 µg/g liver (no detected in control group)	(Magnuson et al., 2018)

^a · The exact amount was not specified in the paper, these data are estimated from Fig. 1 in the paper.

^b · Dietary supplemental 75 mg/kg lycopene with 100 mg/kg vitamin E in the diet at the same time, DM means dry matter.

^c · The α -carotene intake was 4.63 mg/day per hen which can be calculated based on production performance data and contents of carotenoids in carrot.

^d · The β -carotene intake was 7.88 mg/day per hen which can be calculated based on production performance data and contents of carotenoids in carrot.

^e · The paper did not clearly indicate the feeding time. The cows' average weight was 351.3 ± 12.1 kg at the beginning of the experiment, and it was 591 ± 13.9 kg when slaughtered.

^f · The control group in this study was designated as yellow maize + lutein fortification

^g · The control group in this study was designated as yellow maize + lutein fortification, and the exact amount was not specified in the paper, these data are estimated from Fig. 2A in the paper.

^h · Produced marigold flower meal (*Tagetes erectus*, TE) and spinach (*Spinacia oleracea*, SO) as carotenoid sources (mixture of 25% TE and 75% SO).

ⁱ · The exact amount was not specified in the paper, these data are estimated from Fig. 1 in the paper.

2. Basic features of carotenoids

Because of lipophilicity, carotenoids have very low solubility in water and are soluble in most organic solvents. To date, more than 1100 different carotenoids have been identified from various natural sources (Yabuzaki, 2017). However, only a small proportion of carotenoids are present in human foods, and even fewer carotenoids can be found in animal-derived food or applied as feed additives. The most concerned and researched carotenoids mainly include α -carotene, β -carotene, lycopene, lutein, zeaxanthin, β -cryptoxanthin, astaxanthin, and canthaxanthin, which are also the focus subjects of this paper. As shown in Fig. 1A, some carotenoids mentioned above contain 40 carbon atoms with a long carbon chain skeleton that contains a variable number of conjugated double bonds. The special structure of carotenoids that gives them the property to absorb visible light conferring on them the pigment character in the yellow to red range (Ribeiro et al., 2018). Hence, carotenoids provide chromatic colors for many plants, as well as animals, especially the color of yolk is deeply affected by these pigments. In addition, the presence of conjugated double bonds is also the basis for the antioxidant capacity of carotenoids, which allows these compounds to quench free radicals efficiently (Zerres & Stahl, 2020).

There are many ways of classifying carotenoids depending on different definition. According to the chemical composition, those formed only by carbon and hydrogen atoms are termed carotenes

(α -carotene, β -carotene, lycopene), whereas carotenoids containing oxygen besides carbon and hydrogen are known as xanthophylls (lutein, zeaxanthin, β -cryptoxanthin, astaxanthin, and canthaxanthin) (Jing et al., 2022). In xanthophylls, oxygen can be present in different functional groups, such as hydroxyl, carbonyl, epoxide, and other oxygenated groups, these structures lead to a more polar nature than carotene (Saini et al., 2022). Carotenoids can also be divided into provitamin A and non-provitamin A compounds based on whether they can be enzymatically converted into vitamin A. The provitamin A carotenoids possess at least one β -ionone ring along with the polyene chain, and theoretically, β -carotene has the highest vitamin A activity among them because it possesses two β -ionone rings (Debelo et al., 2017). Of note, when the provitamin A carotenoids are ingested by poultry and livestock, they can be converted into vitamin A in the animals' bodies, and can also be accumulated intact in many animal products. We discussed a few relevant literatures in Section 5 of this paper.

In general, natural carotenoids are mostly in their *all-trans* (*all-E*) configuration, which seems to be the most stable (Rodriguez-Concepcion et al., 2018). However, each carotenoid can potentially form multiple geometrical isomers due to a conjugated system of double bonds characteristic of these kinds of compounds (Boon et al., 2010). The most common *cis*-isomers (*Z*-isomers) are 9-*cis*, 13-*cis*, and 15-*cis* carotenoids, Fig. 1B showed the different *cis* β -carotene. Several researchers have investigated the differences in biological functions of

different geometrical isomers carotenoids. Some of them pointed out the *cis*-isomers of lycopene, β -carotene, and lutein had higher bioavailability and tissue accumulation efficiency than the *all-trans* isomers in rats (Honda et al., 2021). Moreover, the *cis*-isomers exhibited greater antioxidant and anti-inflammatory activities compared with the *all-trans* isomers, hence the *cis*-isomers carotenoids might lead to more remarkable health benefits (Honda, 2023; Yang et al., 2019). In addition, there are some carotenoid molecules that contain chiral centers and can be present in the form of the optical isomers, where zeaxanthin is shown in Fig. 1C. Several kinds of geometric or optical isomers of carotenoids have been found in livestock products. For example, a study in our laboratory showed that when supplemented with astaxanthin microcapsules powder (byproduct from *Haematococcus pluvialis*) in the diet of laying hens, the ratio of 9-*cis* and 13-*cis* astaxanthins accounted for about half of the total astaxanthin in astaxanthin-fortified eggs, and the different astaxanthin geometric isomers were all increased in yolks following the supplementation dose (Dansou et al., 2021). Honda et al. prepared tomato oleoresins having different lycopene *cis*-isomers contents and then added to the diet of laying hens. They found that as the *cis*-isomers content in diet increased, the total lycopene and *cis*-isomers lycopene in the egg yolks were also increased (Honda et al., 2019). Levin et al. demonstrated that the 9-*cis* isomer could be stored in the livers of chicks when they were fed oil-soluble mixtures of *all-trans* and 9-*cis* β -carotene (Levin et al., 1994). Rasmussen et al. reported that a small amount of *meso* (3*R*,3'*S*)-zeaxanthin could be detected in egg yolks from hens fed on *meso* (3*R*,3'*S*)-zeaxanthin-containing feeds (Rasmussen et al., 2012). Because of the high cost and difficulty in determining the different carotenoid isomers, most research on carotenoids in animal-derived foods still focuses on the detection of *all-trans* carotenoids, which can be seen in next section. In addition to being present as different isomers, carotenoids can also be associated with other molecules. In particular, a part of xanthophylls that have at least one hydroxyl group can be associated with fatty acids and form xanthophyll esters (Mariutti & Mercadante, 2018). These kinds of xanthophylls, such as lutein, zeaxanthin, β -cryptoxanthin, and astaxanthin, can be found in many fruits and flowers in the free form or acylated with fatty acids. Mass spectrometry or nuclear magnetic resonance spectroscopy is frequently required for identification of xanthophyll esters, and appropriate extraction conditions and instrument parameters need to be explored for different samples. Moreover, almost no standards for xanthophyll esters are commercially available, the standards mentioned in a few studies were obtained by synthesis, making it very difficult to quantitate such kinds of compounds accurately (Mercadante et al., 2017). In the current study involving xanthophyll esters, researchers mostly chose plants as the subject, available information in animal-derived foods is very limited. In the future, it is believed that more and more information about these carotenoid isomers and esters will be available as detection techniques improve.

3. Deposition characteristics of carotenoids in livestock products

Carotenoids have been widely used as feed additives in animal husbandry, and these bioactive compounds produced by microorganisms has reached a high level of maturity in recent years, gradually replacing chemically synthesized carotenoids and playing a better role in health benefits (Jing et al., 2022; Mapelli-Brahm et al., 2020; Saini & Keum, 2019). Numerous studies have confirmed that this class of bioactive compounds can exert positive effects on promoting the growth and reproduction of poultry and livestock (Kerr et al., 2015; Nabi et al., 2020; Noziere et al., 2006), β -carotene and other provitamin A carotenoids are of great significance in preventing vitamin A deficiency in poultry and livestock caused by rapid growth and production pressure (Green & Fascetti, 2016). However, much research only focuses on the physiological functions and health benefits of carotenoids when used as dietary supplementation in the diet of animals, while neglecting the

deposition and distribution of carotenoids in the body after animal uptake. Strikingly, there is an increasing interest in broadening new dietary sources for carotenoids (Meléndez-Martínez et al., 2022), eggs and milk have received great attention as excellent carriers of carotenoids. Some studies have also involved the content of carotenoids in different meat, meanwhile, some animal offal, especially the liver, are also regarded as rich in carotenoids. Therefore, the laws and characteristics of the deposition of carotenoids in poultry and livestock have been gradually revealed by more and more studies. This section will be combined with relevant literatures to introduce and summarize the current situation of carotenoids in livestock products.

For the various studies listed in Table 1, research on the deposition of carotenoids in egg yolks accounted for the vast majority, from which it can be seen that eggs have a special advantage as carriers for the enrichment of these lipid-soluble nutrients. Moreover, the experimental procedures of all studies are basically consistent. Namely, after dietary supplementation of carotenoids in the diet of animals for a period of time, the samples of eggs or milk, as well as meat or liver (after slaughter) were collected. Then, different organic solvents were selected as extraction reagents for different samples, and the techniques of high-performance liquid chromatography or supercritical fluid chromatography (or both of them further supplemented with tandem mass spectrometry) were applied subsequently to identify and detect the corresponding carotenoids. Based on the results of various studies in Table 1, we have summarized some laws and characteristics of the deposition and enrichment of carotenoids in livestock products. First, when poultry and livestock have noncarotenoids fortified feed, the varieties and amounts of carotenoids in the products are very limited. However, with increasing levels of carotenoids supplemented into the diet, regardless of the dietary source, the amount of carotenoids in livestock products was increased accordingly within limits. The different results of lycopene (Honda et al., 2019), β -carotene (Condrón et al., 2014; Jin et al., 2015; Miao, Yang, et al., 2023), lutein (Skřivan, Marounek, Englmaierová, & Skřivanová, 2016; Xu et al., 2014), zeaxanthin (Skřivan et al., 2016) and astaxanthin (Dansou et al., 2021; He et al., 2023) in egg yolks, meat or milk proved this rule generally. Second, there seems to be a certain upper limit for the deposition of carotenoids in livestock products. When the carotenoids in the diet are at a high level, the deposition amount rate of increase slows and efficiency becomes low. The results of Jiang et al. showed that after 21 days of feeding, the amounts of β -carotene in yolk were higher when the supplementation levels were 20 mg/kg feed than 40 mg/kg (Jiang et al., 1994). Other research involved in the enrichment of astaxanthin in eggs pointed out that the deposition rate of astaxanthin in eggs became lower when the diet was supplemented with astaxanthin at 42.6 mg/kg compared with 21.3 mg/kg under the same feeding time (Dansou et al., 2021). In addition, Jin et al. found that there was no significant difference in the β -carotene amount in the liver of steers that received supplementary β -carotene at concentrations of 600, 1200, or 1800 mg/day for 90 days (Jin et al., 2015). Hence, when carotenoid intake by animals was too high, this may lead to its deposition in the body reaching a plateau, and excess carotenoids could be excreted from the body. Third, according to the research about the amount carotenoids in egg yolks with feeding time, the deposition of supplementation carotenoids in egg yolks increased gradually with the feeding time at the early stage of the experiment, and it would take approximately two weeks for carotenoid amounts to reach a steady plateau in the egg yolk (Miao et al., 2023; Ortiz et al., 2021; Zhao et al., 2023). Whether this law applies to other livestock products, further research is needed for verification. Finally, in view of the egg yolk amounts of lutein and astaxanthin being more than that of lycopene and β -carotene under the same addition level in feed, it is supposed that the xanthophyll may be easier to absorb and deposit in laying hens than carotene. Our previous study also showed that even with the fortification of β -carotene in eggs, lutein and zeaxanthin in eggs still account for a large proportion of carotenoids (Miao et al., 2023). However, the situation may be the opposite in cows, a study has pointed

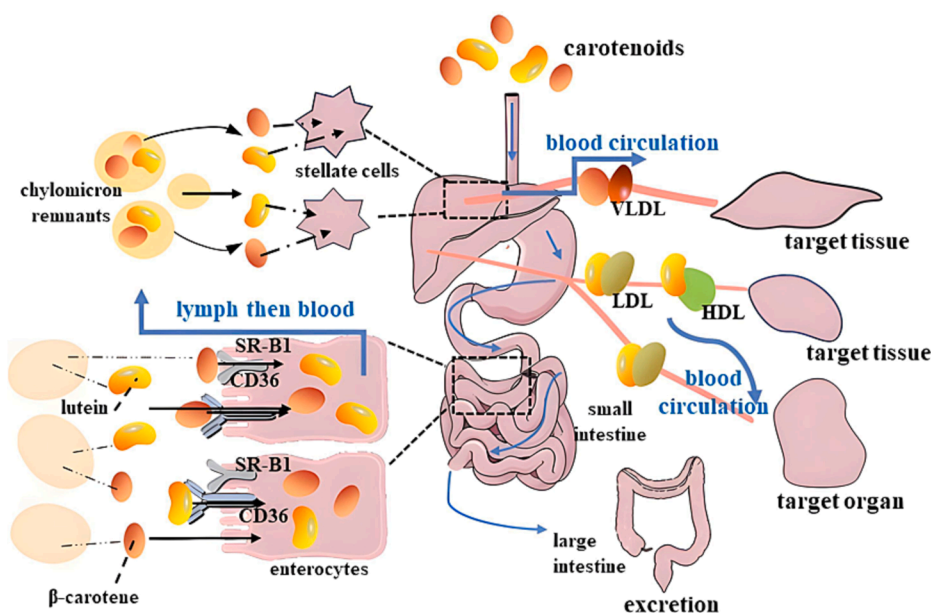


Fig. 2. Simplified schematic of absorption and transport of carotenoids from the digestion to the target organs and tissues (β -carotene and lutein as examples). Carotenoids in the food matrix pass through the esophagus and are digested in the stomach. Then in the small intestinal tract, carotenoids in the food matrix are released and solubilized in mixed micelles. Next, the carotenoids in the mixed micelles pass the enterocytes through the membrane transporters such as SR-B1 and CD36 as well simply passive diffusion. Once in the enterocytes, the intact carotenoids can be packaged into chylomicrons and delivered to the liver by lymph and blood. In addition to being deposited and stored in the liver, a part of intact carotenoids can be transported in the bloodstream to target tissues and organs (such as ovary, muscle and mammary gland) with the assistance of different lipoproteins. Finally, some carotenoids are excreted from the body through the large intestine.

out that β -carotene is the dominant carotenoid in bovine milk, comprising 75 %–90 % of the total carotenoids (Conboy et al., 2021). These might be related to the different bioaccessibility and bioavailability of carotenoids in different animal species (Desmarchelier & Borel, 2017; Lee et al., 1999), although more evidence is needed to validate this hypothesis.

At present, although more and more different carotenoids have been applied in poultry and livestock diets, they still only account for a small portion of the entire carotenoid family. A lot of research has proven that livestock products can serve as excellent carriers of carotenoids, especially for carotenoids that are not easily available in human diets. For instance, the main source of astaxanthin was previously considered to be marine food products (Higuera-Ciapara et al., 2006), but now it has broad accessibility in carotenoid-enriched eggs. In the future, as more varieties of carotenoid additives become available for industrial production, more carotenoid-enriched livestock products will emerge.

4. Metabolic pathways of carotenoids in animals

As mentioned above, after the uptake of carotenoids by animals from feed, these nutrient substances undergo a series of metabolic processes before being deposited in the livestock products, including ingestion, digestion, absorption, bioconversion, and transportation. After years of research, these processes have been studied relatively clearly, meanwhile, the functions of many genes and proteins involved in these processes have also been revealed. In this section, we have provided a brief description to introduce the pathways of carotenoids from feed to livestock products.

At an early stage after the animals eat feed, through oral mastication, stomach peristalsis, and digestive enzyme action, carotenoids can be released from the food matrix, then they are encapsulated into lipid droplets or globules and transferred to the proximal parts of the small intestine (Desmarchelier & Borel, 2017; Geng et al., 2022). In the small intestine, the main site of carotenoids' absorption (Von Lintig et al., 2020), the released carotenoids are combined with bile salts, cholesterol, fatty acids, phospholipids, and other lipid components to form

mixed micelles (Bohn et al., 2019). Next, they are delivered to the apical surface of the enterocytes (Rodríguez-Concepción et al., 2018). Of note, xanthophyll esters can be hydrolyzed to the free form by some lipases in the small intestine lumen for better absorption (Chitchumroonchokchai & Failla, 2006). When the mixed micelles contact the intestine mucous membrane, carotenoids present in them can be absorbed by simple diffusion through the brush border membrane into the enterocytes, and also can be mediated by some receptor-binding proteins (Shilpa et al., 2020). Research has proved that the scavenger receptor class B type 1 (SR-B1) and cluster determinant 36 (CD36) are the two key membrane proteins that facilitate the absorption of carotenoids from mixed micelles. Once taken into the enterocyte, a part of the carotenoids undergoes cleavage by the enzymes β -carotene-15,15'-oxygenase (BCO1) or β -carotene-9,10'-oxygenase (BCO2), resulting in the formation of different cleavage products (Bohn et al., 2022). BCO1 is responsible for catalyzing the bioconversion of provitamin A carotenoids into vitamin A, this process is detailed in the next section. The other part of the carotenoids is unprocessed and can be packaged with other lipid compositions together into chylomicrons intactly, then chylomicrons as well as their encapsulated carotenoids are released into the lymphatic system, and next delivered to the bloodstream, eventually reaching the liver in the form of chylomicron remnants (Rodríguez-Concepción et al., 2018; Shete & Quadro, 2013; Von Lintig et al., 2020). The liver is regarded as the main site that stores carotenoids and distributes them to the peripheral tissues (Bohn et al., 2019). Carotenoids are in association with various kinds of lipoproteins to be transported to target tissues and organs (such as muscle, ovary, and mammary gland) by the bloodstream (Ribeiro et al., 2018; Rodríguez-Concepción et al., 2018). In particular, because of the polar nature of lutein and zeaxanthin, they are more evenly distributed between low-density lipoprotein (LDL) and high-density lipoprotein (HDL) fractions, whereas the β -carotene and other nonpolar carotenoids are found mostly incorporated into very low-density lipoprotein (VLDL) and LDL (Bohn et al., 2019; Rodríguez-Concepción et al., 2018). Finally, these lipid-soluble bioactive compounds accompany the formation of livestock products and are deposited in them. Fig. 2 briefly illustrated the absorption and transport

Table 2

The change in vitamin A amounts in livestock products by supplementation with provitamin A carotenoids.

Carotenoid	Specie	Product	Dietary Source	Supplemental Level	Duration	Change of vitamin A ^a	Reference
β -Carotene	Laying Hens	Eggs	Commercial additive product	15, 30, 60, 120 mg/kg β -carotene in feed (vitamin A level in feed was 8000 IU/kg)	49 days	5.53, 6.01, 6.21, 5.73 μ g/g retinol, 0.11, 0.13, 0.17, 0.19 μ g/g retinyl propionate, 1.01, 1.31, 1.63, 1.82 μ g/g retinyl palmitate, 0.80, 0.86, 1.16, 1.19 μ g/g retinyl stearate, and 9.80, 10.50, 10.71, 10.50 μ g/g total vitamin A in yolk (5.26 μ g/g retinol, 0.07 μ g/g retinyl propionate, 0.87 retinyl palmitate, 0.71 μ g/g retinyl stearate, and 9.48 μ g/g total vitamin A in control group)	(Miao et al., 2023)
β -Carotene	Laying Hens	Eggs	Commercial additive product	5, 10, 20, 40 mg/kg β -carotene in feed (vitamin A level in feed was 9900 IU/kg)	21 days	11.50, 12.03, 13.93 12.88 μ g/g total vitamin A in yolk (11.62 μ g/g in control group)	(Jiang et al., 1994)
β -Carotene	Steers	Meat	Commercial additive product	5.5, 27.5, 137.5 mg/kg β -carotene in feed (vitamin A level in feed was 2200 IU/kg)	Unspecified ^b	114.3, 126.8, 143.0 ng/g retinol, 23.4, 25.7, 29.7 ng/g retinyl palmitate, 16.3, 18.2, 24.2 ng/g retinoic acid in longissimus muscle (85.5 ng/g retinol, 21.6 ng/g retinyl palmitate, 15.9 ng/g retinoic acid in control group)	(Condron et al., 2014)
β -Carotene	Steers	Meat	Commercial additive product	600, 1200, 1800 mg/day of β -carotene for per steer (vitamin A level in feed was 12500 IU/kg)	90 days	36.79, 38.03, 38.85 μ g/g total vitamin A in yolk (36.33 μ g/g in control group)	(Jin et al., 2015)
β -Carotene	Cows	Colostrum	Commercial additive product	800 mg/day of β -carotene for per cow (vitamin A level in feed DM was 6600 IU/kg)	21 days	4.83 μ g/mL milk (4.35 μ g/mL in control group)	(Prom et al., 2022)
β -Carotene	Laying Hens	Liver	Commercial additive product	15, 30, 60, 120 mg/kg β -carotene in feed (vitamin A level in feed was 8000 IU/kg)	49 days	5.64, 5.72, 5.84, 4.76 μ g/g retinol and 1.01, 1.53, 2.96, 3.61 mg/g retinyl palmitate in liver (4.55 μ g/g retinol and 0.67 mg/g retinyl palmitate in control group)	(Miao et al., 2023)
β -Carotene	Pigs	Liver	Commercial additive product	10 mg/kg β -carotene in feed (vitamin A level in feed was 4000 IU/kg)	98 days	13.0 μ g/g retinol, 242 μ g/g retinyl palmitate, 65 μ g/g retinyl oleate, 36 μ g/g retinyl stearate in liver (8.3 μ g/g retinol, 143 μ g/g retinyl palmitate, 36 μ g/g retinyl oleate, 23 μ g/g retinyl stearate in control group)	(Schweigert et al., 2001)
β -Carotene	Steers	Liver	Commercial additive product	600, 1200, 1800 mg/day of β -carotene for per steer (vitamin A level in feed was 12500 IU/kg)	90 days	478.24, 622.30, 740.34 μ g/g total vitamin A in liver (305.09 μ g/g in control group)	(Jin et al., 2015)
β -Cryptoxanthin	Laying Hens	Eggs	Engineered high-carotenoid biofortified maize	0.13 mg/kg α -carotene, 2.86 mg/kg total β -carotene, 3.12 mg/kg β -cryptoxanthin in feed (biofortified maize account for 60 % in feed and no supplementation vitamin A additive)	40 days	4.81 μ g/g total vitamin A in yolk (4.46 μ g/g in control group) ^c	(Heying et al., 2014)
β -Cryptoxanthin	Laying Hens	Liver	Engineered high-carotenoid biofortified maize	0.13 mg/kg α -carotene, 2.86 mg/kg total β -carotene, 3.12 mg/kg β -cryptoxanthin in feed (biofortified maize account for 60 % in feed and no supplementation vitamin A additive)	40 days	about 5.16 mg/g total vitamin A liver (about 2.15 mg/g in control group) ^d	(Heying et al., 2014)

^a · The data of retinol detected in samples after saponification were defined as the total vitamin A content, if the different forms of vitamin A had also been detected in unsaponifiable samples there would be an additional annotation.

^b · The paper did not clearly indicate the feeding time. The cows' average weight was 351.3 ± 12.1 kg at the beginning of the experiment, and it was 591 ± 13.9 kg when slaughtered.

^c · The control group in this study was designated as yellow maize + lutein fortification

^d · The control group in this study was designated as yellow maize + lutein fortification, and the exact amount was not specified in the paper, these data are estimated from the Fig. 1B in the paper.

processes of carotenoids in animals body, taking β -carotene and lutein as examples.

In recent years, the concepts of release rate, micellization rate, bioaccessibility, and bioavailability have been widely discussed as key parameters for evaluating the efficiency of carotenoid use in the body (Geng et al., 2022). Each of these indicators is influenced by several

factors, and many excellent reviews have summarized the related research (Castenmiller & West, 1998; Desmarchelier & Borel, 2017; Geng et al., 2022; Saini et al., 2022; Shilpa et al., 2020; Yonekura & Nagao, 2007). Among these, this paper focuses on the interaction between carotenoids, especially competitive inhibition of different carotenoids. Our laboratory has found that with the increasing uptake of

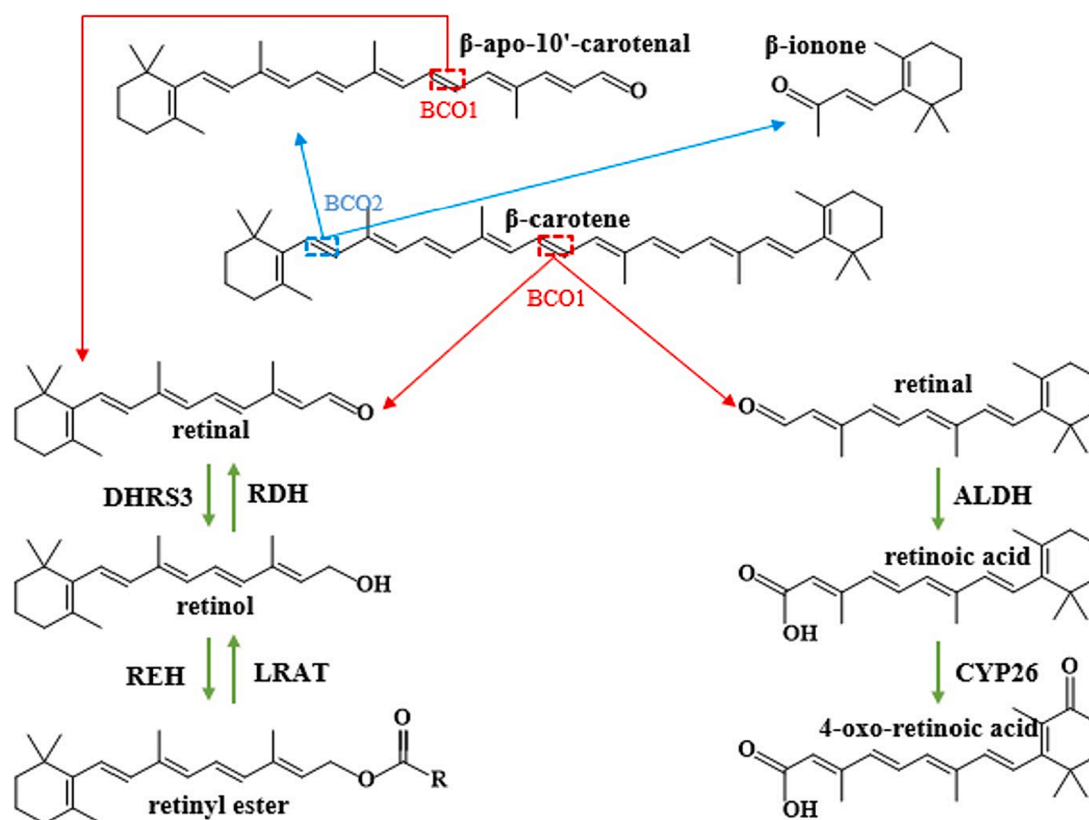


Fig. 3. Overview of β -carotene bioconversion. The β -carotene can be catalyzed by the BCO1 enzyme and results in the generation of retinal, which is subsequently incorporated into vitamin A metabolism. Furthermore, β -carotene can also be converted by mitochondrial BCO2 into apocarotenoids different from retinoids.

β -carotene in laying hens, there is a significant decrease of lutein and zeaxanthin in egg yolks (Miao et al., 2023). The research by Wang et al. showed that the continuous supplementation of large amounts of any one of the three carotenoids (β -carotene, lutein and zeaxanthin) for 28 days could depress the amount of the other carotenoids in plasma, liver and other tissues and organs (Wang et al., 2010). Similarly, after a certain amount of β -carotene was administered to humans, the amount of plasma lutein decreased by more than 50 % (Kostic et al., 1995), this phenomenon has also been reported in the study of mice (Mamatha & Baskaran, 2011). However, not all research results showed competition between carotenoids in animals, Zhao et al. demonstrated that the deposition of astaxanthin in egg yolks might lower the content of lutein, whereas it did not affect zeaxanthin (Zhao et al., 2023). Another study also showed that the enrichment of astaxanthin in egg yolks did not significantly affect the zeaxanthin content (Wang et al., 2022). In an in vitro experiment using caco-2 cells to investigate the competitions between carotenoids for their uptake, the results showed that lutein uptake was not significantly affected by the addition of phytoene and phytofluene. But the β -carotene uptake was reduced by 12.9 % and 21.6 %, respectively, after the same treatment (Mapelli-Brahm et al., 2018). The regulatory mechanism related to competition between carotenoids has not been fully explored, some hypotheses suggest that the competition mainly occurs in the process such as incorporation into mixed micelles, sharing the common membrane transporter (SR-B1), formation of chylomicron remnants, and association with lipoproteins (Mapelli-Brahm et al., 2018; Shilpa et al., 2020; Tyssandier et al., 2002; Van den Berg, 1999).

In fact, when the carotenoids are applied to animal husbandry, the factors that affect the metabolism of carotenoids in the animal body and the deposition of livestock products may become more complex, in consideration of the wide difference in the aspects of species, breeds, age, environment, feed composition, and management style. Therefore,

there is still a lot of work to be done to achieve accurate feeding and efficient utilization of carotenoids in poultry and livestock.

5. Bioconversion of provitamin A carotenoids

In addition to being deposited intact in the tissues and organs after the carotenoids are taken into enterocytes, there are also various cleavage products called apocarotenoids generated under the action of enzymes (Harrison & Quadro, 2018). Specifically, the provitamin A carotenoids can be further converted into different forms of vitamin A, thereby altering vitamin A levels in animals' bodies. We have summarized the effects of provitamin A carotenoids on the vitamin A amount in livestock products which were shown in Table 2. For the dietary supplementation with provitamin A carotenoids in the diet of poultry and livestock, it is not surprising that the different forms of vitamin A in the egg yolks, milk, and meat show increase (Condron et al., 2014; Heying et al., 2014; Jiang et al., 1994; Jin et al., 2015; Miao et al., 2023; Prom et al., 2022). However, the absolute increased amount of vitamin A was still very limited in most cases. By contrast, the change in vitamin A levels in liver was more obvious (Heying et al., 2014; Jin et al., 2015; Schweigert et al., 2001), especially for the retinyl esters. This is because the liver is the main storage site of vitamin A, and retinyl esters (retinyl palmitate) are the main storage form (Blaner, 2019).

Fig. 3 is a schematic diagram of the provitamin A carotenoids' bioconversion and interaction with retinoids metabolism (using β -carotene as an example). In theory, the central cleavage of β -carotene at the 15,15' double bond is catalyzed by the BCO1 enzyme and results in the generation of two molecules of retinal (RAL, also called β -apo-15-carotenal), whereas α -carotene and β -cryptoxanthin only undergo asymmetric cleavage and produce one molecule of RAL. So as mentioned earlier, the β -carotene is always thought to have the highest vitamin A activity (Nie et al., 2019). RAL is considered to be an important

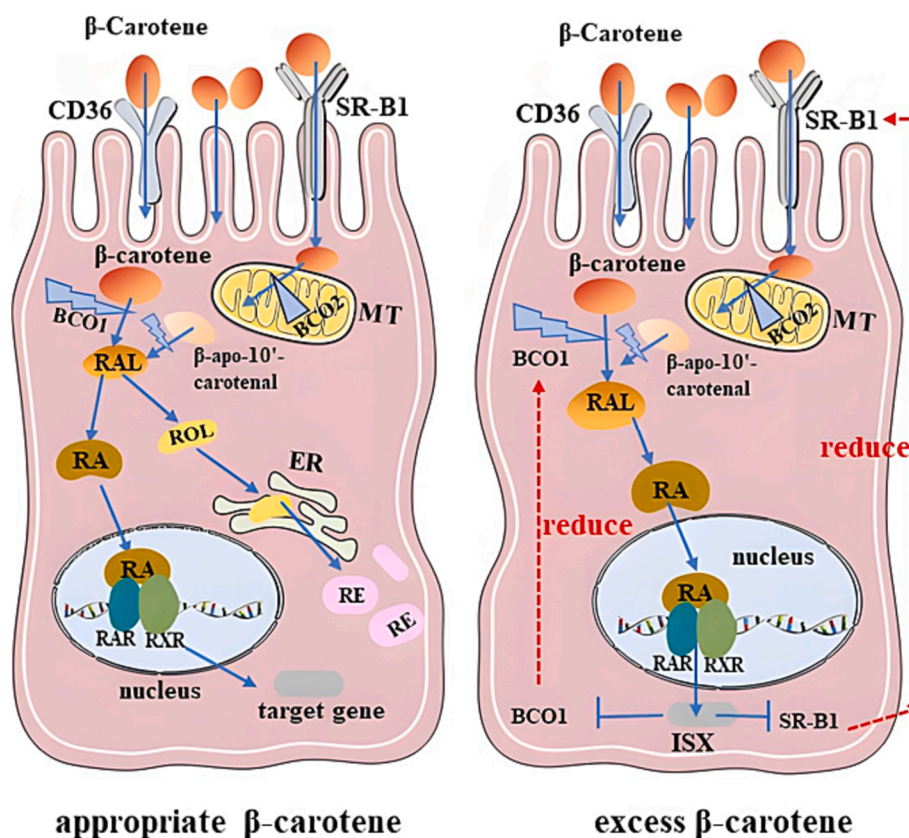


Fig. 4. Simplified schematic of the β -carotene bioconversion under appropriate or excess conditions. When the β -carotene level is too high, the negative feedback mechanism can be activated. RA moves into the cell nucleus, binds to the RARs, and then heterodimerizes with RXR. Next, the ISX was induced to repress the expression of the genes BCO1 and SR-B1.

intermediate product of the retinoids' metabolism (Russo et al., 2021). It can be reversibly reduced to retinol (ROL) by short-chain dehydrogenase/reductase (ROL can also be reversibly metabolized to RAL via the retinol dehydrogenases family), then the ROL is further converted to different forms of retinyl esters (RE) after esterification to fatty acids by the action of lecithin: retinol acyltransferase (LRAT) (Rodríguez-Concepcion et al., 2018; Von Lintig et al., 2020). Meanwhile, RAL can also be further oxidized irreversibly to retinoic acid (RA) under the catalyzation of a series of aldehyde dehydrogenases (ALDH). RA combines with the retinoic acid receptors (RARs), next the complex can heterodimerize with other class of transcription factors called retinoid X receptors (RXR) and then bind to retinoic acid response elements (RAREs) to regulate the expression of more than 500 genes (Blaner, 2019). In addition, RA can undergo further oxidative metabolism catalyzed by cytochrome P450 enzymes (CYP26A1, CYP26B1 or CYP26C1) forming several oxidized products for elimination from the body (Thatcher & Isoherranen, 2009). The various forms of retinoids formed by bioconversion of provitamin A carotenoids would be packed in chylomicron for body distribution together with those intact carotenoids and other lipid compounds for the body. Besides the central cleavage of β -carotene to yield retinal, another feasible route is the eccentric cleavage. The enzyme responsible for catalyzing this process is BCO2, the main function of BCO2 is asymmetric cleaving at the 9,10' double bond both for the provitamin A and non-provitamin A carotenoids which leads to the production of apocarotenoids. This enzyme is different from the BCO1 that is located in cytoplasm, whereas BCO2 is found in mitochondria (Raghuvanshi et al., 2015). The apocarotenoids that possess one β -ionone ring in the structure, such as β -apo-10'-carotenal, which can be further converted under catalyzing by BCO1 and eventually produce one molecule of retinal. In addition to the biological actions of provitamin A activity, apocarotenoids also have the potential to regulate cellular

functions, especially for the activation of important antioxidant signaling pathways (Sharoni et al., 2012; Barros et al., 2018; Harrison & Quadro, 2018), but these molecules have not been thoroughly studied in animal products yet.

As shown in Table 2, the bioconversion efficiency of β -carotene into vitamin A decreased with increasing doses in the diet (Jiang et al., 1994; Jin et al., 2015; Miao et al., 2023), which meant that there was a certain upper limit of the provitamin A carotenoids bioconversion. The key transcription factor, intestine-specific homeodomain transcription factor (ISX) which could be induced by RA via RARs, has been proven responsible for the regulation of negative feedback control of the bioconversion of provitamin A, this special mechanism could maintain the vitamin A homeostasis in the body and avoid hypervitaminosis A (Lobo et al., 2010; Von Lintig, 2012). When the intake of vitamin A or provitamin A carotenoids are in excess, the ISX can be activated and the expression of the genes BCO1 and the SR-B1 in epithelial cells of the intestine are repressed to control the vitamin A production by reducing the carotenoids absorption and cutting off the bioconversion pathway (Von Lintig, 2012; Von Lintig et al., 2020). The proposed regulation route is shown in Fig. 4. In modern animal husbandry, preformed vitamin A is always added to the diet as the formation of synthetic RE at a high level to improve immunity and alleviate stress (Chassaing et al., 2016; Shojadoost et al., 2021), hence the elevation of vitamin A amount in livestock products by supplementation with provitamin A carotenoids will always be limited.

6. Conclusion and prospect

As a class of multifunctional bioactive compounds, carotenoids have been widely applied in animal husbandry with different roles for a long time, including colorants, provitamins, and antioxidants. The

carotenoids can be given more stability and bioavailability due to unique fat composition of livestock products, and have received special attention from researchers and consumers. There is no doubt that available information about the deposition and enrichment of carotenoids in livestock products has made some progress in recent years. The characteristics of different carotenoids have mostly been revealed, and the dietary sources of carotenoids for poultry and livestock have been widened, as well, the production of carotenoids additives or bio-fortified maize has also gradually become easier and cheaper. In addition, the metabolism pathway of the carotenoids from feed to livestock products has been basically clarified, although some regulatory mechanisms have not yet been thoroughly explored. Meanwhile, the enrichment law of several kinds of livestock products, especially for eggs, has also been summarized. On the whole, there will be a broad prospect to produce carotenoid nutrition-fortified food with livestock products as carriers.

Currently, there are still only a few carotenoids that are enriched as nutrients in livestock products. New carotenoids should be used in the diet of poultry and livestock, especially for those carotenoids that are not commonly found in vegetables and fruit. Moreover, except for the all-trans carotenoids, the carotenoid isomers, xanthophylls esters, and apocarotenoids may have special aspects in metabolism and function, future research should contribute to developing a simple, rapid, and accurate determination method for most carotenoids and their derivatives in livestock products. Even more important, although the production of carotenoids has come a long way, more carotenoids products with high bioaccessibility and bioavailability in animals body are needed to meet the demands for carotenoid enrichment in livestock products. The technologies such as nanoparticles delivery systems can be used as a good method and have broad prospects for development. In addition, because animal species handle carotenoids differently with respect to ingestion, absorption, transportation, deposition, and bioconversion, more comparative and mechanistic studies are required to achieve more efficiency for the enrichment of carotenoids in different livestock products in the future. Finally, after the production of livestock products fortified in carotenoids, further evaluations of clinical benefits are required to establish the reduction of diseases related to nutrition. It is believed that carotenoids will continuously show excellent biological activity in the fields of functional food, food additives, animal feed and so on in the future.

CRedit authorship contribution statement

Qixiang Miao: Conceptualization, Methodology, Software, Writing – original draft. **Xueyang Si:** Investigation, Software. **Qingyu Zhao:** Formal analysis, Resources. **Huiyan Zhang:** Writing – review & editing. **Yuchang Qin:** Supervision, Project administration, Funding acquisition. **Chaohua Tang:** Writing – review & editing, Resources. **Junmin Zhang:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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