

## Review

## Diversity, physiology, and evolution of avian plumage carotenoids and the role of carotenoid–protein interactions in plumage color appearance

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## ABSTRACT

The diversity of vibrant plumage colors in birds has evolved as a direct result of social and environmental pressures. To fully understand these underlying pressures it is necessary to elucidate the mechanisms for the creation of novel plumage colors which include the metabolic transformations of dietary carotenoids and spectral tuning of the molecules within the feather protein environment. Recent advances in this field have greatly expanded the number and breadth of avian species for which plumage pigmentation has been characterized, making it possible to reconstruct the phylogenetic history of carotenoid usage in plumage. Resonance Raman and classical Raman spectroscopic techniques have been employed with great effect in the study of carotenoids *in situ*. The application of these methods have two benefits: to identify carotenoids in feathers that are unavailable for destructive sampling; and to study the spectral tuning resulting from the interaction between the carotenoids and the proteins to which they are bound. This review presents a summary of recent advances in the understanding of the molecular factors controlling the coloration of avian carotenoid plumage obtained through the application of both bioanalytical and spectroscopic methodologies.

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## Introduction

Birds constitute one of the most diverse classes of animals on Earth, exemplifying a wide variety of body types, vocalizations, and plumage displays. Their vibrant colors have apparently evolved for a number of potential reasons including social and sexual signaling, and camouflage [1–4]. A wide range of plumage colors can be produced through pigmentation or by light scattering from structural morphologies in the feathers, or by some combination of these factors [1].

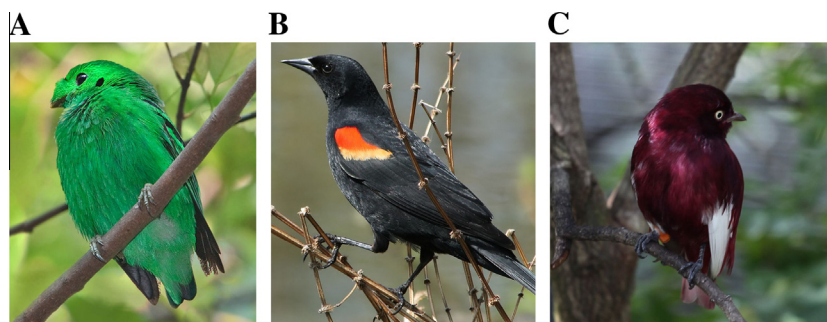
Pigments alone are capable of generating a wide range of plumage hues in the visible region of the electromagnetic spectrum. Carotenoids are a common pigment found in avian plumage, and they can appear yellow, orange, red, pink, and purple. Carotenoids can also combine with other pigments or with structural effects to create an even greater variety of colors [4,5]. A striking example of this is the plumage of the Green Broadbill, *Calyptomena viridis* (Fig. 1A), which arises from a combination of structural color arising from blue spongy medullary bars [6] and the yellow carotenoid, 7,8,7',8'-tetrahydro-zeaxanthin (Fig. 2) [7]. The result is a non-iridescent, vibrant green color that would otherwise be impossible

to create from any known avian pigments [4,8] or color producing nanostructures [5]. Carotenoids also sometimes co-occur with melanins, which span the color range from yellow or orange to brown (pheomelanins) to darker browns and black (eumelanins) [9]. In species of *Euplectes* weavers (Ploceidae) [10] dark melanin-based plumage functions to enhance the color of red patches of carotenoids, the size and hue of which are important in the territorial behavior of males [12,13]. In other species such as *Agelaius* blackbirds (Icteridae, Fig. 1B), melanins have been found to co-occur in the same patches as carotenoids, although the affect on the resulting hue remains unclear [11].

Because of the role of carotenoid pigments in avian sexual and social behavior, scientific literature on avian carotenoids has surged in recent years. Avian carotenoid diversity, physiology, and evolution was thoroughly surveyed by McGraw [4] in 2006, and the role of carotenoid-signals in avian behavior was meticulously reviewed by Svensson and Wong [3] in 2011. However, a large number of research advances since then warrant a new review of the current understanding of avian plumage carotenoids. This paper will review these advances and focus on the diversity of plumage carotenoids, metabolic pathways for the physiological modification of dietary carotenoids by birds, avian perception of carotenoid based plumage coloration, and the evolution of carotenoid use in plumage. Also discussed is the application of resonance

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**Fig. 1.** (A) *Calyptomena viridis*, (B) *Agelaius phoeniceus* and (C) *Xipholena punicea*. Photographs are reproduced under the Creative Commons Attribution-Share Alike license(s) and are attributed to the following individuals and licenses: (A) Doug Janson, (CC BY-SA 3.0); (B) Walter Siegmund, (CC BY-SA 3.0); and (C) Tom Woodward, (CC BY-SA 2.0). Photographs were cropped, but are otherwise unaltered.

Raman (rR) spectroscopy<sup>1</sup> to understanding the role of carotenoid–protein interactions in feathers which are a major factor in determining their color. Due to space limitations, this mini-review will deal only with carotenoid pigmentation in avian plumage. The reader interested in the important topic of avian integumentary carotenoids is referred to the review by McGraw [4] and recent publications by García-de Blas [14,15] and references contained therein for information on the subject.

### Diversity of avian plumage carotenoids

Carotenoids are a diverse class of molecules that typically contain 40 carbon atoms with a central polyene chain (Fig. 2), and can be classified based on their associated oxygen functions (e.g. carotenes or xanthophylls) or end-groups, (e.g. “open-chain” carotenoids denoted by the greek letter psi ( $\psi$ ), or terminal six-membered rings).

The absorption properties of a carotenoid directly correlate with the length of its  $\pi$ -electron conjugation: Carotenoids with long  $\pi$ -electron conjugated chains have a lower excited state transition energy, and thus exhibit red-shifted absorption bands relative to carotenoids with shorter  $\pi$ -electron conjugated chains [17]. The number of double bonds in the  $\pi$ -electron conjugated chain is denoted  $N$ . In carotenoids having twists about C=C double bonds (configurational isomers) or C–C single bonds (conformational isomers), or having functional groups (e.g. carbonyls) that extend the conjugation into and beyond the terminal rings, the effective conjugation length,  $N_{\text{eff}}$ , may not be equivalent to  $N$ , but can be determined by comparing the spectral properties of the molecule with another having the same linear conjugation length [17]. The diversity of carotenoid structures is further expanded by the presence of non-conjugated oxygenated functional groups (e.g. hydroxyls, methoxyls and carbonyls) associated with carbons on the terminal rings.

A review by McGraw in 2006 reported 24 different carotenoids from avian feathers [4]. Since then, careful chemical analysis of non-temperate bird species has expanded the known diversity of avian carotenoids (Fig. 2) and revealed ten carotenoids that are entirely novel [7,18–20]. Additionally, these recent works have helped elucidate the range and specificity of the metabolic transformations available to birds [7,20,21]. For example, a study on neotropical manakins (Pipridae) revealed evidence of endogenous production of rhodoxanthin [21], a carotenoid which is relatively rare in nature [16] and is associated with bright red and purple

hues in feathers [21–24]. Moreover, a broad survey of 25 species of cotingas (Cotingidae) revealed a series of novel methoxy-carotenoids that create unique purple hues (Fig. 1C) [18,19]. A similar study conducted on five genera of broadbills (Eurylaimidae) revealed two novel carotenoid structures and showcased the ability of some species to modify dietary carotenoids in ways that both shorten and lengthen the chromophore, leading to disparate color patches [7].

### Dietary accumulation of carotenoids

Carotenoids are produced *de novo* by bacteria, algae, fungi and higher plants as vital components of the photosynthetic apparatus where they are employed in light-harvesting, photoprotective and structural roles [25]. Animals acquire carotenoids through the dietary consumption of these carotenoid-containing organisms [26]. However, because they are vitamins for all heterotrophic animals [27,28] and are stored in their esterified forms in a number of internal tissues [4], carotenoids will bioaccumulate in the food chain as do other vitamins.

Of the hundreds of naturally-occurring carotenoids, birds are thought to ingest only about a dozen in their diet [4]. The number of bioavailable carotenoids is further narrowed by the ability of birds to absorb them from these complex biological matrices and mobilize them throughout the body [3,29]. The bioavailability of carotenoids varies both on a species level and on an individual level. This is because their polarity and stability, the matrix from which they are to be extracted, the interactions with other carotenoids or dietary components in the gut (fiber, lipids), and individual health status, all impact the potential for the molecules to ultimately be incorporated into carrier lipoproteins [3,4,29]. All birds maintain the capacity to mobilize carotenoids for physiological needs (e.g. in cone oil droplets [30]) but only some groups of birds have evolved the capacity to metabolically modify, transport and deposit them into their feathers [1].

Of all the carotenoids in the avian diet, lutein, zeaxanthin,  $\beta$ -carotene and  $\beta$ -cryptoxanthin (Fig. 2) are the major ones recovered from the plasma of birds [4,31]. A few other dietary carotenoids are known to be absorbed and circulated in some birds without any further modification, including the ketocarotenoids canthaxanthin and rhodoxanthin (Fig. 2) [4], although these carotenoids are likely rare in the diets of most birds. Canthaxanthin is relatively common in orange, pinkish or red feathers, and there is strong evidence from controlled dietary studies that this carotenoid can be deposited directly into the plumage [4,32] or egg yolks [4,32,33] when fed to birds. The carotenoid rhodoxanthin has been implicated in the appearance during the last century of orange coloration in the traditionally yellow tail bands in the Cedar Waxwing (*Bombycilla cedrorum*) [34,35] and of aberrant red pigmentation

<sup>1</sup> Abbreviations used: rR spectroscopy, resonance Raman spectroscopy; HOOP, hydrogen-out-of-plane; SAXS, Small-Angle X-ray Spectroscopy; fwhm, full-width at half-maximum; DDT, dichlorodiphenyltrichloroethane; IMM, inner mitochondrial membrane.

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