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Tracing the roots of avian fauna hues: A review

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Abstract

Human interest in the coloration of bird plumage has fascinated humans since ancient era. Fascination with plumage coloration stems from the rich variety of colors and patterns observed across bird species. Plumage coloration serves many functions, ranging from crypsis and camouflage to social signaling and mate choice. Plumage coloration serves a wide range of functions in aves including species recognition, inter and intra sexual signaling and camouflage. Carotenoids are the second most common pigment found in bird plumage. These are not synthesized by avian body and must be acquired from its diet. It was long thought that color of bird feathers does not change after plumage moult. The avian plumage gamut lacks saturated green, blue, purple, UV-green and UV-red colors. There may be two possibilities: these colors may be very challenging or impossible to create, or simply undesirable or poorly functioning. Plumage coloration serves a number of functions in aves including species recognition, sexual signaling and camouflage.

Keywords: Avian Fauna, Camouflage, Plumage coloration, Sexual Signaling.

Introduction

Human interest in the coloration of bird plumage has fascinated humans since ancient era. Fascination with plumage coloration stems from the rich variety of colors and patterns observed across bird species [1]. Coloration is often a sexually and socially selected trait that can signal individual quality and identity, as well as signal species identity, enhance crypsis provide thermoregulatory benefits and protect against bacteria [2]. These diverse communication signals have likely evolved in response to the avian visual system [3]. Quantifying differences in plumage coloration among morphologically similar species and subspecies can be exploited to identify taxonomic groups in field, without the additional cost in time and materials required for genetic testing. Biologists have only begun to understand how the complexity of tetrachromatic avian color perception has influenced the evolution of avian coloration [4]. Plumage coloration serves a number of functions in aves including species recognition, sexual signaling and camouflage. It is believed to help facilitate species recognition, restricting interspecies gene flow [6].

Nature of plumage coloration

Coloration of feathers is due to the pigments present in them, their structural properties or a combination of both. For most avian taxa pigments are the most important contributors to plumage coloration [7]. Structural characteristics of feathers that impart color are found in a wide range of birds and are often combined with pigments to enhance pigment based colors or create additional colors [8].

The most common avian plumage pigment is melanin. Melanin is responsible for many of the blacks, grays, browns and other earth tone colors seen in avian plumage [9]. Melanin-based pigmentation is the only mechanism of bird color production that occurs under direct cellular control, hence holding the greatest potential to generate complex pigmentation patterns. In fact, it has been shown that birds produce complex plumage patterns by modulating the presence, arrangement or differentiation of melanocytes in the developing feather follicles [4]. There are two classes of melanin, eumelanins which give rise to black and dark brown hues and phaeomelanins which are responsible for reddish brown color. In House sparrows (*Passer domesticus*) both the classes of melanin are present. They give a wide range of greyish brown

colors when present together ^[10]. Moreover, melanins are presumably cheap to produce, can be synthesized by birds themselves and may strengthen feathers ^[11, 12 & 13]. Carotenoids are the second most common pigment found in bird plumage. These are not synthesized by avian body and must be acquired from its diet ^[7]. Deposition of carotenoids or psittacofulvins (in case of parrots) produce colors rich in long wavelength reflectance (red, yellow) ^[16]. Lutein and zeaxanthin are the most abundant carotenoids in the diet and blood of birds (McGraw, 2006). Red ornaments displayed by many animal species are often the result of biotransformation of the cited yellow hydroxycarotenoids in red ketocarotenoids such as astaxanthin or canthaxanthin (17A). The green plumage coloration of many parrot species is a result of yellow coloration from psittacofulvin pigments and a blue reflectance derived from the feather structure, which combine to create the green color that we perceive ^[8]. Parrots produce psittacofulvins, a type of red to yellow pigment that is not found in any other type of vertebrate. The researchers say, it was a surprise that a mutation in MuPKS causes a noticeable color change. In other birds, enzyme is not expressed in feathers ^[23].

The wild phenotype of *Columba livia* is slate blue-grey with a black tail-band and two black wingbars. The grey and black are the result of different distributions of the same amount of black melanin granules. In the grey parts the black granules are clumped and, due to the reflection of the light, what we see appears blue-grey. In the black parts the granules are spread equally and the colour appears black ^[15]. Because the hue and intensity of color in part reflects the quality of diet (at least the quantity of carotenoids in diet) ^[17, 18]. Carotenoid-derived plumage coloration can communicate habitat quality, foraging efficiency and individual health to conspecifics and there has been considerable interest in their role as honest-signals of fitness within the frame work of sexual selection ^[19]. Psittacofulvins and carotenoids largely occupy similar portions of color space, but are never found together ^[20]. Other uncommon classes of pigments include porphyrin pigments which provide reddish-brown plumage coloration in a few avian orders (such as Bustards, Nighthawks, Owls, and Turacos) ^[21].

Structural colors

Over evolutionary time, structural colors have greatly expanded the gamut of avian plumage colors and also created colors unachievable by plants. ^[39]. Structural colors are derived from nano-scale structures that diffuse or reflect light in specific ways. Structural colors are produced from the interaction of light waves scattering across the interface of materials with different physical refraction properties ^[24]. Often structural colors are combined with pigment-based colors, either to reinforce a single color, or to create a new color (such as green in parrots) and in some cases structural coloration can be masked by pigment based coloration ^[25]. In particular, UV reflectance, which is invisible to the human eye and has received considerable interest recently, is a structurally based color ^[26]. Variation in structure coloration appears to reflect genetic variation ^[27] and condition of individuals has been shown to modify UV coloration ^[28, 29] studied origins of avian blue from representatives of almost every group that evolved blue coloration. He discovered that as a blue feather grows, stringy keratin molecules separate from water in each cell. When the cell dies, the water dries away and is replaced by air. This leaves a structure of keratin

protein interspersed with air pockets. When white light strikes a blue feather, the keratin pattern causes red and yellow wavelengths to cancel out each other, while blue wavelengths of light reinforce and amplify one another and reflect back to the beholder's eye. (29A)

Variations in Plumage Coloration

While there is evidence of condition dependent variation in coloration, particularly for carotenoid based pigmentation, these environmental variations influence degrees of color expression, not the color location, pattern, or particular colors expressed. In this sense, plumage coloration could be a valuable character for inferences about taxonomic relationships. Despite the intense interest in avian plumage coloration, the genetic basis for plumage coloration is poorly understood ^[30, 31]. Evidence suggests multiple sources for genetic code of coloration, from single-locus to polygenic effects and different genes presumably control different types of pigment coloration and structural coloration. A number of studies primarily conducted on domestic and cage birds, demonstrated simple Mendelian patterns of inheritance ^[32]. The gene, MC1R, plays an important role in expression of melanin in many vertebrates, where a single point mutation produces dark or light plumage morphs depending on which of the two alleles are expressed ^[33, 34]. Wide variety of vertebrates, from flamingos to trout, loses their bright yellow/orange/red coloration when they are kept in captivity ^[36]. Studies have shown that psittacofulvin pigments can with environmental conditions that directly affect individuals (drought conditions) ^[25] and individual conditions can influence UV coloration ^[28, 29]. These observations show that some birds can utilize the small amount of dietary carotenoid pigments in seeds to fully express ornamental coloration: but even these species will lose their coloration if access to carotenoids drops below a certain level. Early environment is also implicated in causing variation in adult and juvenile plumage coloration. In blue net nestlings, the development of both structural (UV/blue) and carotenoid based (yellow) plumage has been shown to be associated with nestling body condition and nest environment ^[40]. Blue UV coloration depends on the microstructure of the plumage ^[41] whereas yellow coloration is influenced by carotenoid contents ^[42] and by microstructure ^[43]. It was long thought that color of bird feathers does not change after plumage moult. However, the coloration of plumage due to deliberate staining (with uropygeal secretion) i.e. with cosmetic purposes may help individuals to communicate their quality to conspecifics, as observed in flamingos (*Phoenicopterus roseus*) the colour of plumage changes with the application of carotenoid-rich secretions over it by the birds themselves, that the intensity of coloration increases with the quantity of pigments applied on to the plumage, that the concentration of carotenoids in the uropygial secretions changes seasonally in accordance with plumage color, that for the application of such carotenoids the birds use specific behavior and that the more colorful birds start breeding earlier. All this is consistent with the notion that pigments in the uropygial secretions are used as cosmetic, and that this has a signaling function. In addition to cosmetic coloration, the color of feathers can change over time due to physical abrasion of keratin structure UV bleaching of pigments. Several studies have documented seasonal changes in coloration of birds, including a study of Blue Tits (*Parus caeruleus*) where UV coloration declined in lightness, though not chroma and hue ^[38]. While the changes in feathers due to

wear generally reduce color intensity, in some species the overall plumage appears brighter as feathers wear^[39].

Constraints on plumage coloration

The avian plumage gamut lacks saturated green, blue, purple, UV-green and UV-red colors. There may be two possibilities: these colors may be very challenging or impossible to create, or simply undesirable or poorly functioning. Together, physical and physiological constraints on signal production may render certain colors unattainable. Birds can physically evolve such colors, but natural and sexual selection dictate that they do so rarely^[44].

Each class of feather pigments is highly constrained to a relatively tiny volume of the color space. Consequently, there are many regions in the avian color space that cannot be realized with the few classes of available pigments. For example, there are no blue pigments in bird feathers and green porphyrin pigments are very rare^[44] providing a narrow range of colors. Structural colors provide a much broader range of colors than pigments. To some extent, the distribution of avian plumage is an epiphenomenon of tetrachromatic visual system that evolved early in vertebrates and has been maintained in birds for capabilities beyond those required just for signal processing. Evolutionary novelties in exogenous pigment metabolism have clearly permitted phylogenetic expansions of the color gamut. Social and sexual selection for new plumage colors have likely contributed to the evolution of metabolic innovations in carotenoid pigment structure. For example, the physiological alteration of yellow xanthophylls (which are acquired from the diet) into red/orange ketocarotenoids for deposition in the plumage has evolved independently in many different lineages of birds^[45].

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