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YOU CAN'T JUDGE A PIGMENT BY ITS COLOR: CAROTENOID AND MELANIN CONTENT OF YELLOW AND BROWN FEATHERS IN SWALLOWS, BLUEBIRDS, PENGUINS, AND DOMESTIC CHICKENS

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Abstract. The two main pigment types in bird feathers are the red, orange, and yellow carotenoids and the black, gray, and brown melanins. Reports conflict, however, regarding the potential for melanins to produce yellow colors or for carotenoids to produce brown plumages. We used high-performance liquid chromatography to analyze carotenoids and melanins present in the yellow and brown feathers of five avian species: Eastern Bluebirds (*Sialia sialis*), Barn Swallows (*Hirundo rustica*), King Penguins (*Aptenodytes patagonicus*), Macaroni Penguins (*Eudyptes chrysolophus*), and neonatal chickens (*Gallus domesticus*). In none of these species did we detect carotenoid pigments in feathers. Although carotenoids are reportedly contained in the ventral plumage of European Barn Swallows (*Hirundo rustica rustica*), we instead found high concentrations of both eumelanins and phaeomelanins in North American Barn Swallows (*H. r. erythrogaster*). We believe we have detected a new form of plumage pigment that gives penguin and domestic-chick feathers their yellow appearance.

Key words: Aptenodytes patagonicus, *carotenoids,* Eudyptes chrysolophus, Gallus domesticus, Hirundo rustica, *melanins,* Sialia sialis.

No Puedes Juzgar un Pigmento por su Color: Contenido de Carotenoide y Melanina de Plumas Amarillas y Marrones en Golondrinas, Azulejos, Pingüinos y Gallinas Domésticas

Resumen. Los dos tipos principales de pigmentos que las aves incorporan en sus plumas son carotenoi-

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des, para desarrollar plumajes rojo, naranja o amarillo, y melaninas, para adquirir coloración negra, marrón, gris o tonalidades color tierra. Sin embargo, existe información conflictiva sobre la potencial coloración de plumas amarillas basadas en melanina y la presencia de caroteniodes en el plumaje marrón de ciertas especies. En este estudio, usamos cromatografía líquida de alto rendimiento para analizar los tipos y cantidades de carotenoides y melaninas presentes en las plumas amarillas y marrones de cinco especies de aves: el azulejo *Sialia sialis* y la golondrina *Hirundo rustica*, los pingüinos *Aptenodytes patagonicus* y *Eudyptes chrysolophus* y el plumón natal amarillo de la gallina doméstica *Gallus domesticus*. En ninguna de estas especies detectamos pigmentos carotenoides en las plumas. A pesar de que los carotenoides han sido encontrados en el plumaje ventral de la golondrina *Hirundo rustica rustica*, nosotros en cambio encontramos altas concentraciones de eumelaninas y feomelaninas en *H. r. erythrogaster* y en azulejos que variaron entre individuos y regiones de plumaje. Creemos que hemos detectado una nueva forma de pigmento de plumaje que le da a las plumas de pingüinos y pollos domésticos su apariencia amarilla.

Carotenoids and melanins are the two primary types of pigment incorporated into bird feathers (Fox 1976). Red, orange, and yellow plumage colors are typically the result of carotenoid pigments, whereas black, brown, gray, and earth-toned colors are created by the presence of melanins (Fox and Vevers 1960). Many classes of carotenoids exist, based on their molecular structure (e.g., carotenes, xanthophylls), and these may confer different colors on an animal (Goodwin 1984). In contrast, melanin pigments come in only two main forms, eumelanin and phaeomelanin, and the relative ratio of these two melanins can influence feather coloration (e.g., domestic pigeons [*Columba livia*]; Haase et al. 1992). Black and gray feathers are typically thought to contain predominantly eumelanins, whereas earth-toned feathers are dominated by phaeomelanins, much like red human hair (Fox and Vevers 1960).

Interestingly, some have attributed the yellow color of feathers in certain species to melanins. Völker (1934), for example, classified the yellow plumage pigmentation of domestic chicks (*Gallus domesticus*) as melanin based. Still others have reported that brown plumage, particularly in the Barn Swallow (*Hirundo rustica rustica*), contains a host of colorful carotenoid pigments (Stradi 1998, Camplani et al. 1999, Saino et al. 1999). These biochemical reports seem to contradict the normal appearance of the respective plumage colors, so we investigated both the carotenoid and melanin content of yellow and brown feathers from five avian species, including these two mentioned above. We sampled feathers from wild Eastern Bluebirds (*Sialia sialis*) and Barn Swallows from North America (*Hirundo rustica erythrogaster*), from wild King Penguins (*Aptenodytes patagonicus*) and Macaroni Penguins (*Eudyptes chrysolophus*) on the Crozet archipelago, and from domestic chicks. We used high-performance liquid chromatography (HPLC) to determine whether carotenoids, melanins, or both types of pigment were present in the colorful plumage of these species.

METHODS

SPECIES DESCRIPTIONS AND FEATHER COLLECTION

Barn Swallows. The ventral plumage of North American Barn Swallows is rufous or chestnut colored (Brown and Brown 1999). This trait honestly signals mate quality in both males and females and varies most among individuals in the color of specific body regions (e.g., throat, breast, belly, vent; Safran and McGraw 2004). As part of an ongoing study of Barn Swallows in Tompkins County, New York (42°27′N, 76°29′W), RJS collected up to 10 pigmented ventral feathers from three males and three females in March and April 2001. Feathers were stored attached to index cards in the dark at room temperature and analyzed for carotenoids in October 2001 and melanins in December 2001 and January 2002. Carotenoid analyses were performed on a group of five feathers from each bird; the remaining feathers from each body region were pooled for all birds to understand the variation in eumelanin and phaeomelanin pigmentation across the colored plumage areas.

Eastern Bluebirds. Eastern Bluebirds display orange-red plumage on the breast (Gowaty and Plissner 1998) and exhibit marked within- and between-sex variation in the size of this feather patch (Siefferman and Hill 2004). We characterized the pigment composition from a standardized location on the breast patch (the center). As part of a study of bluebirds in Lee County, Alabama (32°36′N, 85°30′W), LMS collected three pigmented breast feathers from six males and six females in March 2002. These feathers were stored in envelopes in the dark at room temperature and analyzed for the presence of carotenoids (in three males and three females) and melanins (the remaining three of each sex) in April and May 2002.

King and Macaroni Penguins. King Penguins have flashy auricular and chest patches of yellow-orange feathers (Jouventin 1982). Macaroni penguins develop yellow-orange filamentous forehead plumes (Warham 1975, Jouventin 1982). As part of a study of penguins on Possession Island, Crozet Archipelago in the Indian Ocean (46°27′S, 51°51′E), PMN and FSD collected ca. 100 breast and auricular feathers from three King Penguins and single feather plumes from two Macaroni Penguins (all of unknown sex) in November–December 2001. These feathers were folded within index cards and stored in sealed plastic packets at 22°C until pigment analysis in March–May 2002. We separately analyzed ca. 10 breast and 10 auricular feathers from all King Penguins and halves of each Macaroni Penguin forehead plume for carotenoids and melanins.

Domestic chicks. Yellow downy feathers were collected from two 1-day-old single-comb white leghorn domestic chicks (Cornell K-strain; one in February 2002 and one in May 2002). All feathers were stored in the dark in a plastic bag. In March 2002 and again June 2002, ca. 10 feathers from each bird were analyzed for both carotenoids and melanins.

CAROTENOID EXTRACTION AND CHROMATOGRAPHY

All carotenoid analyses were conducted in the laboratory of RSP. We used both thermochemical (Hudon and Brush 1992) and mechanical (Stradi et al. 1995) extraction techniques to isolate carotenoid pigments from bird feathers. Prior to both procedures, feathers from all species were washed separately in ethanol and hexane for 30 min each and blotted dry. We trimmed 3–5 mg of pigmented barbules and split them into equal portions for the two extractions. For the thermochemical method, we placed the colored barbules in 1 mL acidified pyridine (3 drops HCl in 50 mL pyridine) and held them at 95°C under argon for 4 hr. The solution was then cooled to room temperature, and we twice extracted the lipids with 1 mL distilled water and 5 mL hexane:*tert*-butyl methyl ether (1:1, v/v). We centrifuged the mixture for 5 min at 3000 rpm, removed the supernatant, and evaporated the solvent to dryness under a stream of nitrogen. For the mechanical extraction, we ground the trimmed barbules for 15 min at 30 Hz in a Retsch® MM200 mixer mill (Retsch Inc., Irvine, California) using a zirconia grinding jar and balls (fitted with a Teflon® O-ring) and in the presence of 3 mL methanol. Again, the solution was centrifuged for 5 min at 3000 RPM and the supernatant removed and evaporated under nitrogen. For both extraction procedures, we ran a positive control (yellow, carotenoid-pigmented contour feathers from American Goldfinches [*Carduelis tristis*]; McGraw et al. 2001, McGraw, Hill, et al. 2002) along with our samples.

For HPLC analysis, the purified extracts were redissolved in 200 μL HPLC mobile phase (acetonitrile: methanol:chloroform, 46:46:8, v/v/v) and 50 μL was injected into a Waters™ 717plus Autosampler HPLC (Millipore Corp., Bedford, Massachusetts) fitted with a Develosil RPAqueous RP-30 column (250 × 4.6 mm ID; Nomura Chemical Co. Ltd., Aichi, Japan) and an Eppendorf TC-50 column heater (Hamburg, Germany) set at 32°C (McGraw, Adkins-Regan, and Parker 2002). We used an isocratic system (Hewlett-Packard 1050 Series Isocratic Pump) at a constant flow rate of 1.2 mL min^{-1} for 90 min to allow sufficient time for both xanthophylls and carotenes to elute. Data were collected from 250–600 nm using a Waters™ 996 photodiode array detector (Waters Chromatography, Milford, Massachusetts). The minimum detection limit of this instrument is 0.0001 absorbance units, which amounts to approximately 0.005 mg of carotenoid per gram of pigmented feather portion using this protocol.

MELANIN EXTRACTION AND CHROMATOGRAPHY

All melanin procedures were performed in the laboratory of SI and KW. Methods of analyzing both phaeomelanins and eumelanins in bird feathers follow those in Haase et al. (1992). To determine eumelanin content, colored feather barbules were homogenized in water (1:100, w/v) and 400 μL of the homogenate were added to 800 μL 1 M H_2SO_4, oxidized with 3% $KMnO_4$. The resulting oxidation product (pyrrole-2,3,5-tricarboxylic acid; PTCA) was analyzed via HPLC (Ito and Fujita 1985, Ito and Wakamatsu 1994). Phaeomelanins were examined by hydrolyzing 200 μL feather homogenate with 500 μL 57% hydriodic acid at 130°C in the presence of H_3PO_2 for 24 hr, and subsequently analyzing the product (4-amino-3-hydroxyphenylalanine; 4-AHP) using HPLC with electrochemical detection (Wakamatsu et al. 2002). Amounts of eumelanin and phaeomelanin were obtained by multiplying the amount of PTCA and 4-AHP by conversion factors of 50 and 9, respectively (Ito and Fujita 1985, Wakamatsu and Ito 2002). Analyses of all samples were performed in duplicate, and we report averages of these values here.

RESULTS

In none of the feathers from the five species studied did we detect carotenoid pigments. Lipid-soluble extracts were colorless; brown and yellow feathers retained their respective hues. In contrast, our feather standards from American Goldfinches yielded 0.2–6 mg carotenoid per g of feather (McGraw, Hill, et al. 2002).

In the chestnut ventral feathers from both Eastern Bluebirds and Barn Swallows, we found substantial amounts of both eumelanin and phaeomelanin (Table 1). Eumelanin concentrations were higher than phaeomelanin in all bluebird and swallow samples except one: Barn Swallow throat feathers. Throat feathers in Barn Swallows also contained the highest concentration of pigments among the four plumage regions we sampled in this species. In our bluebird samples, male feathers tended to contain more pigments overall, and a higher percentage of eumelanin pigments, than those of females (Table 1).

In the breast and auricular feathers of King Penguins, we also detected a small amount of melanin, primarily eumelanin (Table 1). However, there remained much yellow pigment in the feather that could not be accounted for by either carotenoids or melanins. Yellow plumes from Macaroni Penguins similarly contained very low levels of melanin (Table 1) and remained brilliant yellow after pigment analyses. The same was true for the yellow natal down of domestic chicks, as we were unable to detect any appreciable amounts of melanins or carotenoids in these feathers (Table 1).

DISCUSSION

The aim of this study was to analyze the extent to which carotenoid and melanin pigments determine yellow and brown feather coloration in a diverse group of bird species. Although carotenoids and melanins are not the only two forms of yellow or brown pigments in animals (Needham 1974, Brush 1978), several recent behavioral-ecology studies in birds have assumed that yellow integumentary features (e.g., feathers, beaks) are carotenoid based (e.g., Irwin 1994, Massaro et al. 2003), and that certain rust-colored plumage colors contain a high concentration of carotenoid pigments (e.g., Møller and Mousseau 2001).

We first characterized the plumage pigments contained within the chestnut ventral feathers of male and female Barn Swallows and Eastern Bluebirds from North America. We found no carotenoid pigments in the colorful throat, breast, belly, or vent feathers of North American swallows or in the breast feathers of bluebirds. This was a surprising result, as it is reported in the literature that the chestnut-colored facial and throat plumage in the European subspecies of Barn Swallows (*H. r. rustica*) contains carotenoid pigments (e.g., Stradi 1998, Camplani et al. 1999, Saino et al. 1999). Stradi (1998) first published a complete HPLC chromatogram profiling the suite of hydroxy- and keto-carotenoid pigments that are found in the rust-colored

TABLE 1. Mean eumelanin and phaeomelanin concentrations (mg pigment per g pigmented feather barbule) in yellow and brown feathers from swallows, bluebirds, penguins, and domestic chicks. Blank entries indicate that pigment concentrations were below our detection limit (0.01 mg g^{-1}).

Species (Plumage color)	Bird ID	Sex	Body region	Eumelanin	Phaeomelanin
Barn Swallow[a]	pooled	pooled	throat	3.2	6.6
(chestnut or rufous)	pooled	pooled	breast	1.0	0.5
	pooled	pooled	belly	0.7	0.4
	pooled	pooled	vent	1.3	1.0
Eastern Bluebird	1	male	breast	4.5	2.8
(orange-red)	2	male	breast	4.6	2.0
	3	male	breast	4.4	2.9
	4	female	breast	2.8	0.9
	5	female	breast	3.0	0.7
King Penguin	1	unknown	breast	0.4	0.04
(yellow-orange)	1	unknown	auricular	0.4	0.04
	2	unknown	breast	0.2	0.02
	2	unknown	auricular	0.2	0.02
	3	unknown	breast	0.4	0.02
	3	unknown	auricular	0.7	0.05
Macaroni Penguin	1	unknown	head plume		0.16
(yellow-orange)	2	unknown	head plume	0.3	0.2
Domestic chicken	1	unknown	natal down		
(yellow)	2	unknown	natal down	0.06	

[a] North American subspecies. Ventral feathers were pooled from 3 males and 3 females and analyzed by body region.

throat feathers of European *H. rustica*. Saino et al. (1999) later asserted, however, that this reddish color ''is mainly caused by melanin, although small amounts of lutein have also been found in these feathers (R. Stradi, unpubl. data)'' (p. 442).

In fact, we isolated a high concentration of melanin pigments in the chestnut ventral plumage of male and female Barn Swallows and Eastern Bluebirds from North America. Both phaeomelanins and eumelanins were present, and this is typical of brown feathers in other species (e.g., pigeons, ducks; Haase et al. 1992, 1995). Compared to swallows, bluebirds exhibited a richer chestnut hue in the ventral plumage we examined, and these feathers contained a higher overall concentration of melanins. Among the body regions we studied in Barn Swallows, the throat feathers yielded the highest concentration of melanins, and this is invariably the most deeply colored ventral region of plumage in both sexes (Safran and McGraw 2004). Eumelanins are typically darker than phaeomelanins (Ito and Fujita 1985), however, and yet the dark throat plumage in Barn Swallows also yielded the highest percentage of phaeomelanins compared to other feather regions.

Ventral plumage color is a sexually selected trait in North American Barn Swallows (Safran and McGraw 2004) and in Eastern Bluebirds (Siefferman and Hill 2004), with the most colorful birds breeding earliest and producing the most offspring in a year. To reinforce the honesty of these mating signals, there may be physiological costs to producing brightly colored plumage. Animals synthesize melanins from nutritionally dispensable amino acids (e.g., tyrosine; Meister 1965), but phaeomelanin and eumelanin biosynthesis follow markedly different biochemical pathways (Land and Riley 2000) that appear to be differentially sensitive to levels of circulating sex steroids in certain species (Haase et al. 1995). In Mallard drakes (*Anas platyrhynchos*), for example, androgen treatment stimulates phaeomelanogenesis, but not eumelanogenesis, in feather tracts and results in more phaeomelanic head plumage and undertail coverts (Haase et al. 1995). Thus, there may be important and fine-tuned enzymatic and hormonal control over the production and deposition of these two forms of melanin pigments in feathers, so that birds may manufacture optimal levels of phaeomelanins and eumelanins to express bright plumage coloration. There may be sex-related differences in phaeomelanin or eumelanin biosynthesis as well, as suggested by the fact that male bluebird feathers in this study had higher melanin levels, and a higher relative amount of phaeomelanins, than those of females.

Next, we investigated the biochemical nature of yellow feathers in two sub-Antarctic penguin species and from domestic chicks. Again, despite the widespread view that yellow plumage is derived from carotenoids in birds (e.g., in finches, sparrows, woodpeckers; Fox 1976, Stradi 1998), we found that yellow feathers in penguins and domestic chicks lacked carotenoids entirely. We also investigated the possibility that these yellow plumage colors could be attributed to the presence of melanins, as there is evidence in mammals that yellow fur contains melanins (primarily phaeomelanin; Cone et al. 1996, Miltenberger et al. 1999) and as some have speculated about the melanic nature of yellow chick feathers (Völker 1934). In King Penguin feathers, we indeed found small amounts of melanin pigments. These were primarily eumelanins, but occurred nearly one order of magnitude less in concentration than in the brown feathers described above for bluebirds and swallows. Pigmented plumage regions in King Penguins have been occasionally described as orange (Jouventin 1982), and in the hand individual feathers appear yellow at the base but tipped with small amounts of brown. This small amount of melanin is presumably what gives King Penguin feathers their brown edges.

In contrast to King Penguin plumage, only trace amounts of melanin were quantified from yellow Macaroni Penguin and domestic chick feathers. However, like King Penguin feathers, a substantial amount of yellow pigment remained after analysis that could not be classified as either melanin or carotenoid. At present, the only other yellow pigments that have been described from bird feathers are the psittacofulvins found in the plumage of parrots (Stradi 1998) and pterin pigments in the yellow, orange, and red irises of blackbirds, starlings, owls, and pigeons (e.g., Oehme 1969, Oliphant 1988, Oliphant et al. 1992, Oliphant and Hudon 1993, Hudon and Muir 1996). We have gathered preliminary biochemical evidence that these yellow penguin and chick pigments are soluble in mild acids and bases and fluoresce strongly under UV light, characteristics that typify pterins (Needham 1974). This suggests that penguins and domestic chicks color themselves with a class of pigments never before described from bird feathers.

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CAN LANCHESTER'S LAWS HELP EXPLAIN INTERSPECIFIC DOMINANCE IN BIRDS?

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Abstract. We studied the applicability of Lanchester's laws of combat to explain interspecific dominance in birds. We focused on 10 species of Australian birds in the arid zone of New South Wales that foraged at an established locust trap. Consistent with the ''linear law,'' larger species usually dominated smaller species in one-on-one encounters. We found no support for the ''N-square law,'' which predicted that large numbers of smaller species could dominate larger species when more abundant. Further analysis of the most abundant species revealed that it was less likely to visit the locust trap when larger, more dominant heterospecifics were present. Body size, and not numerical superiority, seems to be an important determinant in interspecific foraging decisions in birds.

Key words: *body size, foraging behavior, group size, interspecific competition, Lanchester's laws.*

¿Puede la Ley de Lanchester Ayudar a Explicar la Dominancia Interespecífica en Aves?

Resumen. Hemos estudiado la aplicabilidad de las leyes del combate de Lanchester en explicar la domi-

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