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Comparative Biochemistry and Physiology, Part B 142 (2005) 245 – 250
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Interspecific variation in dietary carotenoid assimilation in birds: Links to phylogeny and color ornamentation

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Received 3 May 2005; received in revised form 27 July 2005; accepted 28 July 2005

Abstract

Many birds use carotenoid pigments to acquire rich red, orange, and yellow coloration in feathers and bare parts that is used as a signal of mate quality. Because carotenoids are derived from foods, much attention has been paid to the role of diet in generating color variation both within and among avian species. Less consideration has been given to physiological underpinnings of color variability, especially among species. Here, I surveyed published literature (e.g. captive feeding studies) on carotenoid assimilation in six bird species and completed additional controlled carotenoid-supplementation experiments in two others to consider the ability of different taxa to extract carotenoids from the diet in relation to phylogeny and coloration. I found that, for a given level of carotenoids in the diet, passerine birds (zebra finch, *Taeniopygia guttata*; house finch, *Carpodacus mexicanus*; American goldfinch, *Carduelis tristis*; society finch, *Lonchura domestica*) exhibit higher levels of carotenoids in circulation than non-passerines like gamebirds (domestic chicken, *Gallus domesticus*; red junglefowl, *Gallus gallus*; Japanese quail, *Coturnix coturnix*; red-legged partridge, *Alectoris rufa*). This difference in carotenoid accumulation is likely due to interspecific variation in micelle, chylomicron, or lipoprotein concentrations or affinities for xanthophyll carotenoids. Passerine birds more commonly develop carotenoid-based colors than do birds from ancient avian lineages such as Galliformes, and the physiological differences I uncover may explain why songbirds especially capitalize on carotenoid pigments for color production. Ultimately, because we can deconstruct color traits into component biochemical, physical, and physiological parts, avian color signals may serve as a valuable model for illuminating the proximate mechanisms behind interspecific variation in signal use in animals.

Keywords: Carotenoids; Galliformes; House finch; Passeriformes; Plasma carotenoids; Plumage coloration; Sexual selection; Society finch

1. Introduction

Carotenoid pigments are common colorants of egg yolk, feathers, and bare parts like the beak and legs in birds (reviewed in McGraw, in press). The role that red, orange, and yellow carotenoid-based colors play as intraspecific signals of mate quality has received considerable attention from evolutionary biologists in recent decades (reviewed in Hill, 1999, in press). Within the last few years, an interest in interspecific patterns of carotenoid use and coloration has also emerged (Hill, 1994, 1995; Mahler et al., 2003; Tella et al., 2004; McGraw and Schuetz, 2004).

Because carotenoid colors are derived from pigments acquired from foods, most phylogenetic studies of carotenoid coloration have focused on the role of diet, with the prediction that species displaying bright carotenoid colors would consume more carotenoid-rich foods (e.g. fruits) than less colorful or non-carotenoid-colored taxa. In fact, there is support for this hypothesis among species of pigeons (order Columbiformes; Mahler et al., 2003) and across a larger sample of avian orders (Tella et al., 2004). However, we also know that important physiological conditions can contribute to color production within a species (e.g. health, McGraw and Ardia, 2003; lipoprotein status, McGraw and Parker, in press). Thus, species might also vary in their abilities to

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doi:10.1016/j.cbpb.2005.07.012

assimilate carotenoids from foods and subsequently use them for coloration. To date, few studies have considered interspecific variation in carotenoid physiology and how it might factor into color signaling (McGraw and Schuetz, 2004).

Here, I surveyed data from the literature and conducted additional dietary-carotenoid-supplementation experiments to determine the extent to which different avian species vary in their ability to accumulate dietary carotenoids in the body. This has the potential to be a quite tractable experimental system for studying proximate control of phylogenetic variation in carotenoid coloration compared to studies of diet in wild birds, where data on food choice and intake are scarce, difficult to gather, and less standardized (for factors such as energy expenditure). Specifically, I gathered information on plasma-carotenoid levels in captive, adult birds from eight avian species (from two avian orders, Passeriformes and Galliformes) for which the concentration of dietary carotenoids was known. These orders are ideal for physiological comparison, since members of both groups are herbivorous and consume and accumulate the same types of carotenoids (xanthophylls). Data on the relationship between plasma-carotenoid concentration and dietary-carotenoid concentration were available from the literature for six species (chicken, *Gallus domesticus*; red junglefowl, *Gallus gallus*; Japanese quail, *Coturnix coturnix*; red-legged partridge, *Alectoris rufa*; American goldfinch, *Carduelis tristis*; zebra finch, *Taeniopygia guttata*); for two additional species (society finch, *Lonchura domestica*; house finch, *Carpodacus mexicanus*), I conducted new carotenoid feeding experiments to examine the relationship between plasma- and dietary-carotenoid concentration.

2. Methods

2.1. Literature review

Published studies that report relationships between dietary- and plasma-carotenoid concentrations (Table 1) used a variety of experimental methods (e.g. carotenoid doses) and report different measures of central tendency and variability, but I attempted to standardize data as closely as possible for interspecific comparisons. Because several experiments administered only two doses of dietary carotenoids (e.g. high versus low), I gathered data at or near these two levels for all species. 'High-dose' values fell $\geq$30 mg/kg and 'low dose' values were $\leq$30 mg/kg (but mostly were ca. 10 mg/kg). These values likely are within the natural limits in wild-bird diets; in house finches, for example, the average concentration of carotenoids in a meal is 12 mg/kg but values range from 1–80 mg/kg (Hill et al., 2002). Moreover, in domestic chickens, a dose of ca. 90 mg/kg (well above the highest dose

Table 1
Relationship between the concentration of carotenoids circulated in blood and dietary carotenoid availability in various bird species

Species	Sex	Dietary carotenoid dose (mg/kg)	Plasma-carotenoid concentration mean (range) (μg/mL)	Plasma: diet ratio	Reference
Passerines					
House finch (*Carpodacus mexicanus*)*	M	17	16 (4–28)	0.94	This study
		46	26 (6–42)	0.57	This study
	F	17	14 (9–30)	0.82	This study
		46	43 (19–67)	0.93	This study
Zebra finch (*Taeniopygia guttata*)*	M	30	28 (20–48)	0.93	1
		60	44 (13–82)	0.73	1
	F	30	13 (2–28)	0.43	2
		60	20 (6–49)	0.33	2
American goldfinch (*Carduelis tristis*)*	M	5	20 (8–35)	4.0	3
		50	62 (43–111)	1.24	3
Society finch (*Lonchura domestica*)	M	8.5	52 (33–67)	6.12	This study
Non-passerines					
Domestic chicken (*Gallus domesticus*)*	F	11	4	0.36	4
		44	12	0.27	4
Red junglefowl (*Gallus gallus*)	M	7	0.9 (0.4–1.5)	0.13	5
		45	1.6 (0.1–2.8)	0.04	5
	F	7	1.4 (0.1–2.3)	0.2	5
		45	2.2 (0.9–3.8)	0.05	5
Japanese quail (*Coturnix japonica*)	M	37	0.7	0.02	6
	F	37	5.0	0.14	6
Red-legged partridge (*Alectoris rufa*)*	F	17	2.1	0.12	7

Data for all species were collected from captive feeding experiments run at non-breeding and non-molting times, with the exception of American goldfinches, which were completing their nuptial molt. I report data separately for the sexes within a species, and ranges in plasma-carotenoid concentration in addition to means, when such information was available. Carotenoid-colored species are denoted with asterisks.
References: 1. McGraw and Ardia (2003); 2. McGraw and Ardia (2005); 3. McGraw et al. (2004); 4. Marusich and Bauernfeind (1981); 5. McGraw (unpublished data); 6. Toyoda et al. (2002); 7. Bortolotti et al. (2003).

considered for this study) is needed to saturate leg coloration (Fritz et al., 1957).

In all cases but one (e.g. molting American goldfinches; McGraw et al., 2004), I used values from birds at non-breeding and non-molting times, in order to control for any seasonal differences in carotenoid allocation (e.g. to egg-yolks or to feathers) that may occur among the species. Birds were assumed to be in reasonable health in all studies (e.g. not suffering from coccidial infections); in some cases, this was ensured because birds were given coccidiostatic drugs (e.g. in the case of American goldfinches; McGraw et al., 2004). I report data for the different sexes and for ranges of plasma-carotenoid concentrations in addition to means when they were available. Data were ultimately summarized for each species by dividing average plasma-carotenoid concentration (in μg/mL) by dietary-carotenoid concentration (in mg/kg), to obtain a "carotenoid extraction–efficiency ratio" for use in interspecific comparisons.

2.2. New carotenoid feeding experiments

2.2.1. Society finches

In January 2005, I held 14 adult males (of varying plumage morphs) in small (39 cm tall × 28 cm long × 21 cm wide) cages of 2–3 birds on a 14 : 10 day / night cycle in an indoor animal-approved room on the campus of Arizona State University. Birds were fed an *ad libitum* diet of ZuPreem® AvianMaintenance™ Natural Premium Diet for Canaries and Finches (Premium Nutritional Products Inc., Mission, Kansas) and tap water for two months prior to determining plasma-carotenoid concentration (see below). This pelleted diet contains a xanthophyll (lutein + zeaxanthin) content of 8.5 mg/kg (unpubl. data; per the methods of McGraw et al., 2001). I isolated plasma carotenoids by drawing 80 μL blood from the brachial vein of each bird and extracting 10 μL plasma with 100 μL ethanol and 100 μL *tert*-butyl methyl ether. The solution was vortexed, centrifuged at 10000 rpm for 4 min, and the supernatant transferred to a new tube and evaporated to dryness under a stream of nitrogen. I resuspended the carotenoid crystals in 200 μL methanol and injected 50 μL into a Waters Alliance 2695 HPLC system (Waters Corporation, Milford, Massachusetts) fitted with a Develosil RPAqueous RP-30 column (250 × 4.6 mm; Nomura Chemical Co. Ltd., Aichi, Japan) and a built-in column heater set at 30 °C. We used a three-step gradient solvent system to analyze both xanthophylls and carotenes in a single run, at a constant flow rate of 1.2 mL/min: first, isocratic elution with 50 : 46 : 4 (v/v/v) methanol : acetonitrile : dichloromethane for 11 min, followed by a linear gradient up to 50 : 15 : 35 (v/v/v) methanol : acetonitrile : dichloromethane through 21 min, held isocratically at this condition until 30 min, and finishing with a return to the initial isocratic condition from 30–48 min. Data were collected from 250–600 nm using a Waters 2996 photodiode array detector. We identified pigments by comparing their respective retention times and absorbance maxima (λ_{max}) to those of authentic reference carotenoids run as external standards. Three dietary carotenoids (lutein, zeaxanthin, and β-cryptoxanthin) and two metabolically derived forms (anhydrolutein and dehydrolutein, derived from lutein; McGraw et al., 2002) were detected in society finch plasma (as in their estrildid-finch relatives; McGraw and Schuetz, 2004); the four xanthophylls comprised >90% of all carotenoids. Total carotenoid concentration was determined using Empower software (version 5.0) by adding xanthophyll peak areas at λ_{max} and fitting these to externally run standard curves.

2.2.2. House finches

In February–April 2005, I held 16 male–female pairs of wild-caught (in October 2004) adult house finches in similar cages within an animal-approved indoor but naturally lit room. Finches were also fed an ad libitum diet of ZuPreem and water for four months prior to study. During the experiment, I randomly divided birds into 8 'low-carotenoid' pairs and 8 'high-carotenoid' pairs. 'Low-carotenoid' birds were fed ZuPreem plus water supplemented with 8.5 μg/mL carotenoids (5% lutein + zeaxanthin starch beadlets, Roche Vitamins Inc., Parsippany, NJ, at a ratio of 90 : 10, as is found in the plasma of wild finches; unpubl. data); 'high-carotenoid' birds were fed ZuPreem plus water supplemented with 37.5 μg/mL carotenoids. Six weeks after beginning carotenoid supplementation, we drew ca. 100 μL blood from all birds via the brachial vein and extracted and analyzed carotenoids from plasma following the methods described above. Lutein, zeaxanthin, and β-cryptoxanthin were the main carotenoids in captive finch plasma; xanthophylls comprised >85% of total carotenoids, and again plasma-carotenoid concentration was calculated for this study by summing HPLC peak areas for xanthophylls.

2.3. Statistics

Ideally, I would have used standard comparative methods to statistically evaluate phylogenetic patterns of carotenoid-extraction efficiency, but data from such a small, taxonomically restricted set of species did not permit these comparisons. Instead, I used a non-parametric Mann–Whitney *U*-test (because data on carotenoid extraction efficiency were not normally distributed) to examine differences in carotenoid accumulation between passerines and non-passerines. My sample of species also included some carotenoid-colored and -uncolored species from each clade, so I pooled species across phylogenetic lines and tested for an effect of coloration on carotenoid extraction efficiency using a Mann–Whitney *U*-test.

3. Results

Dietary carotenoid concentrations in the eight reviewed bird species ranged from 7–60 mg/kg, but average plasma

concentrations ranged from 0.7–64 μg/mL. Thus, there is considerably higher (by an order of magnitude) interspecific variability in carotenoid circulation despite comparably lower experimental variation in dietary carotenoid levels. I found that passerines assimilate significantly more carotenoids from foods than do non-passerines (Fig. 1). If we take the average dietary carotenoid concentration used across all studies in my sample (29 mg/kg) and extrapolate the plasma-carotenoid concentration of passerines and non-passerines from their respective carotenoid-extraction–efficiency ratios (1.55 and 0.15, respectively), then non-passerines (4.4 μg/mL) circulate an order of magnitude (90%) fewer carotenoids through blood, on average and for a given level of dietary carotenoids, than do passerines (45 μg/mL). Because all but one of the passerines had carotenoid coloration (society finches are the exception), carotenoid-colored species also had higher carotenoid extraction–efficiency ratios than carotenoid uncolored species ($U=16$, $p=0.02$).

4. Discussion

Here I uncover phylogenetically and morphologically related differences in carotenoid assimilation among avian species. Historically, work on carotenoid physiology in animals has largely focused on few, model, often domesticated species (e.g. chicken, mouse, human) and is rarely placed in any evolutionary context, despite the variety of theoretical and applied reasons (e.g. for nutritional supplements and health therapies in humans and poultry) for knowing the constraints that species face for carotenoid accumulation.

Variability in carotenoid accumulation among species of wild animal, as well as in plasma-carotenoid uptake (both in terms of carotenoid types and amounts) among species under controlled laboratory conditions, has been recognized by many to be high (e.g. Parker, 1996; Tella et al., 1998; Surai et al., 1998, 2001; Slifka et al., 1999). In birds, at least in this limited preliminary sample of eight species from two major avian lineages, I found that phylogenetic relationships significantly explained the ability of species to assimilate carotenoids from food. In particular, songbirds (order Passeriformes), a more recently derived order of birds, more efficiently extract and accumulate carotenoids from food than do members of a more ancient lineage of birds, the gamebirds (Galliformes). Tella et al. (2004) recently uncovered a similar phylogenetic component to carotenoid accumulation across a much wider sample of birds (80 species from 8 orders), but this was from a study of free-living individuals, where several environmental and life-history factors, such as diet (see more below), could not be wholly disentangled from shared ancestry. My survey offers experimental support for phylogenetic control of interspecific variation in carotenoid accumulation in birds.

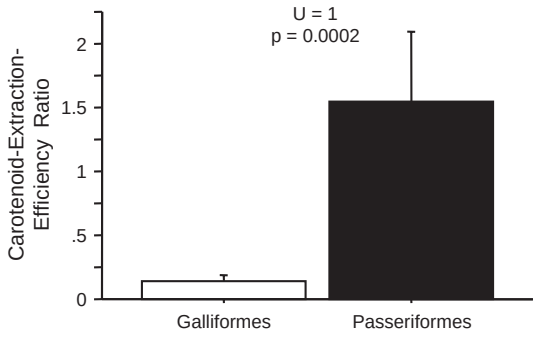

Fig. 1. Differences in the ability of passerines and gamebirds to accumulate carotenoids from the diet, as measured by the ratio of plasma-carotenoid concentration to dietary-carotenoid concentration from controlled captive feeding experiments with four species from each avian order. Mean ratios for each species were used in analyses, since paired t-tests did not reveal an effect of sex ($t_6=-0.58$, $p=0.58$) or dietary carotenoid dose ($t_7=1.4$, $p=0.21$) on utilization efficiency in the species for which such data were available.

An important question begged by these results is: what mechanism might account for such species differences in carotenoid assimilation? One very straight-forward and non-physiological possibility is related to body size: that larger Galliformes (ca. 1 kg in mass) simply eat less food (and thus fewer carotenoids) per unit body mass than much smaller Passeriformes (ca. 0.02 kg in mass). An allometric relationship between body size and food ingestion has long been known, with food-consumption rates increasing with body mass by a power of 0.75 (Peters, 1983). Thus, using the above body-mass estimations and the assumption of a linear relationship between blood volume and body mass (sensu Tella et al., 2004), gamebirds should, on average, circulate 34% fewer carotenoids, based on diet alone, than should songbirds for a given dietary carotenoid concentration. However, I found that gamebirds circulated an order of magnitude (90%) fewer carotenoids through blood than did songbirds for a given dietary dose, demonstrating significant residual, diet-independent, taxonomic variation in carotenoid accumulation. Another extrinsic factor proposed to affect carotenoid uptake is the matrix and digestability of food in which carotenoids are found (Parker, 1996); however, if anything, the gamebirds in this study, which were all fed formulated powdered/pelleted diets, could more easily digest food and take up carotenoids. Instead, it is likely that there are fundamental intrinsic differences in the concentrations or affinities of the molecules that take up carotenoids from food (e.g. micelles, chylomicrons) or that transport carotenoids throughout the blood to tissues in the body (lipoproteins, binding proteins; Tella et al., 2004). To date, little is known of micellar, chylomicron, lipoprotein, or binding protein profiles in any bird species (e.g. Allen, 1987; Mossab et al., 2001; Bernstein et al., 2005; McGraw and Parker, in press), let alone across avian orders.

Apart from the physiological requirements for high carotenoid accumulation, there can also be numerous advantages to accumulating high levels of carotenoids, so it is useful to consider the ultimate evolutionary reasons behind elevated carotenoid accumulation in songbirds compared to gamebirds.

The most widely recognized and supported use for carotenoids in birds is for coloring feathers and bare parts to become sexually attractive (Hill, 1999). Songbirds, compared to gamebirds, have far more representative species that are colored by carotenoids (personal observation), and nearly all of the evidence for the sexually selected benefits of carotenoid coloration in birds comes from passerines, with none yet from gamebirds (Hill, in press). Thus, one viable hypothesis is that sexual selection for bright coloration has favored superior carotenoid-assimilation abilities in songbirds. Results from the present study in fact revealed a difference in carotenoid extraction efficiency in relation to carotenoid coloration, although admittedly this was nearly wholly confounded by phylogeny; clearly a more comprehensive comparative test is needed of this hypothesis, both within and among clades. Another interesting possibility is that, due to the antioxidant and immunoregulatory properties of carotenoids and the fact that songbirds 'lose' large amounts of carotenoids to colorful tissues, songbirds may require more carotenoids for self-maintenance than do gamebirds. In fact, this is one of the themes of Hamilton and Zuk's (1982) hypothesis of parasite-mediated sexual selection, where more brightly colored bird species were found to suffer a greater incidence of parasitism. It is unlikely that health differences among the captive birds in the studies I reviewed explained patterns of carotenoid uptake (e.g. due to medical treatments; infection by coccidians, which disrupt intestinal carotenoid absorption, in both lineages (McGraw and Hill, 2000); and the ongoing debate over the health benefits of carotenoids among birds (Navara and Hill, 2003)), but future considerations of the costs and benefits of carotenoid extraction efficiency across taxa should certainly incorporate a species' immunological needs for carotenoids.

5. Conclusions

There is tremendous variability among animal species in the signals used for communication (e.g. colors, odors, songs, dances; Bradbury and Vehrencamp, 1998). Although several studies have been conducted within animal classes to understand why species vary in their signal repertoire (e.g. Owens and Hartley, 1998; Ptacek, 2000; Badyaev et al., 2002), few have addressed the proximate mechanisms that underlie interspecific patterns of signal use (e.g. De Voogd et al., 1993). Bird colors present a unique opportunity for such an investigation, because we can break down the signal into component parts (e.g. pigments, microstructures) to trace the biochemical, physical, and physiological components of color production and how they vary among species (McGraw and Schuetz, 2004; Hill and McGraw, in press).

Ultimately, this study should serve as an initial observation from which we can now build a stronger foundation of information on the relationship between diet, physiology, phylogeny, and carotenoid coloration in birds. The studies I reviewed from the literature targeted a very simple xanthophyll carotenoid system, when in reality birds consume foods with a range of xanthophylls and carotenes that are not always equally accumulated in the body and can serve both direct and indirect (e.g. as a metabolic substrate) roles in pigmentation. Carotenoid-physiology studies should also be preferentially expanded to clades nearest to passerines (e.g. woodpeckers) and gamebirds (e.g. Anseriformes) and in sister species that exhibit no v. some carotenoid color (or sexually selected v. non-sexually selected color). Last, a major challenge will be to conduct more refined and quantitative physiological studies that account for carotenoids on a per-microgram, per-day basis across a larger time-scale than just the non-breeding, non-molting period, since species have such fluctuating supplies and demands of carotenoids that ultimately serve a variety of signaling and physiological purposes. Only after such work has been completed can we evaluate the relative strength of factors such as diet, physiology, phylogeny, and morphology on the carotenoid-accumulation abilities of birds.

Acknowledgments

I thank J. Badman and S. Schenone for animal care, O. Crino and P. Nolan for assistance with data collection, and two anonymous referees for constructive comments on the manuscript. The School of Life Sciences and College of Liberal Arts and Sciences at Arizona State University provided financial support for this work. The Institutional Animal Care and Use Committee at Arizona State University (protocol # 05-764R) approved all procedures reported here.

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