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DIET-INDUCED PLUMAGE ERYTHRISM IN BALTIMORE ORIOLES AS A RESULT OF THE SPREAD OF INTRODUCED SHRUBS

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ABSTRACT.—Baltimore Orioles (*Icterus galbula*) of unusual redness over large sections of their plumages were recently discovered in southeastern Canada. Reddish feathers from six of nine specimens sampled at the McGill Bird Observatory in Ste-Anne-de-Bellevue, Montreal, Quebec in fall 2006 contained rhodoxanthin, a keto-carotenoid of deep red hue usually found in plants. Rhodoxanthin comprised ~5% of carotenoids in many oriole feathers, and up to 18% in the reddest one. Redness in oriole feathers with rhodoxanthin correlated with amounts of that pigment, rather than with amounts of red 4-keto-carotenoids like canthaxanthin normally present in orange oriole feathers. Redness in feathers with rhodoxanthin also tended to be greatest in feathers with the least amounts of carotenoids. The anomalous rhodoxanthin altered the normal relationship between redness and 4-keto-carotenoid concentration, and total feather carotenoid concentration in Baltimore Orioles. We believe rhodoxanthin and the associated aberrant reddish tones result from consumption of berries of exotic bush honeysuckles (*Lonicera* spp.), now widely propagated in eastern North America and the Midwestern United States. We confirm the presence of rhodoxanthin in the berries of Tatarian honeysuckle (*L. tatarica*). Rhodoxanthin produces a shoulder at ~520 nm of the reflectance spectrum of feathers in which it occurs. *Received 22 September 2011. Accepted 17 July 2012.*

Key words: Asian bush honeysuckles, Baltimore Oriole, carotenoids, diet, *Icterus galbula*, *Lonicera*, rhodoxanthin.

Carotenoids produce most of the bright red, orange, and yellow colors in bird plumages (Brush 1981, Stradi 1998, McGraw 2006). Birds acquire the colorful pigments in their diets (Brockmann and Völker 1934) but can also modify them in a number of ways, for example to produce 'red' pigments (Völker 1962, Brush 1981, Stradi 1998, Inouye et al. 2001, McGraw et al. 2003). Carotenoid displays are believed to be honest indicators of male quality or vigor in many species of birds (Hill 1991, Hill and Montgomerie 1994, Lozano 1994, Dufva and Allander 1995, Griffith and Pryke 2006). Red displays, which are apparently more costly to produce (Hudon 1991, Hill 1996), may be particularly informative. The indicator value of redness is undermined, however, if it can be acquired irrespective of quality, for example as a result of incorporation of foreign red carotenoids into feathers (*cf.* Giersburg and Stadie 1933, Völker 1955, Bruning 1971, Hudon 1994).

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We recently described Baltimore Orioles (*Icterus galbula*) with unusually reddish plumages for their age and sex in three metropolitan centers in eastern Canada, including a large number of orioles banded at the McGill Bird Observatory (MBO) at Ste-Anne-de-Bellevue at the western tip of Montreal Island, Quebec in 2006 (Flinn et al. 2007). The birds, mostly hatching year (HY) individuals, had varying amounts of red color (Chrome Orange [# 16; numbering from Smithe 1975] to Burnt Orange [#116]) on large sections of the plumage normally pigmented yellow to olive (Flinn et al. 2007).

Parkes (1993) previously described six Baltimore Orioles with erythristic plumages from a relatively small area of the northeastern United States (New York and Rhode Island), including two with a striking resemblance to birds banded at MBO in 2006. Parkes (1993) also described erythristic males in alternate plumage. He postulated the aberrant color was likely diet-derived but stopped short of identifying a possible source of the pigment, even though he was investigating a parallel situation in Cedar Waxwings (*Bombycilla cedrorum*) (Mulvihill et al. 1992).

Cedar Waxwings with aberrant orange tail tips began appearing in eastern North America ~50 years ago (Hudon and Brush 1989, Mulvihill et al. 1992, Witmer 1996). The orange parts contained rhodoxanthin (Hudon and Brush 1989), a carotenoid pigment of deep red hue only rarely encountered in birds (Hudon et al. 2007). Hudon

and Brush (1989) suggested a dietary explanation for the orange tail tips, and Brush (1990) later identified a potential exogenous source of the unusual pigment in the berries of Morrow's honeysuckle (*Lonicera morrowii*). This honeysuckle, and a close relative, the Tatarian honeysuckle (*L. tatarica*), were actively propagated in the late 1950s and early 1960s in eastern North America as valuable shrubs for developing farm wildlife habitat (Edminster 1950, Witmer 1996), and are now well established in forest edges, abandoned fields, pastures, roadsides, and disturbed woodlands in eastern North America and the Midwestern United States (Williams 2005). Their propagation largely coincides with the first reports of Cedar Waxwings with orange-tinted tail tips in North America (Mulvihill et al. 1992, Witmer 1996). Controlled feeding experiments confirmed that provisioning waxwings with Morrow's honeysuckle berries at the time of feather molt results in orange tail-tipped waxwings (Witmer 1996).

We collected feathers from several aberrantly-colored Baltimore Orioles banded at MBO in 2006. Our objectives were to: (1) assess whether rhodoxanthin is present in the unusually red feathers, (2) investigate the relationship between redness and keto-carotenoid composition/concentration in oriole feathers with and without rhodoxanthin, and (3) establish the presence of rhodoxanthin in berries of Tatarian honeysuckle.

METHODS

Field Observations.—Fifteen of 34 Baltimore Orioles (23 first captures, 11 recaptures) banded after 15 August 2006 at MBO, including eight of 17 orioles banded on 16 August, had feathers that were considered unusually red. One of us (SL) collected from 2–10 feathers, both red and normally colored in some individuals, from the breast area of nine of these orioles for analysis.

Reddish HYs had plumage patches approaching the color of after hatching year (AHY) males. A particularly red AHY male had breast colors approaching Flame Scarlet [#15]. No bird had reddening of tail feathers. We compared the sampled feathers with those from individuals of known age and sex housed at the Royal Alberta Museum that were collected in Alberta distant from areas with an incidence of erythrism.

We characterized individual feathers from the supplied material both spectrally and biochemically, selecting feathers of similar sizes and color distribution, also uniform coloration, that spanned the range of colors represented in sampled feathers. We washed the feathers first with a dilute aqueous solution of dishwashing detergent (Sunlight, Phoenix Canada, Toronto, ON) and, once dried, with petroleum spirit. We weighed each feather using a Denver Instruments Pinnacle Series PI-225D (Denver Instruments, Arvada, CO, USA) precision analytical balance.

Spectrophotometry.—We acquired reflectance spectra of individual feathers over the range of 350 to 800 nm using an Ocean Optics USB2000 spectrophotometer (Ocean Optics Inc, Dunedin, FL, USA) fitted with an ISP-REF illuminated integrating sphere (10.32 mm^2 sample window) set to exclude mirror-like (specular) reflection. The spectrophotometer was operated with the OOIBase32 Version 2.0.1.4 (Ocean Optics, Dunedin, FL, USA) using the following settings: integration time = 10 msec, spectra averaged = 100, and boxcar smoothing = 5.

The feathers lay with their upper surface facing the observer on a flexible sheet of microcrystalline cellulose made for thin-layer chromatography (Chromagram sheet 13,254, Eastman Kodak Co., Rochester, NY, USA), providing a white surface of uniform, high reflectance across the visible spectrum (85% compared to a 99% Spectralon white standard) to highlight absorption by the feather pigments. The sheet served as both the background and 'light' control for reflectance readings; turning the light source off served as the 'dark' control. We used only the spectrum exhibiting the greatest difference in reflectance between 800 and 456 nm (the peak of absorption) of several (>15) readings of each feather analyzed for calculations, because the spectra were degraded by inclusion of the grayish plumulaceous bases of feathers which varied with feather positioning. We turned the feathers 90 degrees clockwise and repeated the readings for a second spectrum. We also obtained reflectance spectra after carotenoid extraction in warm pyridine, an extraction that leaves the feather structure and most melanin (dull yellow through brown to black) pigments largely untouched (Hudon and Brush 1992).

Redness, which results from absorption of longer wavelengths into the green part of the visible spectrum than for yellow feathers, was measured using the λ_{R50} of the reflectance spectra, the wavelength at which reflectance is at the midpoint between the maximum reflectance

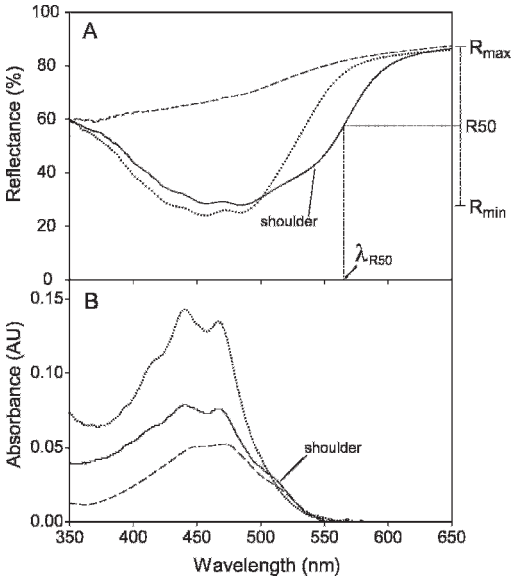

FIG. 1. Reflectance and absorption spectra of feathers of Baltimore Orioles from the McGill Bird Observatory and their respective pyridine extracts. (A). Reflectance spectra of feathers with (solid line: band # 1951-51453) and without rhodoxanthin (dotted line: band # 1951-51469), as well as after pigment extraction (stippled line: 1951-51469). We show graphically how λ_{R50} is calculated for 1951-51453. (B). Absorption spectra of carotenoid extracts of these feathers (solid line: band # 1951-51453; dotted line: band # 1951-51469), and an extract of the berries of a Tatarian honeysuckle, in hexanes (stippled line).

at long wavelengths and the minimum at shorter wavelengths (Andersson and Prager 2006; Fig. 1A). We used the average of measurements made for the two spectra per feather analyzed.

Biochemistry.—We extracted feather carotenoids in warm pyridine after Hudon and Brush (1992) with a few modifications. Acidification, which can be harmful to carotenoids, was not needed. We conducted the extractions in sealed 1-dram borosilicate glass vials flushed with N_2 gas. We transferred the extracted carotenoids into methyl-*tert*-butyl ether (MTBE) with deionized water, which effects a more complete transfer of carotenoids than diethyl ether. We replaced the deionized water several times to remove as much of the pyridine as possible, and transferred the MTBE epiphase with the carotenoids into a clean vial.

We ascertained pigment concentration by evaporating the ether extract over a stream of N_2 gas, redissolving the pigments in a known volume of hexanes (OmniSolv, EM Science, Gibbstown, NJ, USA), and removing traces of water with crystals of anhydrous sodium sulfate. We calculated pigment concentration in mg carotenoid per gram of feather tissue using the formula: (A_{peak} × volume of extract [ml] × 10)/($E^{1\%}_{1cm}$ × feather mass [g]), where A_{peak} is the absorption at the extract's maximum, and $E^{1\%}_{1cm}$ is the extinction coefficient of a generic carotenoid in hexane, taken to be 2,500 (Britton 1985). We extracted the carotenoids in Tatarian honeysuckle berries collected in Edmonton, Alberta in August 2008 with acetone, and transferred the pigments to hexanes with deionised water in a separatory funnel. We produced absorption spectra of the pigment extracts using the Ocean Optics spectrophotometer fitted with a CUV-FL-DA cuvette holder (Ocean Optics, Dunedin, FL, USA). We used a Mikropack DH-2000-Bal deuterium tungsten halogen lamp (Ocean Optics) as light source.

We identified the carotenoids in oriole feathers initially by analytical thin-layer chromatography (TLC) on flexible sheets of silica gel (PE SIL G; Whatman Ltd., Maidstone, Kent, UK) and aluminum oxide (60 neutral; EM Science, Cherry Hill, NJ, USA) using mixtures of hexane and acetone (2:1 and 3:1, respectively). The aluminum oxide plates bind common 3-hydroxy, 4-keto-carotenoids (astaxanthin and adonirubin) tightly which allows detection of rhodoxanthin without interference from these pigments. We based pigment identifications on their color, relative mobility (R_f's), and comparison with known standards. Hoffman-LaRoche (Basel, Switzerland) supplied standards of echinenone, canthaxanthin, lutein, and zeaxanthin. We extracted rhodoxanthin from the red feathers of a male Western Tanager (*Piranga ludoviciana*; Hudon 1991), and astaxanthin from the shells of commercially available black tiger prawns (*Penaeus monodon* Fabricius; Howell and Matthews 1991).

We used high-performance liquid chromatography (HPLC) to quantify individual pigments (mainly rhodoxanthin and canthaxanthin) using a Waters instrument (Waters, Milford, MA, USA) equipped with two Waters 501 pumps, a 712 WISP autoinjector, a System Interface Module, and a Lambda Max 481 UV detector. We separated the carotenoid pigments isocratically using a Vydac C18 reverse phase column (4.6 mm i.d. × 250 mm) (Grace Vydac, Hesperia, CA, USA) assisted with a methanol:acetonitrile (9:1) mobile phase flowing at 0.5 mL/min following Craft (1992). We detected the carotenoids at

450 nm. We used carotenoid standards and pigment extracts to identify the relevant peaks on the chromatograms. We used SigmaScan Pro 5.0.0 (Systat Software Inc., San Jose, CA, USA) to calculate areas under the curve of the peaks of interest and relative abundance after the chromatograms were digitized with a Hewlett Packard Scanjet G3110 scanner.

Rhodoxanthin separated into six peaks (at 14.2, 15.1, 16.2, 17.5, 19.0, and 20.6 min) in this chromatographic system corresponding to stereoisomers of the pigment. Most of these peaks overlapped other carotenoids present in oriole feathers, including one of the 4-keto-carotenoids of interest (canthaxanthin) at 17.7 min, and we used the area under the curve of an unhindered peak at 19.0 min (representing 17.0% of all rhodoxanthin, based on the average of 3 runs) to extrapolate total rhodoxanthin concentration. We calculated canthaxanthin concentration in feathers with rhodoxanthin by substracting rhodoxanthin's contribution (2.12 × the absorption of the peak at 19.0 min) to the area under the curve of the peak at 17.7 min. We calculated a pigment's relative abundance by dividing the areas under the curve of each respective peak by all the areas under the curve.

Data Analyses.—We tested for correlations between λ_{max} (peak of absorption of pigment extract) or λ_{R50} (redness) and the relative concentration of different pigments using Spearman correlation rank tests. We conducted regression analyses and the statistical tests using StatView for Windows 5.0 (SAS Institute Inc. 1998).

RESULTS

Spectrophotometry.—The yellow to orange (and reddish) breast feathers of orioles had a broad peak of absorption in the blue to green part of the reflectance spectrum (Fig. 1A), which was largely eliminated by extraction of the carotenoids with warm pyridine (stippled line, Fig. 1A). The absorption spectrum of the pigment extract that ensues (Fig. 1B) broadly matches the reflectance spectrum of native feathers (Fig. 1A) plotted upside down with two identifiable peaks/troughs. However, the peaks on the absorption spectra shifted to shorter wavelengths by ~16 nm compared to those on the reflectance spectra (Fig. 1B).

The peak at shorter wavelengths (at ~457 nm) was the reflectance minimum for most intact feathers, except the three reddest feathers, where the peak at ~484 nm was the minimum. The peak at shorter wavelengths (at ~441 nm) was also the peak on the absorption spectra of extracts for all feathers except the single reddest feather. The position of the peaks of absorption varied little between feather extracts; the peak at short wavelengths (the main peak in most samples) of absorption spectra varied between 439.01–443.72 nm (mean ± SD; 440.9 ± 1.1 nm; n = 17) with 13 samples peaking between 440–442 nm. The wavelength of peak absorption of extracts correlated weakly with redness (λ_{R50}) (r^2 = 0.206 for feathers of birds from MBO, up to r^2 = 0.217 when the feathers of Alberta birds were included), being highest in the redder feathers; however, this could hardly account for the increased redness.

In contrast, λ_{R50} differed markedly between samples, varying from 523–566 nm in feathers from birds banded at MBO, to 515 nm in birds of normal, non-reddish coloration from the collection at the Royal Alberta Museum. Feathers visually assessed as being reddest had the highest λ_{R50}'s. The increase in λ_{R50} was mainly the result of a shift of the slope of increasing reflectance to longer wavelengths (Fig. 1A). However, many of the aberrantly-colored feathers also exhibited a shoulder above 515 nm on both reflectance and absorption spectra (Figs. 1A, B), an element also expected to increase λ_{R50}. Common 4-keto-carotenoids cannot account for this shoulder because they have a unimodal absorption spectrum centered ~460 nm in the solvent system we used, pointing to the presence of a red pigment that absorbs at longer wavelengths than common 4-keto-carotenoids. Rhodoxanthin is one such pigment. The pigments present in Tatarian honeysuckle berries also had a shoulder at ~519 nm in solution in hexanes (Fig. 1B).

Biochemistry.—Baltimore Oriole feathers naturally contain a complex mixture of eight carotenoid pigments that range in color from yellow to red on TLC. The relative amounts of the different pigments varied with age and sex of birds (data not shown), but the pigments were in order of abundance usually: 3′-hydroxy-ε,ε-caroten-3-one, lutein, canthaxanthin, ε,ε-carotene-3,3′-dione, astaxanthin, adonirubin, and echinenone; zeaxanthin was detected on HPLC.

Some orange-red to red feathers contained in addition to the above pigments a carotenoid that was identical to rhodoxanthin, for example

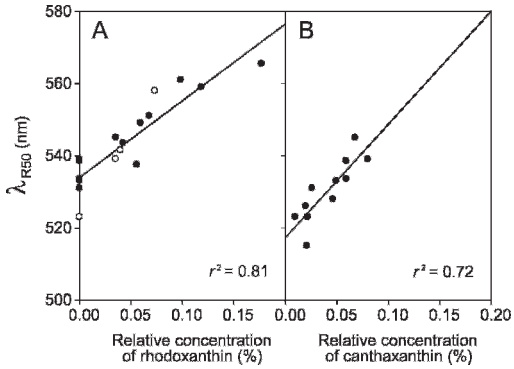

FIG. 2. Relationship between λ_{R50}, a proxy for redness, and (A) the concentration of rhodoxanthin in feathers of Baltimore Orioles from the McGill Bird Observatory (y = 533.9 + 212.6x) (n = 17), or (B) the concentration of canthaxanthin in feathers lacking rhodoxanthin (including specimens from the Royal Alberta Museum; y = 517.4 + 313.5x, n = 11). The open dots are four feathers from a single oriole (band # 1951-51434).

appearing as a tightly-grouped set of three red to red-orange bands on analytical thin-layer chromatography, matching the red pigment in the Western Tanager. The berries of Tatarian honeysuckle also contained the red carotenoid. Reddish feathers from six of nine birds, mostly HY, but also an AHY, sampled at MBO had detectable amounts of the pigment, including the two reddest individuals (band #s 1951-51453 and 1951-51463) (Fig. 2A). Rhodoxanthin accounted for almost 18% of all carotenoids in one sample, although the pigment accounted for ~5% of all carotenoids in most samples. The proportion of carotenoids that was rhodoxanthin in the reddish feathers sampled at MBO was an excellent predictor of redness (λ_{R50}) (rs = 0.902, P < 0.001, n = 17; Fig. 2A). Canthaxanthin concentration in the same feathers was inversely related to redness (rs = −0.438, P = 0.080, n = 17). However, canthaxanthin concentration was an excellent predictor of redness in feathers without rhodoxanthin including the birds from Alberta (rs = 0.916, P = 0.004, n = 11; Fig. 2B).

The total concentration of carotenoids in the sampled feathers varied from 0.14 to 1.7 mg/g of feather, the AHY male exhibiting the highest concentration, averaging 0.373 ± 0.136 mg/g; (mean ± SD, n = 15) in HYs. Redness (λ_{R50}), also the proportion of carotenoids that was rhodoxanthin, varied inversely with total carotenoid concentration, although only the former was statistically significant (rs = −0.569, P = 0.033, n = 15 and rs = −0.395, P = 0.14, n = 15, respectively) in HYs.

DISCUSSION

Six of nine sampled orioles noted as unusually red for their age and sex at MBO in 2006 displayed rhodoxanthin, a retro-carotenoid of deep red hue rarely encountered in birds (Hudon 1991, Hudon et al. 2007) and normally absent in the feathers of Baltimore Orioles (Hudon 1991, this study). Orioles with the red pigment had variegated plumages that combined feathers of contrasting colors (orange vs. yellowish-green in many HYs) unlike the relatively uniform coloration of orioles that inherently were more red. Potentially two-thirds of 15 orioles deemed of unusual redness or 29% of 34 orioles banded at MBO after 15 August had rhodoxanthin in their feathers, based on the proportion in sampled birds. We suspect three individuals banded and photographed before 15 August when the first feather samples were taken also acquired the retro-carotenoid. Rhodoxanthin was recently found in the orange tail tips of aberrantly colored Cedar Waxwings in eastern North America (Hudon and Brush 1989), and suspected in the origin of aberrant orange plumage colors in other songbirds (Mulvihill et al. 1992, Brooks 1994).

The presence of rhodoxanthin altered the normal relationship between 4-keto-carotenoid concentration, total carotenoid concentration, and feather redness in Baltimore Orioles. Redness in normal orange oriole feathers correlates with amounts of red 4-keto-carotenoids like canthaxanthin (and possibly other 4-keto-carotenoids, e.g., astaxanthin, not quantified here), but redness in feathers with rhodoxanthin correlated with amounts of that retro-carotenoid. Redness also tended to be greatest in feathers that had the smallest amounts of carotenoids, when redness would be expected to increase with total carotenoid concentration (Hudon et al. 2003, Andersson et al. 2007). The strong influence of rhodoxanthin on redness is in part because the pigment absorbs at longer wavelengths than natural 4-keto-carotenoids and produces red tones more readily. The relationship between redness and rhodoxanthin is reinforced in our study because the reddest feathers often had little carotenoids in them, feathers where the presence of rhodoxanthin would have the most dramatic effect, which led us to identify them as unusually red.

Red plumages in most birds are associated with 4-keto-carotenoids, such as canthaxanthin and

astaxanthin (Völker 1962, Brush 1981, Stradi 1998, McGraw 2006), which are produced endogenously from dietary, usually yellow, carotenoids (Brush 1981, Stradi 1998, Inouye et al. 2001, McGraw et al. 2003). It has been hypothesized that 4-keto-carotenoids are either costly to produce (Hudon 1991, Hill 1996), or the displays that incorporate them are limited by precursor availability in diets (McGraw et al. 2006) or by other, poorly known, physiological processes (Hudon 1994, Hill 2000, McGraw and Hill 2001), so that redness can act as an honest indicator of individual quality (Hill 1996). Redness produced by 4-keto-carotenoids is at risk of losing its indicator value if it can be produced irrespective of a male's quality, for example as a result of the ingestion and subsequent deposition of unnatural red carotenoids, such as rhodoxanthin, in feathers containing carotenoids (*cf.* Giersburg and Stadie 1933, Völker 1955, Bruning 1971, Hudon 1994).

Jones and others (2010) recently described an uncoupling between plumage coloration and body condition in the Northern Cardinal (*Cardinalis cardinalis*) connected to the spread of introduced shrubs in Ohio. The availability of berries of the Amur honeysuckle (*L. maackii*) in urbanized areas of central Ohio produces a situation where cardinal plumage coloration no longer mirrors body condition in areas where the shrub is abundant (Jones et al. 2010). This may be expected to have reproductive consequences given that coloration is a cue known to promote assortative mating in that species (Jawor et al. 2003).

Amur honeysuckle is related to Morrow's and Tatarian honeysuckles, sometimes grouped together as the Asian bush honeysuckles (Rathfon 2006). Ingestion of the berries of Morrow's and Tatarian honeysuckles, hypothesized to be the cause of aberrantly-colored Cedar Waxwings in eastern North America (Brush 1990, Mulvihill et al. 1992, Witmer 1996), is suspected for Baltimore Orioles in eastern Canada. Baltimore Orioles feed primarily on insects and other invertebrates during the breeding season, but incorporate fruits, e.g., mulberries (*Morus* spp.), raspberries (*Rubus* spp.), and cherries (*Prunus* spp.) in their diet when available (Rising and Flood 1998). MBO has few bush honeysuckles and orioles were not actually observed eating the berries there, but the shrubs are present nearby. Bush honeysuckles are the main berry-bearing shrubs at Tommy Thompson Park Bird Research Station (TTPBRS) in Toronto, where several aberrantly-colored orioles have been documented, including a particularly red individual (Flinn et al. 2007). One of us (DD) observed orioles feeding heavily on honeysuckle berries in late summer and early 'fall' migration (Aug) when the fruit is abundant at TTPBRS. Both Morrow's and Tatarian honeysuckles are available in mid-summer starting in late June–early July until about the end of August at TTPBRS. We now confirm the presence of rhodoxanthin in berries of Tatarian honeysuckle.

The timing of the prebasic molt in Baltimore Orioles also largely coincides with availability of honeysuckle berries. The preformative molt in HYs begins in breeding areas in early July and involves the body feathers but no tertials, rectrices or remiges (Pyle 1997); the adult prebasic molt begins in July and is a complete molt involving the entire plumage. Orioles at MBO were actively molting their contour feathers when the unusually-colored birds were first noted in early August 2006. A HY oriole banded at TTPBRS on 14 August 2007 was undergoing an extensive body molt with many pin feathers. All pin feathers, as well as the recently grown feathers, of this bird were orange-red in color.

Red color in rectrices is only known from a bird with a left 4th rectrix heavily washed with red (Parkes 1993); however, since the feather was the only aberrantly-colored one (rectrices are grown simultaneously in the nest) and it had the broad shape of an adult rectrix rather than the narrower shape of the adjacent greenish rectrices, it was presumed to be the replacement of an accidentally lost rectrix. The implication is that berries are not fed to nestlings at the nest, at least not in quantities sufficiently large to affect the color of the rectrices, although berries seemingly are available at the time.

We can expect feathers of unusual redness to appear in older, after second year (ASY) orioles in breeding areas when they return the following year, because the prealternate molt in Baltimore Orioles is uncertain, being either very limited or does not occur at all in AHY/ASYs (Pyle 1997). Color change in older birds happens largely as a result of the wear of feather tips (Pyle 1997). A particularly red adult (ASY) male oriole was banded at MBO in May 2005 (M. A. Gahbauer, pers. comm.). Retention of aberrantly colored feathers in second year (SY) birds is less certain,

as they undergo a fairly extensive (limited to incomplete) first prealternate molt in spring that involves most of the contour feathers, 0–10 inner greater coverts, 1–2 tertials, and 0–12 rectrices (Pyle 1997). Thus, most SYs may lose the reddened feathers acquired in the fall by the following spring.

Any avian species that have carotenoids in feathers and ingest honeysuckle berries at the time of feather molt could potentially have parts of their plumage imbued with unusual reddish tones. This need not be limited to species that eat a lot of fruit, as many species of birds that are largely insectivorous during the breeding season, like wood warblers (Parulidae), shift to high levels of frugivory in fall and winter (Greenberg 1981, White and Stiles 1990, Parrish 1997, Suthers et al. 2000, Borgmann et al. 2004).

The current availability of rhodoxanthin in much of eastern North America and the Midwestern United States, through the bush honeysuckles, offers a natural laboratory to investigate the role of plumage coloration and redness in mate selection in many birds that display carotenoids. A few possible evolutionary outcomes may be envisioned. Birds with redder phenotypes could be at a selective advantage as mates, at least initially, if redness is preferred. In time, a hard-wired preference for redness may prove detrimental, if redness loses its indicator value, for example causing females of superior quality to mate with red males of inferior quality (Jones et al. 2010). It has been speculated the preference will weaken over time under these circumstances (Schluter and Price 1993, Omland 1996). It is also possible the color change will have minimal impact on assortative mating if individual quality is communicated in other ways (Andersson 1994, Johnstone 1996), for example through other types of pigments or signals, such as melanins or structural elements (Jawor et al. 2003, Grether et al. 2004), or behavior.

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