Diet-induced Plumage Erythrism as a Result of the Spread of Alien Shrubs in North America

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ABSTRACT

Many species normally bright yellow have been turning up with abnormal orange-to-red feathers in eastern North America and the American midwest. In addition to the well-documented orange tail-banded Cedar Waxwings, aberrantly reddened feathers have been recorded on Yellow-breasted Chat, Kentucky Warbler, White-throated Sparrow, Baltimore Oriole and Northern Flicker. The birds are suspected of having acquired a carotenoid of deep red color (rhodoxanthin) *from their diet, likely from the berries of two species of exotic bush honeysuckles (Morrow's and Tatarian honeysuckle and their hybrids) now well established throughout eastern and midwestern North America. Using a set of well-defined criteria, we have compiled a preliminary list of species, plumages, feathers, and feather tracts likely affected by the unusual carotenoid, and the U.S. states and Canadian provinces where they occur. To accomplish this, we consulted banders at banding stations and browsed images of birds posted on the World Wide Web. We report instances of obvious reddening of the plumage (i.e., erythrism) or the presence of rhodoxanthin in 15 species of birds, including several that ingest fruits only sporadically or seasonally, over a span of at least five decades. Our summary includes many examples of aberrantly colored birds in eastern North America, including southern Canada, and the Midwest, but also farther west (Alberta, Montana and Idaho) and in southern areas where these birds overwinter.*

INTRODUCTION

By now, most banders are aware that Cedar Waxwings *(Bombycilla cedrorum)* in eastern North America, on occasion, sport orange tail tips instead of the normal yellow ones. First observed almost 50 years ago, the underlying cause of orange-tailed Cedar Waxwings did not come to light until the 1990s with reports from the Powdermill Avian Research Center (PARC; Hudon and Brush 1989, Mulvihill et al. 1992), Ontario (Pittaway 1991) and New York (Witmer 1996, Levine and Bull 1998).

Hudon and Brush (1989) identified the source of the aberrant coloration as rhodoxanthin, a rare carotenoid pigment of deep red hue that is chemically distinct from the red 4-keto-carotenoid *(astaxanthin)* found in the "waxy" wing appendages that grace a variable number of secondary flight feathers of this species (Brush and Allen 1963). The birds, mostly individuals with juvenal rectrices, were getting the pigment in their diet at the time of rectrix growth (in the nest for the hatch-year birds) and depositing it alongside the yellow carotenoids that normally color these feathers (Hudon and Brush 1989). Potential exogenous sources of the rare pigment were later identified in the berries of two exotic species of Asian bush honeysuckles, the Morrow's (*Lonicera morrowii*) and Tatarian (*L. tatarica*) honeysuckles (Brush 1990, Hudon et al. 2013). The shrubs were actively propagated in the early-to-mid-1960s as valuable wildlife habitat and are now well established in eastern North America and the American Midwest (Edminster 1950, Williams 2005).

The first instances in North America of Cedar Waxwings with variant tail tips largely coincided with the spread of these shrubs (Mulvihill et al. 1992, Witmer 1996). Controlled feeding experiments later confirmed that provisioning waxwings with honeysuckle berries when they grow their rectrices indeed produces individuals

with orange tail tips (Witmer 1996). Rhodoxanthin is otherwise known from only the arils of yew (*Taxus* spp.) trees, which are only occasionally taken by birds (Fordham 1967, Martell 1974).

But observations of birds with abnormally reddened feathers in eastern North America have not been limited to the berry-eating Cedar Waxwings. Mulvihill et al. (1992) mention frequent orange variant Yellow-breasted Chats (*Icteria virens*) and isolated erythristic Kentucky Warblers (*Geothlypis formosa*) at PARC. At about the same time, banders in Connecticut, Minnesota and western New York state were reporting White-throated Sparrows (*Zonotrichia albicollis*) with orange rather than the normal bright yellow lores characteristic of the species (Bilsborough 1987, Brooks 1994, Craves 1999).

More recently, plumage reddening (*erythrism*) was documented in yet another brightly colored species, the Baltimore Oriole (*Icterus galbula*). Orioles with unusually red plumage were reported at three metropolitan centers in eastern Canada in the fall of 2005 (Flinn et al. 2007, Hudon et al. 2013), including a strikingly red individual at the Tommy Thompson Park Bird Research Station (TTPBRS) in Toronto (see Flinn et al. 2007). The fall of 2006 produced even more reddened individuals with several orioles at the McGill Bird Observatory (MBO) at Ste-Anne-de-Bellevue at the western tip of Montreal Island, Quebec, and two more birds at TTPBRS (Flinn et al. 2007). Parkes (1993) had previously described erythristic Baltimore Orioles in New York and Rhode Island, but the study by Hudon et al. (2013) established for the first time that rhodoxanthin was involved in the reddening of feathers in at least six orioles at MBO. Finally, occasional orange to red flight feathers in Yellow-shafted Flickers (*Colaptes auratus auratus* subspecies group) in eastern North America, far from the hybrid zone with the Red-shafted Flicker (*C. a. cafer* subspecies group), were recently ascertained to be caused by rhodoxanthin, not genetic introgression (Hudon et al. 2017). It is apparent that any species of bird that normally has yellow carotenoids in its plumage, and which ingests Morrow's or Tatarian honeysuckle berries during feather molt, likely will have portions of its plumage imbued with unusual reddish tones. Consequently, we compiled a list of species and plumages where we suspect feather reddening as a result of exogenous (i.e., dietary) rhodoxanthin. We think that bird banders are particularly well-positioned to detect and document such variants. By summarizing the information in this article, we hope that there will be a wider appreciation for this emerging phenomenon, and that more attention will be paid to its possible effects on various aspects of bird behavior. We strongly encourage banders to carefully document instances of diet-induced erythrism in the species listed here, as well as any suspected cases in additional species.

METHODS

We searched for examples of birds exhibiting atypically "warm" carotenoid colorations, e.g., orange in place of yellow, or red in place of orange, from a variety of sources. We were assisted in this search by banders at banding stations in eastern North America and the American Midwest who have noted abnormally reddened individuals in species they band, and who kindly shared their observations with us by filling out a questionnaire. We expanded geographic coverage for our study by searching the Internet for images of aberrantly colored birds, using terms like "orange", "orange-red", "red", or "abnormal", posted by bird enthusiasts and nature photographers, including banders. For a few species, such as Northern Flicker, we also examined specimens at various museums and other institutions in the U.S. and Canada.

We identified feathers suspected of carrying rhodoxanthin by applying a set of well-defined criteria that follow from our understanding of how rhodoxanthin gets incorporated into the plumage of birds (Völker 1955, Witmer 1996, Hudon et al. 2017). This largely permitted us to distinguish this process from other processes that could result in reddened feathers. The latter processes include the application of colored material from the environment, e.g., adventitious coloration, or genetic differences that affect the production of red pigments, be it carotenoic or melanic pigments, and their deposition in feathers. These criteria are:

(1) We expect the change in color to be an increase in redness (i.e., warmth) of the feathers as a result of the incorporation of rhodoxanthin, a pigment of a deep red hue. This will usually produce reddish (orange to red) tones, but may also result in brownish tones if the feathers are normally colored green and harbor dark melanins. As a corollary, we can expect much variation between individuals in the resulting color, depending on amount of berries consumed. The reflectance spectrum of a rhodoxanthin-bearing feather may be expected to show a shoulder at about 570 nm (Hudon, Derbyshire et al. 2013, Hudon, Driver et al. 2017).

(2) The warm tones will appear only in areas of the plumage that are normally pigmented by carotenoid pigments, i.e., areas normally colored yellow, orange, red or green, even if only faintly so. This expectation may allow one to rule out the application of applied material, and genetic processes affecting melanin pigmentation.

(3) The warm tones should appear only in feathers grown in the late summer or the fall, during the preformative and prebasic molts, which is when the berries are exclusively available. In many but not all instances, these feathers may be worn only in the fall and winter, until they are replaced in the prealternate molt. If not replaced during the prealternate molt, we would expect the reddened feathers to be lost at the next prebasic molt, unless the bird again ingested rhodoxanthin-laden fruits during the molt. Consequently, the pattern of reddened plumage would be expected to be different from one year to the next, in contrast to what would be expected in a genetic variant.

(4) The warm colors may be expected to produce an uneven or mottled distribution of reddened feathers, if rhodoxanthin-bearing fruits are not consumed for the whole period of feather molt, or if the prebasic and prealternate molts are partial. However, the color should be identical on the two sides (vanes) of individual feathers. A phenotype of this sort would not be expected of genetic variation.

(5) Finally, reddening should occur only in those feather tracts that are molted where and when the fruits are available in a particular area, and this may vary geographically and with the age of the birds (Witmer 1996).

RESULTS

Table 1 lists species in which individuals were observed with abnormally reddened plumage coloration likely due to the ingestion of rhodoxanthin-containing berries (see examples on Figure 1; additional examples can be found in Flinn et al. 2007). Table 1 also identifies the affected plumages and feathers, as well as the seasons when and the states/provinces where the variants were found.

DISCUSSION

Rhodoxanthin has been isolated from aberrantly colored feathers of Cedar Waxwing, Baltimore Oriole, Northern Flicker, White-throated Sparrow and Northern Cardinal (Hudon and Brush 1989, Hudon 1991, Flinn et al. 2007, Hudon et al. 2013, Hudon et al. 2017). The presence of atypical orange to red feathers in a larger suite of brightly colored birds in eastern North America and the American Midwest documented here points to much more widespread acquisition and deposition of this unusual carotenoid in feathers. The list of species affected by this pigment is not limited to species that are well known frugivores, such as Cedar Waxwing. It also includes insectivorous species, such as woodpeckers, wood warblers and tanagers, that undergo a seasonal dietary shift in late summer and fall (see Greenberg 1981, White and Stiles 1990, Parrish 1997, Suthers et al. 2000, Borgmann et al. 2004). We note that fruits are not even mentioned as food items on the breeding grounds for the Blue-winged Warbler, Kentucky Warbler and Common Yellowthroat in their respective *"Birds of North America"* species accounts (Gill et al. 2001, McDonald 2013, Guzy and Ritchison 1999).

As predicted for a pigment source that is only available in the late summer and fall, the majority of individuals with reddened tones were in basic plumage, although individuals of a few species (Northern Flicker, Cedar Waxwing, Prothonotary Warbler, Common Yellowthroat, American Redstart, Prairie Warbler, Yellow-breasted Chat, Scarlet Tanager [female] and Baltimore Oriole) also had unusual colors in Alternate ("breeding") plumage. Surprisingly, the Prothonotary Warblers we uncovered with orange tones were all in Alternate plumage. This must reflect a gap in

Table 1. List of species, plumages and feathers noted with abnormal reddened colors, and the seasons and geographical areas where found.

Common name / *Scientific name*	Number#	Basic	Alternate	HY/SY	AHY/ASY	Male	Female	Feathers affected	Fa	Wi	Sp	Su	States/provinces/countries (broadly arranged from more examples to fewer)
Northern Flicker *Colaptes auratus*	36	✓	✓	✓	✓	✓	✓	Some, but not all, primaries, secondaries and rectrices, underwing coverts	✓	✓	✓	✓	MA ON MI PA NY VA CT WI NJ QC MD IL OH NC IN PE
Cedar Waxwing *Bombycilla cedrorum*	69	✓	✓	✓	✓	✓	✓	Tail band, rarely belly	✓	✓	✓	✓	PA NY MA ON NJ NC* VA VT MI TX* QC IN NH SC* FL* OH MN AB MT ID
Blue-winged Warbler *Vermivora cyanoptera*	2	✓			✓	✓		Crown, throat, underparts	✓				MA PA
Prothonotary Warbler *Protonotaria citrea*	24		✓		✓	✓	✓	Head, throat, underparts			✓	✓	NY ON NC OH IN TX FL NJ IL MD LA UT Costa Rica*
Kentucky Warbler *Geothlypis formosa*	2	✓			✓		✓	Superciliary, chin, throat, breast	✓				PA
Common Yellowthroat *Geothlypis trichas*	7	✓	✓		✓	✓	✓	Chin, throat, breast	✓			✓	MA PA NJ RI NH FL
American Redstart *Setophaga ruticilla*	7	✓	✓	✓		✓	✓	Back, wing coverts, flanks, edges of primaries	✓			✓	QC ON PA OH VT
Yellow Warbler *Setophaga petechia*	4	✓	✓	✓		✓		Face, crown, throat, breast, belly, back	✓				PA, QC
Chestnut-sided Warbler *Setophaga pensylvanica*	1	✓		✓			✓	Crown, back	✓				PA
Prairie Warbler *Setophaga discolor*	11	✓	✓	✓	✓	✓		Crown, face, throat, underparts, bend of wing	✓		✓	✓	FL MA PA NC VA
Yellow-breasted Chat *Icteria virens*	20	✓	✓	✓	✓	✓	✓	Throat, breast, breast, sides, underwings, wing coverts	✓	✓	✓	✓	PA MD MA NJ OH TX RI IL VA NS NL
White-throated Sparrow *Zonotrichia albicollis*	19	✓		✓	✓	✓	✓	Lores, bend of wing	✓	✓			PA MA MI ON NY MN SC* MD* VA* TX*
Scarlet Tanager *Piranga olivacea*	13	✓	✓	✓	✓	✓	✓	Head, throat, back, breast, belly, rump, wing coverts, edges of rectrices	✓		✓	✓	PA NY FL* QC OH
Northern Cardinal *Cardinalis cardinalis*	3	✓		✓		✓		Head, breast, flanks, wing coverts, flight feathers	✓				PA MI CT
Baltimore Oriole *Icterus galbula*	28	✓	✓	✓	✓	✓	✓	Head, throat, breast, belly, back, wing coverts, rectrices	✓	✓	✓	✓	MA ON MI QC NY PA NS RI VT, IL, IN, NB, FL*, Costa Rica*
Total	246												

\# Number of independent reports, not the number of aberrantly colored individuals involved.

Seasons: Fa (Aug, Sep, Oct), Wi (Nov, Dec, Jan), Sp (Feb, Mar, Apr) and Su (May Jun Jul). Note that birds in Juvenal plumage that were molting pre-Formative orange feathers in late July were classified as Fall.

* States/countries where the species does not normally breed.

photographic coverage of the species as the Prothonotary Warbler does not undergo a pre-Alternate molt (Pyle 1997) and should look largely the same in Basic plumage. Prothonotary Warblers were interesting in another respect. Occasionally individuals exhibited reddish tones on their heads (crown, throat) that did not match what we expected from the deposition of rhodoxanthin in feathers. Besides colors that were more rufous in tone, the feathers were also often matted, appearing as if stuck together. We suspect this color variation to be a form of staining acquired as a result of the species' habit of feeding on nectar and placing its head in flowers (Julie Craves, pers. obs.).

We also found examples of thrushes, namely a Veery (*Catharus fuscescens*) and a Hermit Thrush (*Catharus guttatus*), with faint reddish washes on their bellies that did not appear to be from external application (adventitious coloration), for example as a result of staining from the bird's feces. However, it is unclear whether these pink washes were caused by rhodoxanthin as these species do not appear to normally deposit carotenoids (which rhodoxanthin could replace) there. It is possible that porphyrins, which occasionally show up in fresh plumages but fade rapidly afterward, imparted the reddish color. Porphyrins can usually be identified by their pink fluorescence under ultraviolet (black) light, if spectrophotometric or biochemical studies are not possible.

We note that rhodoxanthin did not explain the reddish underwing coverts of a female Rose-breasted Grosbeak (*Pheucticus ludovicianus*) banded at McGill Bird Observatory in 2006 (30 Aug; band #1951-76608). The red color in this instance was caused by 4-keto-carotenoids, mainly canthaxanthin, but also echinenone (Hudon unpublished data), which the female grosbeaks are believed to produce endogenously, since males use them to produce the bright red color of the breast patch and underwing coverts (Hudon 1991). The absence of rhodoxanthin should not come as a surprise, however, as this variation in the color of the underwing coverts of female Rose-breasted Grosbeaks has a long history (e.g., Moyer 1930, Leberman 1984), preceding by many years the active dissemination of Asian bush honeysuckles in North America. Though the color of the coverts of female Rose-breasted Grosbeaks is typically yellow, on occasion they take bright rose colors, rarely as rose-pink as in the male, or various shades of orange and salmon (Moyer 1930, Leberman 1984). Reddened underwing coverts in female grosbeaks should thus be considered a normal, and likely genetically based color variation in the species, possibly the result of incomplete suppression of processes involved in the production of red underwing colors in the male (see examples in Winterbottom 1929).

The color variants reported on here typically mapped to the northeast (New England, New York, Pennsylvania, New Jersey and southern Ontario and Quebec; 66% of records), and parts of the American Midwest (17%), with particularly high concentrations of species and individuals with aberrant plumages in eastern Massachusetts, western Pennsylvania, southern Ontario and southern Quebec, consistent with the distribution of Morrow's and Tatarian honeysuckles and their hybrids in North America (Figure 2). The exotic bush honeysuckles quickly became well established in these areas, following their active promotion in the 1960s as "valuable wildlife habitat." They have become naturalized to a point of being considered highly invasive species in many states (Williams 2005, USDA Forest Service).

We note the observation of aberrant Cedar Waxwings as far west as Alberta, Montana and Idaho (2% of records), where the bush honeysuckles, in particular the Tatarian honeysuckle, occur (Figure 2 Pg.103). Finally, aberrantly colored birds (15% of records) were also recorded in areas where birds from the Northeast spend the winter (the southern U.S. for the Cedar Waxwing and White-throated Sparrow; Costa Rica for Prothonotary Warbler and Baltimore Oriole). Records of aberrantly colored birds go back at least five decades (Mulvihill et al. 1992), and possibly even earlier than that for Northern Flickers (see Hudon et al. 2017). However, the vast majority of records with dates have been documented in the current (2010s; 91 of 197 records; 46%) and the previous (2000s) decade (93 records; 47%). This trend may have more to do with the increased use of the World Wide Web

to disseminate images of birds, through blogs and image-sharing sites like 'Flickr,' than any actual increase in the incidence of reddened birds.

The altered plumage coloration in these brightly colored species has the potential to disrupt color signals used by females to assess a male's quality and underlying genes (Andersson 1994, Griffith and Pryke 2006, Hudon et al. 2013). Jones et al. (2010) for example found that plumage coloration no longer correlated with, or honestly signalled, body condition in cardinals in urban areas of central Ohio as a result of the presence of Asian bush honeysuckles there. The authors surmised that Amur honeysuckle (*Lonicera maackii*) caused the breakdown (Jones et al. 2010). However, since its berries contain only common yellow carotenoids and no rhodoxanthin (Hudon et al. 2017), it is possible that undetected Morrow's or Tatarian honeysuckles present in these locales created this situation; alternatively, the Cardinals may have been second-year birds whose natal dispersal led them away from areas where Morrow's and Tatarian honeysuckles were present. Importantly, the decoupling between plumage coloration and body condition has the potential to reduce the fitness of females that select mates appearing to be more genetically fit (Wolfenbarger 1999), when the alluring coloration could instead be due to the consumption of plumage-altering exotic berries (Hudon et al. 2013). In localities where diet-based erythrism is occurring, plumage coloration should be a less reliable indicator of male quality, providing a natural experiment to investigate the importance of male coloration in mate selection and subsequent reproductive success. The color-altering properties of rhodoxanthin additionally potentially provide an opportunity to identify (1) species previously unknown to incorporate fruits in their diets in late summer and fall, even if infrequently or in small amounts (e.g., Blue-winged and Kentucky warblers, and Common Yellowthroat), (2) feathers not otherwise thought of as normally containing carotenoid pigments (even if only faintly, as potentially in some thrushes), (3) the timing of replacement of bird feathers, and (4) which feathers are not replaced during the pre-Alternate molt.

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Figure 1. Examples of birds with aberrant plumages believed to be the product of the ingestion of rhodoxanthin-containing berries. A. Prothonotary Warbler (Iroquois NWR, NY; 27 May 2006); B. Common Yellowthroat (Wing Island Bird Banding Station, MA; 15 May 2010); C. American Redstart (McGill Bird Observatory, QC; 28 Aug 2006); D. Chestnut-sided Warbler (PARC, PA; 9 Sept. 2014); E. Prairie Warbler (Wing Island Bird Banding Station, MA; 16 Sept. 2010); F. Yellow-breasted Chat (PARC, PA; 2 May 2006); G. Scarlet Tanager (PARC, PA; 16 July 2005); H. close-up of Northern Cardinal (PARC, PA; 15 Aug 2004).

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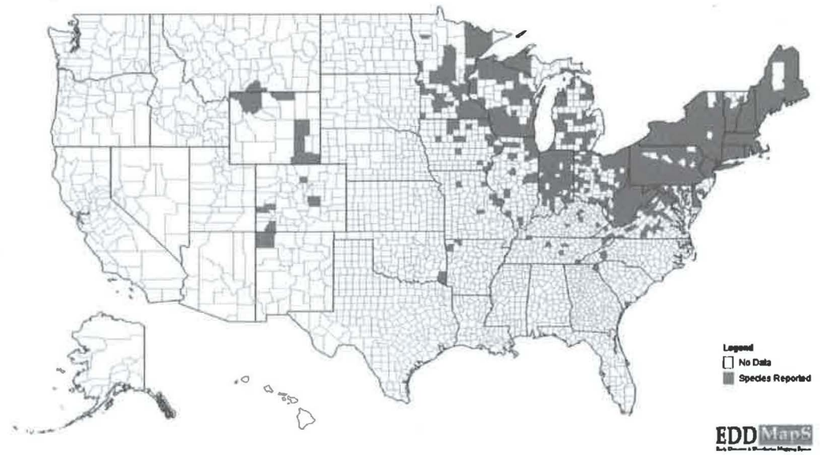
Figure 2. Known distribution of *Lonicera morrowii* and *L. tatarica* by counties in the continental U.S.A. (EDDMapS 2017). Canadian provinces with these taxa are indicated using abbreviations.

Lonicera morrowii

Canadian provinces: SK, ON, QC, NB



Lonicera tatarica

Canadian provinces: AB, SK, MB, ON, QC, NB, NS