The colors of birds provide a wonderful spectacle. They are the result of the interplay of diverse pigments with intricate structural elements. For the casual observer, avian coloration is a source of beauty. For birders and ornithologists, colors and patterns assist in the identification of species, as well as in the aging and sexing of individuals. And for the birds themselves, colors serve a number of purposes, including mate selection, indicator of social rank, camouflage, and species recognition.

Color variation, not including that related to age, sex, or season, can be expected to occur in many species of birds, for example, among geographic races and among genetically based color morphs. Some color variation, however, cannot be assigned to different subspecies and morphs. If you have seen enough House Finches, for instance, you will have noticed males with unusual orange or even yellow hues. This article reports on an unusual color variation in the Baltimore Oriole, a phenomenon observed in Canada only in the past few years and presumed to be dietary in origin.

**A Red Baltimore Oriole!**

Our story begins at the Tommy Thompson Park Bird Research Station (TTPBRS) in Toronto, Ontario. Tommy Thompson Park is the largest area of existing natural habitat on the central Toronto waterfront. The research station was established to deliver monitoring, research, and educational programs focused on birds and the environment. The migration monitoring program at TTPBRS is operated daily during spring and fall migration and involves standardized mist netting, banding, and census and point counts.

In the early morning of 22 August 2005, an unusual-looking first-fall Baltimore Oriole was captured and banded. The individual sported red feathers on its head, breast, and undertail, as well as red highlights on the secondary coverts, back, and belly (Fig. 1), areas normally tinted yellow to orange-yellow in first-basic plumage. The bird was briefly examined, photographed, and released without a clear understanding of its aberrant coloration. Another bird with less-obvious red coloration had been captured earlier that same week; however, it was dismissed as an isolated oddity, a bird that had been stained perhaps. The appearance of this second bird gave notice that further investigation was warranted.
More Red Baltimore Orioles

By the time the 2005 fall season was over, at least two more—seemingly unrelated—cases of reddened Baltimore Orioles would come to light: a migrant observed foraging at Sainte-Catherine in Montréal, Québec, on 9 September 2005 (Fig. 2) and a young male in southern Halifax, Nova Scotia, in late November (Fig. 3). The warm plumage tones of the latter bird initially led to its misidentification as a Flame-colored Tanager, clearly a bird requiring documentation!

The summer and fall of 2006 would produce yet additional red orioles, with at least two more banded at TTPBRS and at least seven at the McGill Bird Observatory at Sainte-Anne-de-Bellevue in Montréal (Fig. 4).

Reddish (or erythristic) orioles have been described only once before. Parkes (1993) reported five instances of aberrantly reddened Baltimore Orioles from the northeastern United States. One was a bird banded on Great Gull Island, New York, in 1985. The second was a bird banded at Block Island, Rhode Island, in 1988. Parkes’s search for similarly affected specimens in museum collections turned up three more individuals in the American Museum of Natural History (AMNH 54807, 521485, and 789315). Two were collected in New York state, and one (AMNH 521485) lacked collection data. Although Parkes did not perform a chemical analysis of the affected feathers, he indicated that the color change was likely diet-related. Could these orioles and the recent Canadian birds represent examples of diet-induced reddening resulting from the ingestion of the berries of an introduced shrub currently taking North America by storm?

Carotenoids and Feather Color

Carotenoid pigments are diverse and widely distributed in the natural world. They are responsible for the bright yellow to red colors found in such plant foods as carrots, tomatoes, and peppers. Their manifestations include most of the bright red, orange, and yellow hues seen in bird feathers worldwide, and almost all of those observed in North American birds.

Like all other animals, birds cannot synthesize carotenoids from scratch, so the biochromes (“building blocks”) must be acquired in the birds’ diets. The sources of dietary carotenoids are numerous and varied. Some carotenoids are ingested and deposited unmodified. Others are modified by birds, yielding compounds that broaden the color palette to include red, orange, and bright yellow hues not attainable with pigments obtained directly in the diet.

Carotenoids manufactured by birds (and many other animals) are derived from dietary compounds, and include the 4-keto-carotenoids, responsible for most of the red hues of birds on this continent, such as Greater Flamingo, Northern Cardinal, Rose-breasted Grosbeak, and Scarlet Tanager (Fox et al. 1969, Hudon 1991, McGraw et al. 2001), and the canary-xanthophylls, which yield bright yellow colors in other species, such as American Goldfinch and Western Tanager (Hudon 1991, McGraw et al. 2001).
suckle \((L.\ tatarica)\), another introduced species, were not tested, but were believed to contain the pigment, based on the plant’s close relationship to Morrow’s honeysuckle and the fact that the two species readily hybridize in the wild (Mulvihill et al. 1992, Witmer 1996).

Confirmation that rhodoxanthin in honeysuckle berries could redden the tail tips of Cedar Waxwings came a few years later, when Witmer (1996) conducted feeding experiments in the controlled environment of an aviary. Waxwings were divided into two groups and fed a diet of either exclusively Morrow’s honeysuckle berries or their choice of dog food or Morrow’s honeysuckle berries. The group having a choice ate primarily berries. All birds from either group that began molting rectrices grew orange-tipped replacements. When they started molting rectrices some birds in each group were switched to a rhodoxanthin-free dog-food-only diet. Rectrices grown before the diet switch were aberrant (orange-tipped) and those grown after the diet switch were normal (yellow-tipped).

**A Short Time Window**

The timing of berry availability relative to tail feather growth explains why most of the waxwings with orange tail bands at Powderrmill were immatures (Mulvihill et al. 1992). At Powderrmill, honeysuckle berries are available from June into early August, when nestling waxwings are actively growing their juvenal rectrices (Mulvihill et al. 1992). Adults do not normally molt their tail feathers until later, in mid-August at the earliest, during the prebasic molt, when the berries are no longer available, so adults nearly always had yellow-tipped tails. Several immature birds with orange tail bands were also found growing yellow-tipped replacement feathers in September and October when honeysuckle berries were no longer available. Two birds with yellow tail bands were found growing orange-tipped replacement feathers in July when honeysuckle berries were available. It was concluded that adults undergoing an adventitious molt of their tail feathers during June and July could grow orange-tipped rectrices (Hudon and Brush 1989, Mulvihill et al. 1992).

In contrast, near Ithaca, New York, where in 1993 79% of adult and 39% of juvenile waxwings had orange-banded tails, honeysuckle berries, mostly of Morrow’s, are available until mid-October (Witmer 1996). Thus honeysuckle berries in this region are still available when adults undergo the prebasic molt of their rectrices.
Rhodoxanthin
Rhodoxanthin ingested at time of feather growth can be deposited in areas of plumage normally pigmented by carotenoids (Volker 1955). Since rhodoxanthin is structurally similar to many of the carotenoids deposited in the plumage of birds, notably the canary-xanthophylls, it should come as no surprise that, where available, it would turn up in the tips of the rectrices of Cedar Waxwings. Although scarce in plants, rhodoxanthin is found in low concentrations in the foliage of many species of conifers, causing the fall reddening of their needles. Rhodoxanthin is also responsible for the red color of the arils of the eastern yew tree (Taxus canadensis) but these may not be eaten by birds, given that the yew is considered toxic. The key is that the appearance of rhodoxanthin-induced color variation is recent; therefore, it is unlikely that any species native to eastern North America is the source of the pigment.

Alien Shrubs
Morrow's and Tartarian honeysuckles were introduced and actively disseminated as desirable wildlife habitat in the late 1950s and early 1960s, based on recommendations from a few years earlier (Cook and Edminster 1944, Edminster 1950); these plants are no longer viewed as beneficial, however (Williams 2006). Bush honeysuckles are currently well-established in many parts of the United States and Canada, notably the northeastern United States (USDA 2006), providing birds with a ready supply of red berries.

At the Tommy Thompson Park Bird Research Station (TTPBRS), both Morrow’s and Tartarian honeysuckles are abundant, and 2005 was a bumper year for the berry crop. Waxwings, orioles, and robins were observed gorging on berries during the first few weeks of August of that year. Orange tail bands on young waxwings have been commonly noted over the past three fall seasons of banding at Tommy Thompson Park (Fig. 5).

A Red Tide
Since the elucidation of the source of color variation in the Cedar Waxwing, many examples of aberrantly colored (reddened) birds have come to light. Invariably, these are birds in which yellow or green areas of the plumage are aberrantly colored orange or red. Rhodoxanthin is suspected in all these cases, but has yet to be chemically demonstrated.

Along with the Cedar Waxwing, the White-throated Sparrow is known to exhibit enhanced garb. In some individuals the lores, the only area of bright yellow color on a White-throated Sparrow, are orange (Fig. 6).

Brooks (1994) reported eight White-throated Sparrows with orange lores banded in western New York state during the 1990–1993 fall seasons. These were from more than 2,700 birds banded during 1985–1993. No orange-ored birds were observed among more than 950 banded during the spring from the same period. Craves (1999) reported a hatch-year White-throated Sparrow with orange lores banded on 27 September 1998 at the Rouge River Bird Observatory in Michigan. This was the first White-throated Sparrow with orange lores banded there among the more than 700 birds of that species banded in 1992–1998. Another hatch-year bird with orange lores was banded at Rouge River on 16 September 1999. The Kalamazoo Nature Center had three orange-ored birds (all hatch-year) out of 1,043 White-throated Sparrows banded during 1990–1998. The TTPBRS banded its first White-throated Sparrow with orange lores on 19 September 2005 and another on 30 September 2006. All of these observations point to the low incidence of this type of diet-induced color variation in the White-throated Sparrow. Although the White-throated Sparrow’s summer diet consists primarily of insects, with some greens and fruit taken, by late summer and fall the diet shifts mainly to fruit and seeds (Falls and Kopachena 1994).

During a five-year interval at Powderrill Nature Reserve, banding results included nine of 28 Yellow-breasted Chats exhibiting bright orange breast feathers and two adult (after hatch-year) Kentucky Warblers with orange-yellow coloration on the supercilium, chin, throat, and breast (Mul-
Adult male Scarlet Tanagers at Powdermill have been observed replacing their scarlet alternate plumage with scattered bright orange, rather than the usual yellow basic feathering (Fig. 7). Also, a hatch-year female Scarlet Tanager in first prebasic molt banded at Powdermill on 16 July 2005 had scattered orange-colored body feathers replacing the streaked gray-and-olive juvenal plumage (Leppold and Mulvihill 2006).

Finally, a hatch-year Yellow Warbler captured on 16 July 2005 at Powdermill had aberrant orange feathering along the sides of its throat and lightly down the center of its belly (Leppold and Mulvihill 2006).

And based on our findings in southeastern Canada, it appears that the Baltimore Oriole has now joined the ranks of unsuspecting snappy dressers.

**Fall Colors**

Although Baltimore Orioles feed primarily on insects during the breeding season, they also incorporate a significant amount of fruit—including berries—into their diet. Rising and Flood (1998) listed the main components of the diet at this time as caterpillars, fruit, adult insects, and spiders. Of particular note regarding the 2005 occurrences at TTPBRS was an oriole nest discovered near the research station. The adult male of this nesting pair was banded, and both parents were observed in an almost frenzied feeding pattern on nearby fruit-bearing shrubs, including bush honeysuckles. Point count surveys on both 8 and 11 July revealed a family group of four Baltimore Orioles feeding near the nest, suggesting that the chicks had fledged. While it cannot be ascertained beyond a doubt that the aberrantly colored orioles had hatched locally, the circumstances indicate that they likely were.

Furthermore, Baltimore Orioles undergo their prebasic molt at a time when bush honeysuckle berries are available. The first prebasic molt is a partial molt that begins in early July and involves the contour feathers of the body, but not the flight feathers of the wing and tail (Pyle 1997, Rising and Flood 1998). The first prealternate molt is incomplete and involves some contour feathers, some inner greater coverts, up to two tertials, and some or all rectrices. The definitive prebasic molt begins in July and involves the entire plumage. Baltimore Orioles generally complete their prebasic molts on the breeding grounds—in other words, before they begin their southward fall migration. The status of further prealternate molts is uncertain. The molt may be very limited or may not occur at all. The definitive alternate plumage aspect is primarily attained by wear on feathers grown during the definitive prebasic molt. This wear reduces or eliminates the pale edges of orange or black contour feathers, and reduces the white edges on black wing feathers (Pyle 1997, Rising and Flood 1998).

**Issues**

Recent chemical analysis by Jocelyn Hudon (unpublished data) has found that the reddened feathers of some of the odd-colored Baltimore Orioles collected at McGill Bird Observatory in 2006 do contain rhodoxanthin. The Baltimore Oriole is thus the second species, after the Cedar Waxwing, proven to have rhodoxanthin in aberrantly colored feathers.

This color change has the potential to cause more than puzzled looks on birders’ faces, should odd-colored males find favor in the eyes of female orioles. Since the prealternate molt in Baltimore Orioles is limited, young and even older birds that acquire aberrantly colored feathers in the fall could still show them the following spring. If adult females find the odd color appealing, will they choose young males over more-experienced ones as mates? Will older males tolerate this intrusion by younger males? Will they end up spending more energy than usual establishing breeding territories because of the increased competition? Would females learn to overcome their fatal attraction to redder males, if they turned out to be poor providers of food for any chick produced? The potential impacts of widespread rhodoxanthin ingestion on the evolutionary ecology of the Baltimore Oriole remains to be determined.

A final issue concerns the potential for more bird
species to exhibit this type of diet-induced color variation. Potentially, any species that harbors carotenoids in its feathers and that incorporates bush honeysuckle berries into its diet during molt could show reddish plumage. This phenomenon need not be limited to species that eat a lot of fruit. Even species considered primarily insectivores, like wood-warblers, have developed orange patches. Based on our understanding of how rhodoxanthin is incorporated in bird plumages, several generalizations can be made to help identify the cases in which diet-induced reddening, as a result of eating the berries of introduced bush honeysuckle, has occurred. Specifically, we would expect:

1. An increase in the redness (warmth) of the coloration as a result of the incorporation of rhodoxanthin, a deep red pigment. Much color variation would be expected, depending on amounts of honeysuckle berries consumed.

2. The warm tones to appear only in areas of the plumage that are normally pigmented by carotenoid pigments, i.e., those areas normally colored yellow, orange, red, or green, even if only faintly so.

3. The warm tones to be found only in feathers grown in the late summer or fall, during the prebasic molt, when the berries are available. For some species, those feathers will be worn only in the fall and winter, that is, until they are replaced during the prealternate molt in spring. In other species, in which the prealternate molt is incomplete, aberrantly colored feathers would appear in the breeding season the year following.

4. An uneven or mottled distribution of the warm tones, appearing in only those feathers grown at the time when honeysuckle berries are available.

5. The aberrantly colored feathers to be found only in those feather tracts that are molted when honeysuckle berries are available, which will depend on a number of variables, like age of the bird, geography, and so forth.

The Future
Proper documentation of the spread of this diet-induced color variation in Baltimore Orioles, as well as other species of birds, will be achieved only through careful involvement of the birding community. Birders are urged to report any examples of color variation they encounter, whatever the species. Such reports could go to state and provincial records committees. This information will aid in understanding which species are affected, as well as in documenting the geographical and temporal scopes of this emerging phenomenon. Migration monitoring stations that encounter birds with variant colors will help define affected areas, along with the age and sex of affected individuals. Importantly, feather collection by authorized personnel will permit a detailed examination of which pigments are causing the color variation. If the phenomenon spreads, studies by ornithologists will provide insight into diet-induced and other types of color variation.

Fig. 6. White-throated Sparrows with orange—rather than yellow—lores have been noted in low numbers since the early 1980s. Other species—for example, Yellow-breasted Chat and Kentucky Warbler—have also been noted in the past several decades to be prone to exhibit unusual amounts of red and orange in the plumage. Toronto, Ontario; 30 September 2006. © Dan Derbyshire / Toronto & Region Conservation.

Fig. 7. Although this article has a geographic focus on southeastern Canada, the increase in frequency of aberrantly red birds appears to be widespread. For example, the Powderrmill Avian Research Center in southwestern Pennsylvania has for several decades been documenting such birds, including this Scarlet Tanager growing orange feathers in its prebasic molt. Rector, Pennsylvania; August 1993. © Robert Mulvihill.
and how it is affecting biological parameters such as mate selection and survivability of affected individuals.

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Literature Cited


