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CONSEQUENCES OF AN ALIEN SHRUB ON THE PLUMAGE COLORATION AND ECOLOGY OF CEDAR WAXWINGS

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ABSTRACT.—Cedar Waxwings (*Bombycilla cedrorum*) with orange (instead of the normal yellow) tail bands have appeared in eastern North America in the last 35 years. Biochemical studies have implicated a dietary cause (Hudon and Brush 1989), specifically the fruits of *Lonicera morrowii* (Brush 1990), for this novel color variant. I show that rectrices replaced while Cedar Waxwings are feeding on *L. morrowii* fruits develop orange tips. Rectrices replaced subsequent to switching the diet of molting waxwings from *L. morrowii* fruits to dog chow were yellow, showing close temporal correspondence between dietary input of rhodoxanthin and the coloration of growing feathers. In the Ithaca vicinity, fruits of *L. morrowii* are eaten by wild Cedar Waxwings from June until mid-October. The extended pattern of availability and consumption of *Lonicera* in this region appears to explain my unique observations of adult Cedar Waxwings growing orange tails during the fall months. Cedar Waxwings maintained body condition and molted while on an extended diet of *L. morrowii* fruits (36 days for two birds and 64 days for two others). Three birds initiated tail molt while on this diet, including one that molted all of its flight feathers. These results emphasize the nutritional specialization of Cedar Waxwings to a diet of sugary, low-protein fruits, and show that molt occurs in an apparently normal manner when birds are eating a low-protein fruit diet. *Received 30 September 1994, accepted 15 April 1995.*

CEDAR WAXWINGS (*Bombycilla cedrorum*) normally have a yellow terminal band on their tails. Within the past 35 years, Cedar Waxwings with orange tail bands have appeared in the northeastern United States and southeastern Canada (Yunick 1970, Hudon and Brush 1989, Pittaway 1991, Mulvihill et al. 1992). Carotenoid pigments (i.e. xanthophylls) cause the yellow tail bands of Cedar Waxwings (Hudon and Brush 1989), as well as the red tips of their secondaries (Brush and Allen 1963). The coloration of the novel orange-tipped rectrices of Cedar Waxwings is caused by the inclusion of a red carotenoid pigment (rhodoxanthin) in the

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FRONTISPIECE. Tail colors of Cedar Waxwings. Bird in upper left (Bird 1) was fed only *Lonicera* fruits during tail molt. Bird in upper right (Bird 2) was switched from *Lonicera* fruits to chow diet midway through tail molt. Bird in lower left is wild bird with orange tail band (Cornell University Vertebrate Collection [CVC] no. 30194; juvenile male, 9 November 1961, Chemung Co., New York). Bird in lower right is wild bird with normal yellow tail band (CVC no. 14422, adult male, 1 June 1942, Tompkins Co., New York).

tail bands (Hudon and Brush 1989). Carotenoid pigments in feathers appear to be derived exclusively from dietary sources, either directly or with modification (Goodwin 1984, Hudon and Brush 1989). Dietary rhodoxanthin has been reported to be deposited unaltered in the carotenoid-containing feathers of several birds (Völker 1955, 1957, 1958). Apparently, this pigment is not distinguished biochemically from the yellow xanthophylls that normally color these feathers. These findings suggest that the recent color variant of the Cedar Waxwing is a result of a dietary shift to a rhodoxanthin-rich food source during the period of tail molt (Hudon and Brush 1989). Of the seven recently introduced plants in the northeastern United States analyzed by Brush (1990), rhodoxanthin occurred only in the fruits of Morrow's honeysuckle (*Lonicera morrowii*).

In western Pennsylvania, virtually all Cedar Waxwings with orange tail bands are birds with juvenal rectrices (Mulvihill et al. 1992). The availability of honeysuckle fruit (*L. morrowii* and *L. tatarica*) coincides with the period during which nestlings are growing their tails (late June through July) but not with the period during which adults replace their rectrices (Dwight 1900). Mulvihill et al. (1992) suggested that this explains the occurrence of orange-banded tails only among young Cedar Waxwings (plumages before first complete molt, which occurs in fall months of second year). Birds molting from one color form to the other also have been noted (Hudon and Brush 1989, Mulvihill et al. 1992), suggesting a dietary (versus a genetic) basis for the phenomenon.

In aviary feeding trials, I tested the influence of honeysuckle fruit consumption on plumage coloration of molting Cedar Waxwings. Based on work conducted in the vicinity of Ithaca, New York, I report information on the historical incidence of orange-tailed Cedar Waxwings, the seasonal phenology of honeysuckle fruit availability, and Cedar Waxwing consumption of this fruit. I also describe body-mass changes and molt progression of captive Cedar Waxwings during periods in which they were fed a diet consisting entirely of honeysuckle fruits.

METHODS

Naturalized honeysuckles.—Eurasian honeysuckles are widely established outside of cultivation in the northeastern United States (Barnes 1972). These shrubs are now common in the Ithaca vicinity (e.g. Stover [1994] recorded alien honeysuckle shrubs at 7 of 12 pasture sites). Muenscher (1950) reported three exotic honeysuckles in the Ithaca area (native ranges from Rehder 1903): *L. morrowii* (Japan), *L. xylosteum* (Europe, Asia Minor, and western Siberia), and *L. tatarica* (central Asia to southern Russia). These species are morphologically similar and are considered to be closely related (Rehder 1903). Although hybrids are rare among the species of this genus in natural situations (native ranges and habitats), *L. morrowii* and *L. tatarica* readily hybridize where they occur together as aliens (Rehder 1903). I identified local honeysuckles by leaf pubescence, pedicel length, bractlet size, flower color, and filament pubescence (Fernald 1950, Muenscher 1950). Honeysuckle shrubs were surveyed on 24 May 1993 during flowering at six local sites (three in Ithaca and three in rural areas). *Lonicera morrowii* and *L. tatarica* can be readily distinguished at this season by flower color (white, turning yellow and pink, respectively; Fernald 1950). I did not find *L. xylosteum* among the shrubs I examined. *Lonicera morrowii* was much more common than *L. tatarica.* Among three transects in Ithaca, 80.5% (n = 354 shrubs, range 71.6–85.1%, 61–201 shrubs per transect) of honeysuckle shrubs were *L. morrowii*, whereas among three rural transects (two streamside sites and one roadside site), virtually all shrubs were *L. morrowii* (n = 215 shrubs, range 98.4–100.0%, 37–117 shrubs per transect). Species identity was based on morphological criteria, but in light of the ease of hybridization among this group of shrubs (Rehder 1903, Barnes 1972), the genetic purity of these plants is uncertain. Rhodoxanthin has been reported from fruits of *L. morrowii* (Brush 1990), as well as fruits of two other species of *Lonicera* (*L. webbiana* and *L. ruprechtiana*; Rahman and Egger 1973), suggesting the widespread occurrence of rhodoxanthin in this genus. I used fruits from shrubs identified as *L. morrowii* (hereafter, *Lonicera*) in this study. Voucher specimens have been deposited at the Bailey Hortorium, Cornell University.

Housing and foods.—I maintained Cedar Waxwings in unheated aviaries (4.00 × 2.15 m) with exposure to natural conditions on the southern side (2.15 m). An opaque fiberglass ceiling slanted from a height of 2.84 m on the southern end to 3.38 m on the northern end. One ceiling panel (0.97 × 2.29 m) was translucent. The mesh of the screened side of the aviary was wide enough to allow entry of flying insects, but insect consumption was assumed to be extremely low because insects were uncommon within the chambers. Birds were given fresh water and food daily.

The foods offered to Cedar Waxwings in this study were *Lonicera* fruits and moistened dog chow (Iams Company, Eukanuba Brand Small Bites Puppy Chow; hereafter referred to as "chow"). I analyzed these foods for hexose sugars (anthrone procedure; Yemm and Willis 1954), lipids (ethyl ether extraction), and nitrogen (Kjeldahl method) as an estimate of protein. Results are reported relative to dry matter (dried at 100°C to constant mass) of fruit pulp and skin. Samples for sugar analysis were extracted with 80% ethanol to exclude polysaccharides. *Lonicera* fruits were high in sugar (73.8 ± SE of 0.7%, $n = 13$ shrubs) and low in lipids ($<2\%$, $n = 2$) and nitrogen (0.53 ± 0.01%, $n = 2$), whereas chow was low in sugars (1.3%) and high in lipids (21.7%) and nitrogen (5.78%). Fruits of *L. morrowii* contain rhodoxanthin (Brush 1990) and other carotenoid pigments (Goodwin and Goad 1970). Rhodoxanthin was presumed to be absent from the chow diet because of the lack of ingredients reported to contain this pigment. The chow diet contained ground corn, chicken fat, and whole eggs, which may have contributed other C_{40} xanthophyll carotenoids, such as zeaxanthin and cryptoxanthin (Belyavin and Marangos 1989).

Diet treatments.—Seven Cedar Waxwings were used in the tail-color experiment. Three birds molted all rectrices while on a diet of *Lonicera* fruits, either with or without supplemental chow. Four others were switched to a chow diet after they initiated rectrix molt on a diet that included *Lonicera* fruits. Bilateral pairs of rectrices are molted from the center outward at intervals of about three to four days (Witmer unpubl. data), so the progression of rectrix molt was easy to monitor. All birds had been maintained in captivity for at least one year, primarily on a diet of wild fruits and chow. The diet manipulations are described below.

Four adult Cedar Waxwings were maintained exclusively on a diet of *Lonicera* fruits from 30 July until 4 September 1992. On 4 September three of these birds were midway through rectrix molt. Two of these three birds were switched to chow (three-day transition with both *Lonicera* fruits and chow offered). The other bird undergoing tail molt and the fourth bird that had not begun tail molt remained on the exclusive fruit diet until 2 October 1992. This fourth waxwing did not replace any rectrices while eating a fruit-only diet but molted one rectrix between 3 and 13 October when it was fed *Lonicera* fruits and chow.

Three other Cedar Waxwings molted rectrices while eating a diet of *Lonicera* fruits and chow offered simultaneously in unlimited amounts. These birds selected a diet that was about 90% fruit (dry matter). Two adults (second-year birds) were maintained on this diet from 30 July until 17 September 1992. On 17 September one of these birds was midway through rectrix molt and was switched to chow. The other bird was already growing a complete set of new rectrices. The third waxwing, an adult female, was provided the fruit and chow diet from 30 July through 10 October 1992, during which time she molted all of her rectrices.

I compared tail coloration of the experimental birds with recent (since 1986) specimens of Cedar Waxwings in the Cornell University Vertebrate Collections (CVC). I did not use older specimens because of potential fading. Tail colors of experimental birds and museum specimens were matched with colors in Smithe (1975). Museum specimens in the CVC were examined to evaluate the historical occurrence of Cedar Waxwings with orange-tipped rectrices in central New York. Specimens acquired since 1986 were salvaged birds, representing a haphazard sample.

Diet of wild Cedar Waxwings.—Monthly values of the proportion of fruit in Cedar Waxwing diets were based on analysis of gut content records from the U.S. Biological Survey (Witmer 1996). I examined these data (1885–1950) for records of the fruits of exotic honeysuckles in the stomachs of Cedar Waxwings. Contemporary use of these fruits by Cedar Waxwings in the Ithaca vicinity was evaluated by feeding records made during daily roadside surveys (ca. 4 km) from 1988 through 1993. I treated each encounter as a single sample of waxwing feeding, not weighted by flock size. I used this approach because individuals within a flock are not independent choice measures (McPherson 1987). This approach also reduced bias created by the greater apparency of larger flocks.

RESULTS

Experimental effects of diet on plumage coloration.—Consumption of *Lonicera* fruits by Cedar Waxwings during tail molt resulted in orange-tipped rectrices (Frontispiece, Table 1). All four birds that were switched to the chow diet subsequently grew yellow-tipped rectrices, whereas each of the three birds not switched continued growing orange-tipped rectrices (Fisher's exact test, $P = 0.03$, df = 1, $n = 7$). Two birds on the diet of only *Lonicera* fruits also molted flank feathers tinged with orange, instead of the normal yellow flank feathers (Frontispiece). Three Cedar Waxwings from this experiment are deposited in the CVC (catalog nos. 39056 [Bird 1], 37981 [Bird 2], and 37554 [Bird 6]).

Tail bands of waxwings fed only *Lonicera* fruits showed more red pigmentation (Flame Scarlet to Chrome Orange) than did orange-tailed museum specimens (Spectrum Orange in eight birds and Chrome Orange in one). Tail-band coloration of birds fed *Lonicera* fruits and chow was similar to that of wild waxwings, but still showed slightly more red pigmentation (Table 1).

Most rectrices molted subsequent to the diet switch from *Lonicera* fruits to chow were yellow. Only one rectrix that erupted immediately after the three-day transition from fruit to chow showed a tinge of orange on the edge of the feather (Frontispiece, Table 1). Thus, the loss of

TABLE 1. Colors (in parentheses; after Smithe 1975) of rectrix tips of Cedar Waxwings maintained on diets including *Lonicera* fruits or switched from fruit to dog chow midway through rectrix molt. "Transition" is a three-day period between diet switch. Rectrices usually were molted symmetrically from center outward. Unless noted otherwise, rectrix numbers refer to bilateral pairs of feathers. Orange colors (in decreasing amount of red): (15) Flame Scarlet; (16) Chrome Orange; (17) Spectrum Orange; (18) Orange Yellow. Yellow color: (56) Straw Yellow.

			Rectrices erupted		
Bird	Sex	Diet	On initial diet	During transition	After diet switch
1	M	Fruit[a]	1-6 (15-16)		
2	M	Fruit/chow[a]	Left: 1-2 (16)	3 (16-17)	4-6 (56; orange edge on 4)
			Right: 1-2 (16)	3 (16-17)	4-6 (56)
3	F	Fruit/chow[a]	1-4 (16)	5 (18)	6 (56)
4	M	Fruit/chow[a]	Right: 6 (16)		All others (56)
5	F	Fruit	1-6 (17)		
6	F	Fruit	1-6 (16)		
7	F	Fruit/chow	Left: 1-4 (16)		5-6 (56)
			Right: 1-3 (16)		4-6 (56)

[a] Fed only *Lonicera* fruits for extended period (see text). Bird no. 4 molted no rectrices on the fruit-only diet but molted one rectrix on the fruit/chow diet between 3 and 13 October.

rhodoxanthin pigmentation from the plumage corresponded very closely with the timing of the diet switch. The yellow rectrices of experimental birds were duller (Straw Yellow; Frontispiece, Table 1) than those of wild birds (14 specimens with Spectrum Yellow tails). All experimental birds had very little yellow pigmentation in their belly feathers.

Molt on a fruit-only diet.—Cedar Waxwings that were fed only *Lonicera* fruits maintained good body condition (Fig. 1) and molted varying amounts of plumage while on this diet. Two birds that were fed this diet for 36 days initiated prebasic molt and showed a slight (Bird 2) or moderate (Bird 3) loss of body mass (Fig. 1, Table 1). Two other waxwings fed only *Lonicera* fruits for 64 days showed much different molting schedules from each other, but exhibited similar patterns of body-mass change (Fig. 1). One of these (Bird 1) molted all of its flight feathers during this period (Table 1). This bird molted at a faster rate than two other waxwings that were at a similar stage of molt on 4 September, and were switched from the fruit-only diet to the chow diet on this date (Bird 1 replaced 23 flight feathers during this period, whereas Birds 2 and 3 replaced 18 and 10 flight feathers, respectively). The other waxwing fed only *Lonicera* fruits for 64 days (Bird 4) molted fewer flight feathers than the other three fruit-only birds by 4 September, and during the subsequent month molted only one primary per wing.

Historical dietary changes.—Fruits of introduced honeysuckles did not occur in gut contents of Cedar Waxwings collected in the northeastern United States from 1885 to 1950 (n = 212; Witmer 1996). Many of these birds (142) were taken from June through October, the period during which *Lonicera* fruits are available in central New York. Fruits of a native honeysuckle, *L. caerulea*, occurred in 20 of 30 waxwings collected in Maine in July 1949 and 1950. Fruits of *L. caerulea* are bluish-black (Muenscher 1950) and probably were not confused with the red-fruited Eurasian honeysuckles. In contrast, fruits of alien honeysuckles are eaten by waxwings from mid-June until mid-October in the Ithaca vicinity (57% of fruit diet, 46% of whole diet; Fig. 2).

Adult waxwings molting orange tails.—I observed flocks of waxwings feeding heavily on *Lonicera* fruits from 23 September until 8 October 1993 on seven days. I judged birds as adults by the presence of molting rectrices (an unambiguous indicator of adult status) or by adult body plumage with distinct red waxy tips on the secondaries and a wide tail band (Pyle et al. 1987). Among adult birds, 79% (n = 53) had some or all of their rectrices tipped with orange. All orange-tailed adults were undergoing tail molt, whereas most yellow-tailed adults were not. Among juvenile waxwings, 39% (n = 97) had orange-tipped rectrices. These observations corroborate previous field observations (1989–1991) of orange-tailed adults in fall flocks that were feeding on *Lonicera* fruits (12 of 18 orange-tailed birds were adults).

Historical occurrence of orange-tailed wax-

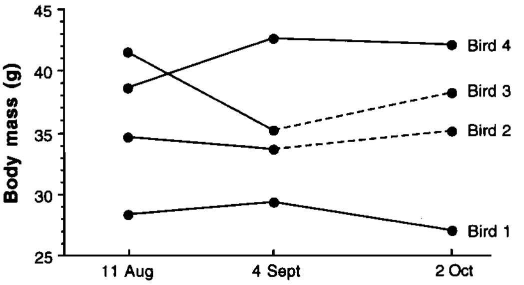

FIG. 1. Body mass changes of birds fed only *Lonicera* fruits for extended periods (solid lines); diet initiated on 30 July. On 4 September, all birds were molting; they were midway through wing molt and three had begun tail molt (see Table 1). At this time two birds were switched to chow diet for remainder of molt period (dashed lines).

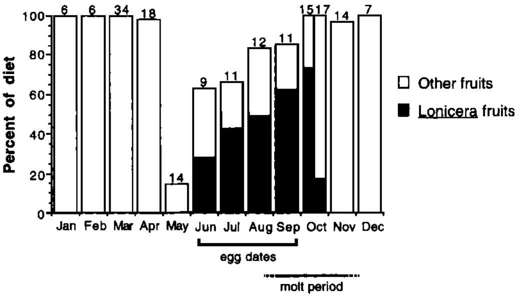

FIG. 2. Frequency of occurrence of *Lonicera* fruits in diet of wild Cedar Waxwings from recent roadside surveys near Ithaca, New York. Monthly estimates of proportion of fruit in diet are from analysis of records of stomach contents; fruit in diet is represented by bars (Witmer 1996). Egg dates from Bull (1974); molt period from Dwight (1900) and Pyle et al. (1987).

wings.—All Cedar Waxwings in the CVC from 1878 to 1950 (n = 47 birds) and from 1951 to 1960 (n = 17 birds) had yellow tail bands. A Cedar Waxwing collected in 1961 was the first record of the orange-tailed variant (see Frontispiece); seven other waxwings from this decade had yellow tails. This phenomenon appears to have arisen in other areas of the northeast at about this time; Mulvihill et al. (1992) first noted orange-tailed Cedar Waxwings in western Pennsylvania in 1964. The incidence of orange-tailed Cedar Waxwings subsequently has increased (2 of 16 specimens from 1986 to 1990, and 7 of 13 specimens from 1991 to 1993). Mulvihill et al. (1992) also reported an increasing incidence of orange-tailed Cedar Waxwings from the early 1960s to 1985. Of recent specimens (1986 to present) that had tails grown as adults, 12 waxwings salvaged during the breeding season (May to September) had yellow rectrices, and one waxwing salvaged in November had some orange rectrices.

DISCUSSION

Experimental effects of diet on plumage coloration.—Pigment deposition in the tail bands of Cedar Waxwings was strongly influenced by dietary inputs of rhodoxanthin at the time of feather growth. Wild waxwings probably never consume *Lonicera* fruits to the extent that any of the experimental birds did. Birds in the wild eat some animal prey during the prebasic molt period (September to November; Witmer 1996) and would likely eat a mixture of fruits. Consistent with the immediate absence of rhodoxanthin in growing feathers upon the removal of *Lonicera* fruits from the diet, the reddish coloration of the tail bands of the experimental waxwings compared with wild birds suggests a positive relationship between dietary intake of rhodoxanthin-laced food and deposition of this pigment in growing feathers.

The capacity of Cedar Waxwings to store carotenoids is unknown, but the skin on the legs, and the subcutaneous fat, of two experimental birds were reddish (Birds 1 and 2). Chickens are known to deposit carotenoids in subcutaneous fat and egg yolks (Goodwin 1984). Cedar Waxwings showed no evidence that they mobilized stored rhodoxanthin for feather pigmentation.

Hill (1992) found no visible effect of stored carotenoids on plumage coloration in male House Finches (*Carpodacus mexicanus*) that were fed a carotenoid-deficient diet just prior ($\leq$1 month) to the initiation of prebasic molt. In contrast, Kritzler (1943) induced molt of display feathers in three species of weaver finches after maintaining them on a carotenoid-free diet for about three months; these birds grew feathers with normal amounts of yellow pigments but with much diluted amounts of red pigments. Test (1969) maintained Northern Flickers (*Colaptes auratus*) on a carotenoid-deficient diet and observed a steady decline in the amount of yellow pigmentation in remiges molted over a 2.5-month period; red pigments were lost immediately, however. Test also observed an immediate (within hours) effect of the addition of dietary carotenoids on feather color. Similarly, Kritzler (1943) induced orange feathers in normally yellow-feathered finches (*Euplectes* spp.) by feeding them paprika, which contains capsanthin, a pigment foreign to their normal diet. Völker (1955, 1957) demonstrated strong effects of dietary rhodoxanthin on feather coloration in Common Canaries (*Serinus canaria*) and Red Crossbills (*Loxia curvirostra*).

The experiments noted above indicate that dietary inputs of carotenoids often appear immediately in molting carotenoid-containing feathers, but the effects of dietary deprivation of carotenoids vary among species in their rates of disappearance. There appears to be variation in the response of plumage pigmentation to dietary inputs due to the amount and/or type of carotenoid involved, both in the food and in the plumage. Carotenoid deposition in chicken egg yolks also is strongly affected by dietary carotenoid content (Goodwin 1984). Quantitative deposition of dietary carotenoids in feathers as a function of their availability in the environment affects plumage color variation in Great Tits (*Parus major*; Slagsvold and Lifjeld 1985, Partali et al. 1987) and appears responsible for habitat-associated color morphs of Tristan Buntings (*Nesospiza acunhae*; Ryan et al. 1994).

If the size and coloration of the tail are important in mate selection (see Burley et al. 1982, Hill 1990), then orange tail coloration may be affecting the attractiveness of waxwings as mates. Mountjoy and Robertson (1988) found that Cedar Waxwing mates tend to associate by the number of secondaries with red waxy tips.

Molt on an exclusive fruit diet.—The performance of molting Cedar Waxwings eating a diet of only *Lonicera* fruits (ca. 2.33% protein based on a nitrogen-to-protein conversion factor of 4.4; Milton and Dintzis 1981) underscores the nutritional specialization of waxwings to a diet of sugary, low-protein fruits (Witmer 1994, 1996). Captive Cedar Waxwings fed an array of fruits maintained stable body mass over a 27-day period (Holthuijzen and Adkisson 1984). Similarly, Berthold (1976) found that Bohemian Waxwings (*B. garrulus*) maintained body mass when fed fruit diets over periods of 10 to 18 days. The adequacy of this diet for molting waxwings is remarkable because of the protein and sulfur amino-acid costs of molt (Robbins 1993). *Lonicera* fruits are low in sulfur amino acids (Witmer unpubl. data), but Cedar Waxwings did not show signs of protein or sulfur amino-acid deficiency (e.g. loss of body mass, shorter feathers, and protracted molt; Murphy and King 1991). This result with captive Cedar Waxwings is consistent with the predominantly fruit diet of wild waxwings during their prebasic molt (see Fig. 2).

Granivorous American Tree Sparrows (*Spizella arborea*) require a dietary protein level higher than 4% for maintenance (Martin 1968). The ability of Cedar Waxwings to thrive on sugary fruit diets is paralleled by the performance of hummingbirds eating sugary, low-protein diets (1.5% protein; Brice and Grau 1991). Murphy and King (1984, 1991) found that molt in White-crowned Sparrows (*Zonotrichia leucophrys*) occurs normally at low dietary protein and sulfur amino acid levels.

Ecology of an introduced shrub and native frugivore.—Fruits of *L. morrowii* have increased dramatically in the diet of Cedar Waxwings within the last 40 years, at least in some localities. In central New York, this fruit is locally abundant and persists until October, well into the period during which adult Cedar Waxwings replace their rectrices (Sherburne 1972, Witmer unpubl. data). Captive Cedar Waxwings perform well on a diet of *Lonicera* fruits, and wild waxwings in Ithaca include much of this fruit in their diet from July to mid-October. As a consequence of these dietary patterns, adult and juvenile Cedar Waxwings produce orange-tipped tails in the Ithaca area. Hudon and Brush (1989) and Mulvihill et al. (1992) reported several adult Cedar Waxwing specimens with some orange rectrices. The demonstration that adult waxwings, both captive and wild, develop orange tails under the influence of diet eliminates hypotheses that suggest that nestling waxwings are more susceptible to this effect because of the idiosyncracies of nestling nutrition and growth (Hudon and Brush 1989). The apparent rarity of adult Cedar Waxwings with orange tail bands in other areas of the northeastern United States (Mulvihill et al. 1992) suggests that the phenomenon in central New York is local. The continued predominance of breeding adults with yellow tail bands in the Ithaca area (Witmer unpubl. data) may reflect a dilution effect due to the lack of philopatry in Cedar Waxwings (Brugger et al. 1994).

Populations of honeysuckle shrubs (*Lonicera* spp.) most likely spread in the northeastern United States during the middle part of this century because of increases in available habitat coupled with aggressive planting programs.

Eurasian honeysuckles were introduced into North America long ago (*L. morrowii* in 1875, *L. tatarica* in 1752; Wyman 1949). By the early 1900s, *morrowii* and *tatarica* had escaped cultivation and were widely naturalized in New England (Rehder 1903). The abandonment of agricultural land in the 1920s and 1930s, however, appears to have created large areas of suitable habitat for these shrubs (Hauser 1966). Honeysuckle shrubs thrive in disturbed sites, such as roadsides, old fields, and streambanks (Barnes 1972). Dispersal of Eurasian honeysuckles throughout the northeastern and midwestern United States was facilitated by government agencies that propagated and dispensed these shrubs because they were deemed to be beneficial to wildlife (Cook and Edminster 1944, Edminster 1950, Edminster and May 1951, Smith 1964, Mulvihill et al. 1992). *Lonicera morrowii* and *L. tatarica* appeared in the naturalized Illinois flora between 1922 and 1955 (Henry and Scott 1981). These shrubs were naturalized in Michigan by the late 1940s, with their hybrid, *L.* × *bella*, establishing by 1957 (Hauser 1966). Mulvihill et al. (1992) reported that *L. morrowii* and *L. tatarica* were planted at their study site in western Pennsylvania in 1960.

Thus, Eurasian honeysuckles have expanded over large areas of North America within the last 50 years. The first appearance of orange-tailed Cedar Waxwings in the early 1960s, and the increasing occurrence of this plumage variant since then, suggests that heavy consumption of honeysuckle fruits by waxwings has followed the plant's widespread establishment by human influences (Mulvihill et al. 1992). The cultivation and spread of alien honeysuckle shrubs in North America have resulted in an abundance of the fruits of these shrubs, an apparent characteristic of many of the foods eaten by Cedar Waxwings (McPherson 1987, Witmer 1996). Although consumption of honeysuckle fruits by Cedar Waxwings and other fruit-eating birds is important in the dispersal of these plants, frugivorous birds do not appear to have been primarily responsible for the rapid spread of Eurasian shrub honeysuckles in North America.

The large difference in the fruiting phenology of honeysuckle shrubs between western Pennsylvania and central New York is interesting, considering that these two locales are relatively close geographically and share similar climate, soil, and vegetation (Vankat 1979). Honeysuckle fruits at the Powdermill Nature Reserve wither by mid-August (Mulvihill et al. 1992, R. Mulvihill pers. comm.). Barnes (1972) reported a similar phenology of fruit persistence in Wisconsin. The contrast between central New York and western Pennsylvania shows that the ecological interactions between animal dispersers and fruiting plants can vary over relatively short distances, contingent upon local fruiting phenology and frugivore abundance. The ecological interactions between Cedar Waxwings and alien honeysuckles, along with the ramifications that this new food has had on the plumage coloration of waxwings, underscore the unanticipated consequences that exotics can have on native organisms. The extent to which introduced honeysuckles may influence the ecology and behavior of Cedar Waxwings remains to be determined.

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