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## Carotenoid Availability and Plumage Coloration in a Wild Population of Northern Cardinals

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Bright red, orange, and yellow ornamental plumage and colors of other exposed tissues in birds are produced by deposition of various carotenoid pigments. Because these pigments cannot be synthesized by birds, they must be obtained through dietary sources (Goodwin 1950). As a consequence, the expression of carotenoid-based color in tissues must result from numerous physiological and behavioral processes that determine carotenoid intake, absorption, transport, and deposition (Brush 1990).

The presence of carotenoid pigments in secondary sexual characteristics in birds and fish has evoked much recent interest in their function as signals of individual quality. Carotenoid deposition may be an indicator of genetic quality (Hamilton and Zuk 1982, Kodric-Brown and Brown 1984, Hudon 1994), foraging ability (Kodric-Brown 1989, Hill 1992), presence of parasites or other diseases (Schaeffer et al. 1988, Houde and Torio 1992), and hormone levels (Brush 1967, Temple 1974).

Hypotheses for the function of carotenoid-based ornaments in sexual selection center on the availability of these pigments in natural food sources. In the absence of direct measurements, researchers have suggested that carotenoids are limiting for some wild populations of birds (e.g. Miskimen 1980; Slagsvold and Lifjeld 1985; Hill 1993 a, b; 1994) and fish (Kodric-Brown 1989), and that differences in expression of color are the result of differential foraging ability. In contrast, Hudon (1994) proposed that

carotenoids generally are not limiting in the environment and that the expression of color results from physiological condition and not foraging ability (see Burley et al. 1992). Carotenoids are ubiquitous pigments and are synthesized by nearly all plants, photosynthetic algae, and some fungi and bacteria. In avian food sources, carotenoids are most abundant in animals (e.g. insects) and fruits.

Despite their different assumptions concerning carotenoid availability, the "foraging hypothesis" (Hill 1992) and the "health hypothesis" (Hudon 1994) make predictions that are not separable under non-experimental conditions. Significant fluctuations in the availability of food sources that contain carotenoids may affect not only foraging efficiency but also the health or physical condition of individuals dependent on these food sources. Indeed, the predictions of these hypotheses may be difficult to distinguish even under experimental conditions (Hill 1994, Hudon 1994). However, under any circumstances, a significant decline in availability of important, carotenoid-rich food sources without an accompanying decrease in ornament expression would call into question both hypotheses.

A natural event that dramatically reduced fruit availability enabled us to determine if fruit scarcity resulted in a decrease in plumage brightness in a wild population of Northern Cardinals (*Cardinalis cardinalis*). Cardinals are sexually dichromatic and socially monogamous. Both sexes possess orange bills and dull red-brown remiges and rectrices that are nearly invariant in color. Males also possess carotenoid-based bright red plumage with especially

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intense red color on the breast. Although much duller in color, females might also be considered ornamented. Body coverts are tan overall, but females display variable red color on the median and marginal secondary coverts of the underwing, and variable numbers of red feathers on the crest, face, upper breast, and flank. The underwing coverts of females always display the brightest red color in their plumage. Cardinal diet includes seeds, fruits, and, during the breeding season, insects (Martin et al. 1951).

*Methods.*—We conducted this study at Aullwood Audubon Center and Farm (39°52'N, 84°16'W), 15 km northwest of Dayton, Ohio, from 1993 through 1996. Cardinals have a single prebasic molt annually. Carotenoids must be ingested before and during molt in order to be deposited in feathers (Hill 1992, Witmer 1996). We studied foraging from 18 September to 12 November 1993 to establish food preferences while cardinals were molting. We followed a focal male for at least 30 min and recorded foraging behavior every 5 min. We collected a total of 29.25 h of observations on 10 mature banded males,  $\leq 10$  mature unbanded males, and  $\leq 10$  immature (i.e. with black rather than orange bill) unbanded males. We observed unbanded birds on different territories and assumed they were different individuals, although we cannot know this with certainty.

Relative amounts of foods in the diet (i.e. 58% fruit, 18% unknown, 16% insects, and 8% seeds) were based on the type of food being consumed at the time of instantaneous focal sampling. Of the fruits consumed, 54% were wild grapes (*Vitis* spp.), 15% multiflora rose (*Rosa multiflora*), 8% honeysuckle (*Lonicera* spp.), and 23% other fruits, including hackberry (*Celtis occidentalis*) and wild cherry (*Prunus serotina*). These results concur with previous studies of stomach contents that indicate cardinal diets consisted of 75% vegetable and 25% animal matter by mass in fall (Martin et al. 1951), and that grapes composed a large portion of the fruits consumed (McAtee 1908).

We captured adults in potter traps or mist nets during the breeding seasons of 1993 through 1996. Each was banded with a United States Fish and Wildlife Service aluminum band and a unique combination of three colored plastic bands. We scored an individual's color by matching plumage color to the most similar Munsell color chip (glossy finish collection, Kollmorgen Corporation). Breast colors were recorded for males, and underwing colors for females. Although we did not recapture birds in the same season, we tested color scoring for reliability with museum skins at the Dayton Museum of Natural History and found scoring to be highly repeatable ( $r_s = 0.93$ ,  $n = 22$ ,  $P < 0.01$ ).

Because color is a three-dimensional categorization, we converted Munsell values to a one-dimensional continuum, similar to the method of Burley and Cooper-Smith (1987). However, we ranked value

primary, hue secondary, and chroma tertiary to prevent the possibility of a highly saturated pink outranking a darker, less saturated red-orange. This ordering of color chips produced a "redness" bright-to-dull continuum that agreed with our perception. For male breast color, scores ranged from 6.0 (Munsell 7.5 4/16) to 0.5 (Munsell 8.75 5/16). For female underwing color, scores ranged from 13.5 (Munsell 8.75 4/16) to 1.0 (Munsell 10 6/13).

During January and February 1994, Ohio experienced record-breaking low temperatures. Winter buds on many trees and shrubs were frozen, and commercial fruit crops were reduced (Ohio Department of Agriculture 1994). At our study site, fruits abundant in the fall of 1993 were reduced greatly in the fall of 1994. We found no grapes present in 10 of 13 locations where they were abundant the previous fall, whereas the remaining three locations had an estimated 50% of their 1993 crop. Although honeysuckles were abundant, this fruit was not consumed frequently by cardinals. Other wild fruits present in 1993 were not present in 1994.

Our goal was to determine if a nearly complete failure of the crops of wild fruits resulted in a decrease in plumage brightness of cardinals. To test for this possibility, we compared male breast color and female underwing color among years (1994 to 1996). We used Kruskal-Wallis one-way ANOVA corrected for ties to test color among the three years and Mann-Whitney rank sum tests for pairwise comparisons between the years 1994 and 1995 and 1995 and 1996 ( $\alpha$  devalued to 0.025 by a Bonferroni correction).

*Results and discussion.*—There was a marginal difference in male breast color among the three years ( $H = 5.76$ ,  $n = 25, 28, 24$ ,  $P = 0.056$ ). Breast color was significantly lower in 1995 after the harsh winter than in 1994 when fruits were abundant during the previous fall molt ( $U = 476.5$ ,  $n_1 = 25$ ,  $n_2 = 28$ ,  $P = 0.025$ ). Breast color increased in 1996, following a rebound in the fruit crop, over the 1995 values, but not significantly ( $U = 391.5$ ,  $n_1 = 24$ ,  $n_2 = 28$ ,  $P = 0.31$ ; Fig. 1A). Female wing color did not differ significantly among the three years ( $H = 3.51$ ;  $n = 29, 35, 27$ ;  $P = 0.17$ ; Fig. 1B).

The sample of birds remaining in the population and recaptured in successive years was small, but it allowed us to test whether color changed in the predicted direction in successive molts of the same individual. Nine males were captured in both 1994 and 1995; their plumage-color scores decreased but not significantly so. Two males with the lowest color scores in 1994 were actually brighter in 1995. Plumage-color scores increased significantly in eight males that were sampled in both 1995 and 1996, but not in eight females sampled in both 1994 and 1995. Plumage-color scores of six females sampled in both 1995 and 1996 increased slightly (but not significantly). These data are reported in more detail elsewhere (Linville et al. 1997).

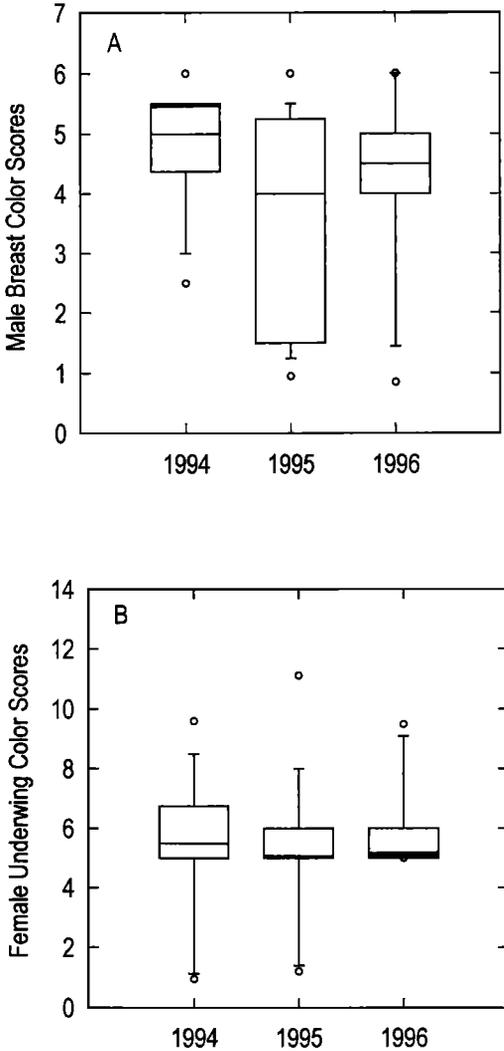


FIG. 1. Box plots of plumage color of (A) male and (B) female Northern Cardinals in the 1994 to 1996 breeding seasons. Horizontal bars in box plots indicate the 10th, 25th, 50th, 75th, and 90th percentiles, and points give data for individuals outside this range. Sample sizes ranged from 24 to 28 males and 27 to 35 females. Note that different scoring schemes were used for the sexes and are thus not interchangeable (see text).

Research on captive birds and fish has demonstrated reductions in color of ornaments with low carotenoid diets. Guppies (*Poecilia reticulata*) fed a canthaxanthin-supplemented diet exhibited brighter red and orange spots than those on carotenoid-free diets (Kodric-Brown 1989). Plumage coloration in House Finches (*Carpodacus mexicanus*) varied in relation to degree of supplementation in oxycaroten-

oids (red pigments) at the time of molt (Hill 1992). Studies of wild populations and experimental evidence suggest that access to carotenoid pigments is responsible for geographic differences in ornamentation of Cedar Waxwings (*Bombycilla cedrorum*; Witmer 1996), Tristan and Wilkins' buntings (*Nesospiza acunhae* and *N. wilkinsi*; Ryan et al. 1994), male House Finches (Hill 1993b), and female Red-winged Blackbirds (*Agelaius phoeniceus*; Miskimen 1980).

Our data provide the first evidence of changes in ornamentation in a single wild bird population associated with changing availability of carotenoid-rich foods. To our knowledge, only one other study of a population of wild birds has demonstrated a relationship between plumage color and diet. Nestling Great Tits (*Parus major*) from two habitats varied in color in relation to the food they received irrespective of genetic differences, as determined by cross-fostering experiments (Slagsvold and Lifjeld 1985). Color of nestling Great Tits also varied among years, and the authors suggested that this was due to availability of carotenoid-rich foods, although they presented no data.

Cardinals shift from a diet high in animal matter during summer to a diet predominated by vegetable matter, particularly fruit seeds and pulp, during fall molt, similar to the shift in House Finch diet from seeds to fruit (Hill 1995). We have found a significant decline in male plumage color when fruit supplies were dramatically reduced, but such a decline is allowed for (if not explicitly predicted) by both the foraging and health hypotheses. However, we note that the significant decrease in male color from 1994 to 1995 was small in magnitude and not detectable when observing males in the field. Indeed, 39% of the birds sampled in 1995 maintained plumage scores equal to or higher than the median color in 1994 (Fig. 1A), despite nearly total failure of the fruit crop. Depending on one's expectations under the foraging hypothesis, the variability in the color change between these two years may be viewed as evidence against the limitation of carotenoids for cardinals under normal conditions.

Admittedly, these data are potentially confounded by age and foraging experience. Wolfenbarger (1996) has shown that male cardinals display increased ornamentation with age, although we have not found such an age effect in this population (Linville et al. 1997). In any case, male cardinals faced with a fruit shortage may have switched to other carotenoid-rich foods (e.g. insects). Alternatively, the dietary carotenoid requirements for building bright red plumage may be considerably less than many investigators suppose to be the case.

The reduction in color displayed by males was not exhibited by females (Fig. 1B). Female underwing color appeared to be unaffected by a reduction in fruit availability. This lack of change may reflect lower requirements necessary for females to maintain

the limited amount of red plumage they exhibit. It is also possible that underwing coverts are protected from light and resultant fading (A.H. Brush pers. comm.).

It should be noted that the link between plumage color in Northern Cardinals and carotenoids present in fruits and other food sources is far from clear. Several carotenoids have been isolated from cardinal plumage (Hudon 1991), but the responsible carotenoids or their precursors available in wild fruits are unknown. Insects also may be a potential source of carotenoids during the fall molt, although the proportion of insects consumed by cardinals drops precipitously after summer.

Our understanding of the function of carotenoids in secondary sexual characteristics in birds is remarkably incomplete. Although much information is available on the influence of carotenoids on the color of domesticated birds (e.g. chickens), the extent to which this information applies to wild species of birds is unclear. Among the things we do not know are the availability of carotenoids in plant and animal foods, rates of ingestion by specific species, metabolic pathways for carotenoids, and mechanisms of their deposition in feathers and other tissues.

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## A Single Functional Testis as a Unique Proximate Mechanism Promoting Sex-role Reversal in Coucals

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Sex-role reversal, where the male provides most or all of the care of eggs and young, occurs in a small fraction of the world's approximately 9,700 living species of birds. Although it is best known in a few temperate-zone shorebirds, sex-role reversal also occurs in ratites, tinamous, and buttonquail, all of which produce precocial young (Ligon 1993). Sex-role reversal also occurs in at least one group of altricial birds, the coucals, genus *Centropus* (Vernon 1971, Irwin, 1988, Ligon 1993, Andersson 1995). Coucals are a distinctive group of nonparasitic cuckoos that occurs over much of the Old World tropics.

The puzzling mating system known as classical polyandry is associated with sex-role reversal. Consequently, the proximate factors that promote this phenomenon should be of interest to students of avian mating systems. Testosterone has a negative effect on parental care in male birds (Wingfield et al. 1990), which leads to the question: What physiological or endocrinological alterations have taken place to bring about sex-role reversal? In two sex-role reversed North American shorebirds, high levels of testosterone are present in preincubating males (Rissman and Wingfield 1984, Fivizzani and Oring 1986, Fivizzani et al. 1986, Oring et al. 1988), but as the male begins to incubate testosterone levels rapidly drop by up to 25-fold (Fivizzani and Oring 1986). The fact that males of these species exhibit normal levels of circulating testosterone prior to incubation led Fivizzani and Oring (1986) to suggest that the internal factors responsible for the preincubation sex-role reversal must be the specificity of neural receptors rather than changes in the gonadal hormonal state typical of each sex.

In coucals, as in precocial species with sex-role re-

versal, the male assumes a role generally considered to be more typical of female birds; i.e. in addition to being smaller, males construct the nest and carry out most or all incubation and care of the chicks (e.g. Vernon 1971, Irwin 1988). A morphological trait possibly related to this sex-role reversal is great asymmetry in size and development of the testes. In at least some species of coucals, the left testis is "atrophied" or "rudimentary," or even absent altogether, whereas the right testis is of normal size (Rand 1933, 1937; Chapin 1939). Based on a sample of 43 male specimens of the Madagascar Coucal (*Centropus toulou*), Rand (1933) reported that, "... the right testis was always larger than the left, which was atrophied, never being firm and oval, and never showing any enlargement in the breeding season, even when the right was at its maximum size." In addition to the Madagascar Coucal, absence or severe reduction in size of the left testis also has been reported in three African species of coucals (Rand 1937, Chapin 1939), including the classically polyandrous Black Coucal (*C. grillii*; Vernon 1971, Irwin 1988).

To obtain additional information on this apparently unique testicular condition, I examined two pickled specimens of males of the Madagascar Coucal in the collections of the Field Museum of Natural History. These birds were collected in October 1989, which is early in the breeding season. Each male had a large right testis (ca. 12.1 × 8.5 mm and 13.7 × 7.8 mm), whereas the left testis was noted by the collector as degenerate in one specimen and was not discernible to me in the other.

Loss of the left testis, rather than the right, is, in itself, peculiar, because in birds the left testis usually is the larger of the two (Lake 1981, Møller 1994; but see Kimball et al. 1997). Although the reasons for this directional asymmetry are not well understood, at the end of embryonic growth the left testis has more

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