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Received 10 October 1991, accepted 19 November 1992.

The Auk 111(1):218-221, 1994

Showiness, Carotenoids, and Captivity: A Comment on Hill (1992)

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Primarily on the basis of the loss of carotenoid pigmentation in captive House Finches (*Carpodacus mexicanus*) and the partially restorative influence of carotenoid supplements, Hill (1992) recently concluded that plumage color variability in male House Finches in the wild is due to differential access to carotenoid pigments at the time of molt, and not to intrinsic differences in the ability of males to use or display carotenoids. While Hill's interpretation appears logical, in many ways extending the work of Brush and Power (1976), it clashes with an imposing body of work from Germany. A probable consequence is that Hill did not really investigate the source of plumage color variation in wild House Finches, as he claimed, but rather evaluated the ability of various pigment-supplementation regimen to reverse color losses incurred in captivity.

German workers have long been aware of the debilitating effects of captivity on carotenoid pigmentation in several birds, notably carduelines, and actively sought ways to remedy these effects (see Völker 1957, Reuter 1964). Heinroth and Heinroth (1926, from the 1966 reprint) discussed possible causes of fading in captive Red Crossbills (*Loxia curvirostra*) and other birds. They found no support for a shortage of carotenoids or an effect of reduced sunlight and surmised that the weakened body condition of captive birds might be responsible instead. Koch (1939) pursued the problem of fading in carduelines further. Red Crossbills and Linnets (*Carduelis cannabina*) replaced their red feathers with yellow ones even in outdoor enclosures in a near-natural setting with an abundance of food and water (Koch 1939). He also found that no vitamin supplements and hormone preparations could reverse the color loss incurred in captivity, although improvements in plumage brightness were seen with certain treatments (Koch 1939).

Weber (1953, 1961) made supplementary observations, and performed a few controlled experiments

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on the Red Crossbill and the Common Redpoll (*C. flammea*). Both carduelines turned pale in captivity, and remained drab even when supplied with large measures of natural sources of pigments. In contrast, individuals that were supplied with similar food items at feeders, but were free to come and go, developed bright red colorations after plucking or molt (Weber 1953). Weber (1961) also found a correlation in redpolls between the plumage brightness of captive birds and the size of their aviaries. Great care was taken in these studies to control the sources of carotenoids in both the captive and free-living birds (see Völker 1957). From this work, Weber (1961) convincingly argued that it was the lack of mobility of the birds or poor body condition or both, and not carotenoid access, that undermined color expression in captive birds.

I personally am aware of additional reports, mostly unpublished and anecdotal, of color losses in captive birds that cannot be attributed to a lack of carotenoids (e.g. Adlersparre 1939). Hill (1992) failed to discuss the possibility that the color loss he observed in captivity could be due to captivity itself. He instead invoked a deficiency of carotenoid intake and lack of internal stores of carotenoid pigments in House Finches.

Hill's success in restoring a more natural-looking coloration with carotenoid supplements, mostly canthaxanthin, does not imply a shortage of carotenoids for his captive birds. Carotenoid supplements have long been used to reverse pigment losses incurred in captivity, but often alter plumage coloration, even to the point of enhancing the natural coloration (Giersberg and Stadie 1933, Völker 1955). With the advent of synthetic canthaxanthin, carotenoid supplementation is now routinely used to alleviate such fading (Reuter 1964, Bruning 1971), but canthaxanthin is not normally encountered by birds in their diets (see below).

Characteristically, color restoration involving pigment supplementation also lacks specificity. Indeed, pigments that rarely are found in the feathers of wild birds—such as capsanthin, rhodoxanthin and β -carotene—often show up in the feathers of birds fed these carotenoids (Kritzler 1943, Völker 1962). The deposition of these unusual carotenoids in feathers suggests that ingested carotenoids can escape the normal controls of carotenoid mobilization, especially when present in large quantities. Carotenoid supplementation, perhaps by making carotenoids available in a nonspecific form, bypasses processes that normally control "pigment traffic" in birds. Hence, feeding experiments should be performed with judgment.

Hill (1992) admitted that his feed mixes, especially the Kaytee Wild Finch Food, are a source of β -carotene, but nonetheless used them as carotenoid-deficient diet(s). Unfortunately, the rape seeds, thistle, flax, canary seed and white millet of the mixes are rich sources of lutein (175, 133, 65, 28 and 22 μg per 10 g of seed, respectively), and carotenes (17, 22, 11,

0, and 0 μg per 10 g of seed, respectively; Brockmann and Völker 1934). Brockmann and Völker (1934) observed that the Island Canary (*Serinus canaria canaria*) maintained its coloration on diets much poorer in carotenoids than Hill's carotenoid-deficient diet even when none of the above sources were represented. Further support for the adequacy of standard feed mixes to provide carotenoids comes from species of birds that are not affected by captivity and maintain bright colors on the common feed mixes (Heinroth and Heinroth 1966), such as the Zebra Finch (*Taeniopygia guttata*; Burley et al. 1992). The reduced post-treatment plumage scores of birds fed the basic seed diet or that supplemented with β -carotene, which Hill reported, agree with an effect of captivity other than carotenoid deficiency, as carotenoids are not limiting in these conditions. More generally, carotenoids in the wild would never be as abundant as in Hill's supplemented diets.

Also, β -carotene and canthaxanthin used by Hill in supplemented diets are not common sources of carotenoids. In fact, no plant is known to produce canthaxanthin or echinenone (see Goodwin 1980). Supplementation, if it is to be attempted at all, should involve hydroxy-carotenoids (the original "xanthophylls") such as lutein or zeaxanthin, which are close or identical to the carotenoids obtained naturally from the diet (Brockmann and Völker 1934, Fox 1976, Hencken 1992). It is hoped that the ingested carotenoids will then be recognized and processed properly.

Hill's comments about carotenoid availability in the wild reveal a common misconception about carotenoids. Researchers seem to think that, because carotenoids cannot be produced endogenously, animals have little control over their carotenoid loads and must be limited in the wild. However, there is little evidence of carotenoid limitation in the wild (but see Slagsvold and Lifjeld 1985). Hill's results certainly are not evidence of it. Given the variety and abundance of potential sources of carotenoids in the wild (Goodwin 1980), it would be more realistic to assume that most birds in the wild are not limited in their access to carotenoids. Hill also implicitly suggests that keto-carotenoids are obtained directly from the diet, to accommodate for the need of canthaxanthin in the brightest colorations (Hill pers. comm.). There is no support for this either. Völker and co-workers demonstrated conclusively that birds manufacture their red carotenoids from yellow plant carotenoids (Brockmann and Völker 1934, Völker 1962, 1964).

It is unfortunate that Hill did not examine the pigments in wild and captive birds to support the contention that the birds vary only in the amount of dietary carotenoids they ingested. I am not convinced that the drab individuals simply have less carotenoids. I suspect that some of these individuals harbor lighter yellow or other carotenoids instead of the usu-

al red ones. Given the probable metabolic interconversion of carotenoids in birds (Davies 1985, Schiedt et al. 1985, Matsuno et al. 1986, summarized in Hencken 1992), including the transformation of yellow pigments into red ones, the discovery of yellow pigments in the pale individuals would weaken the argument of carotenoid insufficiency considerably. For example, I have found that European Goldfinches (*C. carduelis*) with scarlet or orange masks, instead of the crimson mask of some individuals, harbor yellow canary xanthophylls in addition to red carotenoids (unpubl. obs.). Canary xanthophylls are not dietary carotenoids but arise from the metabolism of lutein, as do 4-keto-carotenoids (Brockmann and Völker 1934). It would appear illogical, if indeed the birds were limited in their access to keto-carotenoid precursors, to channel dietary carotenoids to a pathway altogether different from precious keto-carotenoid production. My observations suggest instead that the birds control the fate of ingested carotenoids and, by extension, the color they produce, perhaps, in a health-dependent fashion. This is in accord with the observations of Weber and other German workers.

Of additional relevance is a previous suggestion for plumage carotenoid variability in captive Bullfinches (*Pyrrhula pyrrhula*; Schereschewsky 1929). At least in captive Bullfinches treated with thyroid tissue to enhance the oxidative metabolism and force a molt, the quality of the coloration depended not just on carotenoid uptake but also on the quality of the food itself (Schereschewsky 1929). These observations give further credence to the idea that carotenoid displays are indicators of health or body condition, not carotenoid access.

In conclusion, I believe that the majority of Hill's conclusions, including his storage interpretation, are not justified because the colorations his birds developed in captivity do not embody the normal processes of pigmentation in free-living birds. The studies reported by Hill, to be truly meaningful, should have been performed on free-living birds instead of captives, or on species that are not affected by captivity. Carotenoid supplementation in captive birds is not a substitute for the birds being free-living, because carotenoids are not truly deficient in captivity. Many German workers believed instead that carotenoids were not used properly in captivity, including Weber (1953, 1961) who suggested that the oxidation of dietary carotenoids to keto-carotenoids (then known as "Zersetzungsprodukte") might be defective in captive birds. Weber surmised that the effect might be mediated by an effect of captivity on the oxidative metabolism. However, such metabolic effects have never been conclusively demonstrated, and the physiological process affected by captivity in birds remains unknown. The effects of captivity clearly deserve a much closer look than given by Hill (1992).

Hill's paper puts carotenoids at the center of a very

active area of behavioral ecology, and that is commendable. Carotenoids rightly deserve this role. They are easy to characterize and manipulate, and they are relatively well known biochemically. I suggest that current work should build on truly pioneering studies of plumage carotenoids, and these were performed in Germany over 50 years ago.

Acknowledgments.—I thank Alan H. Brush and Navjot Sodhi for discussion and editorial assistance.

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Received 1 September 1992, accepted 4 April 1993.

The Auk 111(1):221-225, 1994

House Finches Are What They Eat: A Reply to Hudon

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Hudon (1994) raised many interesting points with regard to my aviary studies addressing the effects of diet on expression of carotenoid-based plumage coloration in the House Finch (*Carpodacus mexicanus*; Hill 1992). I captured House Finches from the wild in Michigan and held them in large outdoor aviaries through their prebasic molt. I manipulated the access that groups of captive males had to various carotenoid pigments during molt, and I found a strong effect of dietary access to carotenoid pigments on expression of plumage coloration. I interpreted my results as support for the idea that the plumage brightness of male House Finches is largely a function of access to carotenoid pigments at the time of molt. Hudon countered my conclusion by claiming that the only thing that I demonstrated was a captivity effect. He contends not just that I overemphasized the role of access to carotenoids, but that carotenoid access plays no role in expression of plumage coloration in captive House Finches, in wild House Finches, or in birds in general. I remain convinced that a large part of the changes in plumage coloration that I observed in captive House Finches was a direct result of access to carotenoid pigments and reflects the same processes that are oc-

curring in wild House Finches and in many other species of birds. I will begin by countering some general comments made by Hudon and then present some additional observations of House Finches that support my position.

Hudon contended that I, like many biologists, erroneously assumed that carotenoid pigments are limiting in the environment when actually they exist in "variety and abundance." On the basis of a general reference (Goodwin 1980) he stated that it is more likely to assume that "most birds in the wild are not limited in their access to carotenoids"; however, there is no empirical basis for this assertion. Virtually no data exist on the carotenoid content of the natural diets of wild birds (Goodwin [1980] presented no such data), and the one study that looked at carotenoid access in population of wild birds (Slagsvold and Lifjeld 1985) demonstrated that carotenoids are limiting. Furthermore, there are no data on the quantity of carotenoid molecules needed to produce a particular plumage display. To state matter-of-factly that wild birds are not limited in expression of ornamental plumage by access to carotenoids is a misrepresentation of what little data exist.