

- ways of carotenoids in hen's egg yolk. *Comp. Biochem. Physiol. B Comp. Biochem.* 84B:477-481.
- REUTER, K. 1964. Der Verlust der roten Gefiederfarbe und die Möglichkeit einer Behebung dieses Mangels. *Gefiederte Welt* 32-35.
- SCHERESCHEWSKY, H. 1929. Einige Beiträge zum Problem der Verfärbung des Gefieders beim Gimpel. *Wilhelm Roux' Arch. Entwicklungsmech.* 115:110-153.
- SCHIEDT, K., F. J. LEUENBERGER, M. VECCHI, AND E. GLINZ. 1985. Absorption, retention and metabolic transformations of carotenoids in rainbow trout, salmon and chicken. *Pure Appl. Chem.* 57:685-692.
- SLAGSVOLD, T., AND J. T. LIFJELD. 1985. Variation in plumage colour of the Great Tit *Parus major* in relation to habitat, season and food. *J. Zool. Ser. A* 206:321-328.
- VÖLKER, O. 1955. Die experimentelle Rotfärbung der Vogelfeder mit Rhodoxanthin, dem Arillus-Farbstoff der Eibe (*Taxus baccata*). *J. Ornithol.* 96:54-57.
- VÖLKER, O. 1957. Die experimentelle Rotfärbung des Gefieders beim Fichtenkreuzschnabel (*Loxia curvirostra*). *J. Ornithol.* 98:210-214.
- VÖLKER, O. 1962. Experimentelle Untersuchungen zur Frage der Entstehung roter Lipochrome in Vogelfedern. *Farbenfütterungsversuche am roten Kanarienvogel.* *J. Ornithol.* 103:276-286.
- VÖLKER, O. 1964. Die gelben Mutanten des Rotbauchwürgers (*Laniarius atrococcineus*) und der Gouldamadine (*Chloebeia gouldiae*) in biochemischer Sicht. *J. Ornithol.* 105:186-189.
- WEBER, H. 1953. Bewirkung des Farbwechsels bei männlichen Kreuzschnäbeln. *J. Ornithol.* 94:342-346.
- WEBER, H. 1961. Über die Ursache des Verlustes der roten Federfarbe bei gekäfigten Birkenzeisigen. *J. Ornithol.* 102:158-163.

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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.

Hudon stated that the seeds I fed to House Finches as a carotenoid-deficient diet are "rich sources of lutein . . . and carotenes" and gives values as high as 175 $\mu\text{g}/10\text{ g}$ of lutein based on analyses of Brockmann and Völker (1934). However, Hudon provided no data on the quantities of appropriate carotenoids that are required by male House Finches (or any species of bird) to produce carotenoid-based plumage displays. This is not an oversight on Hudon's part; these data do not exist. Without such data there is no way to know, except in the most general sense, what is a rich source of carotenoids. Moreover, Brush and Power (1976) showed that all House Finch pigments are β -carotene derivatives. No organisms can convert between α - and β -carotenes (Lee 1966, Williams et al. 1967, Fox and Hopkins 1966), so the lutein (an α -carotene derivative) in the seed cannot be used by male House Finches to pigment their plumage. That leaves between 0 and 17 $\mu\text{g}/10\text{ g}$ of carotenes in the seeds, only some of which are the β -carotene molecules required by House Finches. Less than 17 $\mu\text{g}/10\text{ g}$ of seed may provide "a rich source" of carotenoid for male House Finches, but the data at hand suggest that it does not. Hudon cited a study by Brockmann and Völker (1934) showing that canaries (*Serinus canaria canaria*) produced ornamental coloration on a diet with a lower carotenoid content than the seed that I fed to male House Finches in carotenoid-deficient diets. However, canaries with wild-type coloration display only a pale yellow-green coloration, so I am not surprised that they can achieve "normal" coloration on a low-carotenoid diet, and no logical conflict is presented by the fact that male House Finches grow pale yellow feathers on a similar diet.

The body of work conducted in Germany on the effect of diet on expression of carotenoid-based plumage coloration in cardueline finches is imposing. I should have cited such work in my paper. However, none of the studies cited by Hudon clearly demonstrates that captive birds with access to excess carotenoids that are appropriate integumentary pigments or pigment precursors failed to attain full expression of ornamental coloration because of captivity effects. In some studies it was assumed that providing a bit of natural vegetation provided birds with access to the same carotenoid pigments as wild birds (Koch 1939). Other experiments confounded the effects of confinement with effect due to carotenoid access (Weber 1953, 1961; see the second point below). I am certainly not denigrating this body of work. As Hudon correctly pointed out, these were the pioneering studies in the field. They simply do not provide clear proof of a captivity effect.

Hudon stated that there is no evidence that birds use keto-carotenoids from the diet directly as integumentary pigments. To the contrary, extensive work by Fox and coworkers clearly showed that American Flamingos (*Phoenicopterus ruber*) use keto-carotenoids

directly as plumage pigments when they are available, rather than using precursors of keto-carotenoids (Fox and McBeth 1970, Fox et al. 1970, Goodwin 1984). Evolutionary theory predicts that birds should always use integumentary pigments directly, rather than pigment precursors, whenever the integumentary pigments are available and that they should substitute freely among various keto-carotenoids that produce the same ornamental effect. The following passage from Goodwin (1984:166) supports this view:

The question of whether flamingos which accumulate such large amounts of keto carotenoids do so exclusively from their food as preformed pigments or whether they transform non-ketonic food carotenoids, such a β -carotene or zeaxanthin, into keto derivatives is still open to some extent. The likely probability is that both processes are proceeding simultaneously to varying extents according to the nutritional situation the birds find themselves in.

Hudon's suggestion that "unusual carotenoids" escape "normal controls of carotenoid metabolism" and "bypass processes that normally control 'pigment traffic'" indicates a lack of understanding of the ultimate control of carotenoid display. Expression of plumage coloration is the primary determinant of male mating success in the House Finch (Hill 1990, 1991, 1994), so there is strong selection on males to produce bright red plumage. No male House Finch that controlled its "pigment traffic" in a way that did not maximize its expression of plumage coloration would be likely to leave many descendants. Given the importance of color display to reproductive success, male House Finches should use all red pigments and all precursors of red pigments available to them in producing the brightest plumage possible. Available data suggest that this is exactly what they do.

A number of additional observations that I have made of House Finches both in the wild and in captivity over the last six years convinces me that physiological condition alone cannot account for all of the variation in male carotenoid pigmentation and that carotenoid access must play a role in expression of plumage coloration in male House Finches. First, there was certainly no general negative effect of captivity on House Finches. I had several House Finches survive in captivity for four years and many birds for three years, undergoing three or four pre-basic molts. All of the captive birds remained in excellent physical condition. They grew a handsome plumage (ignoring carotenoid pigmentation) with normal melanin pigmentation and no fault bars or shock feathers (both of which are indicators of stress; Newton 1972, Murphy et al. 1988). Moreover, the growth rate of rectrices of captive birds was significantly greater than that of wild birds, undoubtedly because captive birds were in better nutritional condition (Hill and Montgo-

merie unpubl. data). When given a chance, captive birds bred, producing healthy young that responded to diet manipulations exactly like wild-caught birds (Hill 1993a). None of these observations excludes the possibility that captivity affected deposition of carotenoid pigments, but it seems strange that a captivity effect would transcend generations and manifest itself only as an effect on carotenoid pigmentation.

Second, cage size in my experiments did not affect plumage expression. Although I published only the results from experiments conducted in large aviaries, I held House Finches in three cage sizes during feeding experiments: large flight cages ($5.0 \times 2.0 \times 1.2$ m), small flight cages ($2.4 \times 1.8 \times 1.2$ m), and bird cages ($0.5 \text{ m} \times 0.5 \text{ m} \times 0.5 \text{ m}$). In all three cage sizes, male House Finches responded to the diet treatments in the same manner, growing pale yellow feathers when fed only seed, orange plumage when fed β -carotene, and bright red plumage when fed canthaxanthin (Table 1). These were well-controlled experiments in that none of the cages contained any vegetation and the only sources of food and water available to the birds were those that I supplied. These observations on cage size are important because the primary basis for Hudon's criticism of my aviary experiments is a study conducted by Weber (1961) in which Common Redpolls (*Carduelis flammea*) held in cages of different sizes grew ornamental plumage of different coloration. Unfortunately, in Weber's experiment not only did cage size vary, so did the vegetation that was enclosed in the different cages. Despite claims to the contrary by Weber and Hudon, it is clear from descriptions of the experiments that birds in the larger cages had access to a richer diversity of plants (and undoubtedly the insects associated with the plants) than birds in the smaller cages (see particularly the figure in Weber 1961). Thus, the experiments totally confounded plumage effects due to cage size per se and plumage effects due to differential access to carotenoid pigments. Experiments cited by Hudon in which birds were free flying (Weber 1953) are so poorly controlled they do not deserve further comment. Obviously, I do not agree with Hudon's suggestion that one way to test for captivity effects in future research would be to control the diets of free-flying birds.

Third, the House Finches in my experiments displayed a specific response to specific diets. When I switched from one seed mix to another (for composition of the two seed mixes, see Hill 1992), all other conditions being held equal, birds responded by growing plumage of different brightness (Hill 1992). If all diets provided birds with an abundance of carotenoids as Hudon claims and it was a general captivity affect that depressed bird's ability to use carotenoid pigments, then how does one explain this response to a change in carotenoid access? These were not "unnatural" carotenoid pigments as is canthax-

TABLE 1. Plumage brightness scores ($\bar{x} \pm \text{SD}$) of male House Finches after molt on plain seed diets in aviaries of various sizes.^a

Cage size	<i>n</i>	Plumage score ^b
Small	2	103.0 \pm 2.8
Medium	6	101.8 \pm 11.5
Large	13	103.8 \pm 6.5

^a See experiment 2 in Hill (1992) for details of diet.

^b Two-tailed *t*-test comparing the mean plumage coloration of males in medium and large cages yielded $t = 0.49$ ($P = 0.63$).

anthin, but the same carotenoids available to wild birds. I observed a similar difference in the intensity of the plumage grown by male House Finches when I provided canthaxanthin both on apples and in drinking water as opposed to providing canthaxanthin only in drinking water (Hill 1993a). If both of these diets flooded birds with "unnatural" red pigments, why did the birds produce brighter feathers when fed more canthaxanthin? Finally, on the same diet that I fed to male House Finches of the race *C. m. frontalis*, males of the race *C. m. griseocomi* produced significantly brighter plumage (Hill 1993a). The main difference between *frontalis* and *griseocomi* males is that *griseocomi* males have much smaller patches of ventral carotenoid pigmentation than *frontalis* males (Hill 1993a). I explained the different responses to the same diet by suggesting that the birds of both subspecies were limited by access to carotenoids, but that *griseocomi* males had a smaller area to pigment and, hence, achieved brighter coloration (Hill 1993a, 1994). Without invoking carotenoid access, the different response by *frontalis* and *griseocomi* males is hard to explain.

Fourth, female House Finches actually increase in plumage coloration in captivity on the same diet that causes males to lose their coloration. In wild populations, some female House Finches show a wash of carotenoid pigmentation on their crown, underside, and rump that varies from yellow to red but is never as intense as ornamental coloration in males (Hill 1993b). Among populations of House Finches the proportion of females that show detectable carotenoid pigmentation varies from 22 to 56%, with only a very few females showing maximum female color expression (Hill 1993b). When I captured female House Finches from the wild, held them in the same aviaries in which males were housed, and fed them the same plain seed diet that was fed to males, 92% displayed a wash of yellow on their rumps. When canthaxanthin was added to their diet, 100% displayed maximum female coloration (Hill 1993b). Thus, in captivity, females showed a greater expression of carotenoid-based plumage pigmentation than in the wild. If carotenoid access plays no role in expression of plumage coloration in House Finches, how can one explain the observation that females increased in carotenoid expression while males decreased expression in the same cages on the

same diets? In addition, if all wild birds ingest an abundance of carotenoid pigments as Hudon argued, why do so few wild female House Finches display carotenoid pigmentation? All females have the capacity to do so when given access to pigments.

Fifth, the hypothesis that all wild male House Finches have access to more carotenoid pigments than they need to produce bright red plumage and that all variation in male appearance is due to physiological condition cannot explain the remarkable geographic variation in expression of male plumage coloration (Hill 1993a). In many parts of the Hawaiian Islands where House Finches have been introduced, virtually all males are drab yellow and orange rather than bright red in coloration (Grinnell 1911, Hirai 1975, Hill 1993a). In contrast, males introduced to the eastern United States are bright (but they are significantly drabber in Michigan and New York than Alabama; pers. obs.). In coastal California, local populations vary considerably in the mean coloration of males. At two sites only 11 km apart near San Jose males were as bright and as drab as in any populations that I sampled (Hill 1993b). It is hard to imagine that males in these populations have access to the same carotenoid pigments, but are in very different physiological condition. The clutch size, fledging success, and number of broods per season is remarkably similar among drab House Finches in Hawaii, bright and drab House Finches in California, and bright House Finches in Michigan (Hill 1993c). For all variation to be explained by physiological condition rather than carotenoid access one would have to accept that the healthiest males in Hawaii are in poorer condition than the sickest males in Michigan and that simply is not the case.

In conclusion, there is little empirical support of Hudon's claim that male House Finches grew drab plumage in captivity on plain seed diets (Hill 1992), not because of a change in access to carotenoid pigments, but because of captivity effects. In addition, there are no data to support his suggestion that wild birds in general are not limited by access to carotenoid pigments. I certainly agree, however, that it is a topic worthy of further study. The best way to resolve the question of how birds use carotenoid pigments is to take advantage of modern analytical techniques in which molecules can be labeled and tracked from food to feathers or feces.

While the present evidence supports a central role of carotenoid access in determining expression of carotenoid-based pigmentation in birds, I agree that there is good evidence that physiological condition also plays an important part. The study of Zebra Finches (*Poephila guttata*) cited by Hudon, in which birds maintained on the same diet varied in plumage coloration according to physical condition (Burley et al. 1992), and a recent study showing that male three-spined sticklebacks (*Gasterosteus aculeatus*) produce brighter carotenoid coloration on a high-quality than

on a low-quality diet with the same carotenoid content (Frischknecht 1993), provide solid evidence for a role of physiological condition. There also is evidence that parasites inhibit expression of carotenoid pigmentation in both domestic strains and wild strains of Red Junglefowl (*Gallus gallus*; Ruff et al. 1974, Zuk et al. 1990). In the wild, there is likely a complex interaction between physiological condition and dietary access to carotenoids. Individuals in poorer physiological condition probably gain access to fewer carotenoid pigments and are less efficient at using those that they ingest. As in most fields of research, there is more to be gained by keeping a pluralistic approach to investigating the basis for individual variation in expression of carotenoid-based ornaments than in creating false dichotomies.

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LITERATURE CITED

- BROCKMANN, H., AND O. VÖLKER. 1934. Der Gelbe Federfarbstoff des Kanarienvogels (*Serinus canaria canaria* (L.)) und das Vorkommen von Carotinoiden bei Vögeln. Hoppe-Seyler's Z. Physiol. Chem. 224:193-215.
- BRUSH, A. H., AND D. M. POWER. 1976. House Finch pigmentation: Carotenoid metabolism and the effect of diet. Auk 93:725-739.
- BURLEY, N. T., D. K. PRICE, AND R. A. ZANN. 1992. Bill color, reproduction and condition effects in wild and domesticated Zebra Finches. Auk 109: 13-23.
- FOX, D. L., AND J. W. MCBETH. 1970. Some dietary and blood-carotenoid levels in flamingos. Comp. Biochem. Physiol. 34:707-713.
- FOX, D. L., J. W. MCBETH, AND G. MACKINNEY. 1970. Some dietary carotenoids and blood-carotenoid levels in flamingos. II γ -carotene and α -carotene consumed by the American Flamingo. Comp. Biochem. Physiol. 36:253-262.
- FOX, D. L., AND T. S. HOPKINS. 1966. Comparative metabolic fractionation of carotenoids in three flamingo species. Comp. Biochem. Physiol. 17: 841-856.
- FRISCHKNECHT, M. 1993. The breeding colouration of male three-spined sticklebacks (*Gasterosteus*

- aculeatus*) as an indicator of energy investment in vigour. *Evol. Ecol.* 7:439-450.
- GOODWIN, T. W. 1980. The biochemistry of carotenoids. Vol. 1, Plants (2nd ed.). Chapman and Hall, New York.
- GOODWIN, T. W. 1984. The biochemistry of carotenoids. Vol. 2, Animals (2nd ed.). Chapman and Hall, New York.
- GRINNELL, J. 1911. The linnet of the Hawaiian Islands: A problem in speciation. *Univ. Calif. Publ. Zool.* 7:79-95.
- HILL, G. E. 1990. Female House Finches prefer colourful males: Sexual selection for a condition-dependent trait. *Anim. Behav.* 40:563-572.
- HILL, G. E. 1991. Plumage coloration is a sexually selected indicator of male quality. *Nature* 350:337-339.
- HILL, G. E. 1992. The proximate basis of variation in carotenoid pigmentation in male House Finches. *Auk* 109:1-12.
- HILL, G. E. 1993a. Geographic variation in carotenoid plumage pigmentation of House Finches. *Biol. J. Linn. Soc.* 49:63-86.
- HILL, G. E. 1993b. The proximate basis of inter- and intra-population variation in female plumage coloration in the House Finch. *Can. J. Zool.* 71:619-627.
- HILL, G. E. 1993c. House Finch. *In* Birds of North America (A. Poole, P. Stettenheim, and F. Gill, Eds.). No. 46. Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- HILL, G. E. 1994. Geographic variation in male ornamentation and female mate preference in the House Finch: A comparative test of models of sexual selection. *Behav. Ecol.* 5:64-73.
- HIRAI, L. T. 1975. The Hawaiian House Finch. *Elepaio* 36:1-5.
- HUDON, J. 1994. Showiness, carotenoids, and captivity: A comment on Hill (1992). *Auk* 111:218-221.
- KOCH, E. L. 1939. Zur Frage der Beeinflussbarkeit der Gefiederfarben der Vögel. *Z. Wiss. Zool.* 152:27-82.
- LEE, W. L. 1966. Pigmentation of the marine isopod *Idotheamontereyensis*. *Comp. Biochem. Physiol.* 18:17-36.
- MURPHY, M. E., J. R. KING, AND J. LU. 1988. Malnutrition during the postnuptial molt of White-crowned Sparrows: Feather growth and quality. *Can. J. Zool.* 66:1403-1413.
- NEWTON, I. 1972. Finches. Collins, London.
- RUFF, M. D., W. M. REID, AND J. K. JOHNSON. 1974. Lowered blood carotenoid levels in chickens infected with coccidia. *Poult. Sci.* 53:1801-1809.
- SLAGSVOLD, T., AND J. T. LIJFELD. 1985. Variation in plumage coloration of the Great Tit *Parus major* in relation to habitat, season, and food. *J. Zool. (Lond.)* 206A:321-328.
- WEBER, H. 1953. Bewirkung des Fabwechsels bei männlichen Kreuzschnäbein. *J. Ornithol.* 94:342-346.
- WEBER, H. 1961. Über die Ursache des Verlustes der roten Federfarbe bei gekäfigten Birkenzeisigen. *J. Ornithol.* 102:158-163.
- WILLIAMS, J. H., G. BRITTON, AND T. W. GOODWIN. 1967. The biosynthesis of cyclic carotenes. *Biochem. J.* 105:99-105.
- ZUK, M., R. THORNHILL, AND J. D. LIGON. 1990. Parasites and mate choice in Red Jungle Fowl. *Am. Zool.* 235-244.

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Use and Misuse of Bird Lists in Community Ecology and Conservation

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Comparing lists of bird species among sites is an increasingly widespread practice for assessing patterns of species richness, particularly with the accelerating interest in conservation of tropical habitats. Because many researchers believe that problems in species identification and detectability are fewer in birds than in most other taxa, they believe that species richness of birds often can be assessed more quickly

and efficiently than for other taxa. Consequently, species richness of birds is frequently used as an index of overall "biodiversity," thereby assuming a prominent role in conservation decisions. Therefore, comparisons of inventories of avifaunas between sites take on a special significance.

A typical statement that one finds in comparisons of avifaunal surveys might be "341 species were re-