gested (for a detailed discussion of effects of dietary carotenoids on display, see Hill 1992, 1994, Hudon 1994). The latter explanation seems less plausible, but feeding experiments are needed for a definitive test.

The second implication of this study is that, especially for species with red plumage, one can test whether a color display is carotenoid-based by examining plasma during molt. Species with plumage coloration that is carotenoid-based should have orange to red plasma. Species with plumage displays derived from melanins or other biochromes or from feather structures (and lacking carotenoid-based bill or leg color) should have pale yellow plasma. Of course, the best way to determine the basis for color display in a species is to conduct a careful biochemical analysis, but for field biologists examination of blood plasma can provide a quick and useful assay.

Acknowledgments.—I thank J. Willis, J. W. Mathews, J. Belcher and my 1993 Advanced Ornithology class at Auburn University for very capable assistance in sampling birds. A. Brush, J. Hudon, G. Schnell, and G. Hepp provided comments on the manuscript. Materials for this study were provided by the Department of Zoology and Wildlife Sciences and Alabama Agricultural Research Station, Auburn University.

Literature Cited

Abacus Concepts. 1992. Statview. Abacus Concepts, Inc., Berkeley, California.

Brush, A. H. 1978. Avian pigmentation. Pages 141–161 *in* Chemical zoology. Vol. 10, Aves (A. Brush, Ed.). Academic Press, New York.

Brush, A. H. 1990. Metabolism of carotenoid pigments in birds. FASEB J. 4:2969–2977.

Brush, A. H., and N. K. Johnson. 1976. The evolution of color differences between Nashville and Virginia's warblers. Condor 78:412–414.

Brush, A. H., and D. M. Power. 1976. House Finch pigmentation: Carotenoid metabolism and the effect of diet. Auk 93:725–739.

Goodwin, T. W. 1984. The biochemistry of carotenoids. Vol. 2, Animals, 2nd ed. Chapman and Hall, New York.

Hill, G. E. 1992. The proximate basis of variation in carotenoid pigmentation in male House Finches. Auk 109:1–12.

Hill, G. E. 1994. House Finches are what they eat: A reply to Hudon. Auk 111:221–224.

Hill, G. E., R. Montgomerie, C. Inouye, and J. Dale. 1994. Influence of dietary carotenoids on plasma and plumage color in the House Finch: Intra- and intersexual variation. Funct. Ecol. 8:343–350.

Hudon, J. 1991. Unusual carotenoid use by the Western Tanager (*Piranga ludoviciana*) and its evolutionary implications. Can. J. Zool. 69:2311–2320.

Hudon, J. 1994. Showiness, carotenoids, and captivity: A comment on Hill (1992). Auk 111:218–221.

Kornerup, A., and J. H. Wanscher. 1983. Methuen handbook of colour, 3rd ed. Methuen, London.

Pyle, P., S. N. G. Howell, R. P. Yunick, and D. F. DeSante. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, California.

Ralph, C. L. 1969. Control of color in birds. Am. Zool. 9:521–530.

Test, F. H. 1969. Relation of wing and tail color of the woodpeckers *Colaptes auratus* and *C. cafer* to their food. Condor 71:206–211.

Trams, E. 1969. Carotenoid transport in the plasma of the Scarlet Ibis (*Eudocimus ruber*). Comp. Biochem. Physiol. 28:1177–1184.

Received 15 June 1994, accepted 31 August 1994.

The Auk 112(4):1057–1061, 1995

Seasonal Variation in Circulating Carotenoid Pigments in the House Finch

Geoffrey E. Hill

Department of Zoology and Wildlife Science and Alabama Agricultural Experiment Station, 331 Funchess Hall, Auburn University, Auburn, Alabama 36849, USA

Carotenoid pigments are responsible for much of the red, orange, and yellow coloration found in bird plumage (Brush 1978, 1990, Goodwin 1984). They are unique among known avian pigments in that they cannot be synthesized by birds and must be ingested (Goodwin 1950, Brush 1978, 1990). Thus, expression of carotenoid-based plumage coloration depends on a bird's ability to ingest, transport, and modify carotenoid pigments (Brush 1978, 1990). Some bird species are known to have sophisticated mechanisms for efficient absorption, transport, metabolism, and deposition of carotenoid pigments (studies summarized in Brush 1978, 1990, Goodwin 1984). In addition, Hill (1993b, c, 1994a, b, c) proposed that some birds forage to increase the amount of carotenoid that they ingest.

Unlike the carotenoid-based integumentary pigmentation of organisms such as fish, which can change color within weeks or even days in response to changes in diet (Fujii 1969, Nicoletto 1993), the plumage coloration of birds is fixed at the time of molt (Lucas and Stettenheim 1972, Brush 1978). In at least one species of passerine, the House Finch (*Carpodacus mexicanus*), only pigments ingested during feather growth affect plumage color (Hill 1992, 1993b). Given the seasonal need for carotenoids as plumage pigments, I predicted that the volume of carotenoids that birds ingest, process, and transport would be highest during the period of feather growth and relatively low at other times of the year. To test this hypothesis, I studied seasonal variation in the hue of plasma of House Finches.

The House Finch is one of the best-studied passerines with regard to both the proximate and ultimate control of carotenoid-based plumage coloration (summarized in Hill 1993a). Within all populations, male House Finches vary in expression of carotenoid-based plumage coloration from pale yellow to bright red (Brush and Power 1976, Hill 1990, 1993b). Females vary from having no detectable carotenoid pigmentation to having a red rump and a wash of pink on their underparts (Hill 1993c). At least three carotenoid pigments combine to produce the ornamental coloration of male plumage (Brush and Power 1976), and dietary access to those carotenoid pigments at the time of their annual molt appears to determine male appearance (Brush and Power 1976, Hill 1992, 1993b, 1994a; but see Hudon 1994). Female House Finches use male plumage brightness as a primary criterion for choosing mates (Hill 1990, 1991, 1994b) and male coloration appears honestly to signal male quality (Hill 1991, Hill and Montgomerie 1994).

The details of the mechanisms used by House Finches to get carotenoid pigments from food in the gut to developing feathers remain unknown. Hill et al. (1994) reported that the hue of plasma in House Finches can be used as an index of the levels of circulating carotenoid pigments. They found a positive correlation between the redness of the plasma of molting male House Finches and the redness of growing feathers (Hill et al. 1994). They also observed a significant difference in the plasma color of females, which have little carotenoid pigmentation (Hill 1993c), and males, which have extensive carotenoid pigmentation (Hill et al. 1994). In addition, species with carotenoid-based plumage coloration have redder plasma during molt than species lacking carotenoid-based plumage coloration (Hill 1995). These previous studies of plasma hue were conducted on molting birds. In this study, I measured variation in the hue of the plasma of House Finches throughout the year.

Methods.—I captured house finches in mist nets and traps in a residential area of Auburn, Alabama from July 1993 to June 1994. I determined the age and sex of birds using plumage characteristics (Hill 1993a) or extent of skull ossification, and I scored plumage hue by comparing plumage to color chips in the *Methuen Handbook of Colour* (Kornerup and Wansher 1983) following procedures outlined in Hill et al. (1994). I collected about 50 μl of blood from each bird in a heparinized microhematocrit tube after nicking the brachial vein. Blood in the microhematocrit tubes was immediately spun for 2 min at about 10,000 rpm in an IEC Clinical Centrifuge (International Equipment Company, Needham Heights, Massachusetts), and the hue of the plasma portion of the blood was scored by comparison to color chips in the color handbook (for more on plasma-scoring methods, see Hill et al. 1994). Because carotenoids reflect light in a portion of the electromagnetic spectrum that is visible to humans, the presence of carotenoids can be detected with the human visual system (Brush and Power 1976, Hill et al. 1994). However, with such a crude visual assay, there is no way to distinguish between hue changes due to changes in concentration of a particular carotenoid molecule and hue changes due to changes in the type(s) of carotenoids present. Moreover, a critical assumption of my study is that plasma redness was a function of the type or quantities of carotenoids that it contains (for further justification of this assumption, see Brush and Power 1976, Hill et al. 1994). Because hue scores for some classes of birds were not normally distributed (Hill 1993c, Hill et al. 1994), I summarize sampled values as medians and I used nonparametric statistics for all analyses.

Little quantitative data exist on the diets of wild House Finches, or especially how diet might vary seasonally (Hill 1993a). At the turn of the century, Beal (1907) examined the contents of the crops and stomachs of 1,206 wild House Finches collected in California. He summarized the results in a table that showed the proportions of general categories of food items (animal matter, weed seed, fruit, and miscellaneous plant matter) consumed each month of the year. I plotted the data from Beal (1907) to look for seasonal changes in diet that might be related to seasonal changes in carotenoid consumption.

Results.—The median hue of male plasma increased in redness slowly between April and June, increased sharply in July, and peaked in August (Fig. 1). The peak in median plasma hue coincided with the peak in the proportion of House Finches in the Auburn population that were molting (Fig. 1). The median plasma hue of males then declined through September and October, reaching an annual low from December through February (Fig. 1). The median plasma scores of males during molt (July-September) were significantly greater than the median plasma scores of males in the nonmolting period December to February ($U = 333$, $n = 144$ and 94, $P < 0.001$; Fig. 1).

The median hue of female plasma varied across

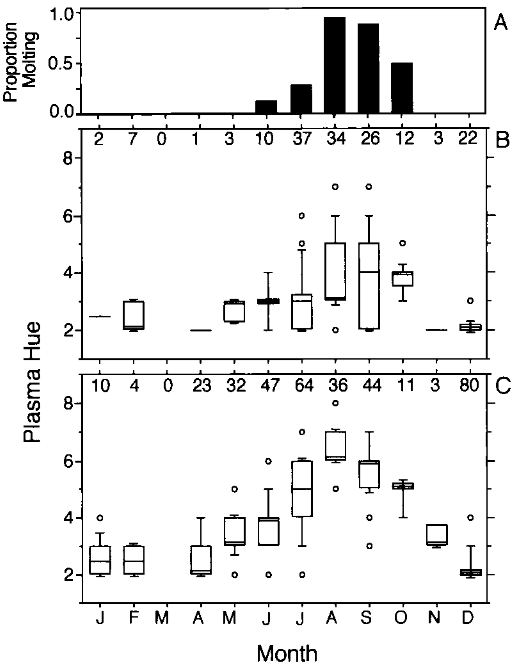

Fig. 1. (A) Histogram of proportion of population of House Finches in Auburn, Alabama molting body plumage by month. (B) Box plot of plasma-hue scores of female House Finches by month. (C) Box plot of plasma-hue scores of male House Finches by month. Horizontal bars in box plots indicate the 10th, 25th, 50th, 75th, and 90th percentiles. Points give data for individuals outside of this range. Numbers above box plots indicate sample sizes.

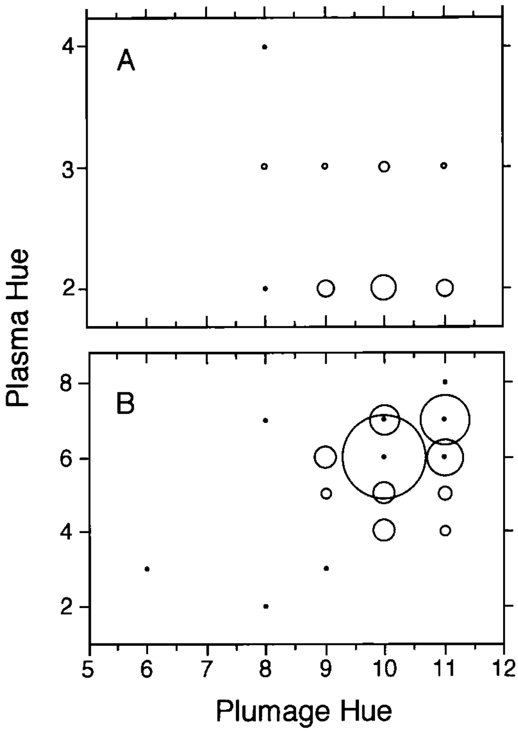

Fig. 2. Relationship between plasma hue and plumage hue for male House Finches sampled in Auburn, Alabama (A) during nonmolting period (January-April) and (B) during molt (July-September). Approximate colors of hues: (2) yellow, (6) orange, (10) red (from Kornerup and Wanscher 1983).

months in a pattern similar to males, although during molt the plasma hue of females was not as red as the plasma hue of males. As in males, the median plasma scores of females during the three months of peak molt (July-September) was significantly greater than the median plasma scores of females in December-February ($U = 540.5$, $n = 97, 31$, $P < 0.001$; Fig. 1).

As reported previously (Hill et al. 1994), there was a significant positive correlation between plasma hue and plumage hue of males during molt (July-September; $r_s = 0.30$, $n = 86$, $P = 0.006$; Fig. 2). However, when the same comparison was made using male plasma samples collected in December-February, the correlation was weakly negative and not significant ($r_s = -0.24$, $n = 28$, $P = 0.21$; Fig. 2).

Plotting the monthly summaries of diets from Beal (1907) provided only the most general indication of seasonal variation in carotenoid consumption (Fig. 3). However, there is a dramatic rise in the proportion of fruit consumed at the end of the summer, coinciding with the onset of molt and with a rise in level of circulating carotenoid pigments in birds. This increase in proportion of fruit consumed is offset by a large drop in the proportion of seeds consumed. A small rise in the proportion of miscellaneous food items consumed (including items such as flower parts) also can be seen (Fig. 3).

Discussion.—I found substantial seasonal variation in the plasma hue of both male and female House Finches. In both sexes, the median redness of plasma hue reached an annual maximum during the period of peak molt by individuals in the population. Assuming that redder plasma hue indicates an increased concentration of carotenoids (or, alternatively, a change in the types of carotenoids) being transported in the blood (Hill et al. 1994), the seasonal variation in plasma hue indicates seasonal variation in pigment physiology. Without additional information, however, there is no way to determine whether changes in circulating levels of carotenoid pigments indicate change in dietary intake of carotenoids, change in the number of carrier proteins in the blood (Trams 1969), change in metabolism of carotenoids (particularly changing yellow carotenoids to red; Brush 1990), or changes in other physiological factors such as intes-

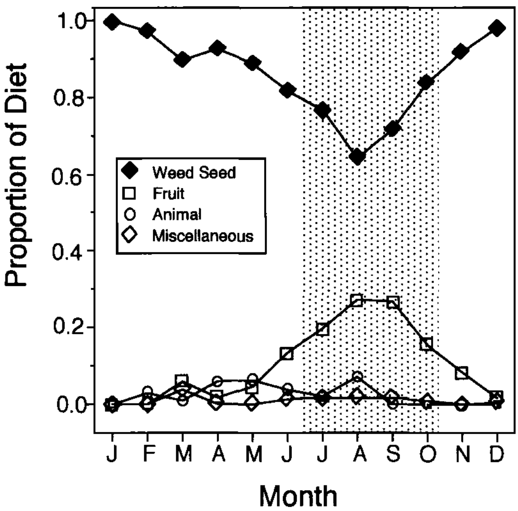

Fig. 3. Proportion of House Finch diets composed of animal matter, weed seeds, fruits, or miscellaneous plant matter in each month of year. Data from Beal (1907) based on analysis of 1,206 stomachs of House Finches collected in central and southern California. Shaded region indicates period of body molt in House Finches.

tinal uptake of carotenoids. Most likely, seasonal variation in carotenoid content of the blood is affected by all of these factors.

In a study of plasma hue, Hill et al. (1994) found a significant positive correlation between the hue of incoming feathers and the hue of plasma in molting male House Finches. I found a similar significant relationship between plumage hue and plasma hue in the current study for months in which males were molting (July-September). However, when I repeated the comparison for a period with no molt (January-March), the relationship disappeared. During the nonmolt period, plasma-hue values were uniformly low, so there was little variation in plasma hue among males compared to the variation among males during molt (Fig. 2). Given the low median plasma hue and the fact that circulating carotenoids cannot affect plumage color except at the time of molt, it would have been surprising if a positive correlation between plumage hue and plasma hue had been found during the nonmolt period. The lack of relationship during the nonmolting period further demonstrates the extent of seasonal variation in circulating levels of carotenoids.

Finally, data from Beal (1907) show that House Finches in California modify their diets substantially in a seasonal pattern with peaks and troughs that correspond to peaks and troughs in molt and plasma hue scores. From midwinter to late summer the proportion of the diet derived from seeds drops from 99.8 to 64.0%, while the proportion of fruit rises from 0.2% to 27.4%. Seeds are generally considered a poor source of carotenoid pigments (Brockmann and Völker 1934, Goodwin 1973, Brush and Power 1976; but see Hudon 1994), and captive male House Finches are unable to attain bright red plumage on a diet exclusively of seeds (Brush and Power 1976, Hill 1992, 1993b, 1994a). The variety and relative abundances of carotenoids in fruits and vegetables are highly variable, but many fruits contain a higher concentration of carotenoid pigment than an equivalent amount of seeds (Gross 1987, Goodwin and Britton 1988, Mangels et al. 1993) and some fruits contain the red pigment rhodoxanthin (Rahman and Eggert 1973), which may be particularly important to male House Finches in acquiring maximum ornamental coloration. The proportion of miscellaneous food items, while never amounting to even 1% of the diet of House Finches, also peaks during molt. A major component of miscellaneous food items is flower parts, which can be a concentrated source of carotenoid pigments (Goodwin 1980, Goodwin and Britton 1988).

Admittedly, the seasonal trends in the diet composition published by Beal (1907) provide only indirect support for the idea that male House Finches adjust their diets to affect intake of carotenoid pigments. Finches may increase their intake of fruit for other nutrients or energy needed for molt. In addition, over the period from midwinter to late summer, fruit becomes more abundant in California, and changes in the diet related to fruit consumption might simply reflect changes in the availability of fruit. However, in central and southern California where this survey was made, fruit is a available year-round and as Beal (1907) stated: "If the bird preferred an exclusive diet of fruit, there is no reason why its taste should not be gratified during the greater part of the year." Moreover, not just fruit is abundant in agricultural areas in late summer, so are a variety of grains that appear to be the preferred food of House Finches at other times of the year (Hill 1993a). That House Finches appear to choose fruit over grain in late summer is again best stated by Beal (1907):

> With the advent of civilization two new articles of food were presented—grain and fruit. It would seem natural for the linnet, especially equipped as the bird is to extract the kernel of seeds, to have chosen the former, as did blackbirds, doves, and some other species; but for some reason best known to itself it selected fruit.

Perhaps the reason "best known to" the finches is that fruit provides more carotenoid pigments.

Acknowledgments.—I thank C. Stockton, J. Mathews, J. Belcher, J Willis, S. Cracroft, R. Oliver, and my 1995 Advance Ornithology class for help in data collection, as well as R. Montgomerie, C. Inouye, J. Hudon, and A. Brush for comments on the paper. House Finches were banded and sampled under a federal banding permit (21661), as well as state of Alabama (#12) and federal (prt784373) collecting permits. Materials for this study were provided by the Department of Zoology and Wildlife Sciences and the Alabama Experimental Research Station, Auburn University.

Literature Cited

Beal, F. E. L. 1907. Birds of California in relation to fruit industry. U.S. Dep. Agric. Biol. Surv. Bull. 30:13-23.

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. 1978. Avian pigmentation. Pages 141-161 *in* Chemical zoology. Vol 10, Aves (A. Brush, Ed.). Academic Press, New York.

Brush, A. H. 1990. Metabolism of carotenoid pigments in birds. Fed. Am. Soc. Exp. Biol. J. 4:2969-2977.

Brush, A. H., and D. M. Power. 1976. House Finch pigmentation: Carotenoid metabolism and the effect of diet. Auk 93:725-739.

Fujii, R. 1969. Chromatophores and pigments. Pages 307-353 *in* Fish physiology (W. S. Hoar and D. J. Randall, Eds.). Academic Press, New York.

Goodwin, T. W. 1950. Carotenoids and reproduction. Biol. Rev. 25:391-413.

Goodwin, T. W. 1973. Carotenoids. Pages 112-142 *in* Phytochemistry (L. P. Miller, Ed.). Van Nostrand Reinhold, New York.

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.

Goodwin, T. W., and G. Britton. 1988. Distribution and analysis of carotenoids. Pages 61-132 *in* Plant pigments (T. W. Goodwin, Ed.). Academic Press, New York.

Gross, J. 1987. Pigments in fruits. Academic Press, New York.

Hill, G. E. 1990. Female House Finches prefer colourful males: Sexual seleciton 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. House Finch. *In* Birds of North America, no. 46 (A. Poole, P. Stettenheim, and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Hill, G. E. 1993b. Geographic variation in carotenoid plumage pigmentation of House Finches. Biol. J. Lin. Soc. 49:63-86

Hill, G. E. 1993c. 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. 1994a. House Finches are what they eat: A reply to Hudon. Auk 111:221-224.

Hill, G. E. 1994b. Geographic variation in male ornamentation and female mate preference in the House Finch: A comparative test of models of sexual selection. Behav. Ecol. 5:20-30.

Hill, G. E. 1994c. Trait elaboration via adaptive mate choice: Sexual conflict in the evolution of signals of male quality. Ethol. Evol. 6:351-370.

Hill, G. E. 1995. Interspecific variation in plasma hue in relation to carotenoid plumage pigmentation. Auk 112:1054-1057.

Hill, G. E., and R. Montgomerie. 1994. Plumage colour signals nutritional condition in the House Finch. Proc. Roy. Soc. B. 258:47-52.

Hill, G. E., Montgomerie, C. Inouye, and J. Dale. 1994. Influence of dietary carotenoids on plasma and plumage color in the House Finch: Intra- and intersexual variation. Funct. Ecol. 8:343-350.

Hudon, J. 1994. Showiness, carotenoids, and captivity: A comment on Hill (1992). Auk 111:218-221.

Kornerup, A., and J. H. Wanscher. 1983. Methuen handbook of colour, 3rd ed. Methuen, London.

Lucas, A. M., and P. R. Stettenheim. 1972. Avian anatomy. Integument, part 2. U. S. Government Printing Office, Washington, D.C.

Mangels, A. R., J. M. Holden, G. R. Beecher, M. R. Forman, and E. Lanza. 1993. Carotenoid content of fruits and vegetables: An evaluation of analytic data. J. Am. Dietetic Assn. 93:284-296.

Nicoletto, P. F. 1993. Female sexual response to condition-dependent ornaments in the guppy, *Poecilia reticulata*. Anim. Behav. 46:441-450.

Rahman, A., and A. Eggert. 1973. Ketocarotinoide in den Fruchten von *Lonicera webbiana* and *Lonicera reprechtiana*. Z. Naturforsch 28:434-436.

Trams, E. 1969. Carotenoid transport in the plasma of the Scarlet Ibis (*Eudocimus ruber*). Comp. Biochem. Physiol. 28:1177-1184.

Received 25 October 1994, accepted 2 March 1995.