Functional Ecology 1994
8, 343–350

Influence of dietary carotenoids on plasma and plumage colour in the house finch: intra- and intersexual variation

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Summary

1. Although carotenoid pigments cause much of the red, orange, yellow and violet coloration in feathers, the processes by which carotenoids are transported from the diet to those feathers are poorly understood.

2. Male house finches (*Carpodacus mexicanus*) display substantial variation in expression of carotenoid-based plumage coloration, an ornamental trait known to influence female choice.

3. To test the hypothesis that variation in carotenoid pigmentation of feathers is caused by processes that occur before the uptake of carotenoids by follicle cells during moult, we compared the hues of blood plasma and growing feathers in three populations (two in California and one in Mexico) of house finches that differed in median male plumage brightness.

4. In all three populations, there was a significant positive correlation between the hues of plasma and plumage in males, but there were no significant correlations between the hues of plasma and plumage in females.

5. In all three populations, the plasma hue of adult males was significantly brighter red than that of adult females; the plasma hue of males from the two brightly plumaged populations was also significantly brighter red than that of males from the drabber population.

6. These results suggest that sex-specific differences in the expression of carotenoid pigmentation and intraspecific variation in the expression of male plumage coloration is the result of processes that occur before carotenoid uptake by follicle cells during feather growth (e.g. due to the influence of foraging behaviour, gut parasites or food quality).

Key-words: Carotenoid pigmentation, *Carpodacus mexicanus*, sexual selection

Functional Ecology (1994) **8,** 343–350

Introduction

Carotenoids are responsible for much of the red, orange, yellow and violet coloration of feathers (Brush 1978). They are unique among known avian pigments in that they cannot be synthesized by birds *de novo*—they must be ingested (Goodwin 1950; Brush 1978, 1990). Because variation in carotenoid-based plumage coloration may influence female choice in some species (Hill 1990, 1991), knowledge about the proximate control of carotenoid pigmentation can help us to understand the mechanisms that influence female choice. Like all physiological aspects of carotenoid pigmentation, however, the transport of carotenoids from the gut lining to follicle cells of growing feathers (Fig. 1) remains poorly understood (see Brush 1978 and 1990 for reviews), particularly for non-poultry species.

Studies of plumage coloration and levels of carotenoids in the plasma have largely been directed either at characterizing species or making interspecific comparisons. These studies have demonstrated (1) that birds with plumage pigmented by carotenoids have specialized mechanisms to transport those carotenoids

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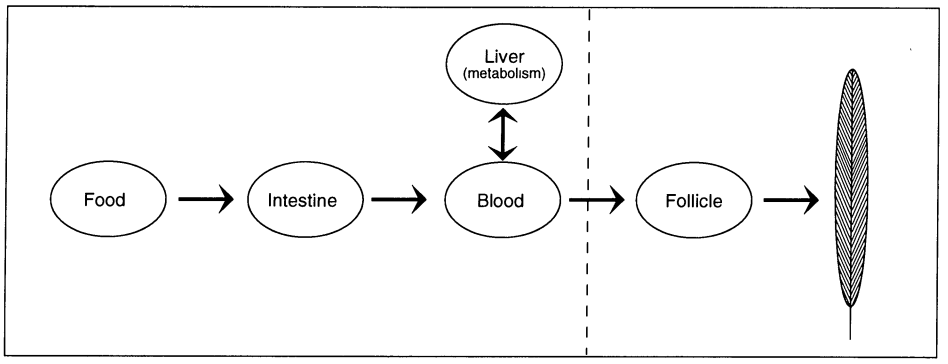

Fig. 1. A diagrammatic representation of the movement of carotenoid pigments from ingestion to eventual deposition in feathers. In this study we tested the hypothesis that differences among individuals in the carotenoid pigmentation of their plumage occur before the uptake of carotenoids by follicle cells (i.e. to the left of the vertical dashed line).

in their blood (Fox, Hopkins & Zilversmit 1965; Trams 1969), (2) that carotenoids are concentrated in developing feathers as they are removed from the blood (Fox 1962), and (3) that dietary intake of carotenoids affects their concentration in both the blood and growing feathers (Fox 1962; Fox & Hopkins 1966; Fox, Smith & Wolfson 1967; Fox, Wolfson & McBeth 1969; Fox & McBeth 1970). To date, no study has focused on the variation in levels of plasma carotenoids among individuals within a species. An analysis of such variation might help us to understand variation in carotenoid-based plumage coloration. The purpose of the study was to test the hypothesis that differences in carotenoid physiology that are responsible for differences in expression of plumage coloration are evident before uptake of carotenoid pigments by the follicle cells of developing feathers. To test this hypothesis we compared the hues of blood plasma to those of growing feathers for both males and females in three populations of the house finch, *Carpodacus mexicanus* (Müller), a species in which variation in expression of carotenoid plumage pigmentation of males is known to influence female mate choice (Hill 1990, 1991, 1994).

We studied a large sample of individuals during autumn moult—the only time of the year when ingested carotenoids can affect plumage coloration in this species (Michener & Michener 1940; Hill 1992, 1993b). One convenient property of the carotenoid pigments of house finches is that easily scorable differences in the hues of both plasma and feathers reflect variation in both the concentration and type of carotenoids present (Brush & Power 1976; Brush 1990).

Materials and methods

STUDY SPECIES

The house finch is a sexually dichromatic passerine bird with ornamental carotenoid pigmentation in the feathers of the crown, rump and underside (Grinnell 1911; Hill 1993a). Ornamental coloration in males varies from pale yellow to bright red (Michener & Michener 1931; Hill 1990, 1992, 1993a). In females, this ornamental coloration is more variable. Many females have no ornamental coloration and a few have reduced expression of the same coloration as males (McEntee 1970; Hill 1993c).

More is known about the carotenoid pigmentation of plumage in house finches than for any other passerine. Males derive their ornamental coloration from a combination of three carotenoid pigments: yellow β-carotene, orange isocryptoxanthin and red echinenone (Brush & Power 1976; Brush 1990). As is true of other birds that derive coloration from carotenoids, house finches must have access to relatively large quantities of carotenoid pigments during moult to attain maximum plumage brightness (Test 1969; Brush & Power 1976; Hill 1992, 1993a). Moreover, feeding experiments indicate that the brightness of plumage grown by both males and females is a function of the type and quantity of pigments that they ingest during moult (Brush & Power 1976; Hill 1992, 1993a,c).

In addition to substantial variation among individuals within these populations, there is also variation among populations in the mean plumage brightness of both males and females, and among subspecies in the distribution of carotenoid pigmentation on the plumage (Moore 1939; Hill 1993a). Among populations of the subspecies *C. m. frontalis*, males in eastern North America (where the species has been introduced by man) average bright red, whereas males in the introduced population on Hawaii average drab orange. There is even considerable variation among native populations in California (Hill 1994)—males that were captured in disturbed rural habitat near Alviso were very drably coloured whereas males captured in suburban San Jose, just 11 km away, were much more brightly coloured (Hill 1994). In addition to this colour variation among *frontalis* populations,

there is substantial variation in the extent of ventral carotenoid pigmentation (patch size) in males from different subspecies. For example, males from the subspecies *griscomi* of south-western Mexico have a much smaller ventral patch of carotenoid-based coloration than males from any of the *frontalis* populations (Moore 1939; Hill 1993a).

Expression of plumage coloration in male house finches is an important criterion in female mate choice (Hill 1990, 1991, 1994). Male plumage coloration also correlates with their overwinter survival (Hill 1991), nest attentiveness (Hill 1991), first nesting date each year (Hill *et al.* 1994) and the probability of nest desertion by their mate (Hill 1991). One explanation for these patterns is that the expression of carotenoid plumage pigmentation is dependent on an individual's condition or quality (Zahavi 1977; Kodric-Brown & Brown 1984; Hill 1990, 1991). To understand how carotenoid-based plumage coloration might serve as an honest signal of such individual quality, it is necessary to understand the proximate basis for variation in expression of this trait.

METHODS

House finches were studied during the autumn moult in southern California and south-western Mexico. In California, birds were captured at three sites in the vicinity of San Jose, Santa Clara County, from 2 to 14 August 1992. Two of these sites were as described by Hill (1994): the Coyote Creek Riparian Station near Alviso and a suburban residence in north-east San Jose. The third site was a suburban residence in south–central San Jose. In Mexico, birds were captured at three locations in the vicinity of Chilpancingo, Guerrero from 9 to 18 September 1992: one 3 km north of Chilpancingo, another near Tixtla (25 km east of Chilpancingo) and the third near Zumpango (25 km north of Chilpancingo).

At Coyote Creek Riparian Station (Alviso), all finches were captured in a large baited trap. At the two other California locations (both in San Jose), finches were netted as they came in to feeding stations. In Mexico (Guerrero), all finches were captured in mist nets in agricultural fields.

At the time of capture, the skulls of all birds were examined to determine the extent of ossification (Pyle *et al.* 1987). The ages of individuals were recorded as either hatch-year (HY; born in the same calendar year in which they were sampled) if they had incompletely ossified skulls, or after-hatch-year (AHY; born in a previous calendar year) if they had completely ossified skulls. Individuals were sexed by examining their gonads (all finches sampled in this study were killed for diet and parasite analysis).

The stage of body feather moult on each individual bird was scored by recording the per cent of body feathers still in their sheaths on five regions of the body [throat, breast, flanks, crown and back/rump; following Rohwer (1986)]. *Body moult score* is the average of the scores from these five body regions (Rohwer 1986). Primaries were scored separately from 0 (old) to 5 (fully grown new feather) following Ginn & Melville (1983); a *primary moult score* was derived by adding the individual scores of the nine primaries on one wing (usually the left).

Approximately 50 µl of blood was taken from each bird by nicking a brachial vein and collecting the blood in a microhaematocrit tube. In California, blood in the microhaematocrit tube was immediately spun for 2 min at *c.* 10 200 ***g*** in an IEC Clinical Centrifuge (International Equipment Company, Needham Heights, Massachusetts, USA). In Mexico, blood in microhaematocrit tubes was spun using a modified model aeroplane motor powered by a 6-V lantern battery. Using this field centrifuge, microhaematocrit tubes were spun for 2 min at *c.* 8500 ± 1500 ***g***, depending on battery voltage.

Immediately after centrifugation, the hue of the plasma portion of the blood was scored by comparison with colour chips in the *Methuen Handbook of Colour* (Kornerup & Wanscher 1983). In California, the blood samples from 70 birds were scored independently by G.E.H. and J.D. Two blood samples were also taken from each of 93 birds and these were spun and scored separately by the same observer. These two sets of *plasma hue scores* were used to calculate the repeatability of hue estimates between observers and within birds, respectively. Plasma hue scores varied from 0 to 7 ($n = 272$).

For each bird, plumage colour was also determined by comparison with colour chips in the *Methuen Handbook of Colour*, similar to Hill (1990, 1992, 1993a). In the present study, however, birds were sampled during the period of moult and we were particularly interested in the colour of new and incoming plumage. Whenever possible (mainly AHY birds), a complete description of an individual's plumage coloration was recorded by scoring the hue, intensity, and tone of new and incoming feathers in seven plumage regions (see Hill 1992). For these birds a *plumage colour score* was calculated as the sum of these 21 measures. Plumage colour scores varied from 21 to 162 ($n = 144$).

For HY birds and birds in heavy moult, however, it was often possible to determine feather hue (and not intensity or tone) for only one or a few plumage regions. For these birds, only a single score was used (*ventral hue score*) for the hue of incoming plumage on their underside (any portion of the throat or upper breast that had enough new feathers to score) as an estimate of their plumage colour. We determined ventral hue score for almost all birds studied by taking the modal value of ventral hues when we were able to determine a plumage colour score. Ventral hue scores varied from 0 to 11 ($n = 343$) and were highly corre-

lated with plumage colour scores of the same individuals ($r = 0{\cdot}91$, $P < 0{\cdot}0001$, $n = 144$).

Nonparametric statistics were used for most analyses because hues for some classes of birds were not normally distributed (see Fig. 2) and could not be normalized with simple transformations. For *post hoc* multiple comparisons following nonparametric analyses of variance (Kruskal–Wallis tests), we used the procedure described by Zar (1984, pp. 199–201).

For trend analyses, model I regressions and analyses of covariance (ANCOVA) were used. Because we estimated hues as integer values, our analyses of plasma hue *vs* ventral hue scores fulfil the requirements for the Berkson case in model I linear regression, where the independent variable is considered as 'fixed by the experimenter' (Sokal & Rohlf 1981). The data were not transformed for these trend analyses because residuals were normally distributed.

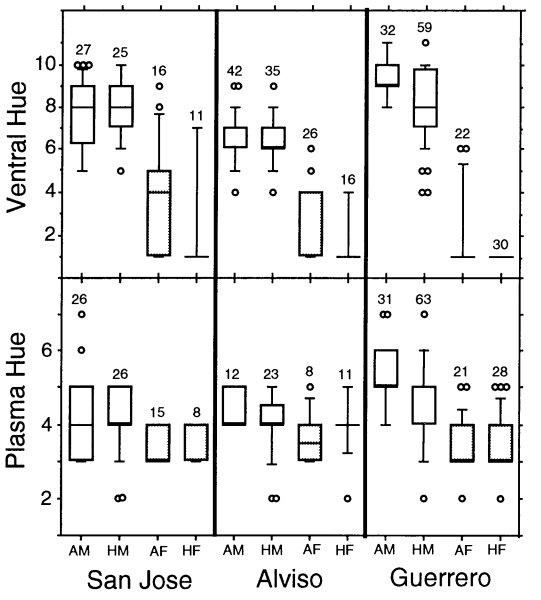

Fig. 2. Box plots of scores for ventral and plasma hues of house finches sampled in three populations. Box plots show the 10th, 25th, 50th, 75th and 90th percentiles as horizontal lines as well as all data points outside this range. AM = AHY male; HM = HY male; AF = AHY female; HF = HY female; box plots for females are shaded. Numbers above box plots indicate sample sizes.

Results

REPEATABILITY OF PLASMA HUE SCORES

We calculated repeatability (r) using the interclass correlation coefficient (Lessells & Boag 1987). Plasma hue scores for individual birds were highly repeatable both between observers ($r = 0{\cdot}96$, $F_{69, 70} = 45{\cdot}5$, $P < 0{\cdot}0001$) and between samples from the same bird scored by the same observer ($r = 0{\cdot}96$, $F_{92, 93} = 53{\cdot}6$, $P < 0{\cdot}0001$).

VARIATION DUE TO MOULT

This study was designed to sample birds at peak moult in both the *frontalis* and *griscomi* populations, as this is the time of year when levels of circulating carotenoids are most likely to influence plumage coloration. Despite this, there was substantial variation among individuals in the progress of their moult. The relations between plasma hue score and either body or primary moult scores (both measures of moult completeness) were not significant for any age or sex class in any population ($P > 0{\cdot}09$ for all analyses; Spearman rank correlations), so we did not control for stage of moult in any analysis.

VARIATION DUE TO SEX AND AGE

In all populations, AHY males had higher plasma hue scores than AHY females (San Jose, $U = 97{\cdot}5$, $n = 26$ males, 15 females, $P = 0{\cdot}005$; Alviso, $U = 20$, $n = 12$, 8, $P = 0{\cdot}19$; Guerrero, $U = 47$, $n = 31$, 21, $P = 0{\cdot}0001$; Mann–Whitney tests; Fig. 2). In Guerrero, HY males also had significantly higher plasma hue scores than HY females ($U = 360$, $n = 63$, 28, $P = 0{\cdot}0001$; Fig. 2), but there were no significant differences between the plasma hue scores of HY males and females in either California population (San Jose, $U = 68$, $n = 26$, 8, $P = 0{\cdot}11$; Alviso, $U = 125$, $n = 23$, 11, $P = 0{\cdot}95$). Because many of the differences between sexes within age classes were significant, we performed separate analyses on data from males and females.

In the two California populations, median ventral and plasma hue scores were not significantly different between AHY and HY males ($P > 0{\cdot}16$ for all comparisons, Mann–Whitney tests; Fig. 2). In the Guerrero sample, however, AHY males had significantly higher scores for ventral hue ($U = 531{\cdot}5$, $n = 59$, 32, $P = 0{\cdot}0004$) and plasma hue ($U = 602$, $n = 63$, 31, $P = 0{\cdot}003$) than HY males (Fig. 2). Separate analyses were performed on data from these two age classes of males.

INTRA- AND INTERPOPULATION VARIATION

Comparing the two study sites in suburban San Jose, there were no significant differences in plumage colour scores of AHY males ($U = 73$, $n = 12$, 14, $P = 0{\cdot}57$; Mann–Whitney test) nor in the ventral hue scores of either AHY ($U = 88$, $n = 12$, 15, $P = 0{\cdot}92$) or HY males ($U = 62{\cdot}5$, $n = 20$, 8, $P = 0{\cdot}36$), so we pooled the data within age classes for these two sites. Similarly, among the three study sites in Guerrero, there were no significant differences in plumage colour scores of AHY males ($H = 2{\cdot}6$, $n = 10$, 4, 17, $P = 0{\cdot}27$; Kruskal–Wallis test) nor in the ventral hue scores of either AHY ($H = 3{\cdot}26$, $n = 10$, 4, 18, $P = 0{\cdot}20$) or HY males ($H = 4{\cdot}64$, $n = 7$, 35, 17, $P = 0{\cdot}10$), so we pooled the data within age classes for these three Mexican sites as well.

Because the plumage coloration of males from the San Jose (two suburban sites) and the Alviso (one rural site) samples differed significantly (AHY plumage colour score, $U=291$, $n=26$, 42, $P=0{\cdot}001$; AHY ventral hue score, $U=360$, $n=27$, 42, $P=0{\cdot}009$; HY ventral hue score, $U=190$, $n=25$, 35, $P=0{\cdot}0002$; see also Hill 1993a), we considered these to be two distinct populations. Also, as the size of the ventral red patch of males of the subspecies *griscomi* (California) and *frontalis* (Guerrero) differed significantly (Hill 1993a), we analysed the pooled Guerrero samples as a distinct population. Thus, data from the Guerrero, San Jose and Alviso populations were analysed separately.

VENTRAL HUE *VS* PLASMA HUE

Overall, there was a significant positive relationship between plasma hue and ventral hue scores for both HY ($r_s=0{\cdot}47$, $n=105$, $P=0{\cdot}0001$) and AHY males ($r_s=0{\cdot}66$, $n=69$, $P=0{\cdot}0001$; Spearman rank correlations, pooling data for all three populations). Moreover, the relationships between plasma and ventral hue scores for AHY and HY males were not significantly different (ANCOVA, $F=0{\cdot}31$, $P=0{\cdot}58$, df = 1, 170), nor was the slope of either relation significantly different from 1·0 (HY, $t=0{\cdot}94$, $P=0{\cdot}35$, $n=105$; AHY: $t=0{\cdot}26$, $P=0{\cdot}80$, $n=69$; Student's t-test; Fig. 3a, b).

When each population was analysed separately, there was a significant positive relationship between plasma hue and plumage colour scores for AHY males from all three populations (Alviso, $r_s=0{\cdot}61$, $n=11$, $P=0{\cdot}05$; San Jose, $r_s=0{\cdot}43$, $n=25$, $P=0{\cdot}03$; Guerrero, $r_s=0{\cdot}67$, $n=30$, $P=0{\cdot}0003$). There were also positive relations between plasma hue and ventral hue scores for both HY and AHY males from both San Jose (AHY, $r_s=0{\cdot}50$, $n=26$, $P=0{\cdot}01$; HY, $r_s=0{\cdot}56$, $n=24$, $P=0{\cdot}007$) and Guerrero (AHY, $r_s=0{\cdot}63$, $n=31$, $P=0{\cdot}0006$; HY, $r_s=0{\cdot}43$, $n=58$, $P=0{\cdot}001$), but not for either HY or AHY males from Alviso (AHY, $r_s=0{\cdot}55$, $n=12$, $P=0{\cdot}06$; HY, $r_s=0{\cdot}05$, $n=23$, $P=0{\cdot}82$), though both relations were still positive. Thus there was a positive relation between plasma hue and the colour of new or incoming plumage (plumage colour or ventral hue scores) in both male age classes in all three populations studied as well as in the pooled data for both HY and AHY males.

As HY females were moulting from juvenile plumage (with no detectable carotenoid pigmentation) into first basic plumage (which may or may not have had detectable carotenoid coloration), we had no way of knowing whether HY females showed no colour because they lacked carotenoid pigmentation in their first basic plumage or because they had not yet grown pigmented feathers. For this reason, only AHY females were analysed. When data for all populations and sampling sites were pooled, no significant relationship was found between scores for ventral and plasma hues in AHY females (Fig. 3c). Likewise,

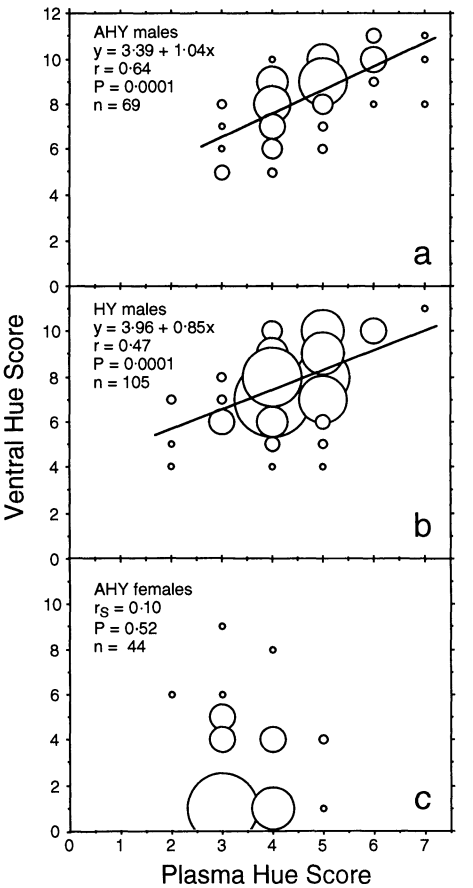

Fig. 3. Relationship between scores for plasma hue and ventral hue for (a) AHY male, (b) HY male and (c) AHY female house finches. Data were pooled for all collecting sites in California, USA and Guerrero, Mexico (see text). The analyses presented are model I regressions for males (a, b) and Spearman rank correlations for females (see Materials and methods). Size of circle indicates the number of coincident data points (for the largest circle $n=14$).

when each population was considered separately, no significant relationship was found between scores for ventral and plasma hues of females from San Jose ($r_s=-0{\cdot}14$, $n=15$, $P=0{\cdot}61$), Alviso ($r_s=0{\cdot}24$, $n=8$, $P=0{\cdot}52$), or Guerrero ($r_s=-0{\cdot}22$, $n=21$, $P=0{\cdot}32$). We further analysed these data by comparing the plasma hue scores of females with and without detectable carotenoid plumage pigmentation and again found no significant differences (all females pooled, $U=219$, $n=20$, 23, $P=0{\cdot}76$; San Jose, $U=17{\cdot}5$, $n=9$, 4, $P=0{\cdot}92$; Alviso, $U=3{\cdot}5$, $n=5$, 3, $P=0{\cdot}19$; Guerrero, $U=31{\cdot}5$, $n=5$, 16, $P=0{\cdot}44$; Mann–Whitney tests).

GEOGRAPHIC VARIATION IN PLUMAGE AND PLASMA COLOUR

The ventral hue scores of AHY males differed significantly among the San Jose, Alviso and Guerrero populations ($H_c=51{\cdot}1$, $n=27$, 42, 32, $P<0{\cdot}0001$;

Kruskal–Wallis test corrected for ties; Fig. 2). Males from Guerrero had the brightest plumage on average, males from San Jose were less brightly coloured and males from Alviso had the drabbest plumage coloration ($P<0{\cdot}002$ for all pairwise comparisons). Females also varied significantly in ventral hue scores ($H_c=6{\cdot}03$, $n=16, 26, 22$, $P<0{\cdot}049$; Fig. 2); those from Guerrero had significantly drabber plumage than females from San Jose ($P<0{\cdot}0001$; Fig. 2), but other pairwise differences were not significant ($P>0{\cdot}10$; Fig. 2).

To see if these differences in male plumage coloration were reflected in plasma hue, we compared plasma hues among the three populations. Plasma hue scores of AHY males varied significantly ($H_c=17{\cdot}9$, $n=26, 12, 31$, $P<0{\cdot}0001$), being higher on average for males from Guerrero than for males from either population in California ($P<0{\cdot}001$ in each case; Fig. 2). Despite the differences in median plumage coloration of AHY males between populations in San Jose and Alviso, there was no difference in median plasma hue scores of AHY males between these populations ($P>0{\cdot}10$; Fig. 2). Finally, there were no significant differences in median plasma hue scores between AHY females from any populations ($H_c=0{\cdot}84$, $n=15, 8, 21$, $P=0{\cdot}66$; Fig. 2).

Discussion

There is a relatively direct relation between the colour of growing feathers and the colour of plasma in house finches. It may seem trivial that house finches growing bright red plumage should have more red pigments being transported in their blood than individuals growing drab yellow plumage, but such a relationship could not be assumed. For example, it would be reasonable to propose that levels of circulating carotenoids are similar for all individuals and that variation in plumage coloration results from follicle cell specificity for available carotenoids during feather growth (Brush 1990). Our observation that there is a relatively strong correlation between plumage colour and plasma colour (i.e. circulating carotenoid pigments) within individuals strongly suggests that, at least for males, differences among individuals in the colour of growing feathers are the result of processes that occur before the uptake of carotenoid pigments by follicle cells (Fig. 1).

Two particularly interesting features of the relationship between plasma and ventral hue scores were evident (Fig. 3). First, the slopes of the regression lines were not significantly different from 1·0. This suggests an approximately one to one relationship between level of circulating carotenoid pigments and the colour of feathers that develop in that follicular environment. Second, the slopes and adjusted means of the regression for HY and AHY males were the same. This similarity in regressions indicates that HY and AHY males do not differ in their capacity to use circulating carotenoid pigments. Rather, differences in plumage colour between AHY and HY males stem from differences in levels of carotenoid pigments in the plasma. This observation corroborates previous results from feeding experiments in which HY males grew feathers of similar colour to AHY males when they were fed the same quantities of carotenoid pigments during moult (Hill 1992).

While variation in plumage coloration among males may be largely a function of the quantity of carotenoid pigments that reaches the blood transport system, control of plumage coloration in females does not appear to be so simple. No significant relationship was found between the plumage coloration and plasma hue for females from any population. However, the plumage coloration of many females is subtle and is difficult to detect in incoming feathers. Consequently, the error in our assignment of ventral hue scores was undoubtedly much higher for females than for males and may have obscured any relationship between plumage and plasma coloration. However, even when we considered only those females with detectable carotenoid pigmentation, which is the subset of females that should have been subject to the least scoring error, we still found no significant relationship between plasma and plumage colours.

Other studies have demonstrated that the ornamental coloration in females is under different proximate control than ornamental coloration in males. For example, on a diet supplemented with canthaxanthin, both *griscomi* and *frontalis* females display maximum female coloration (with a pink wash across the rumps, undersides and crowns; Hill 1993c), but no females ever expressed the highly saturated, brilliant coloration of males (Brush 1990; Hill 1993c). This difference in maximum colour expression may be due to influences of sex hormones. Tewary & Farner (1973) found that male house finches that were either castrated or treated with oestrogen grew female-like plumage that lacked carotenoid pigments. One possible mechanism for such hormone-mediated control of carotenoid deposition in feathers is that hormones control how follicular cells take up carotenoid pigments from the blood (Brush 1990). However, we found significant differences between the sexes in plasma hue, indicating that at least some of the differences between the sexes occur before carotenoids reach the follicle cells. Alternatively, steroid hormones may influence the levels of circulating carotenoid carrier proteins, such that females are capable of transporting fewer carotenoid pigments than males. More likely, though, differences between the sexes in plasma carotenoid levels may result from differences in dietary intake of carotenoid pigments (Hill 1993c).

In addition to the positive relationship between plasma hue and plumage coloration of males within populations, we also found that the median plasma hues of males tended to be higher in populations with brighter median plumage colour. Thus, AHY males in Guerrero had significantly higher plumage colour

scores than males from either California population and their median plasma hue scores were also significantly higher (Fig. 2). In general, it appears that both inter- and intrapopulation variation in plumage coloration is reflected in variation in circulating levels of carotenoid pigments.

These results support and extend previous observations on the proximate control of carotenoid plumage pigmentation in the house finch. Feeding experiments with captive male house finches (from several populations including those studied here) showed that, on a fixed intake of carotenoid pigments, all individuals converged on a similar appearance, regardless of their 'natural' plumage coloration (Brush & Power 1976; Hill 1992, 1993c). We suggest that variation in male coloration arose through differences in access to dietary carotenoid pigments and not through differences in the way in which ingested carotenoids were processed. We are currently investigating dietary variation within and among house finch populations to determine whether plumage colour is correlated with the quantity and quality of carotenoids in an individual's diet. The positive relationship between plumage and plasma coloration provides a second line of evidence that differences in carotenoid pigmentation between bright and drab males occur at least before follicle uptake. There remains, however, virtually no information for house finches or passerines in general on the role of absorption or metabolism in generating intraspecific variation in expression of carotenoid plumage coloration. It is in these areas that additional research is most needed.

Acknowledgements

We thank F. Mewaldt, M. Rigney and the staff at the Coyote Creek Riparian Station for access to collecting sites, and J. Serrano Sr and J. Serrano Jr for assistance in the field. This research was funded by an NSERC grant to R. Montgomerie and an NSERC International Postdoctoral Fellowship to G. E. Hill. Collecting for this study was conducted with permission of the U.S. Fish and Wildlife Service (collecting permit PRT-719116), California Department of Fish and Game (0052) and La Secretaria de Relaciones Exteriores, Mexico (collecting permit 302416).

References

Brush, A.H. (1978) Avian pigmentation. *Chemical Zoology*, vol. X, *Aves* (ed. A. Brush), pp. 141–161. Academic Press, New York.

Brush, A.H. (1990) Metabolism of carotenoid pigments in birds. *FASEB Journal,* **4,** 2969–2977.

Brush, A.H. & Power, D.M. (1976) House finch pigmentation: carotenoid metabolism and the effect of diet. *Auk,* **93,** 725–739.

Fox, D.L. (1962) Metabolic fractionation, storage, and display of carotenoid pigments by flamingoes. *Comparative Biochemistry and Physiology,* **6,** 1–40.

Fox, D.L. & Hopkins, T.S. (1966) Comparative metabolic fractionation of carotenoids in three flamingo species. *Comparative Biochemistry and Physiology,* **17,** 841–856.

Fox, D.L. & McBeth, J.W. (1970) Some dietary carotenoids and blood–carotenoid levels in flamingos. *Comparative Biochemistry and Physiology,* **34,** 707–713.

Fox, D.L., Hopkins, T.S. & Zilversmit, D.B. (1965) Blood carotenoids of the Roseate Spoonbill. *Comparative Biochemistry and Physiology,* **14,** 641–649.

Fox, D.L., Smith, V.E. & Wolfson, A.A. (1967) Carotenoid selectivity in blood and feathers of Lesser (African), Chilean, and Greater (European) Flamingos. *Comparative Biochemistry and Physiology,* **23,** 225–232.

Fox, D.L., Wolfson, A.A. & McBeth, J.W. (1969) Metabolism of β-carotene in the American Flamingo, *Phoenicopterus ruber*. *Comparative Biochemistry and Physiology,* **29,** 1223–1229.

Ginn, H.B. & Melville, D.S. (1983) *Moult in Birds*. BTO Guide 19. British Trust for Ornithology, Beech Grove, UK.

Goodwin, T.W. (1950) Carotenoids and reproduction. *Biological Reviews,* **25,** 391–413.

Grinnell, J. (1911) The linnet of the Hawaiian Islands: a problem in speciation. *University of California Publications in Zoology,* **7,** 79–95.

Hill, G.E. (1990) Female house finches prefer colourful males: sexual selection for a condition-dependent trait. *Animal Behaviour,* **38,** 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 the carotenoid plumage pigmentation of male house finches (*Carpodacus mexicanus*). *Biological Journal of the Linnean Society,* **49,** 63–86.

Hill, G.E. (1993b) House finch. *Birds of North America,* No. 46 (eds A. Poole & F. Gill). Academy Natural Sciences, Philadelphia.

Hill, G.E. (1993c) The proximate basis of inter- and intra-population variation in female plumage coloration in the house finch. *Canadian Journal of Zoology,* **71,** 619–627.

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. *Behavioural Ecology,* **5,** 30–40.

Hill, G.E., Montgomerie, R., Roeder, C. & Boag, P.T. (1994) Sexual selection and cuckoldry in a monogamous songbird: implications for sexual selection theory. *Behaviour Ecology and Sociobiology,* in press.

Kodric-Brown, A. & Brown, J.H. (1984) Truth in advertising: the kinds of traits favored by sexual selection. *Amercian Naturalist,* **124,** 309–323.

Kornerup, A. & Wanscher, J.H. (1983) *Methuen Handbook of Colour*, 3rd edn. Methuen, London.

Lessells, C.M. & Boag, P.T. (1987) Unrepeatable repeatabilities: a common mistake. *Auk,* **104,** 116–121.

McEntee, E. (1970) Age determination of house finches by plumage change. *EBBA News,* **33,** 70–76.

Michener, H. & Michener, J.R. (1931) Variation in color of male house finches. *Condor,* **33,** 12–19.

Michener, H. & Michener, J.R. (1940) The molt of house finches in the Pasadena Region, California. *Condor,* **42,** 140–153.

Moore, R.T. (1939) A review of the house finches of the subgenus *Burrica*. *Condor*, **41,** 177–205.

Pyle, P., Howell, S.N.G., Yunick, R.P. & DeSante, D.F. (1987) *Identification Guide to North American Passerines*. Slate Creek Press, Bolinas, California.

Rohwer, S. (1986) A previously unknown plumage of first-year Indigo Buntings and theories of delayed plumage maturation. *Auk,* **103,** 281–292.

Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*, 2nd edn. W.H. Freeman, San Francisco.

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.

Tewary, P.D. & Farner, D.S. (1973) Effect of castration and estrogen administration on the plumage pigment of the male house finch (*Carpodacus mexicanus*). *American Zoologist,* **13,** 1278.

Trams, E.G. (1969) Carotenoid transport in the plasma of the scarlet ibis (*Eudocimus ruber*). *Comparative Biochemistry and Physiology,* **28,** 1177–1184.

Zahavi, A. (1977) The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology,* **67,** 603–605.

Zar, J.H. (1984) *Biostatistical Analysis*. Prentice Hall, Englewood, New Jersey.

Received 8 March 1993; revised 28 October 1993; accepted 4 November 1993