THE ROYAL SOCIETY

Received 6 December 2001
Accepted 6 February 2002
Published online 7 May 2002

Dietary carotenoids predict plumage coloration in wild house finches

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Carotenoid pigments are a widespread source of ornamental coloration in vertebrates and expression of carotenoid-based colour displays has been shown to serve as an important criterion in female mate choice in birds and fishes. Unlike other integumentary pigments, carotenoids cannot be synthesized; they must be ingested. Carotenoid-based coloration is condition-dependent and has been shown to be affected by both parasites and nutritional condition. A controversial hypothesis is that the expression of carotenoid-based coloration in wild vertebrates is also affected by the amount and types of carotenoid pigments that are ingested. We tested this carotenoid-limitation hypothesis by sampling the gut contents of moulting house finches and comparing the concentration of carotenoid pigments in their gut contents with the colour of growing feathers. We found a positive association: males that ingested food with a higher concentration of carotenoid pigments grew brighter ornamental plumage. We also compared the concentration of carotenoids in the gut contents of males from two subspecies of house finches with small and large patches of carotenoid-based coloration. Consistent with the hypothesis that carotenoid access drives the evolution of carotenoid-based colour displays, males from the population with limited ornamentation had much lower concentrations of carotenoids in their gut contents than males from the population with extensive ornamentation. These observations support the idea that carotenoid intake plays a part in determining the plumage brightness of male house finches.

Keywords: *Carpodacus mexicanus*; honest signalling; condition dependence; sexual selection

> Any male which consumes more carotenoids during foraging will have brighter carotenoid colours. Thus male brightness, at least with respect to carotenoid colours, is a direct indicator of feeding success. (Endler 1983, p. 184)

1. INTRODUCTION

Carotenoid-based colour displays are among the most familiar examples of male ornamental traits that serve as honest signals used by females in making adaptive mate choices (Olson & Owens 1998). Various studies have shown that parasites (Houde & Torio 1992; Thompson *et al.* 1997; Brawner *et al.* 2000) and nutrition (Frischknecht 1993; Hill 2000) can affect expression of carotenoid coloration. Because carotenoids must be ingested by animals, it would also seem that access to dietary carotenoids might limit the expression of carotenoid-based traits, but this idea remains controversial.

Since it was first proposed by Endler (1983), the hypothesis that expression of ornamental carotenoid display is influenced by dietary intake of carotenoid pigments has been widely stated as the primary basis for honest signalling in carotenoid systems (for textbook examples see Gill (1995) and Alcock (2001)). This hypothesis is based on two basic observations: (i) carotenoids cannot be synthesized by animals, so all carotenoid pigments used in display must be ingested (Völker 1938; Brush 1981) and (ii) carotenoid pigments are relatively scarce in the diets of most animals (Goodwin 1984; Hill 1996), though see Hudon (1994) and Thompson *et al.* (1997) for alternative views. Despite an ongoing debate regarding the role of carotenoid access in determining expression of the colour displays of animals (reviewed in Olson & Owens 1998), tests of the carotenoid-limitation hypothesis have been almost entirely restricted to captive-animal studies (Kodric-Brown 1989; Hill 1992, 1993*a*) and these have been criticized (Hudon 1994; Thompson *et al.* 1997). Recently, Grether *et al.* (1999) published a study of guppies (*Poecilia reticulata*) that provided the first direct evidence for limited intake of dietary carotenoid pigments causing reduced expression of ornamental coloration in a wild population of animals. Grether *et al.* (1999), however, compared carotenoid access and integumentary expression among populations of guppies, not among individual guppies. No study has looked at how the carotenoid content of the diet of an individual in the wild affects expression of ornamental coloration.

We sought to test the idea that carotenoid content of the diet affects expression of ornamental coloration in the house finch (*Carpodacus mexicanus*), the best-studied wild bird species with regard to the function and proximate control of carotenoid-based colour display (Hill 2002). Male house finches have carotenoid-based plumage coloration on their heads, undersides and rumps, and they vary

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in expression of carotenoid pigmentation from pale yellow to bright red. Male plumage coloration is an important criterion in female mate choice, with females preferring to mate with males with the reddest and most saturated plumage coloration (Hill 1990, 1991; Hill *et al.* 1999). Parasites (Thompson *et al.* 1997; Brawner *et al.* 2000) and nutritional condition during moult (Hill 2000) can affect expression of this plumage coloration. Intake of carotenoid pigments during moult has also been proposed as an important factor in expression of plumage coloration (Hill 1992, 1994*b*), but there have been no direct field tests of this idea.

Female house finches are generally drab brown, but about half of the females in most populations have a pale wash of carotenoid coloration in the same plumage regions that are coloured in males (Hill 1993*b*). Hill (1993*b*, 1994*a*) proposed that males actively forage for carotenoid pigments while females obtain carotenoids passively in their diets, but this idea has never been tested. The contribution of dietary intake of carotenoid pigments in generating age- and sex-specific patterns of carotenoid display also remains untested. For example, yearling female house finches have, on average, more colourful plumage than older females (Hill 1993*b*) but yearling male house finches typically have, on average, less colourful plumage than older males (Hill 1992). Are these differences due to some sex-related aspect of their physiology or to different diets?

Finally, male house finches vary in expression of carotenoid-based coloration not just within populations but also between populations and subspecies. In most populations, including the subspecies that occurs in most of the US and southern Canada (*C. m. frontalis*), males have red pigmentation extending about half way down their undersides. In a subspecies in southern Mexico (*C. m. griscomi*), however, ventral carotenoid pigmentation is restricted to a small region on the throat and upper breast (Moore 1939; Hill 1993*a*). In mate choice experiments, Hill (1994*a*) showed that females from this small-patched population prefer males with larger patches of colour, which is the ancestral patch size for this subspecies. Thus, despite selection for *griscomi* males to have larger patches of colour, patch size has decreased in this population over evolutionary time (Hill 1994*a*,*b*). Hill proposed that a reduction in the availability of carotenoids in the environment inhabited by the small-patched *griscomi* house finches caused the reduction in male patch size, but so far no data have been available to test this idea.

In this study, we tested the carotenoid limitation hypothesis in two ways. First, we collected moulting house finches from the medium-patched *frontalis* and the small-patched *griscomi* populations and compared the concentration of carotenoids in the gut contents of individual males with the colour of their growing feathers within each population. Second, we compared the mean concentration of carotenoids in the gut contents of males between these two populations. We predicted that, if the carotenoid limitation hypothesis was correct, there would be a positive relationship between the concentration of carotenoids in the gut contents of an individual and the colour of plumage it was growing. Furthermore, we predicted that the mean abundance of carotenoids in the gut contents of males would be lower in the small-patched *griscomi* population compared with the large-patched *frontalis* population (Hill 1994*a*). Finally, to better understand the basis for sex- and age-specific variation in expression of plumage coloration, we compared the carotenoid concentration of gut contents between males and females, and between juveniles and adults.

2. METHODS

(a) *Field sampling*

Using mist nets and traps, we collected male house finches belonging to the subspecies *C. m. frontalis* from one location near San Jose, California from 2 to 13 August 1992 and *C. m. griscomi* from one location near Chilpancingo, Guerrero, Mexico, from 9 to 16 September 1992 (see Inouye *et al.* (2001) for more details on collecting locations). Immediately after capture, moulting individuals were killed, their plumage coloration scored (see below) and the contents of their crop, proventriculus and gizzard removed and placed in a solution of 0.02% w/v butylated hydroxytoluene (BHT) (Sigma, St Louis, MO) in ethanol. BHT is an antioxidant that protects the integrity of carotenoids during storage. Gut-content samples were stored in the dark, refrigerated for 3 to 10 days after collection and then frozen until carotenoid analysis was conducted. The sex of birds was determined by gonadal examination. Birds were aged as either HY (hatch year: hatched in the summer that the collection was made) or AHY (after hatch year: hatched in a previous year) by examining their plumage pattern (see Hill 2002) and extent of skull ossification.

In California, finches were netted or trapped in the vicinity of bird feeders containing sunflower seeds. If present, the large, whitish seeds were conspicuous in the crops and proventriculi of these birds. Although sunflower seeds were found in the crops of several of the birds captured, no sunflower seed was removed from the proventriculus of any of the birds used in this study. The contents of the gizzards of the birds were a finely masticated greenish mash that did not appear to contain any sunflower seed. This indicates that the greatest proportion of the diet sample removed from each bird represented what the bird ate prior to approaching artificial food sources. Thus, it is unlikely that feeders affected the results of this study.

At the time of capture, we scored the coloration of growing or newly grown feathers by visual comparison with colour plates in the Methuen Handbook of Colour (Kornerup & Wanscher 1983). For most AHY males, we were able to score the hue, saturation (intensity) and chroma (tone) of feather patches on the crown, underside and rump following the protocol of Hill (1992, 2002). We summed the 21 plumage scores that resulted from this scoring technique to derive an overall plumage brightness score (Hill 1992, 2002). Most HY males had moulted only small patches of ornamental coloration at the time of sampling, so for these males we could only estimate the hue of growing feathers. The plumage brightness scores were preferable to the single hue scores because they included full tri-stimulus colour descriptions of all coloured regions of the bird. Thus, plumage brightness scores captured more variation in plumage display and increased our power of detecting relationships between dietary access to carotenoids and plumage colour expression. Both hue scores and plumage colour scores are positively correlated with the underlying carotenoid content of feathers in these two populations (Inouye *et al.* 2001).

(b) *Carotenoid analyses*

The ethanol solution in which samples were stored was separated from each diet sample using a Buchner-type filtering funnel equipped with a fine (4–5.5 μm maximum pore size) fritted disc. This ethanol solution was saved for later analysis. The diet samples were then air dried in the dark and weighed after the grit particles were removed.

The diet samples were ground to a fine powder in a small seed mill. This fine powder was then added to a solution of 5% w/v potassium hydroxide in methanol. The ethanol filtrate removed from the original gut samples was added and the entire mixture was bubbled with nitrogen, then left for 4 h, gently stirring in the dark at room temperature. The mixture was centrifuged and the supernatant fluid was removed.

Hexane and methanol were added to the supernatant fluid and this solution was partitioned by the addition of a 10% w/v sodium chloride solution. All hydrophobic substances, including the carotenoids, were incorporated into the epiphase, i.e. the hexane layer. Partitioning was complete once the epiphase was washed three times with water. The epiphase was then filtered through anhydrous sodium sulfate using a Buchner-type filtering funnel with a fine-fritted disc, to remove any residual water. The epiphase was taken to dryness via rotary evaporation and the sample was stored in the dark at −20 °C until further analyses.

Quantitative determination of carotenoids was completed by using visible-light spectrophotometry (Beckman DU-8B Spectrophotometer). Carotenoids were redissolved in hexane and total carotenoid content (μg carotenoids g^{-1} diet) was calculated according to the formula:

$$[A_{450} \times \text{volume of extract (ml)} \times 104]/[E \times \text{diet mass (g)}],$$

where A_{450} is the absorbance recorded at a selected wavelength of 450 nm and E is the extinction coefficient at 1% cm^{-1} of the carotenoid mixture in hexane. Values for E for most carotenoids in most solvents are published in Davies (1976).

3. RESULTS

In all males (ages pooled) in the California population, there was a significant positive relationship between the concentration of carotenoids in the gut contents and both the hue and overall plumage brightness score (hue: Spearman rank correlation, $r_S = 0.23$, $n = 77$, $p = 0.05$; plumage brightness score: $r_S = 0.37$, $n = 43$, $p = 0.02$; figure 1*a–c*). For male house finches collected in Guerrero, Mexico, the relationships between gut carotenoid content and plumage hue ($r_S = 0.41$, $n = 19$, $p = 0.08$) and brightness scores ($r_S = 0.25$, $n = 17$, $p = 0.32$) were both positive but not significant (figure 1*d*). All but one male in the sample from Guerrero, Mexico were AHY, so age classes could not be analysed separately for that population. For the California samples, however, there was a significant relationship between plumage coloration and gut carotenoid concentration for AHY males (hue: $r_S = 0.32$, $n = 42$, $p = 0.05$; plumage brightness score: $r_S = 0.36$, $n = 41$, $p = 0.02$), but not HY males (hue: $r_S = 0.14$, $n = 35$, $p = 0.41$; figure 1*b,c*).

There were also significantly higher concentrations of carotenoids in the gut contents of AHY males (larger patched) from California compared with AHY males (smaller patched) from Guerrero (Mann–Whitney U Test, $U = 672$, $n = 14, 19$, $p < 0.0001$). In AHY males, the median concentration of gut carotenoids in large-patched males was more than three times that of small-patched males (figure 2).

Males and females from the large-patched population (California) did not differ significantly in the concentration of carotenoids in their gut contents ($U = 1890$, $n = 42, 77$, $p = 0.13$; figure 3). Similarly, there were no age-related differences between the concentration of carotenoids in gut contents of HY and AHY males ($U = 756$, $n = 35, 42$, $p = 0.83$; figure 3) or HY and AHY females ($U = 241$, $n = 16, 26$, $p = 0.39$) in this population.

4. DISCUSSION

There were consistent positive correlations between the concentration of carotenoids ingested by male house finches and the ornamental coloration of growing feathers. This relationship was statistically significant only in a medium-patched population (*C. m. frontalis*) sampled in California, but the correlation coefficient was similar in a small-patched population (*C. m. griscomi*) sampled in Guerrero, Mexico. This is the first time, to our knowledge, that the carotenoid limitation hypothesis has been tested by comparing the colour of ornamental display with the carotenoid content of the diets of individual animals. In a similar vein, Slagsvold & Lifjeld (1985) showed that natural variation in the carotenoid content of food provided by parent great tits (*Parus major*) to their nestlings predicted the coloration and carotenoid content of yellow juvenile feathers grown by those nestlings. More recently, Grether *et al.* (1999) showed that male guppies in populations with access to more algae, and hence more dietary carotenoids, had more colourful integumentary displays than males in populations with less access to algae. No other studies, to our knowledge, have investigated the relationship between diet and coloration in free-living animals.

We also found support for the prediction that males from a population with small patches of ornamental coloration consumed lower quantities of dietary carotenoids than males in a population with medium-sized patches (Hill 1994*a,b*). The quantities of carotenoids in the gut contents of medium-patched males (*frontalis*) averaged more than three times higher than that in the gut contents of small-patched males (*griscomi*). While this difference confirms a key prediction of the hypothesis that male patch size was reduced by selection on *griscomi* males in response to reduced access to carotenoid resources (Hill 1994*a,b*), these data do not provide a definitive test of this hypothesis. First, it is possible that, by chance, we sampled localities with relatively high-carotenoid seeds in California and relatively low-carotenoid seeds in Mexico. Thus, our samples might not accurately represent the carotenoid contents of diets across each subspecies range. Second, we did not sample throughout the entire moulting period in each population. Males from the two locations were taken at the same stage in moult, but if carotenoid resources change within a site over the six-week moulting period, this could have affected our assessment of difference in resources between the two sites. Even if our measure of carotenoid resources is representative of the two subspecies, a larger comparative analysis would be required to begin to rule out alternative explanations for the change in patch size, such as change in predation or parasitism rates. Thus, our conclusions about the differences

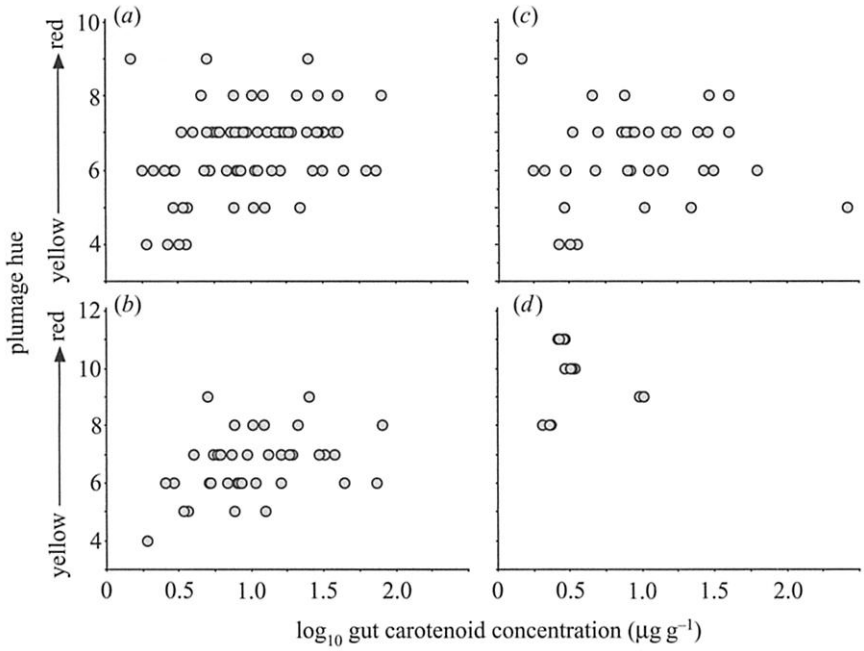

Figure 1. (*a–c*) Relationship between the hue of growing feathers and the concentration of carotenoids in the gut contents of male house finches of the subspecies *Carpodacus mexicanus frontalis* sampled in San Jose, California, and (*d*) *C. m. griscomi* sampled in Guerrero, Mexico. Illustrated are (*a*) all *frontalis* males, (*b*) AHY *frontalis* males, (*c*) HY *frontalis* males, (*d*) AHY *griscomi* males. Hue is a unitless measure derived from comparison with a standard colour reference (Hill 2002).

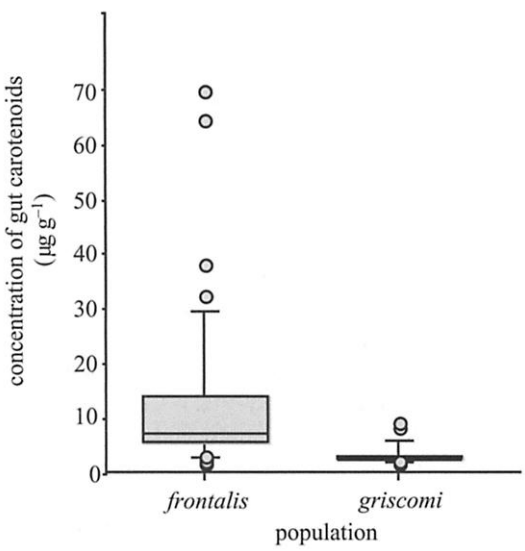

Figure 2. A comparison of the carotenoid concentration of gut contents of AHY male house finches of the subspecies *Carpodacus mexicanus frontalis* ($n = 42$) sampled in San Jose, California and *C. m. griscomi* ($n = 18$) sampled in Guerrero, Mexico. All birds were collected during feather moult. Horizontal bars indicate the 10th, 25th, 50th, 75th, and 90th percentiles and points give data for individuals outside this range.

between these two populations being influenced by dietary carotenoids will require more extensive sampling to see whether they generally apply.

Griscomi males not only have smaller patches of ventral pigmentation than *frontalis* males, but they have crown and breast patches that are more discrete and sharply bounded than those of *frontalis* males (Hill 1993*a*, 2002). This difference in patch conformation has also been proposed to have evolved in response to reduced carotenoid availability (Hill 1994*a*, 2002). Interestingly, despite having smaller patches of colour, the mean concentration of cartonenoids in the plumage of *griscomi* males was more than twice the concentration in the feathers of *frontalis* males (Inouye *et al.* 2001). One interpretation is that smaller and more discrete patches of ornamental coloration allow for more efficient use of dietary carotenoid pigments in *griscomi* males. When they have access to the same carotenoid pigments in captivity, small-patched *griscomi* males grow significantly brighter plumage than larger-patched *frontalis* males (Hill 1993*a*), further supporting this idea.

In the California sample, males and females did not differ in the mean concentration of carotenoid pigments in their gut contents, yet male and female house finches are highly sexually dichromatic. Female house finches show, at most, a vestige of the carotenoid-based plumage coloration displayed by males and about half of the females in any population have no detectable carotenoid coloration in their plumage (Hill 1993*b*). Females also have lower levels of circulating carotenoid pigments during moult than do male house finches (Hill 1995). One explanation for this difference in plumage and plasma carotenoids between the sexes, despite the similarity in total dietary carotenoids, is that male and female house finches differ in the component carotenoids in their diets, with males ingesting carotenoids that are of greater value as plumage pigments. The amount of food that we collected from the guts of individual birds was too small for component carotenoids to be identified, so we have no way to test this idea. It seems more likely, however, that the lack of difference in dietary carotenoids between the sexes is real and the sexual dichromatism reflects a fundamental difference between the sexes in the physiological processes governing

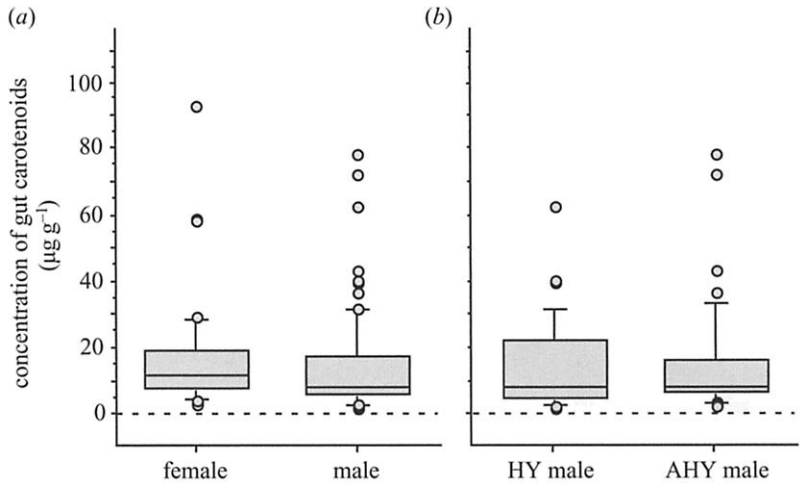

Figure 3. A comparison of the carotenoid concentration of gut contents of (*a*) female ($n = 42$) and male ($n = 19$) house finches and (*b*) HY ($n = 35$) and AHY ($n = 42$) male house finches. All birds were collected in San Jose, California during feather moult. Horizontal bars indicate the 10th, 25th, 50th, 75th, and 90th percentiles and points give data for individuals outside this range.

carotenoid deposition. Females may be using pigments less efficiently than males or they may be using carotenoids for purposes other than plumage pigmentation. Similar sexual dichromatism, despite the same carotenoid intake by males and females, has been observed in American goldfinches (*Carduelis tristis*) in an experimental situation (McGraw *et al.* 2002). Despite having diets with identical carotenoid content, male and female goldfinches grew plumage with different coloration containing different carotenoid pigments. We also found no differences in concentration of carotenoids in the gut contents of HY and AHY male house finches, but this is not surprising given that there were no differences in the mean plumage coloration of HY and AHY males in this sample (Inouye *et al.* 2001).

Overall, the relationships between male plumage coloration and carotenoid concentration of gut contents were relatively weak, but we expected a weak pattern for three reasons. First, to obtain sufficient carotenoids for analysis, we pooled all dietary carotenoids to calculate a single carotenoid concentration and used this as an index of a bird's access to plumage pigments. However, not all dietary carotenoids are equally useful to a house finch (Hill 1996, 2002). Some carotenoids appear to contribute little as plumage pigments. Others can be used as plumage pigments but only after they are metabolically altered. Still other carotenoid pigments are used unaltered as plumage pigments by finches (Inouye *et al.* 2001; Hill 2002). By pooling carotenoids in our analysis, we lost details of carotenoid utilization and these details could explain some of the variation in plumage coloration among males.

Second, by necessity, we took one gut sample per bird, representing only a portion of one meal for each individual. Assuming that male house finches eat several meals (full crops of food) per day and that it takes about 30 days to completely moult body plumage (Michener & Michener 1940), the food sample that was analysed for each male represented only a small fraction of food ingested during the production of ornamental coloration. The fact that we found consistent associations between dietary carotenoids and plumage coloration despite this very limited sampling protocol suggests that males who grow bright plumage consistently ingest greater concentrations of carotenoid pigments than males who grow drab plumage.

Finally, it is well established that environmental factors other than access to carotenoid pigments can affect expression of ornamental carotenoid pigmentation in this species. For example, parasites are known to affect expression of plumage coloration in male house finches. In aviary experiments, isosporan coccidia and mycoplasmal conjunctivitis both had a significant negative effect on expression of male plumage coloration (Brawner *et al.* 2000). In the field, males with lower infections of avian pox and feather mites had significantly redder plumage coloration than males with more severe infections (Thompson *et al.* 1997). In addition, nutritional condition at the time of moult, independent of carotenoid access, can also affect male plumage coloration (Hill & Montgomerie 1994; Hill 2000). For the carotenoid content of diet to be highly correlated with plumage coloration, these other environmental factors would have to be relatively unimportant.

A gauntlet of challenges stand between a male house finch and maximum expression of ornamental plumage coloration. It must first ingest sufficient quantities of the appropriate carotenoid pigments, then avoid parasites and maintain good nutritional condition. Only males that do all of these things well are able to grow bright red feathers. The debate has been whether carotenoid access played any role in this process. Here we show that it does.

We thank the individuals and families who provided logistical support and hospitality during collecting trips, particularly Jorge Serrano Sr, Jorge Serrano Jr and the Serrano family in Mexico, and Fran Mewaldt, Mike Rigney and the staff at Coyote Creek Riparian Station in California. Jim Dale assisted with the field work in California. Birds were collected under a joint US Fish and Wildlife and California Fish and Game Scientific Collecting Permit in California and a scientific collecting permit from La Secretaria de Relaciones Exteriores in Mexico. This study was approved by the Chancellor's Animal Research Committee at UCLA and the Animal Care Committee at Queen's University. Funding was provided in part by the American Museum of Natural History (Frank M. Chapman

Memorial Fund), American Ornithologists' Union, Los Angeles Audubon Society and Sigma Xi grants to C.I., and Natural Sciences and Engineering Research Council of Canada (NSERC) research and equipment grants to R.M. G.E.H. was supported during field work by an NSERC International Postdoctoral Fellowship and during write-up by NSF grants IBN9722172 and DEB0077804. Hoffman–La Roche, Basel, Switzerland generously donated carotenoid standards used in this study. Kevin McGraw, Herman Mays, Paul Nolan and the Hill and Montgomerie Lab Groups provided valuable comments on the manuscript.

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