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Geographic variation in the carotenoid plumage pigmentation of male house finches (*Carpodacus mexicanus*)

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Geographic variation in both the colour and pattern of carotenoid plumage pigmentation displayed by males in two subspecies of house finches (*Carpodacus mexicanus frontalis* and *C. m. griscom*) was quantified. The extent of ventral carotenoid pigmentation (patch size) differed markedly between these two subspecies; *frontalis* males from the U.S. (New York, Michigan, California and Hawaii) displayed a medium patch extending from their throats to their lower bellies, while *griscomi* males sampled in Guerrero, Mexico displayed small patches restricted to their throats. *Frontalis* males sampled in Michigan and New York and *griscomi* males were relatively bright in colouration, while *frontalis* males sampled in Hawaii were relatively drab. Populations of *frontalis* in California showed substantial local variation in average male colouration: in two areas only 12 km apart males were as colourful and as drab as any population sampled. In aviary experiments in which they were fed either a plain seed diet or a diet supplemented with red carotenoid pigments during moult, males from all populations converged on a similar appearance, except that *griscomi* males attained a brighter plumage than *frontalis* males when their diet was supplemented with red pigments. Regardless of diet, the difference in patch size between *frontalis* and *griscomi* males persisted after moult in captivity. The author concludes that the difference in patch size between *frontalis* and *griscomi* males reflects genetic differences between these populations, but that the differences in the mean plumage colouration of males among populations reflect differences in the access that males have to carotenoid pigments during moult.

ADDITIONAL KEY WORDS:—Sexual selection – morphology – diet – taxonomy.

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INTRODUCTION

Plumage pigmentation is the most widely used character in avian systematics to distinguish both subspecies and closely related species (Mayr, 1963). Geographic variation in colourful plumage and other display characters has long been attributed to selection for species-isolating mechanisms (Dobzhansky, 1937, 1951), but such variation is now more generally viewed as having been shaped by intersexual selection (Lande, 1981; West-Eberhard, 1983). In virtually all studies of geographic variation, the different morphologies displayed in different parts of a species' range are assumed to reflect genetic differences among populations, but this assumption has seldom been tested (James, 1983). The proximate basis of geographic variation in the pattern and colouration of plumage pigmentation has been examined through biochemical analysis of feathers in a few species (Brush, 1970; Brush & Johnson, 1976; Troy & Brush, 1983), but the importance of environmental variables such as diet or temperature in generating geographic variation in plumage pigmentation remains largely unstudied.

The proximate basis of geographic variation in the pattern and colouration of plumage pigmentation was investigated in the house finch (*Carpodacus mexicanus*), a small sexually dichromatic passerine. Female house finches are uniform grey-brown above with heavy grey-brown streaking over buff on the underside. Male house finches display the same ground-colour (melanin) pattern as females but they also have patches of bright carotenoid pigmentation on their rump (hereafter rump patch), crown/eyestripe (hereafter crown patch), and throat/breast/belly (hereafter ventral patch). A few females display a diffuse wash of carotenoid colouration restricted to the same patches of feathers as the carotenoid pigmentation displayed by males (Gill & Lanyon, 1965; McEntee, 1970; Hill, 1993a). Within all populations males vary in carotenoid colouration from pale yellow to bright red (Michener & Michener, 1931; Gill & Lanyon, 1965; Hill, 1990), but the mean plumage colouration and the distribution of carotenoid pigmentation differs markedly among populations (Moore, 1939; Hirai, 1975; Aldrich & Weske, 1978; Brush & Power, 1976).

House finches are native to western North America from S. British Columbia to Oaxaca, Mexico and from the Pacific coast to the edge of the great plains (American Ornithologists' Union, 1983; Moore, 1939; Fig. 1). House finches originating from coastal California were introduced to the Hawaiian Islands sometimes before 1870 (Grinnell, 1911) and to Long Island, New York in 1940 (Elliot & Arbib, 1953). In Hawaii, house finches had become abundant on all major islands at least by 1901 (Grinnell, 1911). In eastern North America, the introduced population has grown exponentially and expanded its range (Bock & Lepthien, 1976) so that in 1992 the house finch is an abundant breeding bird throughout the north-eastern and midwestern United States and south-eastern Canada. The western boundary of this eastern population's range has expanded as far west as Montana and Oklahoma (*American Birds* seasonal surveys; Fig. 1).

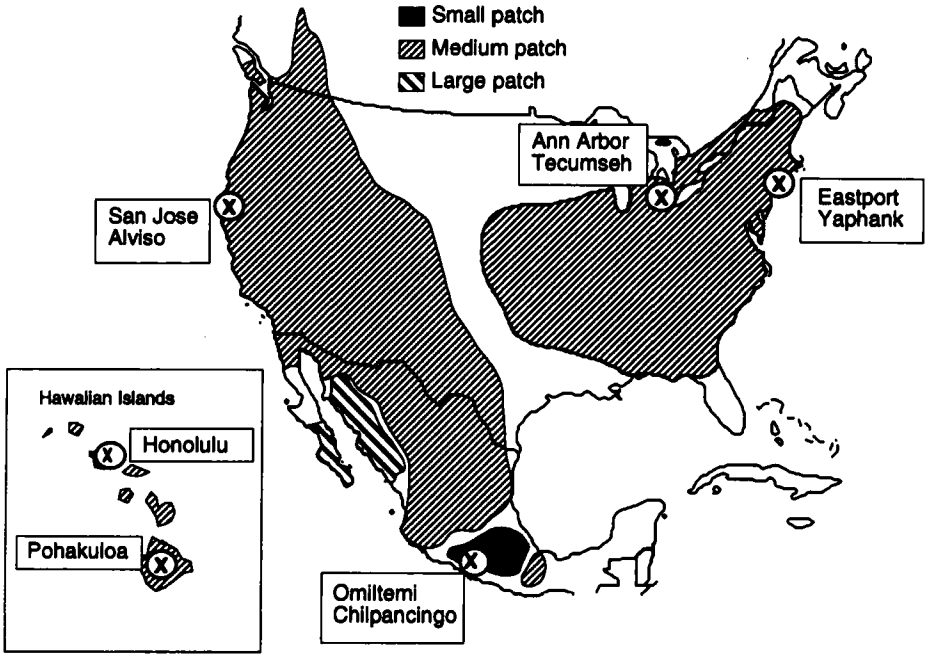

Figure 1. Approximate range of the house finch (*Carpodacus mexicanus*) in 1992 and the areas sampled in this study (indicated with an x). The distribution of the three distinct expressions of ventral patch, each of which comprise several subspecies of house finches, is indicated with different shading (see Fig. 2).

Across their range house finches display variation in body size, bill size and shape, wing and tail length, tarsus length, and plumage colouration (Moore, 1939; Aldrich & Weske, 1978; Aldrich, 1982). Much of this variation is clinal (Moore, 1939; Aldrich & Weske, 1978), but there are also several well-differentiated populations (Moore, 1939). In his detailed treatment of population differentiation in the house finch, Moore (1939) divided the group into four species comprising 18 subspecies. Subsequent treatments of the U.S. and lower California populations (American Ornithologists' Union, 1957, 1983; Grinnell & Miller, 1944) largely followed Moore's taxonomy except that (1) the Hawaiian population is ascribed to the subspecies of the California population (*C. m. frontalis*) from which it was introduced, (2) the two island species of house finches recognized by Moore (*C. amplus* and *C. mcgregori*) are considered subspecies of *C. mexicanus* (*C. m. amplus* and *C. m. mcgregori*), and (3) four western U.S. populations (*C. m. frontalis, C. m. grinnelli, C. m. smithi, C. m. solitudinis*) recognized as distinct by Moore are subsumed under *C. m. frontalis*. When referring to house finch populations, I follow the taxonomy of the American Ornithologists' Union (1957, 1983) for populations occurring in the U.S. (including Hawaii) and Canada and Moore (1939) for populations occurring only in Mexico.

One consistent and conspicuous difference among some populations of house finches is the size of the ventral patch of carotenoid pigmentation. House finches from two populations in southern Mexico (*C. m. mexicanus* and *C. m. griscomi*; Fig. 1) display a very restricted ventral patch with red colouration limited to a small bib under the bill (Fig. 2A; see also Moore, 1939). This very restricted ventral patch size contrasts with the patch expression of populations from the

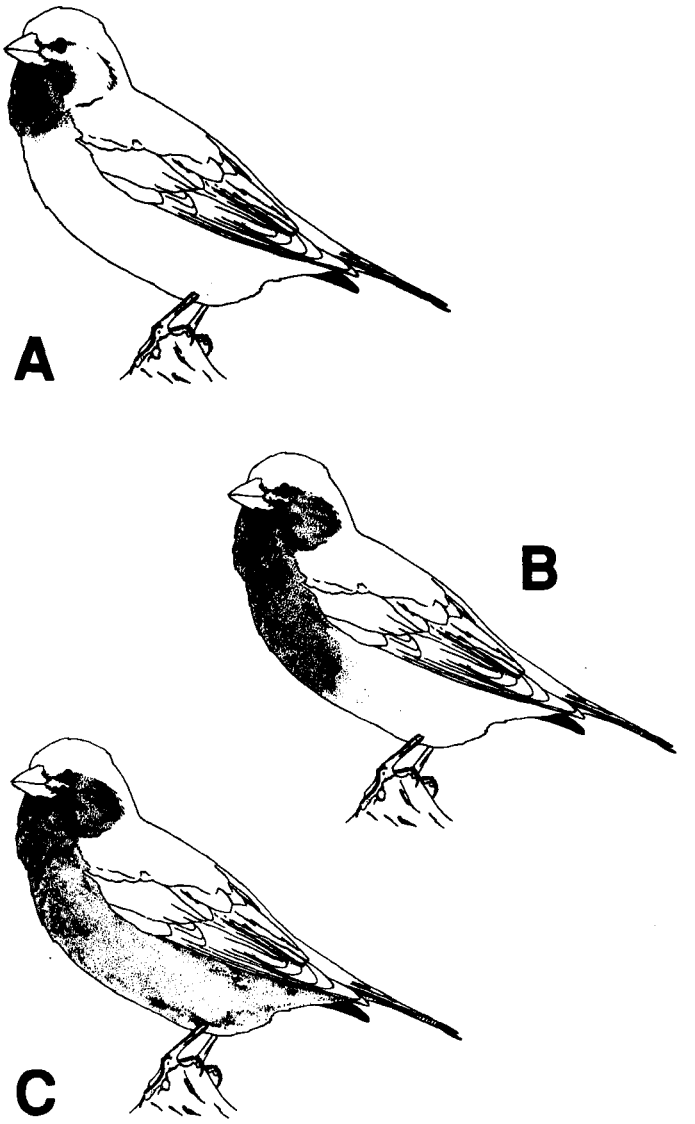

Figure 2. Variation in the extent of ventral carotenoid pigmentation displayed by different subspecies of house finches. A, Typical *C. m. griscomi* male, specimen UMMZ 117647; B, typical *C. m. frontalis* male, specimen UMMZ 227087; C, typical *C. m. ruberrimus* male, specimen UMMZ 95706. Illustration by Phillip C. Chu.

United States, Canada, central Mexico, and a third population in southern Mexico (*C. m. frontalis, C. m. clementis, C. m. nigrescens, C. m. potosinus, C. m. centralis, C. m. coccineus, C. m. altitudinis,* and *C. m. roseipectus*; Fig. 1) in which carotenoid pigmentation extends from under the bill to the belly region (Moore, 1939; Fig. 2B). A third unique form of ventral carotenoid pigmentation is found in populations on the Pacific coast of Mexico (*C. m. ruberrimus* and *C. m. rhodopnus*; Fig. 1) in which the entire ventral surface from the chin to undertail is pigmented with carotenoids (Moore, 1939; Fig. 2C).

The mean plumage brightness of carotenoid pigmentation of males also varies substantially among populations of house finches, particularly among the eastern

U.S., Hawaiian and the parent California populations (hereafter referred to collectively as *frontalis* populations, since they are all recently derived from the *C. m. frontalis* population of coastal California). In Pasadena, California, Michener & Michener (1931) found that about 82% of the 1226 males that they banded were red and the remaining 18% were yellow, orange or red-orange. In contrast, males from the introduced population in Hawaii tend to be orange or yellow in colouration; red individuals are relatively rare (Grinnell, 1911; Hirai, 1975). This difference in mean male colouration between California and Hawaii is so striking that it prompted Grinnell (1912), and later Moore (1939), to recognize the Hawaiian population as a separate species, *Carpodacus mutans*. A shift in the average colouration of males in the opposite direction occurred in the introduced eastern population; most males are red with relatively few yellow or orange individuals (Gill & Lanyon, 1965; Hill, 1990). More subtle differences in male colouration occur among many of the subspecies of house finches recognized by Moore (1939), and these colour differences were often the primary basis for distinguishing subspecies.

Although carotenoid pigmentation is one of the most important morphological characters used in diagnosing geographic races of house finches, recent studies indicate that expression of carotenoid colouration can be sensitive to environmental variation. Birds cannot synthesize carotenoids and must obtain carotenoid plumage pigments through their diet (Goodwin, 1950; Brush, 1978). It has long been known that many species of birds lose plumage colouration after moult in captivity and that selective feeding enables some species to retain their colouration (Delacour, 1928; Bruning, 1971). Research on the biochemical basis of carotenoid pigmentation has demonstrated that individual variation in plumage colouration in the house finch reflects the abundance and proportion of three carotenoid molecules (red echinenone, orange isocryptoxanthin, and yellow β-carotene) present in the feathers (Brush & Power, 1976; Brush, 1990). Variation in overall plumage brightness (which is the interaction of the hue, intensity and tone of the pigmentation; Hill, 1990) is a function of dietary intake of these three carotenoid pigments (Brush & Power, 1976; Hill, 1992).

Because variation in male plumage colouration within at least some populations of house finches is a consequence of differential intake of carotenoid pigments during moult, I hypothesized that variation in male colouration among populations might also reflect differences in access to carotenoids, rather than genetic differences among populations. In this study, I first quantified variation in the colouration and pattern of male carotenoid pigmentation both within and among populations of house finches. I then conducted captive feeding experiments with males from different populations to test the extent to which dietary access to carotenoid pigments might explain geographic variation in plumage colouration. Finally, I discuss the implication of this study to both avian systematics and general theories of sexual selection.

METHODS

Scope

I present observations only on male morphology, although female house finches also vary in carotenoid pigmentation (see Hill, 1993a). I sampled house

TABLE 1. Sampling locations and dates

Region	Site	Coordinates		Date	Males captured
Michigan	Ann Arbor	42°10′N	83°40′W	February-July 1988–90	548
	Tecumseh	42°01′	83°56′	December 1989	46
New York	Yaphank	40°50′	72°54′	December 1989	13
	Eastport	40°40′	72°40′	December 1989	25
California	Alviso	37°20′	121°55′	February 1990	81
	San Jose	37°21′	121°58′	February 1990	37
Oahu	Honolulu	21°19′	157°50′	January 1989	7
Hawaii	Pohakuloa	19°45′	155°33′	January 1989	49
Guerrero, Mexico	Omiltemi	17°30′	100°50′	January 1990	11
	Chilpancingo	17°33′	99°30′	January 1990	37

finches from six geographical regions including much of the natural and introduced range of *C. m. frontalis* as well as the range of the southern, small-patched race, *C. m. griscomi* (Fig. 1). In New York, Michigan, California and Mexico I also sampled two local populations separated by at least 12 km. All sampling was conducted between December and February, except in Ann Arbor, Michigan where sampling was conducted between February and July. Table 1 summarizes sample locations, dates and the number of males examined.

Males were captured by mist nets in Hawaii and Mexico and in traps at feeding stations in California, Michigan and New York. In all cases, the proportion of colour types among birds that I sampled seemed to reflect the proportion of colour types that I observed among free-ranging birds. A bias in sampling is of particular concern when baited traps are used because birds may compete for access to bait causing subordinate individuals to be underrepresented in the sample. To test the assumption that trapping is a reasonable means for randomly sampling house finch populations with respect to plumage colouration, I used data from an intensively studied population in Ann Arbor, Michigan (Hill, 1990, 1991a). In the first year of a population study, before individuals gained trap experience, I found no relationship between the date on which a bird was captured in a trap at a feeding station and its plumage score ($r = 0.002$, $N = 147$, $P = 0.98$; see below for details of scoring technique). Over 90% of males in the population were eventually sampled, and if there was a tendency for bright or drab males to get into traps more readily, one would have expected a positive or negative correlation as either bright or drab males were depleted from the sample pool.

Body size, plumage colouration and patch size

At the time of capture, I measured wing arc (maximum flattened wing), tail length, tarsus length (intertarsal joint to the last undivided leg scale), bill length (nostril to tip), plumage brightness and patch size (see Pyle *et al.*, 1987 for details of morphological measures).

I measured the extent of ventral pigmentation with a gridded transparency overlay. I positioned the transparency over the ventral side of a male and counted the number of squares over feathers bearing carotenoid pigment (see

Hill 1992 for details). I then divided the number of squares with feathers pigmented with carotenoid by the total number of squares on the grid to derive the proportion of the ventral surface pigmented by carotenoids.

I quantified plumage brightness by measuring the hue, intensity, and tone of colouration in seven plumage regions by comparison to colour chips in the *Methuen Handbook of Colour* (Kornerup & Wanscher, 1983; see Hill, 1990, 1992 for details of the scoring technique). To derive an overall plumage brightness index, I then added the resulting 21 scores (see Hill, 1990, 1992). I also derived separate indices for overall hue and overall intensity by summing the hue and intensity scores across regions 1–3 and 5–7. Region 4 was excluded from both indices because it was not pigmented in *griscomi* males (see below).

Because *griscomi* house finches have a very restricted ventral patch, individuals from this population lacked carotenoid pigmentation in the lower ventral region (patch 4) of my scoring system [see Hill (1992) for a detailed description of the division of ventral regions]. A lack of plumage score from this region artificially deflated the overall plumage brightness scores of *griscomi* males relative to *frontalis* males. To compensate, I used plumage data from all *frontalis* males sampled to regress the plumage score of the second-lowest ventral region (patch 3) on the plumage score of patch 4. I found a significant positive relationship between the plumage scores of these regions ($r = 0.88$, $N = 759$, $P = 0.0001$), indicating that patch 3 colouration is a reasonable predictor of patch 4 colouration. I then multiplied the slope of the regression line (0.942) by the plumage score of patch 3 for *griscomi* males to derive a correction value for the missing lower patch. The correction value was then added to the total plumage score giving a corrected plumage score for *griscomi* males that was comparable to the scores of *frontalis* males. This approach is equivalent to dropping the lowest ventral plumage region from the plumage score calculations for all males ($r = 0.99$, $N = 759$ for the two plumage values); I opted to increase the scores of the *griscomi* males rather than to decrease all other scores so that the plumage values discussed in this paper would be directly comparable to the plumage values published elsewhere (Hill, 1990, 1991, 1992).

Controlled feeding experiments

I transported males from Michigan, Hawaii, California and Guerrero to avaries at the University of Michigan. All males except those from Michigan were captured and transported in mid-winter (December–February) at least five months prior to the start of their annual moult, which in all populations occurs between July and November (Michener & Michener, 1940; Stangel, 1985; personal observations). *Griscomi* males from Guerrero were held in quarantine in Los Angeles for 30 days prior to shipment to Michigan, during which time they experienced a southern California photoperiod. After transport to Michigan, all males were maintained on a natural Michigan photoperiod.

Beginning in June 1990, at least a month before the onset of moult, I divided males randomly into two groups to be housed in separate flight cages. One group was fed a nutritious but carotenoid-deficient diet of seed and water (the same seed and water diet used as the 'basic diet' in 1989 feeding experiments with Michigan house finches; see Hill, 1992). The other group was fed the same diet but with canthaxanthin added to their water (Roxanthin Red 10 WS,

Hoffman-LaRoche; *c.* 0.001 g ml^{-1} water). Canthaxanthin is a red carotenoid not found in the plumage of wild male house finches (Brush & Power, 1976; Brush, 1990) but readily used by house finches to pigment their plumage (Brush & Power, 1976; Hill, 1992).

I conducted more extensive feeding experiments with males from south-eastern Michigan in 1988 and 1989; the results have been summarized elsewhere (Hill, 1992). Hawaiian males were also used in feeding experiments in 1989. The basic seed diet and the sources of supplemental carotenoids used in 1988 feeding experiments were different from those used in the 1990 feeding experiments (Hill, 1992), so the results of these experiments are not directly comparable to subsequent feeding experiments and will not be discussed here. The feeding experiments conducted with Michigan and Hawaiian house finches in 1989 were identical to the 1990 feeding experiments except that in 1989 canthaxanthin was provided on apples as well as in drinking water. Also, in 1989 a third group of both Michigan and Hawaiian males had β-carotene, rather than canthaxanthin, added to their drinking water (water dispersible 10% β-carotene beadlets; *c.* 0.001 g ml^{-1} water) and apples (Hill, 1992).

I quantified the plumage score and extent of ventral pigmentation for each male in late October or early November after the completion of moult.

Breeding experiments

Throughout the year I maintained captive house finches in unisexual flocks that were isolated visually from captive house finches of the opposite sex. In May 1990, I introduced 12 pairs of finches to cages containing nest sites and nest-building material. These pairs were composed of either Michigan males and Michigan females or Mexican males and Michigan females.

House finches nest readily in captivity and females in all nesting cages quickly built nests and laid eggs. Owing to initial overcrowding, many nests failed at the egg or small-chick stage, but seven young fledged from three nests, including three males produced by Michigan × Michigan pairs and one male produced by a Mexican × Michigan pair. All fledged young survived and moulted in synchrony with adult birds. These captive-born finches were maintained on a canthaxanthin-supplemented diet from fledging, and I recorded their plumage colouration and extent of ventral pigmentation at the same time as other males in the captive feeding experiment.

Statistical analysis

I performed principal components analysis (PCA) on size measures (wing, tail, bill and tarsus) for all sampling localities (local and regional), and I retained factor scores for the two components with eigenvalues of > 1. I averaged the factor scores of the components for each sampling site, and I plotted the mean PC1 vs PC2 scores for visual assessment of grouping among sampling sites with respect to morphological measures.

To compare both size and plumage measures between sampling localities within regions I conducted paired two-tailed *t*-tests. I used the results of these paired comparisons along with patterns of clustering in the PCA analysis to justify pooling between some sampling localities and removing some sample data

from regional comparisons. I compared the resulting six populations with an analysis of variance (ANOVA) and, where significant differences among populations were found, a Scheffé's test. I analysed the results of captive feeding experiments with paired *t*-tests for dichotomous comparisons within a treatment group and an ANOVA for comparisons among groups.

RESULTS

Microgeographic variation

In most comparisons of morphology, males from localities within a region were more similar to each other than they were to males from other regions (Table 2; Fig. 3). The two exceptions to this pattern occurred in Michigan and Hawaii (Table 2; Fig. 3). House finches from throughout the Hawaiian chain have generally been treated as a single population (Grinnell, 1911, 1912; Moore, 1939), but there is probably little or no gene flow among the islands (Berger, 1981) and the populations on some of the major islands may represent independent introductions of Californian birds. Grinnell (1911) discussed how little is known about the origin of Hawaiian populations. I sampled only seven males on the island of Oahu. Such a small sample limits the power of comparisons with other populations, but I still found that males from Oaha had significantly shorter mean wing, tail, and tarsus length and significantly greater mean bill length than males from the island of Hawaii (Table 2). Males from these two islands did not differ in plumage colouration or patch size (Table 2). Because of these morphological differences, I did not feel justified in pooling data from these islands, so I included only the larger sample of males from the island of Hawaii in morphological comparisons among populations.

The average wing length of males captured in Tecumseh, Michigan was significantly greater than the average wing length of males captured 35 km away in Ann Arbor, Michigan (Table 2). Wear of primary feathers can significantly affect wing-length measurements (Payne & Payne, 1989). Thus, feather wear

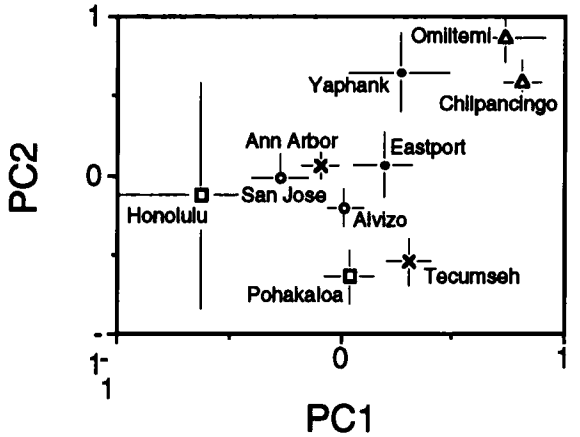

Figure 3. Size measures of males house finches as described by the two principal components. Mean factor scores for each sampling site are plotted with standard errors. Wing and tail length were the major component of variations in PC1; bill and tarsus were the major components of variation in PC2.

TABLE 2. Comparison of morphometrics and plumage brightness of local populations

Character	Population	N	$\bar{x} \pm SE$	t^*	P
Plumage brightness	Ann Arbor, MI	548	145.0 ±0.51	1.71	0.09
	Tecumseh, MI	48	141.8 ±2.26		
	Eastport, NY	25	138.9 ±0.29	0.79	0.44
	Yaphank, NY	13	134.4 ±5.60		
	San Jose, CA	37	140.5 ±2.74	5.86	0.0001
	Alviso, CA	81	122.4 ±1.67		
	Honolulu, HA	7	124.0 ±2.44	0.61	0.55
	Pohakuloa, HA	49	126.5 ±1.51		
	Omiltemi, Mex	11	141.2 ±9.16	0.35	0.73
	Chilpancingo, Mex	37	144.2 ±3.86		
Ventral patch size	Ann Arbor, MI	548	0.659±0.005	0.72	0.48
	Tecumseh, MI	46	0.647±0.017		
	Eastport, NY	25	0.692±0.119	1.40	0.17
	Yaphank, NY	13	0.624±0.050		
	San Jose, CA	37	0.652±0.020	1.37	0.17
	Alviso, CA	81	0.611±0.160		
	Honolulu, HA	7	0.614±0.039	0.023	0.98
	Pohakuloa, HA	49	0.613±0.013		
	Omiltemi, Mex	9	0.240±0.011	0.18	0.86
	Chilpancingo, Mex	35	0.243±0.007		
Wing length (mm)	Ann Arbor, MI	546	80.1 ±0.09	2.33	0.02
	Tecumseh, MI	46	80.8 ±0.25		
	Eastport, NY	24	80.7 ±0.31	0.59	0.56
	Yaphank, NY	13	81.1 ±0.77		
	San Jose, CA	35	79.8 ±0.27	1.01	0.32
	Alviso, CA	81	80.1 ±0.17		
	Honolulu, HA	6	79.3 ±0.61	2.06	0.04
	Pohakuloa, HA	49	81.0 ±0.30		
	Omiltemi, Mex	11	80.8 ±0.67	0.09	0.92
	Chilpancingo, Mex	37	80.8 ±0.31		
Tail length (mm)	Ann Arbor, MI	543	59.5 ±0.09	0.63	0.53
	Tecumseh, MI	46	59.7 ±0.30		
	Eastport, NY	24	59.8 ±0.35	0.64	0.53
	Yaphank, NY	13	60.3 ±0.64		
	San Jose, CA	35	59.0 ±0.36	1.72	0.09
	Alviso, CA	80	59.7 ±0.21		
	Honolulu, HA	6	58.1 ±0.63	0.68	0.50
	Pohakuloa, HA	49	58.8 ±0.36		
	Omiltemi, Mex	11	62.8 ±0.90	0.01	0.99
	Chilpancingo, Mex	37	62.8 ±0.30		
Tarsus length (mm)	Ann Arbor, MI	547	17.2 ±0.03	1.00	0.32
	Tecumseh, MI	46	17.3 ±0.07		
	Eastport, NY	23	17.1 ±0.14	1.53	0.14
	Yaphank, NY	13	17.4 ±0.15		
	San Jose, CA	34	17.2 ±0.07	0.76	0.45
	Alviso, CA	81	17.1 ±0.06		
	Honolulu, HA	4	16.5 ±0.42	2.28	0.03
	Pohakuloa, HA	49	17.3 ±0.10		
	Omiltemi, Mex	11	17.7 ±0.13	1.68	0.09
	Chilpancingo, Mex	37	17.4 ±0.09		
Bill length (mm)	Ann Arbor, MI	547	8.7 ±0.02	1.51	0.13
	Tecumseh, MI	46	8.8 ±0.05		
	Eastport, NY	23	8.8 ±0.06	1.60	0.12
	Yaphank, NY	13	9.0 ±0.09		
	San Jose, CA	34	8.7 ±0.06	0.33	0.74
	Alviso, CA	81	8.6 ±0.05		
	Honolulu, HA	4	9.0 ±0.09	4.11	0.0001
	Pohakuloa, HA	49	8.2 ±0.05		
	Omiltemi, Mex	11	9.0 ±0.12	0.387	0.70
	Chilpancingo, Mex	37	9.1 ±0.05		

*Two-tailed t-test comparing mean plumage scores of males at the two different sites in each region.

can probably account for the differences in wing length between the Michigan populations, since Tecumseh males were sampled in December (just after moult) while Ann Arbor males were sampled between February and July. Feather wear is also known to affect plumage brightness in male house finches (Grinnell, 1911), and Ann Arbor males had higher mean plumage scores than Tecumseh males, although the difference was not significant. To reduce the possible confounding effects of sampling date, I used only males sampled in Tecumseh for interpopulation comparisons, because the dates on which these males were sampled were close to the sampling dates for other populations.

The mean plumage colour of males sampled at Alviso, California was much drabber than the mean plumage colour of males sampled 12 km away at San Jose (Table 2). This difference was not an artifact of sampling as it was obvious even in causal observations of free-flying birds at these two capture localities. Because of the difference in the mean plumage colouration of these two populations, I considered Alviso and San Jose males separately in the interpopulation comparison.

In New York and Guerrero, there were no differences among local populations in mean patch size, plumage colouration, or body size (Table 2; Fig. 3), so for the New York sample I pooled data from Eastport and Yaphank and for the Guerrero sample I pooled data from Chilpancingo and Omiltemi.

Interpopulation variation

Males from all populations were relatively uniform in size and shape. I found no significant differences in the mean wing, tail, tarsus or bill length among Michigan, New York or California populations (Table 3). Males from the island of Hawaii had significantly smaller bills than males from any of the other *frontalis* populations, and shorter tarsi than Michigan males (Table 3). The mean tail length of *griscomi* males from Guerrero was significantly greater than that of all other populations (Table 3), and the mean bill length of *griscomi* males was greater than that of all populations except New York (Table 3). *Griscomi* males also had significantly longer tarsi than males from Michigan or Alviso (Table 3).

Populations fell into two groups with respect to plumage brightness scores. Males from Michigan, New York, San Jose, and Guerrero displayed similar high mean plumage scores, while males from Hawaii and Alviso displayed similar, relatively low mean plumage scores (Table 3; Fig. 4). The mean plumage scores of males from the former localities were signficantly brighter than the mean

TABLE 3. Summary of significant ($P < 0.05$, Scheffé's test) differences between populations in morphological measurements*

	New York	Alviso	San Jose	Hawaii	Guerrero
Michigan	ND	p,h	ND	p,h,l,b	i,v,l,t,b
New York		p,h	ND	b,h	i,v,t
Alviso			p,h	b	p,i,h,v,l,t,b
San Jose				p,h,b	v,t,b
Hawaii					p,h,v,t,b

*ND = No significant differences; letters indicate significant differences between populations: p = plumage brightness, h = plumage hue, i = plumage intensity, v = extent ventral pigmentation; t = tail length; l = tarsus length; b = bill length; no differences among populations were found for wing length.

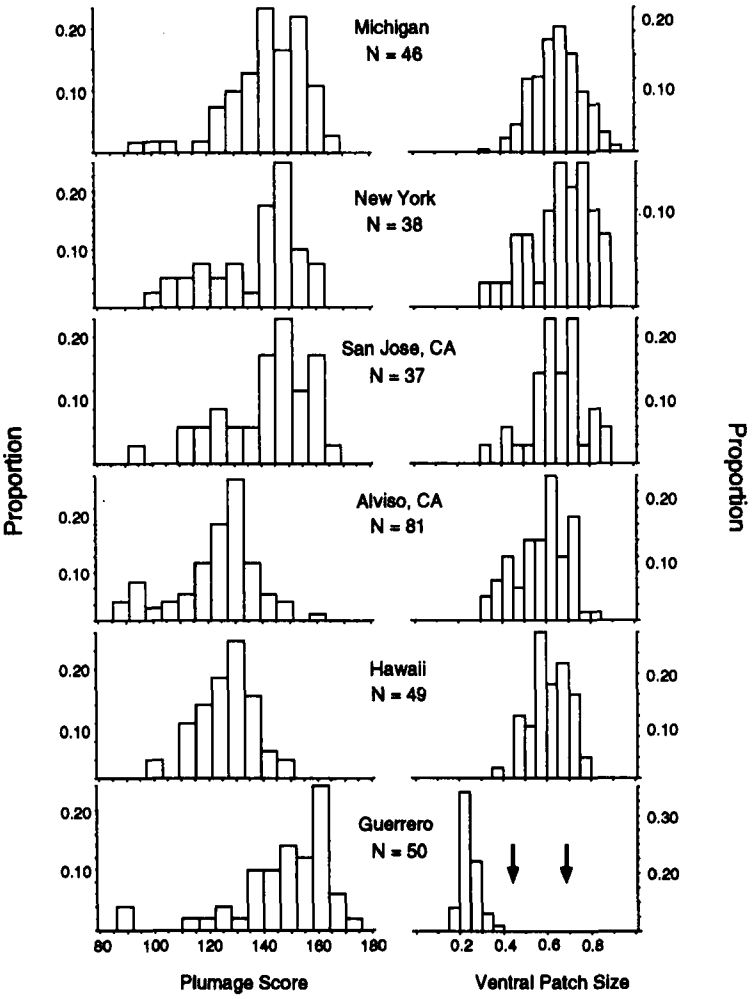

Figure 4. Frequency distributions of plumage brightness scores and ventral patch size (proportion of underside with carotenoid pigmentation) for sampled populations. The arrows in the lower right histogram indicate the ventral patch size of the single *frontalis* × *griscomi* hybrid male (left arrow) and the three *frontalis* × *frontalis* males (right arrow) raised in captivity.

plumage scores of males from the latter in all comparisons, except that New York males did not differ significantly from Hawaii (Table 3, Fig. 4).

Because overall plumage brightness score is a composite of the three main components of colour — hue, intensity and tone (Kornerup & Wanscher, 1983) — males can potentially achieve the same plumage brightness score in different ways (e.g. high hue and low intensity scores or low hue and high intensity scores, etc.). To look for different effects of these colour components among populations, I compared total hue and intensity across populations. (Tone is less variable than hue or intensity among populations and contributes relative little to differences among populations.) The hue scores of populations fell into the same two groupings (Hawaii and Alviso vs all other populations) as did the overall plumage brightness scores of populations (Fig. 5). However, the pattern of intensity scores was somewhat different than the pattern of overall

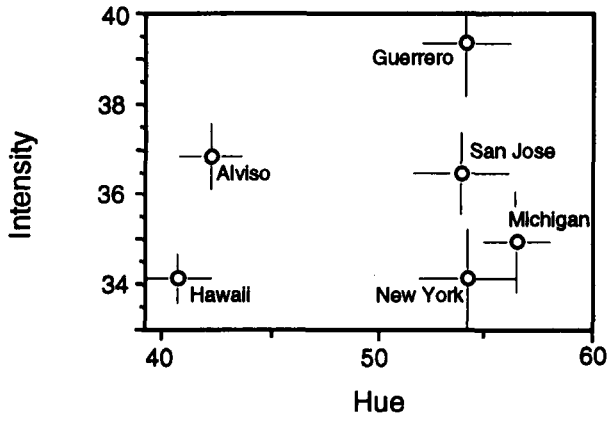

Figure 5. Mean (±SE) intensity of plumage colouration plotted against mean (±SE) hue of colouration across populations (see text for details of intensity and hue scores).

plumage brightness scores. Only the Guerrero populations differed significantly in intensity compared to other populations (Table 3; Fig. 5), but the six populations fell into three groups. Despite their differences in hue, populations in Michigan, New York and Hawaii had similar low mean intensities; populations in Alviso and San Jose had similar intermediate mean intensities; and Guerrero males had the most intensely pigmented plumage (Fig. 5).

Populations also fell into two groups with respect to patch size. *Griscomi* males had distinctive, small ventral patches that were signficantly smaller than the mean patch size of all *frontalis* populations (Table 3; Fig. 4). There were no differences in patch size among the *frontalis* populations (Table 3; Fig. 4). One other consistent difference between *griscomi* and *frontalis* males was in the discreteness of their patches of carotenoid pigments. In *frontalis* males, carotenoid pigmentation was most conspicuous in the bright crown, rump and ventral patches, but in many individuals from all populations there was also a heavy wash of carotenoid pigment over the dark feathers of the head, nape, back and wing coverts. The extent of this red wash varied with plumage colouration and was most conspicuous in bright red males and absent in pale yellow individuals. In *griscomi* males carotenoid pigmentation was always ($N = 50$) confined exclusively to sharply defined crown, rump and ventral patches; there was no detectable pigment outside of these discrete patches.

Plumage colouration in relation to diet

In feeding experiments conducted in 1989, both Hawaiian and Michigan males moulted into pale orange plumages when maintained on a diet supplement with β-carotene and into bright red plumages when maintained on a diet supplemented with canthaxanthin. There were no significant differences between the post-treatment scores of Michigan and Hawaiian males in either the β-carotene-($t = 1.32$) or canthaxanthin-supplemented treatments ($t = 0.72$; $P > 0.20$ for both comparisons, two-tailed t-tests; Table 4). For both populations, the mean post-treatment plumage score of males supplemented with β-carotene was significantly drabber than the pre-treatment scores, while males supplemented

TABLE 4. Plumages brightness and extent of ventral carotenoid pigmentation of male house finches from different populations before and after captive moult on specified diets

Origin	Diet treatment*	Trait†	N	Pre-treatment $\bar{x} \pm SD$	Post-treatment $\bar{x} \pm SD$	t‡	P
Michigan	Deficient 89	c	12	149.3± 7.5	105.8±7.7	11.7	0.0001
	β-carotene	c	10	148.7± 9.1	114.4±4.2	6.5	0.0001
	Canthaxanthin 89	c	22	138.8±17.3	146.0±3.6	1.9	0.0001
	Canthaxanthin 90	c	5	—	139.8±3.6	—	—
	Deficient 89	p	12	0.67±0.11	0.70±0.05	1.0	0.33
	β-carotene	p	10	0.65±0.16	0.69±0.02	0.8	0.43
	Canthaxanthin 89	p	22	0.60±0.10	0.84±0.06	9.7	0.0001
	Canthaxanthin 90	p	5	—	0.74±0.11	—	—
Hawaii	Deficient 90	c	5	117.8±11.6	100.0±8.5	2.21	0.05
	β-carotene	c	4	125.0± 3.8	111.5±4.1	6.09	0.004
	Canthaxanthin 89	c	3	120.3± 1.5	144.8±1.5	4.83	0.02
	Canthaxanthin 90	c	5	121.8± 3.6	141.2±3.7	7.63	0.001
	Deficient 90	p	5	0.62±0.08	0.70±0.07	1.58	0.19
	β-carotene	p	4	0.62±0.05	0.73±0.04	14.50	0.001
	Canthaxanthin 89	p	3	0.60±0.09	0.77±0.07	2.15	0.16
	Canthaxanthin 90	p	5	0.60±0.04	0.78±0.03	11.20	0.0002
California	Deficient 90	c	7	133.6±20.3	102.1±3.7	3.86	0.004
	Canthaxanthin 90	c	7	127.4±27.8	140.1±3.6	1.20	0.14
	Deficient 90	p	7	0.63±0.06	0.66±0.06	0.68	0.52
	Canthaxanthin 90	p	7	0.62±0.19	0.76±0.05	2.46	0.02
Guerrero	Deficient 90	c	6	157.3±11.1	104.5±9.9	7.78	0.001
	Canthaxanthin 90	c	11	148.4±18.7	169.3±4.5	3.97	0.003
	Deficient 90	p	6	0.24±0.01	0.23±0.06	2.53	0.05
	Canthaxanthin 90	p	11	0.23±0.04	0.25±0.04	0.70	0.50

*Deficient 89 = carotenoid-deficient: untreated water and plain apples; deficient 90 = carotenoid-deficient; untreated water; β-carotene supplemented: water and apples treated with 10% β-carotene beadlets; canthaxanthin 89 = canthaxanthin supplemented: water and apples treated with 10% canthaxanthine beadlets; canthaxanthin 90 = canthaxanthin supplemented: water treated with 10% canthaxanthin beadlets (see text for details).

†c = Plumage brightness score; p = extent of ventral carotenoid pigmentation.

‡Paired two-tailed t-test comparing pre- and post-treatment means.

with canthaxanthin moulted onto a plumage that was significantly brighter than their plumage before captive moult (Table 4). On a carotenoid-deficient diet, Michigan males moulted into pale yellow feathers, as expected from previous feeding experiments (Hill, 1992).

In feeding experiments conducted in 1990, I found that males from all populations responded to standardized diets in a similar manner (Table 4; Fig. 6). Males maintained on a carotenoid-deficient diet all grew pale yellow feathers, significantly drabber than their pre-treatment plumage colouration (Table 4; Fig. 6). There were no differences in post-treatment plumage colouration among males from Californian, Hawaiian, or Mexican populations ($F = 1.49$, d.f. = 3, 26, $P = 0.24$, one-way ANOVA; Table 4; Fig. 6). The plumage scores of these males did not differ from the plumage scores of Michigan males maintained on a similar carotenoid-deficient diet in 1989 ($F = 1.49$, d.f. = 3, 26, $P = 0.24$, one-way ANOVA; Table 4; Fig. 6). On a diet supplemented with canthaxanthin, males from all populations produced bright red plumage, but the plumage colouration of Mexican males was significantly

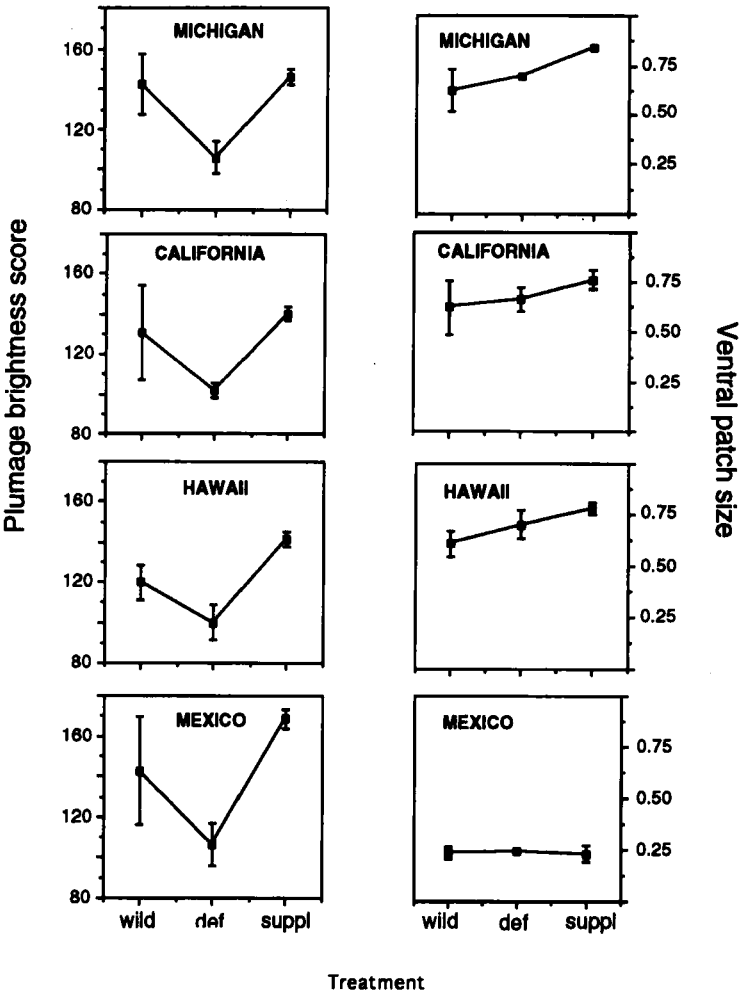

Figure 6. The response (mean ± SD) of plumage brightness score and ventral patch size of male house finches from different populations to standardized diets. Wild = plumage score at the time of capture; def = plumage score after moult on a seed and water diet (see text); suppl = plumage score after captive moult on a seed and water diet supplemented with canthaxanthin (see text).

brighter than the plumage colouration of Californian, Hawaiian, or Michigan males ($P < 0.05$ for all comparisons; Scheffé's test, Table 4; Fig. 6), with no significant differences among the latter populations ($P > 0.05$ for all comparisons; Scheffé's test). Michigan and Hawaiian males supplemented with canthaxanthin both in water and on apples in 1989 were significantly brighter than Californian, Hawaiian or Michigan males that were supplemented with canthaxanthin just in their water in 1990 ($P < 0.05$ for all comparison; Scheffé's test), but Hawaiian and Michigan males from 1989 treatments were still less colourful than Mexican males fed canthaxanthin just in their water in 1990 (Table 4; Fig. 6).

After moult on a canthaxanthin-supplemented diet, all *frontalis* males displayed a heavy wash of red across their crown, nape, back and wing coverts. No reddish wash was apparent on *frontalis* males maintained on a β-carotene-

supplemented diet or on a carotenoid-deficient diet, but a pale yellow or orange wash would be difficult to detect on the dark plumage outside the carotenoid patches. In contrast, no *griscomi* males displayed any trace of carotenoid pigmentation outside their crown, rump and ventral patches regardless of their diet at the time of moult.

Patch size in relation to diet

After moult on a canthaxanthin-supplemented diet in feeding experiments conducted in 1989, the mean patch size of males from Hawaiian and Michigan populations increased substantially relative to pre-treatment patch size (Table 4). Only three Hawaiian males were supplemented with canthaxanthin, so only males from the Michigan population had significantly larger post-treatment patch sizes (Table 4). The mean post-treatment patch size of Michigan males from the β-carotene supplemented and carotenoid-deficient groups was not different than the mean pre-treatment patch size, but the mean post-treatment patch size of Hawaiian males from the β-carotene supplemented group was significantly greater than the mean pre-treatment patch size (Table 4).

In 1990 feeding experiments, the post-treatment patch size of Hawaiian and Californian males on both carontenoid-deficient and canthaxanthin-supplemented diets was significantly larger than the pre-treatment patch size (Table 4; Fig. 6). The patch size of *Griscomi* males increased after moult on a canthaxanthin-supplemented diet but decreased on a carotenoid-deficient diet (Table 4; Fig. 6). The general pattern was for all males to display an increase in patch size after moult on a canthaxanthin-supplemented diet, but for only those males with low initial plumage scores to show an increase in patch size on β-carotene-supplemented or carotenoid-deficient diets (change in mean patch size vs mean pre-treatment plumage score for deficient and β-carotene treatment groups: $r = -0.71$, $N = 6$, $P < 0.03$).

Diet manipulations had no effect on the gross differences in patch size among *griscomi* and *frontalis* males (Table 4). After moult on either a carotenoid-deficient or canthaxanthin-supplemented diet, *griscomi* males had significantly smaller ventral patches than *frontalis* from any population ($P < 0.05$ for all comparisons, Scheffé's test; Table 4, Fig. 6). Within a treatment, there were no differences in patch size among *frontalis* populations ($P > 0{\cdot}05$ for all comparisons, Scheffé's test).

Breeding experiments

Three male offspring resulting from Michigan × Michigan crosses moulted into plumage typical of *frontalis* males maintained on a canthaxanthin-supplemented diet (plumage score $\bar{x} = 141.3$, SD = 3.8; patch size: $\bar{x} = 0.71$, SD = 0.054; compare to Table 4). These captive-born males did not differ in either mean plumage colouration or patch size from other *frontalis* males maintained on a canthaxanthin-supplemented diet (plumage score: $F = 1.36$, d.f. = 2, 24, $P = 0.28$; patch size: $F = 0.49$, d.f. = 2, 24, $P = 0.62$; Fig. 4). Also, like all *frontalis* males maintained on a canthaxanthin-supplemented diet, the captive-born males had a heavy wash of red across the crown, nape, back and

wing coverts. The single male offspring from a Michigan × Guerrero (*frontalis* × *griscomi*) cross had plumage colouration like the offspring of the Michigan × Michigan crosses (plumage score = 139), but this hybrid male was intermediate in patch size (proportion ventral pigmentation = 0.412) to the two parent populations (Fig. 4). It also was intermediate in the discreteness of its crown, rump and ventral patches. Unlike *griscomi* males, several crown and back feathers outside the carotenoid patches displayed a wash of colouration but this was restricted to only a few feathers and hence was much less extensive than is displayed by all *frontalis* males.

DISCUSSION

Proximate control of plumage colouration

By sampling male house finches at different sites across North America I was able to confirm some general patterns of geographic variation in plumage colouration previously reported in the literature (Moore, 1939; Gill & Lanyon, 1965; Hirai, 1975; Brush & Power, 1976). Male house finches that I sampled in Hawaii were mostly drab orange and yellow in colouration with relatively low mean plumage brightness scores, while males sampled in the eastern United States were mostly bright red in colouration with relatively high mean plumage brightness scores. In contrast to previous reports (Grinnell, 1911; Moore, 1939; Michener & Michener, 1931; Aldrich & Weske, 1978; Aldrich, 1982), however, males sampled in coastal California displayed a remarkable amount of local variation in plumage colouration. Males from suburban San Jose averaged as bright as males from the eastern U.S., while males sampled 12 km away in Alviso averaged as drab as males from Hawaii. *Griscomi* males that I sampled in southern Mexico and for which I had no *a priori* expectation of plumage colouration displayed a mean plumage colouration similar to the plumage colouration of *frontalis* males from the eastern U.S.

Several lines of evidence support the argument that the differences in plumage colouration among *frontalis* populations are not due to genetic differentation among populations. First, recent studies have shown that individual variation in plumage colouration within California and Michigan populations of house finches is due to the differences in the type and quantity of carotenoids ingested at the time of moult (Brush & Power, 1976; Brush, 1990; Hill, 1992) and not to intrinsic differences among males in their capacity to be colourful or drab (Hill, 1992). Second, the *frontalis* populations in California, Hawaii and the eastern U.S. are all recently derived from a common ancestral California population (Grinnell, 1911; Elliot & Arbib, 1953; Aldrich & Weske, 1978), so the differences in plumage colouration among these populations have appeared after a very brief period of independent evolution. The change in plumage colouration between Hawaiian and California populations was obvious at least by 1901 (Grinnell, 1911), about 36 years (= generations) after introduction, and the high proportion of red males in the eastern U.S. population was recorded in New York in 1963–64 (Gill & Lanyon, 1965), about 24 years after introduction. Finally, the two local populations that I sampled in California were located only 12 km apart, but they differed dramatically in mean plumage colouration. These populations were separated by no barrier to house finch dispersal and merely

represented two convenient capture localities amidst a very large area occupied throughout by house finches. One might argue that founder effects or natural selection on small populations could have caused rapid genetic changes among the introduced populations in Hawaii or the eastern U.S., but this argument cannot be used for the local variation observed in California.

Controlled feeding experiments provided compelling support for the idea that differences in the mean colouration among *frontalis* males from Hawaii, California, and the eastern U.S. are due to differences in access to carotenoid pigments at the time of moult. When their carotenoid intake was standardized, regardless of whether they were placed on a high- or low-carotenoid diet, *frontalis* males from all populations converged on a similar appearance, with no sigificant differences among males from any location. After moult in captivity, *griscomi* males also displayed plumage colouration like that of *frontalis* males, except that on a canthaxathin-supplemented diet they attained significantly brighter red plumage colouration than *frontalis* males.

Proximate control of patch size

In contrast to the similarity in plumage colouration between *griscomi* and some *frontalis* populations, I found consistent differences in ventral patch size between *griscomi* and all *frontalis* males. The very restricted ventral patch of *griscomi* males persisted after captive moult on either a canthaxanthin-supplemented or carotenoid-deficient diet. Moreover, the *frontalis* × *griscomi* hybrid male had a ventral patch intermediate in size to the two parent populations. These observations indicate that, although diet has some effect on patch size, particularly among *frontalis* males, the gross difference in patch size between *griscomi* and *frontalis* males reflects genetic differences among these subspecies.

Griscomi and *frontalis* males also had consistent differences in discreteness of their patches of carotenoid pigmentation. *Frontalis* males frequently displayed a heavy wash of carotenoid pigment outside their crown, rump, or ventral patches, while *griscomi* males never had feathers with carotenoid pigmentation outside of these patches. As with patch size, the degree to which *frontalis* males displayed carotenoid pigmentation outside their crown, rump and ventral patches was affected by diet, but the gross differences between *griscomi* and *frontalis* males persisted even when males from both populations were fed the same canthaxanthin-supplemented diet. The *frontalis* × *griscomi* hybrid male displayed intermediate plumage; unlike *griscomi* males it displayed some pigmentation outside its crown, rump and ventral patches, but this extra-patch colouration was much less extensive than that of any *frontalis* male on diets supplemented with canthaxanthin. Again, these observations support the idea that differences in the discreteness of carotenoid patches reflect genetic differences among the subspecies.

Plumage colouration and carotenoid access

The large differences in mean plumage colouration that I observed among house finch populations suggest that across their range male house finches experience dramatic differences in the availability of carotenoid pigments. Virtually nothing is known about natural sources of carotenoid plumage

pigments used by male house finches, let alone how the abundance of plumage pigments varies across environments. However, some of the patterns of variation in plumage colouration observed in house finches are consistent with some general features of carotenoid distribution.

Island species or subspecies of several groups of birds display a reduction in carotenoid plumage pigmentation relative to their mainland counterparts (Bateson, 1913; Mayr, 1942, 1963; Lack, 1947; Grant, 1965), including at least two endemic island populations of house finches (*C. m. mcgregori* and *C. m. amplus*; Grinnell, 1911; Moore, 1939). Thus, it is perhaps not surprising that house finches on Hawaii show reduced plumage brightness, with the lowest mean hue and intensity scores of any population that I sampled. Islands in general provide a depauperate flora relative to mainland habitats (MacArthur & Wilson, 1967), and few or none of the plant species that provide house finches with red pigments in California may be present in Hawaii. It is interesting to note that domestic strains of canaries (*Serinus canaria*) introduced to Midway Island lost most of their yellow colouration with "some [being] almost pure white, some brownish, and [with] many intermediate grades" (Munro, 1960). However, other species with carotenoid pigmentation that have been introduced to Hawaii have shown no reduction in or loss of carotenoid colouration (e.g. northern cardinal (*Cardinalis cardinalis*), red-crested cardinal (*Paroaria coronata*), red-billed leiothrix (*Leiothrix lutea*), saffron finch (*Sicalis flaveola*); personal observations).

The dramatic differences in the colouration of males at the two sites in California might seem puzzling, but despite their proximity, these sampling sites were located in very different habitats. In San Jose, males were sampled in a suburban area, while in Alviso males were sampled in a disturbed riparian habitat adjacent to a salt marsh. Moreover, 68% of the males that I sampled at Alviso (which is an active banding station) had been banded at the same location at least 6 months before I captured them. These band-recovery data suggest that many individuals were permanent residents in the locality in which they were sampled and supports the idea that local differences in carotenoid availability would be reflected in the plumage colouration of male house finches. Substantial differences in plumage colouration among local populations inhabiting different environments may occur throughout coastal California (personal observations; R. Gibson, personal communication). It is interesting to note that most of the difference in overall plumage score between San Jose and Alvaso was due to differences in hue; males from the two California populations had very similar mean intensity scores (Fig. 5). This may indicate that while the two populations have access to about the same quantities of carotenoids, they differ in their access to red pigments.

Interestingly, Slagsvold & Lifjeld (1985) observed that both nestling and adult great tits (*Parus major*) show local variation in carotenoid plumage colouration, and that plumage brightness is correlated with habitat and nesting date. Moreover, through cross-fostering experiments and biochemical analysis of the diets fed to nestlings, they demonstrated that the differences in colouration of nestlings were due to differences in the carotenoid content of the nestling diets, and that these differences reflected relative carotenoid levels in various environments at different seasons (Slagsvold & Lifjeld, 1985; Partali *et al.*, 1987). One could imagine that similar environmental variation in carotenoid

availability accounts for both local and geographic variation in male house finch plumage colouration.

The similarity in plumage colouration of male house finches from the eastern U.S. and San Jose might reflect the similarity of the suburban habitats in which both were sampled. Such suburban habitats contain a wealth of ornamental trees and shrubs that produce red fruits and berries and that could provide an abundant source of red carotenoids, allowing many males to attain bright red plumage. While house finches in the eastern U.S. are found almost exclusively in artificially landscaped habitats (Hill, 1993b), house finches in California reside in a variety of natural as well as artificial habitats (Hill, 1993b), which may provide very different access to carotenoids. This heterogeneity of habitats could account for the relative uniformity of mean plumage colouration among house finch populations in the eastern U.S., and the variation among local populations in California.

The relatively high mean plumage colouration of *griscomi* males from Guerrero suggests that males from this region have access to quantities of carotenoid pigments like males in the eastern U.S. or suburban San Jose. However, by distributing carotenoid pigments over a smaller ventral patch and by not pigmenting dark feathers outside the crown, rump or ventral patches, *griscomi* males may simply use ingested carotenoid pigments more efficiently than *frontalis* males. Indeed, *griscomi* males attained significantly brighter plumage than *frontalis* males when both were fed the same canthaxanthin-supplemented diet. Also, *griscomi* males had greater colour intensity than males from any *frontalis* population, suggesting that they concentrate plumage pigments more. Thus, *griscomi* males may have access to smaller quantities of dietary carotenoids than *frontalis* males with equivalent mean plumage scores (see Hill, 1993c).

Implications for taxonomy

As in many species of birds, variation in plumage pigmentation and particularly carotenoid colouration is the main criterion for distinguishing subspecies of house finches (Mayr, 1963; Moore, 1939). The recognition of the introduced population of house finches on Hawaii as a distinct species solely on the basis of carotenoid pigmentation (Grinnell, 1911, 1912; Moore, 1939) shows the extent to which avian taxonomists rely on colouration. The results of my feeding experiments, however, indicate that plumage colouration resulting from carotenoid pigmentation is very sensitive to environmental variation (namely carotenoid availability) and should be employed as a systematic character very cautiously. Within house finches, carotenoid colouration is probably of no value in distinguishing evolutionary lineages and many of the subspecies recognized by Moore (1939) on the basis of plumage colouration should be re-evaluated. Moreover, despite the striking differences in male colouration among house finch populations, my observations indicate that house finches in the eastern U.S. and Hawaii have differentiated little from birds in their parent population in California. Size measurements of males from California, Michigan, and New York failed to support the differences between eastern and western populations of house finches in wing length, bill size and tarsus size reported by Aldrich & Weske (1978) and Aldrich (1982). I did find differences in the size of Hawaiian vs mainland *frontalis* populations; males from the island of Oahu had short wings

and tarsi and large bills, and males from the island of Hawaii had small bills. However, the environmental effects on the development of these characters must be tested (James, 1983) before claims regarding the evolutionary origin of these differences can be considered.

In contrast to the dietary basis for variation in plumage colouration, the differences in the pattern of carotenoid pigments between the endemic populations included in this study do appear to reflect genetic differentiation. Thus, within the house finch complex, and perhaps in birds generally, variation in the pattern of pigmentation is a much better systematic character than colouration. The house finch population in Guerrero is genetically distinct from the northern population of house finches in the U.S. and Canada as diagnosed by the different patch size, and subspecific status seems warranted. The fact that *frontalis* and *griscomi* individuals freely inbred in captivity suggests that these lineages have not diverged greatly. However, patterns of hybridization provide little information in reconstructing historical relationships (Cracraft, 1983), and a better understanding of the systemic relationships of these and other proposed lineages of house finches will require biochemical comparison.

Implications for sexual selection theory

Female house finches prefer to mate with the most colourful male available (Hill, 1990, 1991, 1993c) and by choosing a colourful mate they gain resources and possibly genetic benefits for offspring (Hill, 1991). Thus, a male's reproductive success is directly tied to its success at garnering red pigments and displaying colourful plumage. In addition, mate choice trials with females from Michigan, Hawaii, California and Guerrero indicate that, although plumage brightness is the primary criterion in female mate choice, females prefer large ventral patches of colour over small ventral patches of colour (Hill, 1993c). Given that there is strong sexual selection on males to display large bright patches of ventral carotenoid pigmentation, the loss of brightness and particularly the reduction in patch size displayed by some populations is intriguing.

As I propose throughout this paper, the loss of plumage brightness in some populations is likely a consequence of reduced carotenoid resources in the local environment. No matter how strong the selection to be bright red, males are constrained by their access to carotenoid pigments. On the other hand, patch size seems much less dependent on diet or other environmental factors, and one would expect an evolutionary response by males to the mate preference of females.

One possible explanation for the small ventral patch of *griscomi* males is that there are tradeoffs between patch size and colouration. If, as suggested by feeding experiments, a smaller ventral patch allows male house finches to attain brighter plumage colouration from a limited intake of carotenoid pigments, then it is interesting to speculate that, over time, male house finches might adjust their ventral patch size to correspond to the availability of carotenoids in their environment. In regions with scarce carotenoid pigments, patch size would be reduced, as males traded a large display of colouration for bright colouration. Conversely, in regions with abundant carotenoid pigments, both a large and bright carotenoid display would be attainable, and males would adopt a larger

patch of colouration. Alternatively, patch size might be shaped by differences in natural selection via forces like predation or heat exchange, in which case patch size would have no relationship to carotenoid availability.

Patch size as a function of carotenoid availability could explain the rapid changes in plumage colouration displayed by males in introduced populations. If carotenoid availability changed suddenly, a corresponding genetic change in ventral patch size would require many generations. In the mean time, males would either overextend themselves with a patch size too large to be pigmented adequately and hence mean male colouration would be drab, or they would display a patch size that was too small to take full advantage of the available carotenoids and mean male colouration would be very bright. This hypothesis predicts that carotenoid availability should correlate with mean plumage colouration among *frontalis* populations and with patch size among subspecies of house finches. Alternatively, differences in patch size among populations may have evolved through arbitrary sexual selection (Lande, 1981; West-Eberhard, 1983) with no causal relationship between resource availability and patch size. A survey of carotenoid availability in relation to plumage pattern and colouration is needed to distinguish between these competing sexual selection hypotheses and could provide general insight into the role of diet in generating patterns of geographic variation in the external colouration of birds.

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