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Female house finches prefer colourful males: sexual selection for a condition-dependent trait

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Abstract. Male house finches, *Carpodacus mexicanus*, vary in plumage coloration from pale yellow to bright red. Mate preferences of wild-caught female house finches relative to male coloration were tested in controlled laboratory experiments. In experiments in which they had a choice of four males, test females displayed a significant association preference for the most colourful male presented. Male coloration was independent of age, size, dominance, vocal activity and movement rate in these experiments, and females showed no significant association preference for any of these male characters. When they had females to choose among, test females displayed no association preference. In a concurrent field study in south-eastern Michigan, paired males were significantly more colourful than males in the population at large. Variation in male plumage coloration is a function of dietary intake of carotenoid pigments. Female choice based on such a condition-dependent trait supports a key prediction of the honest advertisement model of intersexual seletion.

Plumage coloration has long been assumed to function in intersexual selection (Darwin 1871; Hamilton & Zuk 1982; Kodric-Brown & Brown 1984), although a number of alternative hypotheses have also been proposed (see Butcher & Rohwer 1989; Ten Cate & Bateson 1988 for recent reviews). To date, however, few experiments have been conducted to test the idea that female birds select mates, at least in part, on the basis of male plumage coloration. Most studies on the role of coloration in mate selection have been conducted on fish, in which females of some species prefer to mate with the most brightly coloured male available (Nobel & Curtis 1939; Kodric-Brown 1985; Houde 1987).

Colourful plumage that results from carotenoid pigmentation (which accounts for most yellow, orange, red and violet colours in birds, amphibians, fish and invertebrates; Fox & Ververs 1960) is particularly interesting because animals cannot synthesize carotenoids de novo; they must derive them from food (Goodwin 1950; Brush 1978). Thus, although the distribution of carotenoids on an organism (i.e. its pattern) is generally inherited (Brush & Siefried 1968; Buckley 1987; Kodric-Brown 1989), variation in carotenoid pigmentation (i.e. the hue, intensity and tone of the patch coloration) is a result of variation in the type and quantity of carotenoids ingested (Brush & Power 1976; Kodric-Brown 1989). Carotenoid pigmentation therefore represents a condition-dependent trait, where condition is access to carotenoids at the time of moult.

In this study, I tested female mate preference relative to male carotenoid pigmentation in the house finch, *Carpodacus mexicanus*, a small, sexually dichromatic passerine that is socially monogamous (Gill & Lanyon 1965; personal observation). Unlike many passerine species, house finches do not defend territories during the breeding season (Thompson 1960; Gill & Lanyon 1965; personal observation), so if females choose mates, they probably respond to characteristics of males and not the quality of resources associated with a male. Within populations, male house finches display substantial variation in plumage coloration, ranging from pale yellow to bright red (Michener & Michener 1931; Brush & Power 1976; see below). This variation reflects the type and quantity of carotenoids (yellow B-carotene, orange isocryptoxanthin and red echinenone) in an individual's plumage (Brush & Power 1976), which, in turn, is a function of the type and quantity of carotenoids ingested at the time of moult (Brush & Power 1976; Hill, unpublished data). Yearling male house finches tend to be less colourful than older males (Gill & Lanyon 1965), but there are no age-specific plumage types (Michener & Michener 1931; Hill, unpublished data); the full range of plumage coloration occurs in all age classes of males.

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I conducted controlled mate-choice experiments using wild-caught house finches that were maintained in captive flocks. My aim was to determine whether carotenoid pigmentation is a basis for female mate choice in the house finch and in so doing to test the hypothesis that females use a condition-dependent trait in selecting mates.

GENERAL METHODS

I captured house finches in southeastern Michigan and southwestern Ohio in the summer and autumn (July–December 1987 and 1988) before they were to be used in mate-choice trials. Males and females were collected at locations at least 20 km apart. Except during experiments, the birds were held in unisexual flocks in an outdoor aviary on the campus of the University of Michigan. The sexes were visually but not vocally isolated throughout the study.

Male house finches vary continuously in coloration from pale yellow to intense red. In the wild, one seldom encounters intensely pigmented yellow males or red males that are very pale; the transition from 'dull' to 'bright' entails a change from pale to intense coloration as well as a shift from yellow and orange to red. The term 'plumage brightness' as I will use it throughout this paper refers to the approximate point along this colour continuum at which an individual's plumage falls. I scored the plumage of males by quantifying the coloration of seven plumage regions (four areas on the underside, plus the crown, eyestripe and rump). I recorded the plumage coloration of each region as a three-number code that scored the hue, intensity and tone by comparison to colour chips in Kornerup & Wanscher (1983). I set up the scoring system so that higher scores along all three colour axes corresponded to brighter plumage. Hue scores ranged from no carotenoid pigmentation (1) through yellow (ca. 2–4) and orange (ca. 5–8) to red (ca. 9–11). The intensity or saturation of the coloration ranged from 1 to 8 (very little colour present to very intense coloration). The tone or amount of black present ranged from 1 to 6 (nearly black to pure coloration). I added the 21 scores to derive a single index value that I used as an estimate of overall plumage brightness. Because of the way I set up the scoring system, adding plumage scores to derive an index value and collapsing scores into principal components yielded a very similar result; the correlation coefficient between PC1 and my additive plumage index was 0·99. I used index values in my analysis rather than principal component scores because I found these values easier to work with. I scored the plumage coloration of all males at the time of capture and again after the completion of a moult in captivity.

To conduct mate-choice trials, I use a mate-choice box consisting of a central chamber measuring 0·41 × 0·41 × 0·94 m with four side compartments measuring 0·31 × 0·31 × 0·74 m (see Burley et al. 1982). At the end of each side compartment was a Plexiglas window connected to an exterior cage. During a trial, each exterior cage contained one stimulus bird (visually isolated from all other stimulus birds) and the main chamber housed the test female. The test female could view only one stimulus bird at a time by hopping or flying under one of four doorways (0·33 m high) leading to a side compartment and up on to a perch. The test female and all stimulus birds were in full vocal contact through the screen lid of the chamber, but the Plexiglas windows precluded any physical contact (see Burley et al. 1982 for details of the chamber design).

An experiment consisted of 14–21 trials, each run with a different female. I counted only trials in which all stimulus birds were visited at least once by the test female. A few trials were discarded because of equipment malfunction. In experiments 1, 2, 3 and 5, I used the same four males or females as stimulus birds throughout an experiment, but to eliminate position effects I rotated stimulus birds among the external cages in such a way that each individual spent an equal number of trials in each compartment.

Trials lasted 3 h and were conducted in the first 7 h of daylight between 21 March and 10 June 1988 and 1989 (a period of intense breeding activity in local wild house finches). Males were introduced into side chambers first and then the test female was released into the central chamber and allowed to move freely about the apparatus for 3 h. The movement pattern of the test female was recorded by an event recorder connected to perches adjacent to viewing windows. I used the time spent by females in association with the four potential choice birds as a measure of mate preference. I designated the first hour of each trial as an adjustment period, during which the birds were given a chance to become accustomed to the chamber. I counted time in association with stimulus birds in the second and third hours of a trial to determine female preference.

In experiment 4, I wired the front perch (adjacent to the viewing window) in each external cage to the event recorder to monitor the movement rate of males, and I installed a sound-activated microphone connected to the event recorder in each male cage to record the vocal activity of each male. The microphones that I used had sensitivity settings and permitted me to record only the male in whose cage a microphone was placed. I verified this by observing vocalizing males in practice trials and by playing back recorded male chirps and song at normal volume in each of the four cages.

When they were not being used in a mate-choice trial, the 12 males used in experiment 4 were housed together in an aviary. I determined the dominance relationships of these twelve males so that I could test whether male dominance influenced female mate preference. House finches are gregarious and I observed little overt aggression (prolonged chasing, feather pulling, etc.) in any of the captive flocks. However, individuals frequently displaced each other from perches, usually with a clear winner and loser in each encounter. I recorded these pairwise encounters in about 2 h of observation and used the relative success of individual males to construct a dominance hierarchy.

I analysed data from the mate-choice experiments by ranking the four stimulus birds from 1 to 4 (least to most preferred) in each trial according to the total amount of time that the test female associated with them. I then compared the observed distribution of ranks among the four stimulus birds across all trials with a Friedman's test to determine whether the observed pattern of association by the test females deviated from random. In cases where the pattern of association was different from random, I conducted a posteriori multiple comparisons to see which stimulus birds differed significantly in their ranks (Burley et al. 1982; Zar 1974). In experiment 4, in which I had data on male vocal activity, movement rate and dominance rank, I performed a similar Friedman's analysis with each variable.

EXPERIMENTS 1 AND 2

Methods

The three least colourful stimulus birds in experiments 1 and 2 came from a group of 10 males captured in southeastern Michigan in September 1987. I did not score the plumage of these males until January 1988 at which time all 10 males had plumage scores substantially below the population mean for southeastern Michigan ($\bar{X}\pm\textsc{se}=119{\cdot}5\pm9{\cdot}1$, $N=10$ for the captive group; $\bar{X}\pm\textsc{se}=146{\cdot}2\pm0{\cdot}8$, $N=149$ for southeastern Michigan population; $t=6{\cdot}80$, $df=157$, $P<0{\cdot}0001$, Student's t-test). Males in this group undoubtedly underwent most or all of their annual moult in captivity and owed their dull pigmentation primarily to their diet rather than to intrinsic features such as foraging ability.

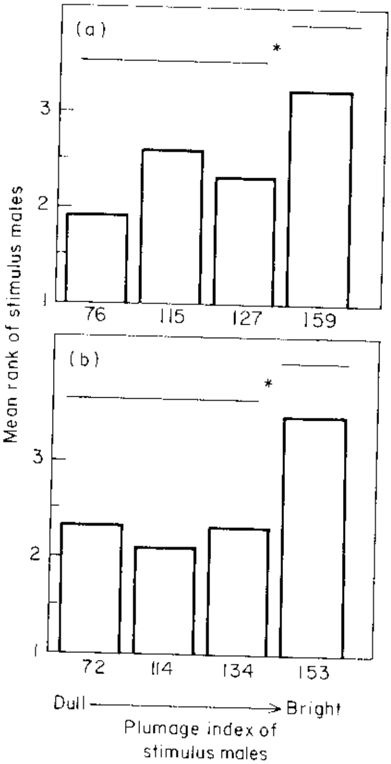

Figure 1. Response of female house finches to males of different plumage coloration in experimental choice trials. Bars represent the mean female preference rank of each stimulus male. The magnitude of plumage index scores corresponds to the overall brightness of a male's coloration (see text). Lines above the bars indicate which males share statistically similar ranks, where successive levels are statistically different from one another. $*P<0{\cdot}05$. (a) Experiment 1, $N=14$, and (b) experiment 2, $N=17$.

I used a different set of four males in these two experiments, but for each experiment I chose four males that represented the full range of plumage variation found in wild populations of house finches (Fig. 1). For the orange-red to pale yellow colour types in each experiment, I used three males from the group described above; for the bright red male in each of these experiments, I used males captured a few weeks later, after they had completed their fall moult in the wild. The age of all birds used in experiments 1 and 2 was unknown.

Results

House finches adapted quickly to captivity and both stimulus birds and test females appeared to adjust readily to the confined space of the experimental chamber. After an initial adjustment period, females generally visited all four males in spurts of activity and then perched near one male for 5–30 min before again visiting all stimulus birds. This pattern of searching and then associating with one bird was generally repeated until the end of the trial. No observers were present in the room during trials, but observations immediately after several trials showed that males and females interacted intensely, with males courting vigorously and females posturing to preferred males.

Females diplayed a non-random association preference in both experiments (experiment 1: $\chi^2=8{\cdot}31$, $df=3$, $N=14$, $P=0{\cdot}040$; experiment 2: $\chi^2=10{\cdot}27$, $df=3$, $N=17$, $P=0{\cdot}016$; Friedman's test), and a posteriori tests indicated a significant preference for the most colourful male ($P<0{\cdot}05$ for both experiments; Fig. 1a, b). Discrimination among the other three males was rather ambiguous and none of the differences was significant.

EXPERIMENT 3

Methods

From a group of males captured in November (after completion of their autumn moult), I chose four males of approximately the same size, weight and coloration (all were orange-red; Fig. 2). I then made the plumage of one male redder by dyeing it with bright red human hair dye (Ardell Really Red Color Enhancer mixed 3:1 with Oreor Creme Color Developer), and I made the plumage of a second male less colourful by applying human hair lightener (Clairol Pure White 40 Creme Developer mixed 1:1 with Clairol 71RG Creme Formula Tint) to coloured areas of its crown, breast and rump. The dyeing process gave the former male a very intense red coloration, very much like the brightest wild male house finches. The lightening process made the latter male more orange, but still more colourful than the drabbest wild males. As in experiments 1 and 2, I used the same four males as stimulus birds throughout the experiment and the ages of all birds were unknown.

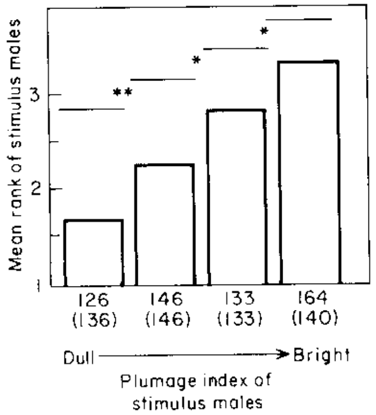

Figure 2. Response of female house finches to males of different plumage coloration in experimental choice trials. Colour variation among males was created with hair dyes and lighteners. Pre-manipulation plumage scores are given in parentheses below post-manipulation scores. Lines above the bars as in Fig. 1. $^*P<0{\cdot}05$, $^{**}P<0{\cdot}01$. $N=18$.

Results

Females again displayed a non-random association preference ($\chi^2=15{\cdot}4$, $df=3$, $N=18$, $P=0{\cdot}002$; Friedman's test), and multiple comparisons tests indicated that the mean preference ranks of all four males differed significantly ($P<0{\cdot}05$ for all comparisons) with the most colourful male ranking the highest and the least colourful male ranking the lowest (Fig. 2). Preference for the two males intermediate in coloration was reversed relative to their plumage brightness (Fig. 2).

EXPERIMENT 4

Methods

In each of the three previous experiments, the same set of four males was presented to each female. The advantage of this approach is that all females were presented with the same variation in male coloration. The disadvantage is that trials within an experiment were not truly independent (Hurlbert 1984; Kroodsma 1989). To reduce the problem of pseudoreplication, in experiment 4 I chose three males to represent each of four colour types. For each trial I would select one of the three males in each type in such a way that I did not repeat combinations of males and all males were

Table I. Pre- and post-manipulation plumage scores of the twelve males used in experiment 4

	Colour-group assignment							
	Red		Orange-red		Orange		Yellow	
	Pre-	Post-	Pre-	Post-	Pre-	Post-	Pre-	Post-
Male 1	140	140	147	134	147	121	148	88
Male 2	143	143	153	132	153	115	155	97
Male 3	148	148	142	130	140	115	142	93
Group mean	143·7	143·7	147·3	132·0	146·7	117·0	148·3	92·6

used in an equal number of trials. Thus, each female in the experiment was presented with a unique combination of stimulus males, but all were presented with the same range of plumage coloration among stimulus males.

All males used in this experiment were known to be at least 2 years old and all were colourful males in the year before they were used in mate-choice experiments (Table I). To create variation in plumage coloration among males, I randomly assigned males to appearance groups by assigning them to specific dietary regimens in late summer prior to autumn moult. Males for the least colourful group were fed a nutritious diet low in carotenoids, and when they moulted, they grew in pale yellow feathers. Males for the second least colourful group were given the same diet but chopped carrots and sweet potatoes were added to provide carotenoids. These males grew in orange feathers. I was not able to induce orange-red plumage through diet manipulation, so I dyed orange males from the previous treatment group with a 2:1:1 mixture of Ardell Really Red Color Enhancer, Sunset Color Enhancer, and Orcor Creme Color Developer, making them red-orange. The coloration of these dyed males closely matched that of wild red-orange males in hue, intensity and tone. And finally, males for the most colourful group were captured a few weeks later, after they had completed their fall moult in the wild (Table I). Thus, there were no differences in the natural coloration of males in these four groups (Table I); colour variation among these males was artificially induced by dyeing and by controlling the quantity of carotenoids that they ingested at the time of moult.

Results

As in the previous experiments, females displayed a non-random association preference ($\chi^2 = 31{\cdot}34$, $df = 3$, $N = 21$, $P < 0{\cdot}0001$; Friedman's test) and the most colourful males were consistently most preferred (Fig. 3). The brightest males were ranked first in 18 out of 21 trials and second in the remaining three trials ($P < 0{\cdot}0001$). The ranks of the other three sets of males were ordered as expected, but the differences were small and not significant. Moreover, the ranks of the three males within an appearance group were consistent; individual differences among the males within a group seemed to be unimportant relative to the plumage colour differences among groups. Also, yearling and older females (females that had not previously paired and those that had probably paired in the wild in the previous year) both displayed a significant preference for the most colourful male (adult: $\chi^2 = 10{\cdot}9$, $df = 3$, $N = 8$, $P =$

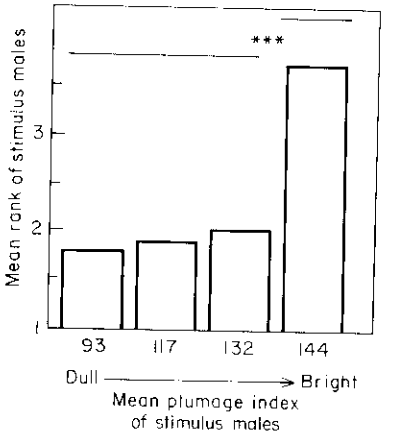

Figure 3. Response of female house finches to males of different plumage coloration in experimental choice trials. Colour variation among males was created with dyes and feeding regimens (see text). Three males were used to represent each type; plumage index score is the mean of these three males. Lines above the bars as in Fig. 1. $^{***}P < 0{\cdot}001$, $N = 21$.

		Winner											
		B1	O1	B2	O2	Y1	O3	R1	R2	Y2	B3	Y3	R3
Loser	B1	☒	1	1									
	O1	25	☒										
	B2	8	14	☒									
	O2	1	1	4	☒								
	Y1	1	4	1		☒	6						
	O3	2	2	1		15	☒						
	R1	2	3	1	6	2		☒					
	R2	6	4	2	4	6	1	2	☒				
	Y2	1	7	3	1	2	4	5	3	☒			
	B3	1		2	1	2	1	1		3	☒		
	Y3	2	4	4		5	2	1	8		1	☒	
	R3	7	3	4	7	3	1	1	2	4			☒

Figure 4. Dominance relationships of the 12 males used in experiment 4. Birds are listed in rank order (top to bottom) based on success in supplanting other males. Number of losses sustained by each male is given in the boxes to the right of its identification code. Each colour type (R: red; B: orange-red; O: Orange; and Y: yellow) is represented by three males (e.g. R1, R2, R3).

0·012; yearling: $\chi^2=21{\cdot}2$, $df=3$, $N=11$, $P<0{\cdot}0001$; Friedman's test; age was not known for 2 of 21 females tested). Thus, the breeding experience or inexperience of females did not seem to alter their mate preferences.

No female association preference was observed for the other male characteristics that were measured. No appearance group of males was significantly more or less active or vocal than another (movement rate: $\chi^2=2{\cdot}64$, $df=3$, $N=21$, $P=0{\cdot}45$; vocalizations: $\chi^2=3{\cdot}80$, $df=3$, $N=18$, $P=0{\cdot}28$; Friedman's test), and female responses relative to male movement rate or vocal activity was not different from random (movement rate: $\chi^2=1{\cdot}38$, $df=3$, $N=21$, $P=0{\cdot}71$; vocalizations: $\chi^2=1{\cdot}0$, $df=3$, $N=18$, $P=0{\cdot}80$; Friedman's test). In the large flight cage in which the 12 males used in this experiment were housed, the red males did not dominate less colourful males (Fig. 4), and female association preference relative to male dominance did not differ from chance ($\chi^2=7{\cdot}17$, $df=3$, $N=21$, $P=0{\cdot}067$; Friedman's test).

EXPERIMENT 5

When given a choice among four females that lacked carotenoid pigmentation, the association preference of test females did not differ from random ($\chi^2=6{\cdot}28$, $df=3$, $N=15$, $P=0{\cdot}099$; Friedman's test; Fig. 5).

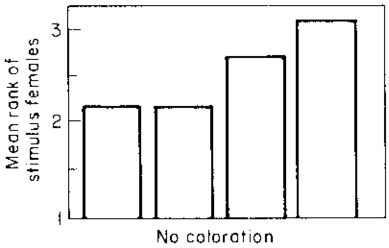

Figure 5. Response of female house finches to females presented as stimulus birds in experimental choice trials. There were no significant differences in the mean ranks of the four stimulus females. $N=15$.

FIELD OBSERVATIONS

Observations of wild house finches on the University of Michigan campus corroborate laboratory results. I banded 149 male house finches between 1 February and 1 July 1988. I subsequently located 66 pairs in which the male was banded. If plumage coloration is a criterion for female mate choice, then males in the breeding population should be more colourful on average than males in the population at large. Thus, I compared the mean coloration of all males banded to the mean coloration of males that paired with a female and I found that paired males were significantly more colourful ($t=1{\cdot}74$, $df=213$, $P=0{\cdot}042$, Student's t-test; Fig. 6). There were no significant differences in the size (wing length or weight) of males from the two samples (wing length: $t=0{\cdot}74$, $df=212$, $P=0{\cdot}46$; weight: $t=-0{\cdot}027$, $df=213$, $P=0{\cdot}98$; Student's t-test).

DISCUSSION

In all four experiments using males as stimulus birds, female house finches displayed a significant preference for the most colourful male presented. By assigning males to colour groups by dyeing or diet, these experiments controlled for the potential confounding effects of male characteristics that may be correlated with plumage coloration. In addition, when I quantified the vocal activity, movement rate and dominance rank of stimulus males, I found no association preference by test

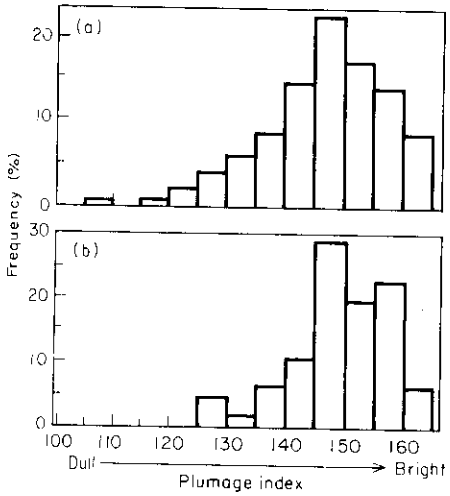

Figure 6. Distribution of plumage scores (see text) of male house finches captured in Ann Arbor, Michigan, between January and July 1988. (a) All males captured ($N = 149$) and (b) paired males ($N = 66$).

females related to any of these features. Thus, it appeared to be the red pigmentation of males and not a correlated character that female house finches were choosing.

One potential problem with experiments 1, 2 and 4 is that males used to represent the brightest plumage class were not captured until after their autumn moult, while males representing the three less-colorful plumage classes were captured prior to their autumn moult. This difference in time of capture could confound the effects of captivity with the effects of plumage coloration. For a number of reasons, however, it seems unlikely that a few weeks difference in time in captivity had a significant effect on these experiments. The health of the house finches that I have kept in outdoor flight cages does not deteriorate noticeably even after 2 years. Males used to represent the brightest class of plumage were captured only 8–10 weeks after males used to represent the other classes of plumage and 20–45 weeks before being used in mate-choice trials. Moreover, in experiment 3, females displayed a significant preference for the most colourful male even though all four stimulus males in this experiment had been in captivity for the same period of time.

Inference regarding female mate preferences in these experiments hinges on the assumption that patterns of association in the mate-choice chamber reflect sexual preference. Various observations support this assumption. First, both males and females in the captive flocks remained in breeding condition throughout the experimental period. Females repeatedly built nests and laid infertile eggs and males sang persistently. Second, the movement pattern displayed by test females (visiting all four stimulus males in spurts of activity and then associating repeatedly with one male) was as expected if females were choosing among potential mates. Third, in contrast to their behaviour in the three trials using males as stimulus birds, test females showed no preference for a particular bird when females were presented as choices. This difference argues against a non-sexual association preference in trials involving males. Finally, as a follow-up to the mate choice trials, I released two females and four males into an outdoor aviary measuring 3·5 × 3·5 × 10 m in June 1988. The males were the most and least colourful (and most and least preferred) from the first and third experiments (Figs 1a and 2). The females paired with the two colourful males within 24 h and one pair proceeded to nest and fledge two broods of young. In this experiment there was no way of distinguishing between female preference and male–male interactions, but the behaviour of these birds substantiated the assumption that females would pair with the male that they sat near in the mate-choice box.

In support of my observations in the laboratory, I found that in a wild population of house finches in southeastern Michigan, the mean plumage coloration of males that paired with a female was significantly greater than the mean coloration of males in the population at large. This observation is relatively weak because I could not eliminate the possibility of pairing success being due to some character that was correlated with male coloration, although male size did not appear to be a factor. However, when the laboratory and field studies are considered together, they present a convincing case for the coloration of male plumage as an important criterion for female mate choice in the house finch.

These results constitute the first experimental evidence for female mate preference relative to the carotenoid pigmentation of male plumage. Most studies dealing with the reproductive consequences of plumage coloration have focused on the function of subadult plumage rather than on the significance of plumage variation among individuals in definitive (adult) plumage (see Lyon & Montgomerie 1986; Butcher & Rohwer 1989 for recent reviews). The few studies that have addressed variation among males in definitive plumage have found that more colourful individuals hold territories of higher quality (Studd & Robertson 1985; Hill 1988; Møller 1988) and enjoy enhanced reproductive success (Studd & Robertson 1985; Hill 1988; Møller 1988; but see Alatalo et al. 1984). However, in such non-experimental field studies, it is not possible to assess the relative importance of intermale interactions and female choice or whether female choice is based on resource quality or plumage characteristics of males (Røskaft & Jarvi 1983; Alatalo et al. 1986; Lifjeld & Slagsvold 1988).

In the only experimental study of female mate choice relative to male plumage coloration, Johnson (1988) found that iridescent (non-carotenoid) pigmentation is one of several male features that female pinyon jays, *Gymnorhinus cyanocephalus*, use to select mates. Experimental studies on zebra finches, *Poephila guttata*, have shown that females use the leg and bill coloration of males as a criterion in selecting mates (Burley 1981; Burley et al. 1982, Burley & Coopersmith 1987), and this coloration appears to be at least partly due to carotenoid pigmentation (Burley & Coopersmith 1987). Similarly, experiments with jewelfish, *Hemichromis bimaculatus*, three-spined sticklebacks, *Gasterosteus aculeatus*, and guppies, *Poecilia reticulata*, demonstrated female preference for the most brilliantly coloured male presented (Noble & Curtis 1939; Semler 1971; Kodric-Brown 1985).

According to current sexual selection theory, females might benefit from choosing males with extreme expression of a display trait such as plumage coloration in two ways. The runaway model (Fisher 1930; Lande 1981; Kirkpatrick 1982) proposes that in choosing a mate with extreme expression of a sexually selected trait, females gain a direct mating advantage for sons. By this model, sexually selected characters evolve entirely due to such an arbitrary mating advantage; there are no overall fitness benefits associated with the characters. Alternatively, the honest advertisement model (Zahavi 1975; Andersson 1986; Kodric–Brown & Brown 1984) proposes that traits that arise via sexual selection permit females to assess the genetic or phenotypic quality of mates and thereby choose a mate that will provide good genes to offspring or good material benefits such as parental care. The crucial difference in these two models is in the basis for variation in expression of the sexually selected character. The runaway model requires that variation in expression of a character that arises through sexual selection reflect additive genetic variance, at least during the evolution of the trait (Lande 1981; Heisler 1984). Alternatively, the honest advertisement hypothesis proposes that character expression is phenotypically plastic and reflects the outcome of an individual's interaction with its environment (Dominey 1983; Nur & Hasson 1984; Andersson 1986).

Carotenoid pigmentation in male house finches appears to be extremely plastic. Variation in plumage coloration in the house finch reflects the quantity and type of carotenoids that a male ingests at the time of moult. Brush & Power (1976) were able to elicit the opposite extremes of character expression in the same male house finches by manipulating their intake of carotenoid pigments. In a similar feeding experiment with a larger sample, I found that standardizing the carotenoid intake of male house finches nearly eliminates variation in coloration within a population and that the relative coloration of a male before treatment is independent of its coloration after treatment (i.e. on a fixed intake of carotenoids, males that are relatively colourful in the wild do not attain a brighter plumage than males that are relatively dull in the wild; Hill, unpublished data).

It is not difficult to imagine how success at acquiring carotenoids might be a good indicator of overall male quality. Endler (1980, 1983) suggested that guppies living in clear, gravel-bottomed streams have limited access to foods containing carotenoid pigments. Only a few males succeed in gaining sufficient carotenoids to display maximum coloration and these are the males that compete the best for limited resources and forage most efficiently (Endler 1980, 1983). Moreover, male guppies that acquired bright carotenoid coloration were at greater risk from predators (Endler 1978, 1980). In house finches, as in guppies, male competitive and foraging abilities, as well as the capacity to escape predators, might be reliably reflected in carotenoid coloration and these features are probably good indicators of overall male quality.

Female mate choice based on a condition-dependent trait such as carotenoid pigmentation supports a key prediction of the honest advertisement model of sexual selection. However, the observation is also consistent with the runaway model if one accepts the argument that sexual selection on male coloration has exhausted additive genetic variance for the trait and that the present pattern of female preference is a holdover from past runaway selection. Ultimately, until plumage coloration in

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house finches is linked to some fitness component of males, carotenoid coloration as an indicator of male quality will remain an interesting speculation.

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