



## Food Color Preferences of Molting House Finches (*Carpodacus mexicanus*) in Relation to Sex and Plumage Coloration

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Received: April 16, 2009

Initial acceptance: June 14, 2009

Final acceptance: July 29, 2009

(S. A. Foster)

doi: 10.1111/j.1439-0310.2009.01697.x

### Abstract

Food color can be indicative of specific nutrients, and thus discrimination based on color can be a valuable foraging behavior. Several bird and fish species with carotenoid-based body ornamentation show color preferences for presumably carotenoid-rich red and orange foods. However, little is known within species about whether or not individuals with (or growing) more colorful ornaments show stronger food-color preferences than those with drabber coloration. Here, we examine food color preferences in house finches (*Carpodacus mexicanus*) – a species with sexually dichromatic and selected carotenoid coloration – as a function of sex and plumage coloration during molt. We captured wild, molting juvenile house finches over 4 wk in late summer/early fall, quantified the color and size of plumage ornaments being developed in males, and determined food color preference in captivity by presenting individuals with dyed sunflower chips (red, orange, yellow, and green). On average, finches showed an aversion to yellow-dyed chips and a preference for red- and green-colored chips. We found no significant difference between male and female preferences for specific food colors, and food color preference was not significantly related to male plumage ornamentation. However, we did find that redder birds demonstrated a higher degree of food selectivity, measured as the proportion of their preferred food color consumed. These results suggest that food color is not a major factor determining food choice in molting house finches, but that there still may be aspects of foraging behavior that are linked to the development of colorful plumage.

### Introduction

The dietary choices of animals are generally considered adaptive, being shaped by the availability of food items in the environment and the nutritional needs of the consumer (Stephens & Krebs 1986). Animals are known to discriminate among food items based upon a wide variety of cues, including caloric content (Sprenkle & Blem 1984), nutrient composition (Schaefer et al. 2003), antioxidant content (Schaefer et al. 2008a), and coloration (Willson et al. 1990). Responses to these cues can be innate or learned through social transmission and/or

association with post-ingestive consequences (Yearsley et al. 2006). Extensive research has focused on the food color preferences of birds because they are highly visual animals and play an important role in the seed dispersal of fruiting plants (Willson & Whelan 1990). Red is a particularly common color for bird-dispersed fruits and is thought to attract avian frugivores by enhancing the conspicuousness of fruits against background foliage (Schaefer & Schmidt 2004), as well as signaling palatability. Recently it has been suggested that birds may use food color as an indicator of antioxidant content (Schaefer et al. 2008a). This is a particularly

intriguing idea because the expression of sexually selected carotenoid-based coloration in birds and fishes is affected by dietary intake of carotenoids (McGraw 2006) and other antioxidants (Bertrand et al. 2006; Pike et al. 2007; but see Karu et al. 2008).

A link between dietary and mate-choice preferences is a key assumption of the sensory bias hypothesis, which proposes that male ornamental signaling evolved as a result of female color preference in the foraging context (e.g. Grether 2000; Rodd et al. 2002). This hypothesis suggests that food color preferences would exist in both sexes, as both males and females could be attracted to the same food types for their nutritive value. Experiments on guppies (*Poecilia reticulata*), which display carotenoid-containing and sexually selected orange spots, show that both sexes have a strong preference for orange food (Rodd et al. 2002). Selective foraging for orange foods may allow guppies to obtain the carotenoids necessary to produce their bright spots (Rodd et al. 2002). Three-spined sticklebacks (*Gasterosteus aculeatus*), which display sexually selected carotenoid-based red throat coloration, have also demonstrated selective foraging by biting at strips of red plastic more than any other color presented (Smith et al. 2004). Olson (2002) found food color preferences in breeding female zebra finches (*Taeniopygia guttata*), which strongly preferred red food over yellow. This preference may be driven by the physiological need for carotenoids during reproduction. Despite these intriguing observations, comparatively little is known within species about inter-individual variation in food color preferences, i.e. whether individuals of different sex, coloration, age, or at different times of year show varying degrees of food choice. For example, degree of male coloration could be positively linked to food color preference because the consumption of specific foods might enhance an individual's coloration.

Male house finches (*Carpodacus mexicanus*) display carotenoid-based plumage coloration ranging continuously from pale yellow to bright red, and it has been shown that males with high carotenoid diets develop redder, more saturated plumage and are preferred as mates by female house finches (Hill 2002). Size of colorful plumage patches also varies among males and is positively correlated with plumage coloration (Hill 2002). Stockton-Shields (1997) tested preferences for red foods in captive molting and non-molting male and female house finches and found that both male and female house finches preferred red food (dyed apple slices) over yellow and

blue, but that there was no seasonal effect on this preference. Redder wild male house finches consume more carotenoids than yellower males (Hill et al. 2002), but we do not yet know if or how males select carotenoid-rich foods. The works of Stockton-Shields (1997) and Rodd et al. (2002) suggest that males may use food color to select carotenoid-enriched foods. However, further study of these color preferences, especially as a function of the color phenotype of individual animals, is needed to clarify the associations between food selection and carotenoid color signaling.

We studied food color preference of recently captured molting male and female juvenile house finches in relation to plumage coloration. This afforded us the opportunity to control feeding conditions carefully (as opposed to studying feeding habits of birds in the wild, which are difficult to quantify) and examine the relationship between recently developed (within days) plumage color and current food color preferences. Consistent with Stockton-Shields (1997), we predicted that both male and female house finches would prefer red foods. Because males growing colorful red-to-yellow plumage (to be displayed in their first breeding season) should have higher carotenoid demands than drab females, we predicted that males would show stronger preferences for red food items than females and that the strength of this preference would positively correlate with plumage coloration and patch size. An underlying assumption of this prediction is that food redness positively reveals carotenoid concentration and/or red carotenoid content, which may not always be true (Schaefer et al. 2008a). We focused our study on juvenile birds because they are abundant, relatively naïve, easy to catch, and have a high degree of plumage color variation (Hill 2002). The limited foraging experience of juvenile birds also offers an insight into innate food color preferences (Schmidt & Schaefer 2004).

## Methods

One hundred eighteen wild juvenile house finches (58 males, 60 females) were captured from Aug. 31 to Sept. 26, 2008 in basket traps at baited feeding sites on the campus of Arizona State University in Tempe, AZ, USA. Upon capture, sex was determined by plumage coloration (i.e. presence of colorful plumage patches on crown and breast in males; Hill 1992), and a U.S. Fish and Wildlife numbered metal band was placed on each bird for individual identification. The study began in approximately the middle

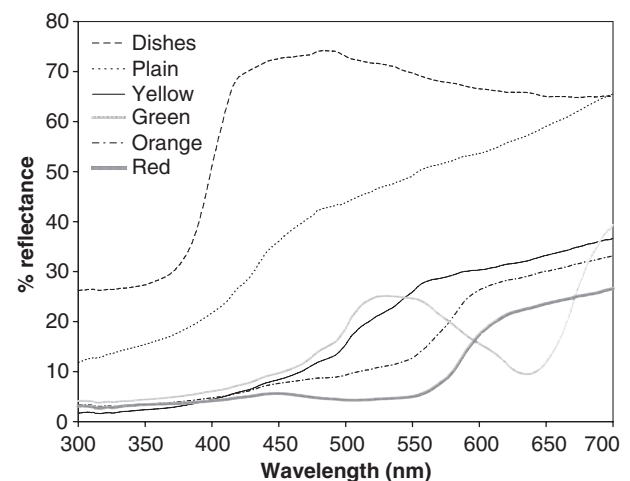
of the molt period (Hill 1993) and all birds included in the study were at least 50% molted; thus, plumage coloration was a reliable indicator of sex. We measured body mass using an electronic balance (to the nearest 0.01 g) and the average hue of crown, breast, and rump plumage of each male using a handheld Colortron II reflectance spectrophotometer (see Hill 1998 and McGraw et al. 2006 for methods and justification). Females very rarely have hints of carotenoid pigmentation on the rump in our population (K.J.M., pers. obs.), so their coloration was not studied here. Using a Canon EOS Digital Rebel DS6041 camera (Canon U.S.A. Inc., Lake Success, NY, USA), photographs were taken of each male's three colorful patches and imported into Adobe Photoshop CS (Adobe Systems, Inc., San Jose, CA, USA), which was used to measure the number of pixels per patch. Pixels were then converted to cm<sup>2</sup> based on comparisons to a size standard that appeared in each photograph, and total colorful plumage area was calculated by summing the values for the three body regions. The birds were then housed for 48 h in individual wire cages (0.6 m × 0.4 m × 0.3 m) in an IACUC-approved greenhouse room (see McGraw 2005 for details). The greenhouse environment provided natural day length and illumination levels, but the spectrum of light differed because the greenhouse was not transparent to ultraviolet wavelengths (<400 nm). Birds were fed a base, *ad libitum* diet of tap water and plain sunflower seed chips, and were released back into the wild after food color preferences were assessed (see below).

#### Food Color Preference Test

Stockton-Shields's (1997) prior study of house finches used dyed apple slices to examine food color preference. In this experiment, dyed sunflower chips (whole kernels, without the hull) were used to ensure color consistency and to simplify the quantitative analysis of amount eaten. Whole sunflower seed chips were dyed red, orange, yellow, and green by spraying them with 20–25 drops of generic food coloring (Target Corporation, Minneapolis, MN, USA) diluted in 175 ml water. These colors were chosen because they represent a spectrum of food colors consumed by house finches, which naturally eat green plant matter as well as flowers and fruits (Beal 1907). While there is the potential for differences in palatability among dyes, it is unlikely that birds were avoiding specific chemicals because the most (green) and least preferred (yellow) colors (see Results below) both contain tartrazine (FD&C Yellow 5). The dyed chips

were color scored using an Ocean Optics S2000 reflectance spectrophotometer (Dunedin, FL, USA; Fig. 1). To determine whether the experimental colors were discriminable in the avian visual system, we calculated the chromatic and achromatic contrasts between the colored chips and with the background of the presentation dish, following Vorobyev et al. (1998) and using the vision parameters of the blue tit (*Cyanistes caeruleus*; Hart et al. 2000). With this model, all of the colored chips differed considerably from one another, as well as from the presentation dish (contrasts ranged from 7 to 33 jnds, discrimination threshold = 1 jnd; data not shown).

For the feeding trials, 20 whole chips of each color were combined and evenly distributed in a plastic presentation dish (4 cm long × 4.5 cm wide × 4.5 cm high). Twelve hours before testing, the base diet was removed from each cage to ensure adequate motivation for foraging during our preference trials. The food trials began at 07.00 hours and ended at 10.00 hours on each testing day. These hours were chosen after several preliminary runs revealed that these were the hours in which the birds ate the most food. Prior to introduction of the colored food, paper cage liners were changed to allow us to detect and collect dropped chips after each trial. Dyed chips of all colors were presented to the birds in their housing cages for an undisturbed 3-h period, after which time any remaining whole chips in the dish and cage floor were collected and counted to determine the number of each color eaten. The inclusion of seeds from the cage floor with the eaten chips in the analysis did not significantly change the results, so we



**Fig. 1:** Reflectance spectra of each chip color and the white presentation dish across the bird-visible spectrum, as determined using UV–VIS reflectance spectrophotometry.

limited our analysis to eaten chips only. We used two metrics of food choice – (1) *color preference* was determined as the relative frequency that a given color of chip was eaten; and (2) *strength of selectivity*, as the number of chips of the most preferred color by an individual divided by the total number of chips eaten during the trial. This measure is a variation on the preference ratio used by Mastrotta & Mench (1995); a highly selective individual that ate exclusively from one color (regardless of what that color was) would score 1.0, while a non-selective individual that ate equally from all four colors would score 0.25.

### Data Analysis

We excluded eight birds from statistical analyses, one because it ate a very small amount of food (five chips of one color only) and seven because a true color preference may have been masked by the fact that they ate all ('ran out of') chips of one color type and more than 10 chips of another color. Including or excluding these birds in the analyses did not change the outcomes of the tests, and we present only the analyses with these birds excluded. Body mass data were not used in full models because they were taken at the time of capture, 2 d prior to the foraging trials, and were not significant predictors of food color preference (mass:  $F_{1,107} = 1.45$ ,  $p = 0.23$ ; chip color  $\times$  mass:  $F_{2,38,254.65} = 2.32$ ,  $p = 0.090$ ). We examined the effects of chip color, sex, and week on the number of chips eaten with a repeated-measures analysis of variance (rMANOVA), with chip color as the repeated within-subject factor, and sex and week as the between-subjects factors. To examine the relationship between food color preference and male ornamentation, we conducted a repeated-measures analysis of covariance (rMANCOVA), with chip color as the within-subjects factor, week as a between-subjects factor, and the first principle component of male coloration and patch size (PC1 plumage coloration) as a covariate. We calculated a principle component of male plumage hue and total carotenoid patch size because these measures were significantly intercorrelated ( $n = 55$ ,  $r = -0.53$ ,  $p < 0.001$ ). PC1 had an eigenvalue of 1.525 and explained 76% of the variation in hue and patch size. Hue loaded negatively ( $-0.873$ ; with lower hue scores assigned by the Colortron corresponding to redder plumage) and patch size loaded positively (0.873) on PC1, such that individuals with a higher score were redder with a larger patch.

We also determined which seed color was most preferred numerically by each individual and used

Pearson's chi-squared tests to analyze the frequency distribution of these designations among individuals and in relation to sex and week. We arcsine-square-root transformed our strength of selectivity measure to meet the assumptions of parametric statistics and examined the effects of sex and week with a univariate ANCOVA. Because we only had plumage color data for males, we used a separate ANCOVA to evaluate the effects of week and PC1 plumage coloration on strength of selectivity. In all of our analyses, non-significant between-subject interaction terms were omitted from the models and the significance level was set at  $p < 0.05$ .

### Results

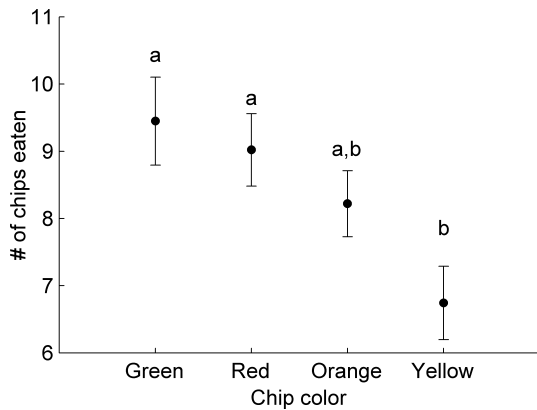
#### General Chip Color Preferences and Differences as a Function of Sex and Week

Finches showed significant chip color preferences (Table 1), with birds tending to eat more red and green chips than yellow chips (Fig. 2). There were no significant effects of week or sex on the number of chips eaten (Table 1). The frequency of the most preferred food color differed significantly from random and, excluding ties ( $n = 8$  out of the 118 birds), 39.6% of birds ate more green chips than any other type, 25.7% ate more red chips, 22.8% more yellow, and 11.9% preferred orange ( $\chi^2 = 15.79$ ,  $df = 3$ ,  $p = 0.001$ ). Males and females did not differ significantly in the frequency of their most preferred color ( $\chi^2 = 1.004$ ,  $df = 3$ ,  $p = 0.808$ ), and there were no significant differences among weeks ( $\chi^2 = 12.44$ ,  $df = 9$ ,  $p = 0.189$ ). The strength of selectivity for the most preferred food color differed significantly across the 4 wk of the study (Fig. 3), but did not differ significantly between males and females (Table 2).

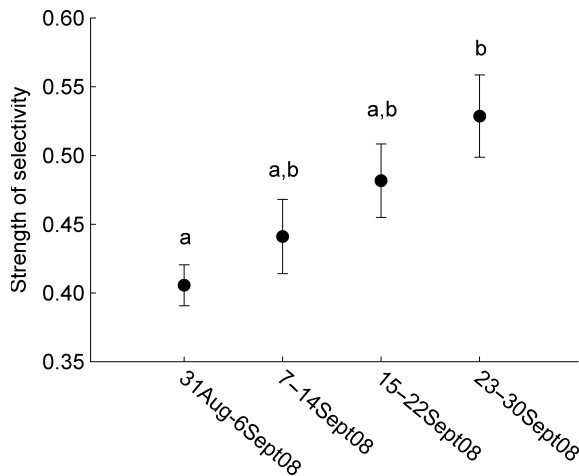
**Table 1:** Repeated-measures ANOVA testing the effect of sex, week, chip color, and relevant interaction terms on number of chips of different color (dyed red, orange, yellow, or green) eaten by molting juvenile house finches during 3-h captive feeding trials

Source	df	MS	F	p
Within subjects				
Chip color <sup>a</sup>	2, 35	246.92	212.89	6.09
Chip color $\times$ sex <sup>a</sup>	2, 35	246.92	34.58	0.42
Chip color $\times$ week <sup>a</sup>	7, 06	246.92	38.12	1.09
Between subjects (effects on average of all colors)				
Sex	1, 105		67.03	1.303
Week	3, 105		63.49	1.23

<sup>a</sup>Greenhouse-Geisser corrected to account for deviations from sphericity.



**Fig. 2:** Mean  $\pm$  SE number of differently colored chips eaten by recently captured molting house finches. Birds were given three undisturbed hours to consume food in a small cage. Points that do not share a letter in common are significantly different (Bonferroni *post-hoc* comparisons, all  $p < 0.026$ ).



**Fig. 3:** Mean  $\pm$  SE strength of food selectivity across the 4 wk of the study. Weeks that do not share a letter in common are significantly different (Bonferroni *post-hoc* comparisons, all  $p = 0.007$ ).

**Table 2:** Results of the univariate anova testing the effects of sex and week on strength of food selectivity in molting house finches (see text for description)

Source	df	MS	F	p
Sex	1, 105	0.009	0.54	0.46
Week	3, 105	0.066	4.11	0.008

**Plumage Coloration and Food Color Preferences**

Food color preference was not related to male plumage ornamentation, as there was no significant interaction effect of chip color and PC1 plumage coloration on the number of chips eaten (Table 3). However, males with more elaborate carotenoid

**Table 3:** Repeated-measures ANOVA testing the effects of plumage coloration (PC1), week, and chip color on number of sunflower chips eaten in male house finches

Source	df	MS	F	p
Within subjects				
Chip color <sup>a</sup>	2, 22	110.90	155.43	0.009
Chip color $\times$ PC1	2, 22	110.90	2.40	0.95
plumage color <sup>a</sup>				
Chip color $\times$ week <sup>a</sup>	6, 65	110.90	25.93	0.69
Between subjects (effects on average of all colors)				
PC1 plumage color	1, 50		35.79	0.61
Week	3, 50		97.62	1.66

<sup>a</sup>Greenhouse-Geisser corrected to account for deviations from sphericity.

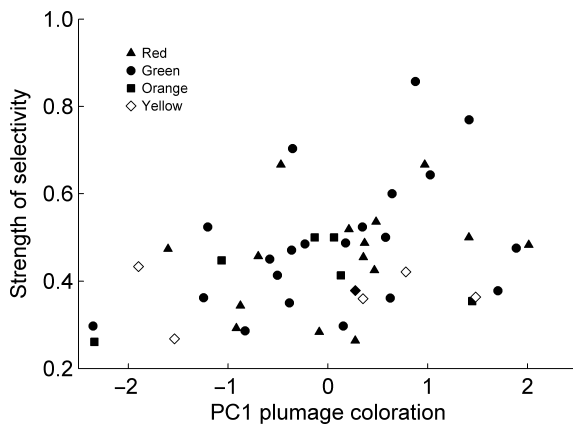
**Table 4:** Results of the univariate ANOVA testing the effects of plumage coloration (PC1) and week on strength of food selectivity in male house finches

Source	df	MS	F	p
PC1 plumage color	1, 50	0.085	6.16	0.016
Week	3, 50	0.063	4.51	0.007

coloration showed significantly stronger selectivity for their most preferred food color (Table 4, Fig. 4).

**Discussion**

Across molting juvenile house finches generally, we found a preference for green and red chips over yellow, with the amount of orange chips consumed falling between these extremes. This pattern is not entirely consistent with the red preference observed in house finches by Stockton-Shields (1997), but in her study birds were only offered a choice between red, yellow, and blue food items. A preference for green foods is not surprising, because house finches commonly consumed fresh plant matter (Beal 1907), which is abundant locally during molt when deserts are replete with green vegetation following monsoon rains. Our results are also consistent with previous studies that indicate that birds do not strongly discriminate between red and green plant-based food items (Gamberale-Stille & Tullberg 2001; Gamberale-Stille et al. 2007). Weak preferences for red vs. green foods in frugivorous species (Willson et al. 1990) may occur due to shifting responses to nutrient or chemical content of food items (Stanley et al. 2002; Rowe & Skelhorn 2005; Tsujita et al. 2008) and to effects of previous foraging experience (Schaefer et al. 2008b). Although the birds in our study were juveniles, we had no knowledge of previous foraging experience, which may have influenced their food color preferences.



**Fig. 4:** Strength of food selectivity of male house finches is positively correlated with plumage coloration (PC1). A higher PC1 value indicates a redder bird with a larger patch size. The preferred food color for each individual is indicated by the symbols listed in the figure legend.

We found no significant relationship between the plumage coloration of actively molting male house finches and either preferences for specific food colors or the total amount of food eaten. If we assume that pursuit of red foods yields a carotenoid-pigmentary benefit (as some models suggest; Rodd et al. 2002), then our results suggest that house finches do not use red food color as a reliable indicator of carotenoid availability. House finches are primarily granivores, but they also eat various fruits and occasionally insects along with vegetable matter (Hill 2002). A study of fruits consumed by neotropical forest birds shows that fruit skin color is a good predictor of antioxidant (especially anthocyanin pigment) content, but not carotenoid levels (Schaefer et al. 2008a); thus red food color may not guarantee high carotenoid intake. Many chlorophyll-rich green foods contain high carotenoid concentrations, in addition to other nutrients (Goodwin 1980). Therefore, focusing on red foods alone may not maximize the intake of carotenoids. It is also important to consider the requirements of other nutrients in the diet, as birds may be attracted to colors that represent molecules other than carotenoids. Schmidt & Schaefer (2004) showed that fruit colors such as yellow, orange, and blue signal the presence of nutrients such as proteins and carbohydrates. As birds are likely to have increased requirements for all of these nutrients during molt (Murphy & King 1992), a diet of varied color and composition may be required to meet these needs; it is noteworthy here that a manipulation of caloric content, independent of carotenoid intake, significantly affected the expression of house finch plumage coloration (Hill 2000).

Therefore, food choices of molting birds likely involve the balancing of a broad suite of dynamic nutrient and caloric needs, and more carefully controlled experimental manipulations are needed to disentangle the effects of specific nutrient demands and food color on food selection.

Birds tended to avoid eating yellow chips compared with other colors. Avoidance of yellow foods has been observed in other species both with and without carotenoid-based coloration (e.g. *Taeniopygia guttata*, Olson 2002; *Dumetella carolinensis*, Willson et al. 1990), suggesting that many birds are adept at identifying unripe yellow foods (Diesselhorst 1972) or possibly less-valuable carotenoid sources. Ingested carotenoids, especially orange forms like beta-cryptoxanthin, must be metabolically modified into red pigments if the bird is to become bright red (Hill 2002). Ingestion of yellow pigments only generates yellow plumage (Hill 2002), and these birds would face reduced mating success during the breeding season, as females are less attracted to yellow males (Hill 2002).

The finding that redder birds did not preferentially forage on red foods begs two questions: (1) how is it that some birds are getting more carotenoids to develop their red plumage and (2) is plumage color still a reliable signal of nutritional quality? Hill et al. (2002) showed that the carotenoid concentration of the gut contents of male house finches was positively correlated with their plumage coloration. If food hue is not used to select food items (as suggested by our study), it is possible that food chroma or brightness reveals carotenoid characteristics or that carotenoids are being detected in food using means other than color (Schaefer et al. 2008a). Variation in the UV spectrum has also been shown to affect food selection (Church et al. 1998, 2001); therefore it is possible that similarities between the UV reflectance peaks of the food colors used in this study resulted in the lack of significant color preference. With respect to nutritional quality, in previous studies redder birds were also found to grow feathers faster (Hill & Montgomerie 1994), adding further support to the idea that there are still key nutritional aspects to coloration. We must not overlook physiological aspects to color acquisition (McGraw 2006), however, especially in house finches, where important red feather pigments like 3-hydroxy-echinone are metabolically derived (Inouye et al. 2001).

Although the preference for any one food color was not significantly related to male plumage coloration, the strength of food selectivity was significantly correlated with plumage coloration. Redder birds consumed more of their preferred food color type,

whereas drabber birds consumed more balanced amounts of all chip colors. Therefore, it may not be a specific color preference that allows individuals to maximize their consumption of carotenoids and other nutrients needed for the colorful plumage molt, but rather that a selective foraging strategy allows them to identify and efficiently exploit profitable food items. Among neotropical frugivorous birds, selectively foraging on fruits of similar ripeness, rather than searching for riper fruits, has been shown to maximize energy intake per unit time (Schaefer & Schaefer 2006). A link between foraging specialization and plumage coloration has been noted in the siskin (*Carduelis spinus*), where individuals with larger carotenoid-based yellow wing patches were less likely to call when isolated from other birds or join simulated foraging flocks of decoys (Senar & Escobar 2002). The authors interpreted these behaviors as indicating that individuals with larger patches were superior foragers and did not need to rely on conspecifics to locate food (Senar & Escobar 2002).

Foraging selectivity also differed significantly across the 4 wk of the study and increased in a pattern that tracked the progression of molt. The highest levels of selectivity occurred in the last week of the study, when many birds were nearly completing or had just completed molt (A.L. Bascuñán and E.A. Tourville, pers. obs.). However, it should be noted that these were not repeated samples and each week represents a different set of individuals. A potential explanation for this temporal variability in selectivity is that birds in earlier stages of molt had greater energetic demands (Murphy & King 1992), were hungrier during the trials, and therefore less selective. Hunger is known to decrease the selectivity for feeding location in European starlings (*Sturnus vulgaris*; Talling et al. 2002), and house finch selectivity for seed types decreases with declines in ambient temperature (Sprenkle & Blem 1984) when the energetic demands of thermoregulation are increased.

In conclusion, our study suggests that food color preference may not be intimately associated with development of elaborate plumage ornaments in house finches. Rather, colorful individuals may rely on other cues to identify profitable food items and employ a selective, individual-specific foraging strategy to maximize nutrition, molt, and coloration.

### Acknowledgements

We thank the Barrett Honors College and School of Life Sciences at Arizona State University for funding

this experiment and Dale DeNardo, Melissa Rowe, and the McGraw and Rutowski laboratories for offering support, useful advice, and/or use of space and equipment. We also thank the two anonymous reviewers of this manuscript for their helpful comments. The Department of Animal Care Technologies at ASU provided housing and husbandry for our animals throughout the experiment.

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