ORIGINAL ARTICLE

# Can House Finches (*Carpodacus mexicanus*) use non-visual cues to discriminate the carotenoid content of foods?

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**Abstract** Carotenoid pigments are involved in different physiological processes (e.g., immunoenhancement, antioxidant activity) in addition to coloring plumage and integuments. As animals cannot synthesize these pigments de novo, it has been proposed that carotenoids constitute a limiting resource that birds may specifically seek in their food. Confirming this hypothesis, it was recently found that birds can discriminate between carotenoid-enriched diets and control diets, even if both have the same color, suggesting that there may be underlying non-visual (e.g., olfactory, taste) mechanisms for detecting carotenoid presence or enrichment in foods. In this study, we performed two experiments with male House Finches (*Carpodacus mexicanus*) to test if this species is able to discriminate between (1) carotenoid-enriched and plain sunflower seeds (while controlling for food coloration), and (2) plain seeds scented with $\beta$-ionone, which is a carotenoid-degradation product that is common in many fruits and is one of the most powerful flavor-active organic compounds, or a sham odorant. We found that finches did not show significant food preferences in either experiment, indicating that they did not use odor or flavor cues associated with carotenoids to discriminate between foods. However, our results do not rule out the possibilities that other flavors or odors can be used in discrimination or that finches may learn to discriminate flavors and odors over longer periods of time or at other times of year through post-ingestive feedback mechanisms.

**Keywords** Carotenoids · Foraging · Olfaction · House Finch

**Zusammenfassung**

**Können Hausgimpel (*Carpodacus mexicanus*) andere als optische Informationen verwenden, um den Karotinoid-Gehalt ihrer Nahrung einzuschätzen?**

Über die Farbgebung von Gefieder und Haut hinaus sind Karotinoid-Farbstoffe an diversen physiologischen Prozessen beteiligt (Stärkung des Immunsystems, Antioxidantien-Aktivität). Da Tiere diese Farbstoffe nicht selbst synthetisieren können, wurde bereits die Idee präsentiert, Karotinoide stellten einen Ressource-Faktor dar, den Vögel gezielt in ihrer Nahrung suchen. Als Bestätigung dieser Hypothese wurde kürzlich herausgefunden, dass Vögel zwischen Karotinoid-angereicherter und Kontroll-Nahrung unterscheiden können, auch wenn beide die gleiche Farbe haben. Dies legt nahe, dass es außer optischen noch andere Informationen geben muss (z. B. Geruch, Geschmack), die als Mechanismen dienen können, das Vorhandensein von, und den Gehalt an, Karotinioden in der Nahrung festzustellen. In unserer Untersuchung führten wir ein Zwei-Stufen-Experiment mit männlichen Hausgimpeln (*Carpodacus mexicanus*) durch, um zu testen, ob diese Art unterscheiden kann zwischen (1) Karotinoid-angereicherten und reinen Sonnenblumensamen (bei gleicher Farbe), und (2) reinen, mit $\beta$-Iononen parfürmierten Samenkörnern und solchen

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mit einem anderen, ähnlichen Duft (β-Ionone sind ein in vielen Früchten vorkommendes Abbauprodukt von Karotinoiden und eine der am stärksten duftenden organischen Verbindungen überhaupt). Wir stellten fest, dass die Finken in den Experimenten keinerlei signifikante Bevorzugung einer der Nahrungsstoffe zeigten, was darauf hinwies, dass sie in der Wahl ihrer Nahrung keine mit Karotinoiden zusammenhängende Geschmacks- oder Geruchs-Informationen benutzten. Andererseits schließen unsere Ergebnisse aber auch nicht die Möglichkeit aus, dass in der Unterscheidung von Nahrungsstoffen ein anderer Geruch oder Geschmack benutzt wurde, oder dass die Finken die Unterscheidung anhand von Geruch oder Geschmack über einen längeren Zeitraum oder zu anderen Jahreszeiten über Rückkopplungsmechanismen in der Verdauung lernen.

## Introduction

Most food items in nature offer animals a variety of nutrient types and concentrations (Pulliam 1975). However, animals often need particular nutrients to meet somatic or reproductive demands and in some instances have developed foraging strategies to pursue food that contains these specific limiting nutrients (Murphy and King 1987). Detection and discrimination of foods enriched with calcium, sodium, or amino acids are widespread (e.g., Murphy and King 1987; Shulkin 1992; Tordoff 2001).

Carotenoids are valuable nutrients that have attracted much research attention by behavioral ecologists in recent years (Svensson and Wong 2011). Carotenoids generate the yellow, orange, and red color of many animals (McGraw 2006) and are involved in different physiological processes, such as immunomodulation, antioxidant activities, and visual tuning (McGraw 2006). As animals cannot synthesize these pigments de novo, it has been proposed that carotenoids constitute a limiting resource for birds (Blount 2004; Costantini et al. 2007), and have become a model system for examining the costs and functions of bright coloration (Blount and McGraw 2008).

Given the diverse benefits of carotenoids, natural selection may favor the evolution of specific capacities to detect food containing high levels of carotenoids (McGraw 2006; Senar et al. 2010). Color has been proposed as the primary means of identifying carotenoid-rich foods (McGraw 2006), but there are currently conflicting reports in the literature on this mechanism. First, in a survey of 60 bird-dispersed fruiting tree species, Schaefer et al. (2008) showed that fruit coloration was not linked with carotenoid content. In contrast, a recent experimental study with Great Tits (*Parus major*) found that birds are able to discriminate between carotenoid-enriched diets and control diets, even if

both have the same color (Senar et al. 2010). Moreover, Catoni et al. (2011) found that individual Garden Warblers (*Sylvia borin*) did not select food for the maximum amount of carotenoids, but choose for a highly consistent carotenoid intake during the course of different dual-choice experiments where they had the choice between carotenoid-enriched and control diet, both with the same color. Taken together, these results suggest that there may be underlying non-visual (e.g., olfactory, taste) mechanisms for detecting carotenoid presence/enrichment in foods.

To test this idea, we performed two captive experiments with House Finches (*Carpodacus mexicanus*)—a North American passerine species with sexually selected carotenoid-based male plumage coloration (Hill 2002). We repeated Senar et al.'s (2010) experiment and offered males a choice between carotenoid-enriched and plain sunflower seeds, while controlling for food coloration by dyeing the seeds green and presenting the food under filtered light. Thus, this first experiment offered the birds the opportunity to discriminate carotenoid content of food based on smell or taste. In the second experiment, we isolated the olfactory component by presenting the birds with a choice of plain seeds scented with β-ionone or a sham odorant. β-ionone was chosen because it is a product of carotenoid degradation, is common in many fruits, is a known attractant for invertebrates, and is one of the most powerful flavor-active organic compounds known (Britton 2008). We predict that birds may prefer seeds scented with β-ionone if they discriminate between foods using their smell. Finally, to determine if the ability to detect carotenoids in food is related to a male's plumage carotenoid-based coloration, we examined the link between food preference and plumage coloration in both experiments.

## Methods

### Study animals

From 1 September to 3 October 2010, we captured 15 male House Finches using baited basket traps (McGraw et al. 2006) from each of three sites in the Phoenix metro area: Estrella Mountain Regional Park, Goodyear, AZ (Site 1); Arizona State University (ASU) Campus, Tempe, AZ (Site 2); and a private residence in Chandler, AZ (Site 3). Birds were caught at the different sites as part of a separate ongoing study of finches in different urban/rural settings. We housed birds individually in small wire cages (0.6 × 0.4 × 0.3 m) in an environmental chamber on the ASU campus, at a constant temperature of 20°C and a photoperiod that mimicked natural conditions. Birds were fed an *ad libitum* diet of black oil sunflower seeds and tap water.

## Plumage coloration

Plumage coloration was quantified using digital photography, following standard published methods for this species (Oh and Badyaev 2006) and others (e.g., McGraw et al. 2002). Because House Finch plumage does not significantly reflect in the UV (Keyser and Hill 1999; McGraw and Hill 2000), techniques that rely on visible-light are sufficient to capture variation in bird-visible and carotenoid-relevant coloration. Using a Canon PowerShot SD1200S, we took two separate photographs of the head, breast, and rump of each bird against a gray-board, using identical distances from camera to object, shutter, exposure, and flash settings for each photograph, and including a color/size standard in each photo to control for any slight variations in object illumination. Ambient lighting was kept constant by photographing finches in the shade of buildings. Digital images (JPEG, 3,648 × 2,736 pixels) were imported into Adobe Photoshop to extract plumage hue of the carotenoid coloration. Values for the two pictures of each bird were averaged for statistical analyses (repeatability = 0.99 calculated using the method of Lessells and Boag 1987).

## Carotenoid discrimination test

To examine whether House Finches can non-visually discriminate foods on the basis of carotenoid content, we prepared two types of experimental seed—control and carotenoid-enriched. Control seed consisted of plain whole sunflower seed kernels, which contain very low levels of carotenoids (see below), while carotenoid-enriched seed consisted of the same seeds coated with zeaxanthin (OptiSharp$^{TM}$; DSM, Heerlen, Netherlands). To apply the carotenoid to the seed, we suspended 4.5 mg of zeaxanthin in 150 ml of water, spread it over 450 g of seed, then dried the seeds overnight at 50°C. This supplementation significantly enhanced the carotenoid content of the seeds ($t = 9.62$, $df = 2.45$, $p = 0.0052$). The high-carotenoid seed contained $3.72 \pm 0.25$ μg/g of total carotenoids, while the regular seeds contained $1.21 \pm 0.08$ μg/g. Both concentrations are in the range of carotenoid concentrations found in natural House Finch food (Hill et al. 2002).

In an effort to remove possible color-visual cues generated by the addition of carotenoids (carotenoid-enriched seeds were more orange), we dyed both seed types with 30 drops of green food coloring (McCormick, Sparks, MD, USA), a preferred food color of House Finches (Bascuñán et al. 2009), and presented the seeds under filtered light. We placed red filters (Roscolux Fire #19; Rosco Laboratories, Stamford, CT, USA) over standard fluorescent light bulbs (Sylvania, 34 W, T12 rapid start Super Saver; Osram-Sylvania, Danvers, MA, USA) to produce a light environment limited to wavelengths >550 nm (Toomey and McGraw 2011). We measured the spectral properties of both seed types with a UV–Vis spectrophotometer (Butler et al. 2011), and assessed the chromatic and achromatic contrast of the types using an avian visual model (Vorobyev et al. 1998; supplemental methods). The spectral sensitivities of the House Finch are not known, so we used parameters from the Canary (Serinus canaria), the most closely related species for which these data are available (Das et al. 1999). We found that the carotenoid-enriched seeds were visually indistinguishable from the control seeds when all were dyed green and presented under red-filtered light; in other words, the avian visual chromatic and achromatic contrast between plain and carotenoid-enriched seeds did not differ significantly from the amount of contrast within each seed type (Table 1). We are confident that the unnatural light environment used in this experiment did not affect bird behavior, as they ate the same amount of seed (2–3 g) as did birds in a similar experiment with non-filtered light (Bascuñán et al. 2009).

For the food choice tests, we measured out 10 g of each seed type into separate white dishes and presented them simultaneously to each bird for 1 h (Bascuñán et al. 2009). The dishes were 15 cm apart, and we randomized the spatial presentation of the carotenoid-enriched and control food. We carried out two feeding tests per bird on separate days (11 and 13 November 2010), beginning at 0700 hours and following an overnight period of food deprivation. At the conclusion of each test, we quantified food consumption by measuring the mass of the food remaining in each dish. We did not take into account the spilled seeds because the number of seed on the floor of the cage were negligible compared to the amount of seed eaten by the birds.

**Table 1** Avian visual model contrast values within a seed type and between plain and carotenoid-enriched seeds under experimental lighting conditions

| | Contrast within (jnds) | Contrast between (jnds) | $t$ | $df$ | $p$ |
|---|---|---|---|---|---|
| Chromatic plain | $2.33 \pm 0.20$ | $2.54 \pm 0.12$ | $-0.95$ | 328 | 0.34 |
| Chromatic carotenoid | $2.34 \pm 0.13$ | | $-0.93$ | 328 | 0.35 |
| Achromatic plain | $11.78 \pm 0.88$ | $12.58 \pm 0.62$ | $-0.74$ | 328 | 0.46 |
| Achromatic carotenoid | $12.52 \pm 0.83$ | | $-0.059$ | 328 | 0.95 |

## Odor discrimination test

To test whether or not finches prefer to feed on foods scented with a carotenoid-derived aroma, we presented two dishes of the plain seed, as described above, and affixed a 5-cm$^2$ piece of $\beta$-ionone-scented or sham-scented filter paper above the dishes. We did not scent the food directly with $\beta$-ionone because we did not want to change the food taste. The $\beta$-ionone scent consisted of a mixture of 20 µl $\beta$-ionone (96% I12603; Sigma-Aldrich, St. Louis, MO, USA) in 980 µl sunflower oil applied to the filter paper. This mixture yields a $\beta$-ionone concentration of 1.89 µg g$^{-1}$ seed, which is consistent with the concentrations found in ripe fruits (Beekwilder et al. 2008). The sham stimulus was simply 1 ml plain sunflower oil applied to the filter paper. We carried out a single test per bird on 22 November 2010, following the same procedure as the carotenoid discrimination test above.

## Statistics

All statistical analyses were carried out with SPSS 13.0 (SPSS, Chicago, IL, USA) with α set at 0.05. To test for food preferences, we used repeated-measures analyses of variance (rmANOVA), with seed type or odor treatment as the within-subjects factor and capture location as the between-subjects factor. In the comparison of carotenoid-enriched and control foods, one of the samples from a Site 3 bird was lost (spilled), resulting in a final sample sizes of 15 from Site 1, 15 from Site 2, and 14 from Site 3. Plumage color was not included as a factor in the rmANOVA because finches trapped at the three sites have significantly different colors (unpublished data) and color measures were only available for a subset of the males: 12 from Site 1, 12 from Site 2, and 13 from Site 3. Instead, we ran correlations between the proportion of carotenoid-enriched seeds eaten and plumage hue for the three sites. We tested the statistical power of our tests using the pwr package (Champely 2009) in R 2.10 (R Development Core Team 2010) and the effect sizes reported by Senar et al. (2010).

## Results

Finches did not consume significantly different amounts of plain versus carotenoid-enriched seeds in the first experiment ($F_{1,40} = 0.725$, $p = 0.40$; Fig. 1a), nor did they consume significantly different amounts of seed from the $\beta$-ionone-scented versus control dishes ($F_{1,41} = 1.22$, $p = 0.28$; Fig. 1b). There was no significant effect of capture location on food preference (carotenoid discrimination test: $F_{2,40} = 2.29$, $p = 0.12$; odor discrimination test: $F_{2,41} = 1.6$, $p = 0.21$) or the total amount of food eaten (carotenoid

discrimination test: $F_{2,41} < 1.31$, $p = 0.28$; odor discrimination test: $F_{1,40} = 2.29$, $p = 0.12$) during either experiment. Finally, we did not find any significant regressions between plumage coloration and food preference during the carotenoid discrimination test (Site 1: $F_{1,11} = 0.63$, $p = 0.45$; Site 2: $F_{1,11} = 0.002$, $p = 0.96$; Site 3: $F_{1,12} = 1.9$, $p = 0.19$) and the odor discrimination test (Site 1: $F_{1,11} = 0.74$, $p = 0.41$; Site 2: $F_{1,11} = 0.008$, $p = 0.98$; Site 3: $F_{1,12} = 0.26$, $p = 0.62$).

With our sample size ($n = 45$), we had sufficient power (0.973) to detect the magnitude of carotenoid preferences
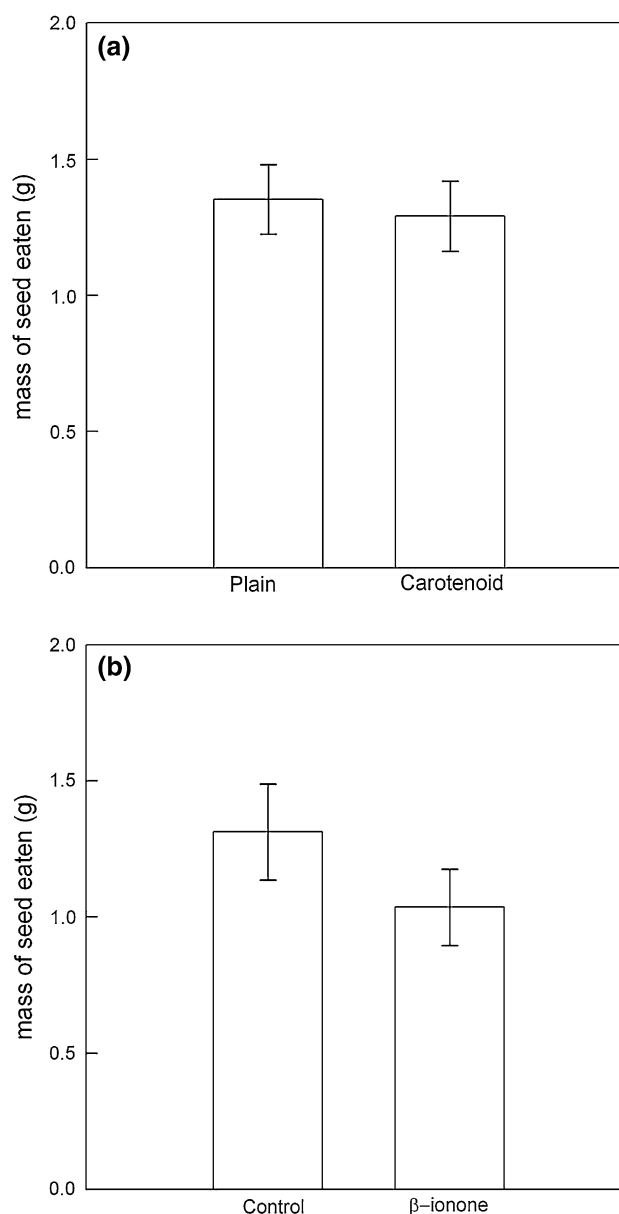


**Fig. 1 a** Mean ± SE mass of plain and carotenoid-enriched seeds eaten by House Finches (*Carpodacus mexicanus*). **b** Mean ± SE mass of plain and $\beta$-ionone-scented seeds eaten

similar to those reported by Senar et al. (2010) (i.e., approx. 40% difference in food intake between treatments).

## Discussion

To consume foods that meet nutritional and physiological requirements, animals may employ foraging preferences for specific nutrients using different cues like food color, taste, or smell. For example, in food choice experiments, European Blackcaps (*Sylvia atricapilla*) selected food containing anthocyanins (antioxidant compounds) over food without anthocyanins (Schaefer et al. 2008). Recently, Senar et al. (2010) observed that Great Tits discriminate between carotenoid-rich and -poor foods that were visually indistinguishable, and suggested that they may use non-visual cues such as taste or smell to assess carotenoid content.

Avian olfaction has been seldom considered in behavioral ecology research (i.e., mostly in navigational studies; Wallraff 2004), and very few studies have examined how birds use smell in the context of foraging (Nevitt et al. 1995; Roth et al. 2008; Kelly and Marples, 2004). This is especially the case in passerines, for which olfactory bulb size is very small compared to other species (Bang and Cobb 1968). Previously, a study on Blue Tits (*Cyanistes caeruleus*) showed that birds are more attracted to feeder boxes with lavender odor than odorless feeder boxes, after a period during which birds were trained to associate lavender odor with food (Mennerat et al. 2005). Another study found an additive effect of novel color and novel odor on food consumption in Zebra Finches (*Taeniopygia guttata*; Kelly and Marples 2004). However, in the same study, birds did not react to the novel odor alone.

In our study, we tested the possibility that House Finches detect carotenoids in their food using smell. We did not find evidence for non-visual carotenoid discrimination. These negative results obtained are unlikely to have resulted from experimental limitations for several reasons. First, we used a greater difference in carotenoid concentration between carotenoid-enriched and plain seed than did Senar et al. (2010). Second, we used a larger sample size ($n = 45$), giving us ample power to detect the effects reported in previous food-choice experiments with birds (Senar et al. 2010; Schaefer et al. 2008). Finally, our manipulation of food color and lighting conditions ensured that visual cues could not influence food preference.

Several hypotheses could explain the absence of food preference in our experiments. First, natural sources of carotenoids potentially contain flavors and odorants not present in our experimental manipulations. Many of the flavors and aromas of fruits are generated through the specific enzymatic cleavage of carotenoids during ripening (Britton 2008), and may have been absent in the purified

carotenoid supplement we used in our study. In addition, $\beta$-ionone is one of the numerous carotenoid-derived aromas ($\beta$-damascenone; for example, Winterhalter and Rouseff 2002; Beekwilder et al. 2008), but it is possible that other specific aromas or flavors could be used by birds to discriminate carotenoid content. Second, it remains possible that House Finches use non-visual cues to find carotenoids in the diet at other times of the year, especially during molt when House Finches are most likely to be avid carotenoid-seekers to develop carotenoid-based coloration (Hill et al. 2002). Third, a species' foraging ecology may affect the likelihood and strength of carotenoid detection in food as well as what detection cues are used. For example, House Finches eat primarily seeds and fruits (Hill 1993), which often use color to attract birds (Willson and Whelan 1990). Thus, finches may rely heavily on these visual cues to locate and discriminate food. For example, House Finches have distinct food color preferences, with an aversion to yellow and a preference for red and green (Bascuñán et al. 2009; Stockton-Shields 1997). In contrast, tits primarily eat insects that tend to be camouflaged or display aposematic coloration with chemical defenses (Royama 1970), such that coloration may not be a reliable indicator of food quality, and non-visual cues like taste and smell may be used instead.

In our experiments, plumage color did not influence food preference during the carotenoid and odor discrimination tests. Previously, Bascuñán et al. (2009) found that redder birds demonstrated a higher degree of food selectivity, measured as the proportion of their preferred food color consumed. Thus, it is possible that redder birds may be more selective, using non-visual cues, on the specific food with the amount of carotenoids physiologically needed, but our study does not rule out this hypothesis. Future experiments may examine this question by giving repeatedly different foods (with the same color) with several levels of carotenoids and assessing the potential link between food selectivity and coloration.

Birds may also develop preferences for carotenoid-rich food sources through post-ingestive feedback mechanisms (Yearsley et al. 2006). Carotenoids may provide a positive feedback through their antioxidant and immune-enhancing effects (McGraw 2006), and studies of other bird species demonstrate the conditioned discrimination of certain nutrients and by-products through negative or positive post-ingestive feedback (Clark and Mason 1987; Werner et al. 2008). Our study does not rule out this possibility because birds had access to carotenoid-enriched food only two times during 1 h. If such learning is an important part of carotenoid foraging, it will be particularly interesting to examine which cues (e.g., color, aroma, flavor) are the most salient because such foraging preferences may influence mate choice and shape sexual selection. For example, the

evolution of carotenoid-based sexually selected coloration in guppies (*Poecilia reticulata*) and sticklebacks (*Gasterosteus aculeatus*) has been linked to foraging preferences for carotenoid-rich foods (Rodd 2002; Smith et al. 2004). This linkage has typically been discussed as a heritable bias for particular traits; however, recently, learned biases have been recognized as important selective forces, with a unique influence on the evolution of sexual signals (Cate and Rowe 2007). Thus, learning the cues associated with specific nutrients, like carotenoids, has the potential to influence the direction and intensity of sexual selection (e.g., Rodd 2002).

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