

# Carotenoid-rich mouth colors influence the conspicuousness of nestling birds

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**Abstract** When allocating investment among offspring, parents might maximize their fitness by biasing investment toward offspring with the best direct fitness prospects. The observed preferences of avian parents for carotenoid-rich mouth colors that advertise good condition has been interpreted as support for this hypothesis. However, because these condition-dependent visual signals might also make offspring more visually conspicuous, active parental preferences for carotenoid-rich traits are difficult to distinguish from passive responses to differences in detectability among offspring. Here, we used a visual model to examine how mouth colors influence the visual conspicuousness of nestling house sparrows (*Passer domesticus*) to parents under a suite of realistic ambient light conditions. We found little evidence that mouths rich in carotenoids provided more conspicuous targets to parents than mouths poor in carotenoids. While other features of

mouth color may have evolved to increase conspicuousness, our results suggest that carotenoid-based coloration is not a product of detectability pressures and rather may serve as a signal of nestling quality.

**Keywords** Begging · Carotenoids · Detectability · Mouth color · Visual signaling · *Passer domesticus*

## Introduction

Offspring influence the allocation of limited parental care. This influence may be the product of competition between siblings (Kacelnik et al. 1995; Parker et al. 2002) or may be exerted when parents seemingly control how resources are distributed (Lyon et al. 1994; Kilner 1995). To the extent that parents actively bias distribution, they are expected to do so nonrandomly with respect to variation in the fitness prospects of individual offspring (i.e., the return on investment that each offspring offers; Trivers 1974; Godfray 1991, 1995). For example, vocalizations (e.g., Price and Ydenberg 1995), stereotyped postures (e.g., Smith and Montgomerie 1991), and specialized morphologies (e.g., Kilner 1997; Saino et al. 2000; Jourdie et al. 2004) expressed during begging displays by avian nestlings all vary with offspring state (i.e., hunger and/or condition), and all influence the allocation of parental care (references above).

While positive parental responses to signals of hunger (Mondloch 1995; Kilner 1995, 1997) suggest that fair allocation is the parents' goal, parental response to variation in offspring condition paints a very different picture. In many nestling birds, the mouth is decorated with carotenoid-based colors (Hunt et al. 2003; Loiseau et al. 2008; Thorogood et al. 2008) that vary reliably with

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standard measures of condition (body mass in the house sparrow (*Passer domesticus*; Loiseau et al. 2008), immune response in the barn swallow (*Hirundo rustica*; Saino et al. 2000, 2003), and tarsus length in the hihi (*Notiomystis cincta*; Ewen et al. 2008)), mirroring the more familiar condition dependence of carotenoid-based sexual ornaments expressed by adults (e.g., Hill 2002). When parents respond to variation in carotenoid-based mouth colors, they do so by delivering more food to mouths that are, or are manipulated to appear, carotenoid-rich (Saino et al. 2000; Loiseau et al. 2008; Ewen et al. 2008; Dugas 2009), paralleling the common female mating preference for carotenoid-rich male ornaments in a wide variety of taxa (e.g., Houde 1997; Hill 2002).

A critical question is whether parents actively favor offspring in good condition or whether allocation differences are merely a function of variation in nestling detectability (Royle et al. 2002; Galván et al. 2008). In the latter case, the evolution of nestling mouth colors might have been driven, largely or exclusively, by properties of the parental visual system, as might proximate parental responses to variation in this trait. The perception of color signals is restricted by ambient light conditions as well as the visual system of the receiver (Endler 1993a), and variation in ambient light can drive the evolution of visual signals (e.g., Marchetti 1993; Stuart-Fox et al. 2008). Because many birds nest in relatively dim locations (e.g., dense vegetation, cavities (Avilés et al. 2008)), mouth parts may have evolved simply to increase the conspicuousness of nestlings, facilitating efficient food transfer from parent to offspring (Ingram 1920; Kilner and Davies 1998; Avilés et al. 2008). Consistent with this detectability hypothesis, comparative evidence suggests that evolution of the nestling mouth has been influenced by nest lighting environment (Ficken 1965; Kilner and Davies 1998; Kilner 1999; Hunt et al. 2003; Avilés et al. 2008). Experimental manipulation also suggests that parental responses to nestling mouth colors are driven by an interaction between colors and ambient light: under low-light conditions only, artificially reducing mouth-color contrast in nestling great tits (*Parus major*) reduced nestling mass gain when parents provisioned (Heeb et al. 2003; but see Götmark and Ahlström 1997).

Parental responses to carotenoid-rich mouths could indicate that parents use this condition-dependent trait to direct resources to especially promising offspring, but any such insights are limited by our lack of knowledge about how carotenoids influence visual conspicuousness. Here, we used a visual modeling approach (Gomez and Théry 2007) to determine how carotenoid-based flange color of nestling house sparrows, a condition-dependent trait (Loiseau et al. 2008, this paper) to which parents respond positively (Loiseau et al. 2008; Dugas 2009),

influences the conspicuousness of the flanges of nestling house sparrows. If carotenoid-rich mouths are more detectable than carotenoid-poor mouths, an active parental preference is indistinguishable from an essentially passive response to the most conspicuous visual target. If, however, carotenoid-rich mouths are not more detectable, parental response can be interpreted as the result of parental favoritism.

## Materials and methods

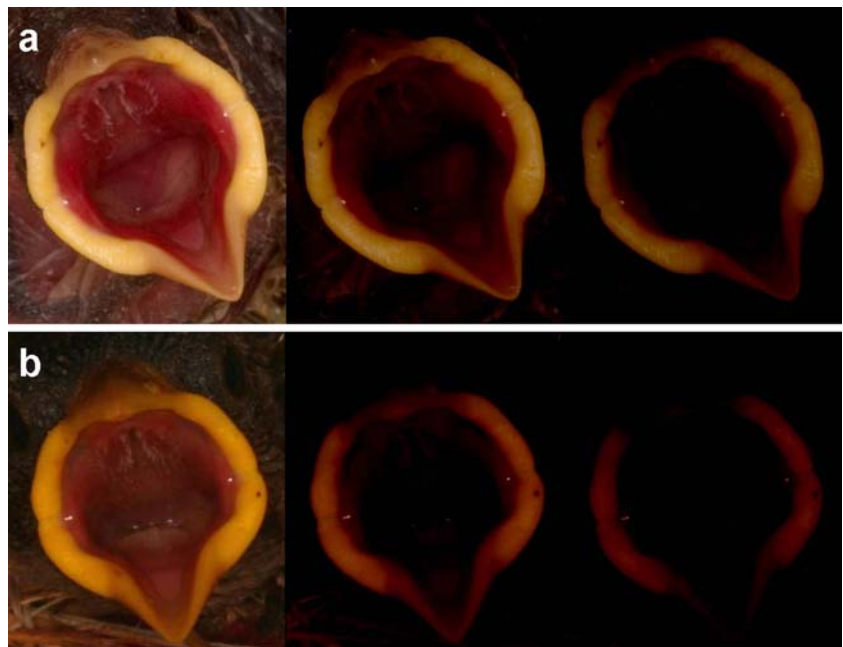
Study animals were drawn from a free-living population of house sparrows occupying nest boxes in Norman, Oklahoma, USA (for details see Schwagmeyer et al. 2002) from May to July 2006. Clutches were monitored regularly to establish day of hatching (day 0). On days 2, 3, and 5, chicks were removed from nests briefly (10 min) and taken to a nearby car, hidden from the view of parents, where they were weighed to the nearest 0.01 g on an electronic balance and assessed for mouth part coloration. On the first day of measurement, marker was applied to the legs of chicks to identify individuals on subsequent days. We sampled entire broods, but to avoid potential desertion by parents, at least one nestling remained in the nest at all times.

House sparrows are typically cared for in the nest for 14 days posthatching (Anderson 2006). Because parental attendance to visual signals requires parental control of allocation, we focused on younger ages, when parental control is likely maximized (Royle et al. 2002; Dugas 2009). Although we would have liked to sample chicks even earlier in the nestling period, handling and color sampling was limited by the small size of young nestlings; we sampled day-2 chicks only after considerable experience with the larger day-3 nestlings.

### Measuring reflectance

In house sparrows, gaping nestlings display a red palate bordered by clearly delineated yellow flanges (Fig. 1) colored by carotenoids (Loiseau et al. 2008; Dugas and McGraw, unpublished data). We measured the reflectance of these two regions using a USB4000 spectrometer (Ocean Optics, Dunedin, FL, USA). Tissue was illuminated by light produced by a deuterium–tungsten halogen lamp (Ocean Optics DT-MINI-2-GS), and spectrometer output was recorded using SpectraSuite software (Ocean Optics). Reflectance is quantified as the percentage of light that tissue reflects at each wavelength relative to a uniformly reflective white standard (WS-1). To control ambient light, which might interfere with accurate color measurements, the color of nestling mouth parts was measured inside a

**Fig. 1** Images of **a** carotenoid-poor and **b** carotenoid-rich house sparrow nestling mouths manipulated to illustrate how ambient light influences achromatic detectability. Mouths were photographed digitally under identical lighting conditions with identical camera settings. The brightness (total red/green/blue value) of both photos was then reduced incrementally (moving left to right) using ImageJ (Abramoff et al. 2004) to illustrate for human vision the effect of low ambient light on the conspicuousness of the two mouths



portable “dark box” constructed with wood and dark cloth. The nestling’s mouth was gently held open, and the reflectance probe was placed at a 90° angle to the tissue (Andersson and Prager 2006). Four reflectance measurements were taken from both the palate and the rictal flanges, and medians for each tissue were used for further analysis. White standards were resampled every four measurements (e.g., between flange and palate measurements), and dark standards, which calibrate the spectrometer to background noise (e.g., that generated by heat), were taken between each brood.

Because visual conspicuousness is defined, in part, by the contrast between the flange and the nest, we also sampled reflectance from nesting material. Older nestlings compact and soil nesting material as they approach fledging, and so we collected ten nests in which eggs were laid but did not hatch and sampled their color in the lab. Ten reflectance measurements were taken from each nest (evenly spaced in the nest cup), and a mean of these 100 measurements was used to represent the average nesting material background.

#### Measuring ambient light

House sparrows occupy a wide variety of nest sites including dirt burrows, free-standing nests within tree branches, and natural and artificial cavities; in all, light illuminates nestlings through a narrow opening (Anderson 2006). We measured ambient light in an empty nest box (boxes have a 2.5-cm round opening that is 12.5 cm above the 11×11-cm floor) with a USB4000 spectrometer and a 600-nm ultraviolet/visible irradiance probe fitted with a

cosine corrector (CC3-UV) and calibrated with an LS-1 Cal lamp (Ocean Optics). The irradiance probe passed through a small hole in the bottom of the nest box and was fixed into position. Dark cloth was used to prevent light from entering the box from below.

To model signals under realistic lighting conditions, we sampled light in the center of the box at two vertical positions (7 and 9 cm above the floor) based on likely positions of chicks within the nest. We estimated these as modal nest height (distance from the wooden floor to bottom of the nest cup, 2 cm)+mean body length (mean±1 SD; day 2 chicks, 5.2±0.6 cm; day 5 chicks, 7.1±0.7 cm). Ambient light was measured at three times of day: 20 min after sunrise, 1 h after sunrise, and at noon (times are, hereafter, referred to as dawn, morning, and noon). In this population, feeding rates are highest in the 2 h after sunrise (Schwagmeyer and Mock 1997). The nest box was rotated so that all measurements were taken with the box facing each cardinal direction. To approximate the lighting conditions parents experienced before entering a box, we also sampled ambient light directly above the box at each measurement time. The habitat near nest boxes is homogenous and almost entirely open (free from trees or other obstructions which would change the composition of irradiance spectra (Endler 1993a)), so this irradiance is a good estimate of light conditions experienced by parents prior to feeding bouts.

#### Quantifying color

To estimate the carotenoid content of colors nonlethally, we calculated the chroma, or saturation, of the reflectance

curve (sensu Endler 1990). Carotenoids produce colors rich in long wavelengths (e.g., yellow, orange, red) via absorption of short-wavelength light (e.g., blue and green; Fox and Vevers 1960; Andersson and Prager 2006). Comparison of reflection at short and long wavelengths is, therefore, a commonly used proxy for the carotenoid concentration of tissues (see Montgomerie 2006 for review). We chose chroma (Endler 1990) to serve a carotenoid proxy because it has been empirically demonstrated to predict the carotenoid content of tissues (Saks et al. 2003) including the flange tissue of nestling house sparrows (Dugas and McGraw, unpublished data).

### Quantifying contrast

To capture the conspicuousness of nestling flanges, we determined their contrast with both the nesting material and the palate, using the model of Gomez and Théry (2007) to calculate chromatic and achromatic contrast. We began by computing quantal catch:

$$Q_i = \int_{300}^{700} R(\lambda)I(\lambda)S_i(\lambda)d\lambda$$

where  $\lambda$  is the wavelength in nanometers,  $R$  is reflectance,  $I$  is spectral irradiance, and  $S_i$  refers to the spectral sensitivity of each of the  $i=4$  cone classes in house sparrows (Chen and Goldsmith 1986). Quantal catch was computed for reflectance functions  $R$  of each nestling flange color, for the corresponding palate color, and for average nest reflectance, using the 24 measured irradiance functions  $I$ : ambient light measurements taken at two positions within the box at all four cardinal directions at three times of day.

We, then, corrected quantal catch to take into account receptor saturation and model color constancy (Gomez and Théry 2007):

$$q_i = \frac{Q_i}{Q_i + Q_i^B}$$

For  $Q_i^B$ , we used irradiance measurements taken directly above the nest box (parent eyes were adapted to current outside lighting conditions, i.e., dawn, morning, and noon). Our logic for this was that parents entering the box for short periods are likely to remain light adapted to outdoor conditions between entering the nest cavity and feeding nestlings (see Reynolds et al. 2009 for review; for a sample of 11 house sparrow pairs, the modal time that parents spent in the box before delivering food averaged  $4.5 \pm 2$  s, D.W. Mock, unpublished data). Corrected  $q_i$  were normalized to relative excitations after Gomez and Théry (2007), producing a three-dimensional, tetrahedral color space defined by the

maximal responses of each cone class. Chromatic contrast between two color patches (flange vs palate or flange vs nesting material) was defined as the Euclidean distance between them. Achromatic contrast was defined as the square root of the squared difference in the summed response of double cones (modeled by combining medium and long-wavelength absorbance spectra) to each color patch (Gomez and Théry 2007).

### Data analysis

With ambient light measurements taken at two positions within the box at all four cardinal directions at three times of day, there were 24 potential variables that captured the chromatic and achromatic contrast of each flange against both the nesting material and the palate. For each of four contrast elements (achromatic and chromatic contrast for flange vs nest and flange vs palate), contrast scores were entered into a principal components analysis to reduce the number of potential dependent variables for later analysis.

To confirm a relationship between flange color and mass in this population (such a relationship was previously reported in a French population of house sparrows; Loiseau et al. 2008), we used a general linear model (GLM) with mass entered as the dependent variable, brood as a random factor, and flange chroma as a covariate (sensu de Ayala et al. 2007). Because some chicks were measured at more than one age, each age group (day 2: 22 chicks from six broods, 3: 65 chicks from 19 broods, and 5: 34 chicks from 11 broods) was considered separately. To examine the relationship between nestling age and color, we used a repeated measures analysis of variance with chicks measured at all three ages (14 chicks from four broods) and on larger subsets of chicks measured on two of the 3 days. Brood of origin was included as a between-subjects factor.

We then examined the relationship between the chroma of each flange and the associated contrast principal components (PC) using correlations ( $N=121$ ). First, because we were interested only in how carotenoid content influenced detectability, and to maximize the range of colors included, we considered each individual flange measurement as an independent data point. However, because it is at least possible that this relationship could be influenced by other features of reflectance (e.g., brightness) which could be associated with brood of origin or individual identity, we also analyzed a reduced data set in which we included only one nestling per brood and each brood only once (final  $N=23$ ). When broods were measured more than once, we excluded brood samples so that the distribution of ages would be as even as possible, and chose one chick per brood randomly (final  $N$  at day 2=6, day 3=10, and day 5=7). Alpha was set at 0.05 throughout.

## Results

### Flange colors and nestling mass

Chroma was positively associated with nestling mass on day 2 and 3, but not on day 5 (see Table 1). Average chroma increased with age (repeated measures  $F_{2,20}=4.11$ ,  $p=0.032$ ). Analysis of chicks measured on two of the 3 days revealed a similar pattern; chroma increased from day 2 to 3 (repeated measures  $F_{1,11}=7.31$ ,  $p=0.021$ ) and from day 3 to 5 (repeated measures  $F_{1,20}=8.89$ ,  $p=0.007$ ). Although we considered a relatively narrow age range here, variation in flanges of these day 2–5 nestlings (range=0.10–0.35, mean  $\pm$  SD =  $0.237 \pm 0.05$ ) actually exceeded the variation in a sample of day 3–9 nestlings in 2008 (range=0.13–0.32, mean  $\pm$  SD =  $0.238 \pm 0.04$ ).

### Principal components analysis of contrast scores

Both achromatic and chromatic flange–palate contrasts were explained by single PCs with eigenvalues greater than 1 (28.83 for achromatic, 23.52 for chromatic), explaining 99% and 98% of variance, respectively. Both were characterized by highly positive loadings under all conditions. Flange–nest achromatic contrast had two PCs extracted, explaining 99% of the variance together (PC1: 67%, eigenvalue=16.10; PC2: 32%, eigenvalue=7.74). Flange–nest achromatic PC1 had highly positive loadings for all morning and noon lighting conditions, while PC2 had highly positive loadings from only dawn conditions. Chromatic flange–nest contrast was described by two PCs, together explaining 95% of the variance (PC1: 89%, eigenvalue=21.34; PC2: 6%, eigenvalue=1.55). PC1 had highly positive loadings at the high position at dawn

and noon, but highly negative loadings at the low position at dawn and under morning conditions. PC2 had positive loadings at the low position at dawn, facing east at morning, and west at noon. Details of PC loadings are presented in [online supplementary material](#).

### Flange colors and contrast

#### *Achromatic contrast*

Flange chroma was negatively associated with contrast between the flange and nest under morning and noon light conditions (flange–nest PC1), but was not associated with flange–nest contrast at dawn (flange–nest PC2), or contrast between the flange and palate (flange–palate PC; Table 2).

#### *Chromatic contrast*

Flange chroma was negatively associated with the first flange–nest PC, meaning that a high-chroma (carotenoid-rich) flange had higher chromatic contrast with nesting material in the morning and at the low position at dawn, but lower contrast at the high position at dawn and at noon. Flange chroma was also negatively associated with the second flange–nest PC, which had positive loadings from the low position at dawn and facing east in the morning and west at noon (Table 2). Flange chroma was, however, positively associated with chromatic contrast between the flange and palate (flange–palate PC; see Table 2). While the relationships between chroma and the second flange–nest PC and the flange–palate PC were not significant in the reduced data set, the patterns were in similar directions as in the full data set (Table 2).

**Table 1** Results of GLMs assessing the relationship between flange chroma and mass at three ages (2, 3, and 5 days posthatching)

Age	Mass				
	Num. <i>df</i>	Den. <i>df</i>	<i>F</i> ratio	<i>p</i> value	Beta (SE)
2					
Chroma	1	15	12.11	0.003	26.40 (7.59)
Brood	5	15	2.61	0.069	
3					
Chroma	1	45	5.58	0.023	27.36 (11.59)
Brood	18	45	1.63	0.094	
5					
Chroma	1	22	1.81	0.192	NS
Brood	10	22	0.74	0.683	

Mass was entered as the dependent variable, chroma as a covariate, and brood ID as a random factor

*Num* numerator, *Den* denominator, *SE* standard error, *NS* not significant

## Discussion

Flange chroma, a proxy for carotenoid content, was positively associated with nestling mass (a reliable predictor of recruitment in this population (Schwagemeyer and Mock 2008)) and age. In the achromatic channel, the only effect of flange chroma was a slight reduction in the contrast between the flange and nesting material. Flange chroma positively influenced chromatic contrast between the flange and palate, but the effect of chroma on chromatic flange–nest contrast was inconsistent across lighting conditions. Overall, we found little support for the idea that carotenoid-rich flanges would be more visually detectable to parents than carotenoid-poor flanges. This result suggests parental preferences for carotenoid-rich mouth parts (Saino et al. 2000; Loiseau et al. 2008) can be safely interpreted as parental choices rather than essentially passive responses to detectability.

**Table 2** Correlations between flange chroma and achromatic and chromatic contrast PCs

	Chroma			
	All nestlings ( $N=121$ )		One nestling per brood ( $N=23$ )	
	$R$	$p$ value	$R$	$p$ value
Achromatic				
Flange–Nest PC1	–0.237	0.009	–0.635	0.001
Flange–Nest PC2	0.141	0.124	0.188	0.390
Flange–Palate PC	–0.023	0.798	–0.381	0.073
Chromatic				
Flange–Nest PC1	–0.439	<0.001	–0.752	<0.001
Flange–Nest PC2	–0.565	<0.001	–0.381	0.054
Flange–Palate PC	0.303	0.001	0.369	0.083

We included all nestling mouths in one analysis, and in a second, used a reduced data set with only one chick per brood

While birds use both achromatic and chromatic contrast to detect objects (Osorio et al. 1999; Schaefer et al. 2006), both experimental and comparative evidence suggest that the achromatic channel is more likely to mediate parental location of nestling mouths. Experimental tests suggest that birds rely principally on achromatic contrast for the detection of movement, edges, and patterns (Osorio et al. 1999; Jones and Osorio 2004), needed for the task facing provisioning parents: detecting the flanges bordering a moving mouth and placing food at its center. The general signal design of mouth colors also suggests that high achromatic contrast is a conserved feature of the mouth: flanges and palates contrast greatly in brightness, even when they have similarly shaped reflectance curves (i.e., are the same color (Hunt et al. 2003)). Differences between cavity and open nesters also support the achromatic detectability hypothesis: flanges of cavity nesters are brighter (Hunt et al. 2003; Avilés et al. 2008) and less densely colored (closer to white) than those of open nesters (Kilner and Davies 1998; very dense carotenoids should also decrease chromatic contrast, see Andersson and Prager 2006). We found the effect of carotenoid-based colors on achromatic contrast to be negligible or negative, suggesting that carotenoids are unlikely to influence parental allocation by making chicks more visually detectable (see Fig. 1).

A reduction in achromatic contrast is an unavoidable consequence of carotenoid deposition. Carotenoids create colors by subtracting short-wavelength light (Shawkey and Hill 2005; Andersson and Prager 2006), and so, the deposition of these pigments in the flanges decreases the brightness of these structures. Because flanges are brighter than both surfaces with which they are juxtaposed, the palate and nesting material (Hunt et al. 2003; Avilés et al. 2008), subtractive carotenoid-based colors necessarily lower the achromatic conspicuousness of the flange. When animals are illuminated by light relatively rich in medium-wavelength light (e.g., below green leaves), the negative effect of carotenoids on overall brightness will be greater

than when light is rich in long wavelengths (Endler 1993a, b). Of course, the absolute effect of pigment deposition on signal conspicuousness will depend on the absolute light levels at the nest (Avilés et al. 2008). In cavity nests, nestling behavior (e.g., stretching the neck upwards, begging at the cavity portal) can offer nestlings, especially older ones, some control over their signaling environment, and this will be an important factor to consider in future behavioral studies.

Yellows more often color the mouths of cavity nesters than the orange or red carotenoids (Ficken 1965, but see Kilner and Davies 1998) that might more accurately signal quality (Hill 1996) or exploit parental sensory biases (Kilner 1999), but would impose an even higher detectability cost (Andersson 2000). While the detectability hypothesis can explain interspecific patterns of mouth colors, it does not explain the presence of carotenoid-based colors in nestling mouths. Rather, our results indicate that carotenoids are signal components that come at the cost of impaired detectability (see also Andersson 2000) and suggest that nestlings may have faced competing pressures to produce a trait that is detectable and reflects quality. The yellow (i.e., not orange or red) colors of cavity nesters (Ficken 1965; Kilner 1999) could, then, be interpreted not as an adaptation that increases detectability per se, but rather the result of constraints imposed by detectability requirements.

While achromatic contrast is probably used for detecting the mouth, Osorio et al. (1999) suggest that the chromatic channel might be better suited to encode information about color differences between individuals. Color parameters associated with high carotenoid content enhanced chromatic contrast between the flange and nest only under a few lighting conditions (and lowered contrast in most conditions), but increased chromatic contrast between the flange and palate under all light conditions. This contrast between the flange and palate (both intrinsic to the chick) might be the most reliable component with

which to assess quality. While birds display preferences for colors mediated by factors other than chromatic contrast (Ham and Osorio 2007), this effect of carotenoids is intriguing and supports the hypothesis that these colors have evolved in a signaling context. A context-dependent response to skin color in parent birds (Bize et al. 2006) also strongly suggests that parental preferences for visual signals can be mediated by active choice rather than a passive response to signal intensity.

The field of sensory ecology has traditionally focused on overall detectability as an important determinant of behavioral preference (e.g., Ryan and Keddy-Hector 1992; Endler 1993b; Cummings 2007), but recent theoretical (Arnqvist 2006) and empirical (Macías García and Ramirez 2005; Wong and Rosenthal 2006) evidence suggests that sensory detectability can be decoupled from signal attractiveness. Future research could benefit from a nuanced approach that considers the varied effects of pigment-based coloration on surface reflectance and their effects on receiver behavior.

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