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Female American goldfinches use carotenoid-based bill coloration to signal status

Troy G. Murphy,[a,b] Malcolm F. Rosenthal,[c] Robert Montgomerie,[a] and Keith A. Tarvin[c]
[a]Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada, [b]Department of Biology, Trinity University, One Trinity Place, San Antonio, TX 78212, and [c]Department of Biology, Oberlin College, Oberlin, OH 44074, USA

Interest in female ornamentation has burgeoned recently, and evidence suggests that carotenoid-based female coloration may function as a mate-choice signal. However, the possibility that females may signal status with coloration has been all but ignored. Bill coloration of female American goldfinches (*Spinus tristis*) changes seasonally, from dull gray in winter to bright orange in the breeding season. We conducted a series of aviary experiments in the breeding season to examine the signaling role of female bill color during both intra- and intersexual contests as well as during male mate choice. We tested for status signaling by examining whether caged females and males avoided feeding adjacent to female taxidermic models as a function of the model's bill color, which was experimentally augmented or dulled. We tested for a mate signaling function by giving captive males a choice between 2 live females with experimentally altered bill colors. Females avoided feeding near model females with colorful bills, but males showed neither avoidance of nor preference for females with more colorful bills. These results indicate that the female's carotenoid-based bill coloration signals status during competitive interactions and suggest that female bill color does not function as a mate-choice signal. This represents the first experimental evidence that a carotenoid-based coloration of females functions to mediate contest competition over food. *Key words:* American goldfinch, bill color, carotenoid signal, intrasexual selection, ornamental female, social selection, *Spinus* (*Carduelis*) *tristis*, status signaling. *[Behav Ecol 20:1348–1355 (2009)]*

Whereas an enormous amount of effort has been allocated to the study of male secondary sexual traits (Darwin 1871; Andersson 1994; Mead and Arnold 2004; Clutton-Brock and McAuliffe 2009), female signaling generally has been neglected in studies of ornamentation. Recent theoretical interest in female ornaments has resulted in studies showing that female traits indicate phenotypic or genetic quality, and that those traits are assessed by males during mate choice (Amundsen et al. 1997; Torres and Velando 2005; Amundsen and Pärn 2006). However, the role of elaborate female traits in signaling status has been virtually ignored. This is surprising because females, like males, often compete over limited resources, such as mates, food, territories, and nest sites. Thus, we should expect female signals of status to evolve to reduce investment in agonistic interactions by allowing competitors to assess the fighting ability of potential opponents, as has been reported often for males (for review see Senar 2006).

Status signals allow individuals to assess the relative dominance of potential competitors without risking injury or wasting time and energy fighting (Rohwer 1985; Senar 1990; Moore et al. 2002; Searcy and Nowicki 2005). Rohwer (1975) proposed that subordinates could signal their status to avoid inducing attacks from individuals that had greater fighting ability, and that dominant individuals could thereby avoid escalating during interactions that they could clearly win. When status signals play a role in mediating conflicts over non–mate-based resources (e.g., food), but do not necessarily provide access to more or higher quality mates, social selection (sensu West-Eberhard 1979, 1983) rather than sexual selection would account for the ornament's maintenance.

Examples of carotenoid-based status signals are rare. Among birds, there are only a few known examples of such signals, most of which have been found in males (Pryke et al. 2001; Pryke and Andersson 2003; Pryke and Griffith 2006; Griggio et al. 2007; see Murphy et al. 2009 and Crowley and Magrath 2004 for examples in females). In contrast, there are many examples of male melanin-based signals of status (for review see Senar 2006). Researchers have long thought that the high costs associated with carotenoid acquisition, assimilation, and conversion—and tradeoffs with certain physiological functions—render carotenoid signals reliable indicators of condition and thus ideal targets of mate choice but not particularly useful as status signals (McGraw and Hill 2000, but see Griffith et al. 2006). In contrast, melanin signals are thought to be favored as signals of status because they are often testosterone-limited (Evans et al. 2000), and hence, their expression can be directly linked to physiological allocation that enhances aggressiveness. Recent evidence, however, has shown that testosterone can also increase carotenoid bioavailability (Blas et al. 2006) and that there is a positive link between carotenoid ornamentation and testosterone (McGraw et al. 2006). Thus, carotenoid signals should also be expected to function as status signals. Because the honesty of status signals is thought to be partially maintained by the negative physiological effects of testosterone (Gonzalez et al. 2001), such as immunosuppression (Folstad and Karter 1992), selection should be expected to favor both carotenoid and melanin signals of status. Moreover, even if a carotenoid signal evolves primarily in a mate-choice context, the information it provides about individual quality or condition could be easily exploited by individuals engaging in competitive interactions (Griffith and Pryke 2006).

American goldfinches (*Spinus* [formerly *Carduelis*] *tristis*) have sexually dichromatic plumage during the breeding season, but, in both sexes, bill color changes from dull gray in the winter nonbreeding season to rich orange during the summer breeding season (McGraw and Middleton 2009). Just before the onset of laying, female bills are almost as colorful as those of males (Murphy TG, Tarvin KA, unpublished data).

Male bill color appears to function as a sexual signal that influences female choice. Mate-choice experiments have shown

Address correspondence to T.G. Murphy. E-mail: troy.murphy@trinity.edu.

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that females prefer to court males with more vivid yellow plumage and more colorful bills (Johnson et al. 1993), and other experiments link male plumage and bill color to diet and parasite status during the previous molt (McGraw and Hill 2000, 2001; McGraw et al. 2004). Additionally, both plumage color and bill color are correlated with current male body condition (Rosen and Tarvin 2006).

Bill coloration may also play a signaling role in female goldfinches. Recent work has shown that female and male goldfinch bill color reflects current immune status and probably stress level (Rosenthal MF, Murphy TG, Darling N, Tarvin KA, unpublished data). Furthermore, goldfinch bill color is at least in part carotenoid-based (Mundinger 1972), and bills become more orange when the diet is supplemented with carotenoids (tested in males only, McGraw et al. 2004; see Alonso-Alvarez et al. 2004 for similar results with female zebra finches, *Taeniopygia guttata*). Similarly, both sexes in other species with red–orange bills exhibit a positive correlation between bill color and plasma carotenoid levels (zebra finch, McGraw et al. 2003; Alonso-Alvarez et al. 2004; red-legged partridge, *Alectoris rufa*, Pérez-Rodríguez 2008). The development of an orange bill in female goldfinches immediately prior to the breeding season also suggests that there is a signaling function to the bill. This seasonal change indicates that the benefits of a colorful bill exceed the costs during the breeding season, possibly because the costs due to predation risk (e.g., Wiens 2001) or changes in physiological demand for or access to circulating carotenoids (e.g., Eraud et al. 2007) exceed the benefits during the nonbreeding season.

Using a series of aviary experiments, we investigated whether female bill color functions as a signal during both mate choice and contests over food. To test the intrasexual status-signaling hypothesis, we asked whether females avoided feeding adjacent to a competitor female as a function of the competitor's bill color. To do this, we presented individual female goldfinches with a choice between 2 feeders in an aviary, and adjacent to each feeder, we placed a female taxidermic model with either dulled or augmented bill color. According to the status-signaling hypothesis, females were predicted to perceive the augmented-bill model as signaling high competitive ability and as a result to feed from the feeder adjacent to the dulled-bill model.

We also tested for intersexual status signaling, and for male mate preference based on female bill color. We used the same experimental setup as for the female–female competition experiment but instead presented males with the choice of 2 feeders (again with female models that differed in bill color placed adjacent to the feeders). According to the intersexual status-signaling hypothesis, males were predicted to feed next to the less threatening, dulled-bill model; however, males were predicted to associate with the augmented-bill model if female bill color functions as a signal used in mate choice. As a second test of the male mate-choice hypothesis, we gave males a choice between 2 live females that differed in experimentally manipulated bill color. By testing birds in both intra- and intersexual competition and in mate-choice arenas, our research represents the first study to experimentally test both the status-signaling and mate-choice hypotheses for the maintenance of a carotenoid-based female trait.

MATERIALS AND METHODS

Study species

The American goldfinch is a socially monogamous passerine with biparental care (McGraw and Middleton 2009). In southern Ontario, pairs begin forming in spring and first clutches are initiated in early July. A successful nesting attempt requires about 31 days from beginning of egg laying to nest departure, and the entire breeding season for a local population lasts just over 2 months. Because of nest predation, few pairs raise more than one brood per season. In addition to feeding nestlings, males invest heavily in feeding their mates during incubation and early brooding. Both sexes defend the immediate vicinity of the nest (Stokes 1950; Coutlee 1967; Middleton 1979). In captivity, both sexes defend access to food (Popp 1987). Goldfinches appear to be most aggressive during the breeding season, but are also agonistic in winter flocks, particularly when feeding (McGraw and Middleton 2009). Females appear to be more aggressive than males during the nesting period and are often observed chasing intruders from the nest site (Coutlee 1967). Both sexes perform stereotypic head-up and head-forward threat displays (Coutlee 1967), suggesting a possible signaling role of coloration on or near the head.

General

This study was carried out in southern Ontario, Canada, at the Queens University Biological Station (44°33′N, 76°19′W). From 13 to 29 July 2008, we tested intra- and intersexual dominance and male mate choice by presenting females and males to model females placed adjacent to bird feeders in an aviary. From 22 June to 18 July 2007, we tested male mate choice by presenting males with 2 live females in a large outdoor aviary.

In both years, we captured birds in mist nests placed around Nyjer Seed Feeders. Sex and age-class were determined by plumage (Pyle 1997). On capture, basic morphological features and body mass were measured, and birds were banded. T.G.M. measured the color of upper mandible and plumage (throat and breast) of all individuals with an Ocean Optics USB2000+ spectrometer and PX-2 pulsed xenon lamp (Ocean Optics Inc, Dunedin FL) with the probe both providing illumination and measuring reflectance at 90° to the feather or bill surface. The probe was mounted in a holder that minimized ambient light and held the tip of the probe approximately 7 mm from the surface. We quantified reflectance (R) as the proportion of light reflected off the measured substrate compared with a Spectralon white standard (Labsphere Inc, NH), at 1-nm intervals across the avian visual range (320–700 nm). The instrument was calibrated against this standard for each bird. In 2008, we calculated the mean reflectance of 5 measures for each body region; in 2007, we calculated the mean reflectance of 2 measures for bill and the mean of 5 measures for plumage patches. Measures of plumage and bill were taken at different, haphazardly chosen locations within each color patch. Using mean reflectance curves, we calculated mean luminance ("brightness"; mean R from 320 to 700 nm), hue (wavelength where $R = [R_{max} + R_{min}]/2$), and yellow chroma ([sum of R from 550 to 625 nm]/mean luminance) using CLR 1.05 (Montgomerie 2008); see table 3.2 in Montgomerie (2006) for further details.

Female–female dominance: model females

To test the intrasexual status-signaling hypothesis for females, we examined whether they avoided feeding adjacent to a competitor female as a function of the competitor's bill color. We used 12 female taxidermic models—6 with experimentally augmented bill color and 6 with experimentally dulled bill color. Models were adult females collected 4–5 km from the study site to ensure that they were not familiar to the focal birds we tested. Before assigning models to treatment groups, we prepared them as lifelike taxidermic models (models were given glass eyes and were mounted in a lifelike perched posture) and

Table 1
Distribution of yellow chroma of the bills of female American goldfinches, showing both free-flying birds and stimulus birds used in dominance and mate-choice experiments

		Model stimuli		Live stimuli	
	Free-flying[a]	Augmented (+)	Dulled (−)	Augmented (+)	Sham (=)
Mean	0.250	0.270	0.214	0.271	0.260
Range	0.220–0.298	0.250–0.302	0.205–0.230	0.242–0.309	0.230–0.296
N	90	6	6	33	33

[a] Free-flying adult females sampled during the 2007–2008 breeding seasons.

ranked them based on yellow chroma of the bill color (yellow chroma). We then alternately assigned each bird in the ranking to different treatments, thus balancing the models for natural bill color. Models in the 2 treatments did not differ significantly in size (Wilcoxon rank sums tests [$N = 12$, degrees of freedom {df} = 1 in all analyses]: bill length, $\chi^2 = 0.01$, $P = 0.94$; tarsus, $\chi^2 = 0.17$, $P = 0.68$), throat coloration (hue: $\chi^2 = 0.03$, $P = 0.87$; yellow chroma: $\chi^2 = 0.03$, $P = 0.87$; mean luminance: $\chi^2 = 0.03$, $P = 0.87$), or bill coloration (hue: $\chi^2 = 0.23$, $P = 0.63$; yellow chroma: $\chi^2 = 0.23$, $P = 0.63$; mean luminance: $\chi^2 = 0.01$, $P = 0.99$).

To augment bill coloration, we applied a mix of nontoxic Prismacolor felt-tipped art markers (PM-14 pale vermillion, PM-19 canary yellow) to the bills of models; to dull bill color, we applied a gray Prismacolor marker (PM-100 warm gray). Because yellow chroma is the best indicator of carotenoid deposition (Saks et al. 2003), we manipulated bill coloration of augmented- and dulled-bill models so that the yellow chroma of manipulated bills resembled those of females with the most, or least, colorful bills, respectively, in the population during the breeding season (Table 1). After color manipulation, mean yellow chroma of the bills was significantly different between augmented- and dulled-bill models (Wilcoxon rank sums: $\chi^2 = 8.31$, $P = 0.004$, $N = 12$), and dyads of stimulus females' bills differed significantly in yellow chroma (Wilcoxon matched-pairs, tests with focal females: $z = 95.0$, $P < 0.0001$, $N = 19$ dyads; tests with focal males [see below]: $z = 138.0$, $P < 0.0001$, $N = 23$ dyads). Color spectra of augmented and dulled bills resembled the spectra of bills of free-flying adult females during the breeding season (Figure 1).

We placed one female into each aviary ($1.2 \times 1.2 \times 1.2$ m) on the day of capture. Each aviary was visually isolated from the others, with 3 sides made of wood and one of screen (Figure 2). Focal birds were allowed to acclimate inside their aviary for approximately 7 h. During this acclimation period, there were no taxidermic models present, and focal birds ate and drank each from a single food and water source placed on the center of the screened wall in its aviary. All birds were removed from their aviaries at dusk and placed in metabolic chambers overnight, as part of another experiment. Before we reintroduced each focal bird back into its aviary the following morning, we removed the single feeder and placed 2 feeders, separated by 1 m, at opposite ends of the screen wall. Adjacent to each feeder, we placed a taxidermic female model with its bill positioned approximately 1 cm above the feeder's small trough. We randomly selected each female model from a pool of 6 models for each treatment, and no 2 models were paired more than once. Model placement was balanced, so that half of the trials had a model with an augmented bill color placed on the left. Focal birds were tested once, then released.

We ran trials in up to 5 aviaries per day. Focal birds were always reintroduced into the same aviary where they were previously held, between 06:20 and 07:30 local time (GMT –5), except for one case in which the bird was reintroduced at 16:30. A trial began when the focal female was reintroduced into its aviary, after which we video recorded feeding behavior for 90 min. We designated the first feeder from which a focal female fed to be the preferred feeder. To test if bill color of focal females was related to their own dominance status, we measured the latency between reintroduction into the

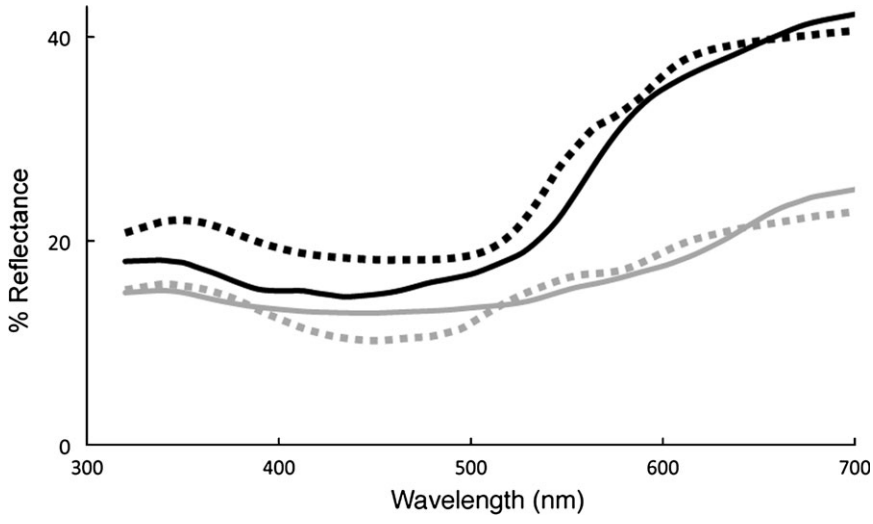

Figure 1
Reflectance spectra from the bills of female American goldfinches. Dotted lines represent reflectance of a naturally colorful bill (top) and of a naturally dull bill (bottom) during the breeding season. The black solid line is from an augmented-bill model, and gray solid line is from a dulled-bill model.

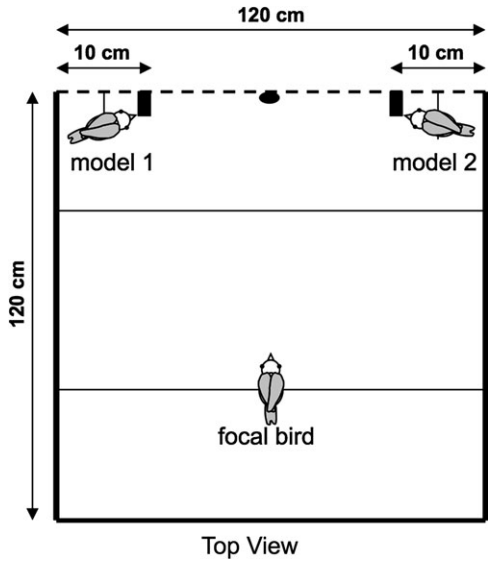

Figure 2
Schematic diagram of aviary used in the status-signaling experiment: 3 sides of the chamber were opaque wooden panels (heavy solid lines); the front and top were screen (dashed lines); wooden perches were at the front and rear of the chamber; 2 small plastic feeders (dark rectangles) were attached to the front wall of the chamber; a water vessel was between the 2 feeders (circle). Adjacent to the feeders were taxidermic models of female goldfinches that differed in experimental bill color.

aviary and the first feeding. We removed 6 trials from all analyses because the females did not eat from either feeder within 90 min, resulting in a sample of 19 focal females (18 adults, 1 yearling).

Female–male dominance and male mate choice: model females

To test whether female bill color functions as an intersexual status signal or as a male mate-choice signal, we followed the protocol described for the female–female dominance test but instead introduced focal males into the aviaries. As before, we placed female models above the feeders. We identified which feeder the focal male fed from first and quantified the latency between reintroduction and the first feeding. We removed 3 trials from the analysis because the males did not eat from either feeder within 90 min; the final sample was 23 focal males (21 adults, 2 yearlings). Focal males were tested once and released.

Male mate choice: live females

To test whether female bill color functions as a male mate-choice signal, we conducted a male mate-choice experiment in a T-shaped aviary divided into 3 compartments (Figure 3). A single male was placed in the large compartment of the aviary, and a female was placed in each of 2 small (38 × 38 × 38 cm) cages attached to the screen separating the small compartments of the aviary from the larger compartment. The 2 females were visually isolated from one another by an opaque partition. We defined the choice zone as the area within 48 cm of the screen dividing the male from the female compartments. A visual barrier between the 2 choice zones prevented a male in one choice zone from seeing the female in the other choice zone (see below; Figure 3).

Birds were captured 1–3 days prior to each trial. Males and females were captured from different locations, separated by

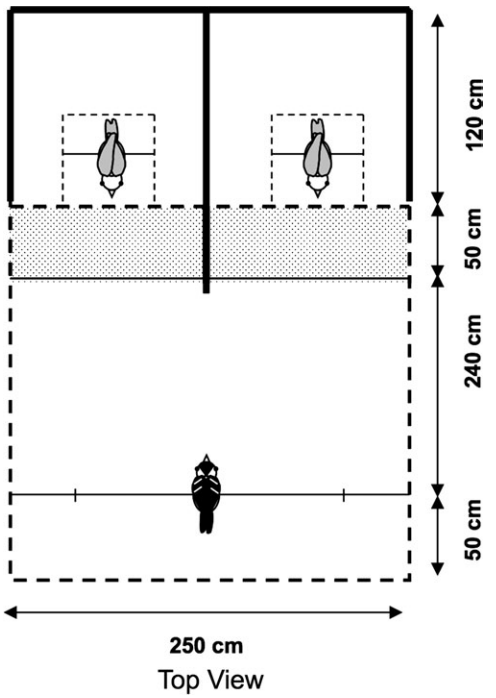

Figure 3
Schematic diagram of the aviary used in the male mate-choice experiment: heavy solid lines are opaque walls; dashed lines are screen walls; thin solid lines are perches. Live females were housed in small cages (light dashed lines) approximately 1.5 m above the ground within compartments that were opaque on 3 sides (heavy solid lines) and separated from the larger male compartment by screen. An opaque partition prevented the focal male from seeing both females when the male was in the "choice zone" (stippled area). When on the perch in the no-choice zone, a male could simultaneously see both females if he was between the 2 points indicated by short vertical lines.

4–5 km, to ensure that males were not familiar with the females. Before each trial, birds were held in individual cages (38 × 38 × 24 cm), and sexes were kept visually isolated. On the day of the trial, the focal male was acclimated in the choice aviary for approximately 30 min before the introduction of the females into their respective compartments.

Dyads of females were matched for age-class and bill size class and were then randomly assigned to treatment groups. Females placed in the 2 treatments did not differ significantly in size (Wilcoxon matched-pairs tests, $N = 33$ dyads in all analyses; bill length: $Z = 40.0$, $P = 0.46$; tarsus: $Z = 57.0$, $P = 0.25$), throat coloration (hue: $Z = 31.5$, $P = 0.54$; yellow chroma: $Z = 7.5$, $P = 0.90$; mean luminance: $Z = 73.5$, $P = 0.19$), or natural bill coloration (hue: $Z = 23.4$, $P = 0.64$; yellow chroma: $Z = 76.5$, $P = 0.18$; mean luminance: $Z = 16.5$, $P = 0.77$).

To augment female bill coloration, we used the same markers as above. However, in this experiment, we created a sham control treatment (instead of a dulled bill treatment) by applying a clear Prismacolor marker (PM-121 clear blender). After color manipulation, mean yellow chroma of the bill was significantly different between augmented and sham control models (Wilcoxon rank sums: $\chi^2 = 10.24$, $P = 0.001$, $N = 66$), and the bills of dyads of stimulus females had significantly different yellow chroma (Wilcoxon matched-pairs test: $Z = 154.5$, $P = 0.004$, $N = 33$). Yellow chroma of the bills of treatment birds approximated the extremes of yellow chroma of the bills of free-flying adult females captured during the breeding season (Table 1).

After manipulation of female bill coloration, we placed females simultaneously into the 2 small cages of the mate-choice aviary. Treatment side was balanced so that approximately half of the trials had an augmented-bill female on the left. Once females were introduced, we video recorded male behavior for 90 min. To quantify male preference, we measured: 1) the amount of time spent in the choice zone in front of each female during a 30-min observation period (see below) and 2) the amount of time spent in close proximity to the female (defined as time on the horizontal screen that divided the male from each female, plus time spent on the perch directly in front of the female) during this 30-min period. We considered the second measure to be a more robust indicator of male preference because, when the male was close to the female, they often interacted (i.e., physically following, visually tracking movement, or calling to each other).

For video analysis, we began scoring male behavior as soon as the male could see both females. We inferred that this occurred either when a male first moved to the central portion of the large chamber of the apparatus, from which he had a view of both females, or when a male had entered both choice zones. Trials lasted 30 min after the point at which the male could see both females. Trials were run throughout the day (06:00–18:30 local time), with up to 6 trails per day. We excluded 5 trials because trial duration was less than 30 min (i.e., the male had not seen both females until after the 60th min of the 90-min recording). We did not analyze 5 trials where the male appeared listless and sat still for over half of the 30-min trial. In total, 33 trials were analyzed (24 with a dyad of adult females, 9 with a dyad of yearling females). Focal males and stimulus females were used in the experiment once and then released.

RESULTS

Female–female dominance: model females

The overwhelming majority of females fed first from the feeder underneath the female model with the dulled bill (dulled bill = 17, augmented bill = 2; Binomial Test, $P = 0.0006$). Thus, focal females avoided feeding near the female model with augmented bill color, as predicted by the intrasexual status-signaling hypothesis.

Latency of females to feed from either feeder was highly variable (mean, 95% CI (confidence interval) [range] = 30.3, 18.3–42.3 [2.3–88.3] min, $N = 19$) but was not significantly correlated with bill or throat color of the focal female (Spearman rank correlations, rho < 0.20, $P > 0.40$, $N = 19$, for all 6 tristimulus color variables). Conclusions were the same when the analyses were restricted to the 18 adult females.

Female–male dominance and male mate choice: model females

Bill color of model females did not affect which feeder males fed from first (dulled-bill female model = 11, augmented-bill female model = 12; Binomial Test, $P = 0.84$, $N = 23$). These results were not qualitatively different if analyses were restricted to adult males ($P = 0.83$, $N = 21$). Thus, focal males neither avoid feeding near the augmented-bill female model (as predicted by intersexual status-signaling hypothesis) nor prefer feeding near the augmented-bill model (as predicted by the male mate-choice signal hypothesis).

Latency of males to feed from either feeder was also highly variable (21.9, 13.9–29.9 [0.1–57.8] min, $N = 23$ males) and was not significantly correlated with the male's bill or throat colors (Spearman rank correlations, rho < 0.30, $P > 0.20$, $N = 23$, for all 6 tristimulus color variables), and conclusions were the same when the analyses were restricted to adult males.

Table 2
Comparison of morphology and plumage coloration between females that were preferred versus unpreferred in male mate-choice trials

	Preferred		Unpreferred			
Variable	Mean	SE	Mean	SE	Paired t	P
Mass (g)	12.0	0.1	12.0	0.1	0.00	1.00
Tarsus (mm)	13.3	0.1	13.1	0.1	−1.43	0.16
Throat luminance	0.247	0.006	0.260	0.006	1.67	0.10
Throat yellow chroma	0.283	0.003	0.282	0.002	1.84	0.08
Throat hue	500.5	0.4	501.3	0.3	1.69	0.10
Breast luminance	0.308	0.007	0.317	0.008	1.06	0.30
Breast yellow chroma	0.268	0.002	0.267	0.002	−0.31	0.76
Breast hue	498.1	0.2	498.2	0.3	0.49	0.63

$N = 33$ for all analyses; SE, standard error.

Male mate choice: live females

Female bill color did not influence the amount of time males spent in the choice zone in front of each type of female (augmented bill: mean [95%CI] = 531.7 [362–701] s; sham control bill: 628.6 [449–808] s; paired t-test, $t = 0.63$, $P = 0.53$, $N = 33$) or the amount of time spent in close proximity to each type of female (augmented bill: 328.7 [201–456] s; sham control: 419.2 [257–582]s; paired $t = 0.77$, $P = 0.45$, $N = 33$). However, males spent significantly more time in the left choice zone of the mate-choice apparatus (paired $t = 2.7$, $P = 0.01$, $N = 33$), potentially due to differences in the vegetation surrounding the left and right side of the mate-choice cage, although side bias for time spent in close proximity to the female was weak (paired $t = 1.70$, $P = 0.10$, $N = 33$). To test whether this apparent side bias confounded our ability to detect a preference for female bill color, we added to our analysis a between-subjects factor specifying the side with the augmented female. After controlling for the apparent side bias, there was still not a significant preference for female bill color (repeated measures analysis of variance: $F = 0.20$; df = 1, 31; $P = 0.66$). Thus, we conclude that males did not show a systematic preference for live females as a function of their bill color.

We compared several traits of "preferred" and "unpreferred" females to test whether male choice was influenced by female plumage or morphology. Preferred females were defined as the member of each dyad on whose side the male spent the most time in the choice zone during the 30-min observation period. Preferred females did not differ significantly from unpreferred females in plumage color or morphology, although throat hue and luminance tended to be greater and throat yellow chroma lower, in unpreferred females (Table 2). These results were not qualitatively different when the preferred female was defined based on time spent in close proximity (all $P > 0.1$).

DISCUSSION

Through a series of aviary dominance experiments, we found that female American goldfinches generally avoid feeding next to taxidermic female goldfinch models with colorful bills, providing strong evidence that the orange, carotenoid-based, bill color of females is perceived as a signal of status during intrasexual competition for access to food. Males, however, did not discriminate female bill color under these experimental conditions.

Our study indicates that female bill color signals status during the breeding season; however all the natural contexts in

which bill color mediates social interactions are not known. Based on our results, bill coloration clearly has a signaling role during competition for food resources, suggesting that social selection (i.e., a form of natural selection for social signaling during competition for non-mate resources; West-Eberhard 1979, 1983) may account for the maintenance of this colorful trait. However, we cannot exclude the possibility that female bill coloration also functions during competition for access to mates and is thus maintained via sexual selection. Indeed, our failure to find evidence that males respond to female bill color suggests that the signal may mediate competition over resources that only females compete with each other for, such as mates or nest sites.

Although we show that female bill coloration mediates interactions among competitors, we do not yet know what underlying physiological factors make this signal reliable and thus allow females with more colorful bills to win competitive interactions. Elsewhere, we show that female bill color in this species changes rapidly in response to an immune challenge (Rosenthal MF, Murphy TG, Darling N, Tarvin KA, unpublished data), so bill coloration may indicate an individual's overall health, and thus, its ability to invest in aggression. Several mechanisms could account for such a relationship. For example, females with more colorful orange bills may be better able to shunt valuable carotenoids into the integument and away from the immune system and other physiological functions, and this might be accomplished only by high-quality, healthy individuals. Alternatively, because bill color is mediated in part by testosterone (Mundinger 1972), bill coloration may indicate physiological state and readiness for aggression, as well as an individual's ability to buffer the negative effects of high levels of circulating testosterone. Furthermore, because bill color changes seasonally, coloration may indicate physiological preparedness to breed. It is possible that breeding readiness is related to a female's motivation to compete for food, nest sites, or mates, so bill color may convey information about willingness to engage in an aggressive interaction. Dominant females may also gain increased access to carotenoid-rich foods, potentially providing a direct link between dominance and bill color.

It is possible that augmented-bill female models were perceived as males because their bills were similarly colored. However, goldfinch plumage is strongly sexually dimorphic, so it seems unlikely that females would have mistaken the sex of taxidermic models.

It is also worth noting that we did not detect an effect of bill color on latency to feed, as might be expected if bill color was related to dominance status. Thus, birds having more vividly colored bills might be expected to be bolder and thus visit feeders less hesitantly. However, latency to feed was likely influenced by many factors that we failed to control, such as differences in hunger and motivation to feed, and also differences in time in captivity and stress response. Therefore, we feel that our methods were too crude to properly test this prediction, and we suggest that future research should address this possibility.

We found no evidence that female bill color functions as a mate-choice signal, and, indeed, we found weak evidence for male preferences for some female plumage characters in the opposite direction to that expected. The lack of evidence for male mate choice is surprising because male goldfinches invest substantially in parental care (McGraw and Middleton 2009), so discriminating among potential mates should be advantageous to males (Trivers 1972; Clutton-Brock and Vincent 1991). Furthermore, the frequent flocking behavior and lack of resource-based territoriality in this species should lead to high encounter rates with potential partners, which would reduce the costs of evaluating potential mates and promote male mate choice (Kokko and Monaghan 2001; Kokko and Johnstone 2002). Moreover, MacDougall and Montgomerie (2003) found assortative pairing for plumage color in this species, suggesting that males may discriminate among potential mates based on carotenoid-based traits. Our lack of evidence for male mate choice of female bill color is especially puzzling because female bill color appears to function as a signal of status among females, and it seems likely that males could benefit by exploiting information revealed by the signal (i.e., condition, quality, and foraging success), as it is likely the same type of information that would be important to males seeking a partner.

Our finding that males apparently ignore a trait that females pay attention to may be explained in a few ways. First, it is possible that our mate-choice arena did not reflect natural conditions. This seems unlikely because female American goldfinches have shown strong mate preferences in similar choice arenas (Johnson et al. 1993). Alternatively, because we conducted our mate-choice experiments in the middle of the breeding season, we may have run our tests after the period when most individuals typically exhibit mate choice. However, this species often forms new pairs throughout the season following nest failure (McGraw and Middleton 2009), so it seems unlikely that our results were influenced by the stage of the breeding season. It is possible that our mate-choice apparatus may have more closely mimicked an opportunity for males to engage in extrapair mating than the conditions that occur during social pair formation. As the benefits of exhibiting choice for an extrapair partner may be low, and we might not expect males to discriminate between females. Finally, it is possible that males simply gain no selective benefits from choosing among different females, and so female bill color plays no role in mate choice. This could be the case if male choosiness is highly costly, as might be expected in this system given the strongly male-biased adult sex ratios (McGraw and Middleton 2009), where the costs of rejecting a low-quality female in hopes of attracting a more preferred one could result in failure to pair or in pairing with a lower quality female. It is worth noting, however, that we failed to find evidence for male mate choice in 2 experiments that differed substantially in design. This lends weight to our conclusion that males do not respond to female bill color when making mate-choice decisions. In any case, our work suggests that additional study on male choosiness in natural contexts would be fruitful.

Most previous work on female status signaling has provided only correlative evidence that there is a link between female plumage color and dominance (pinion jays *Gymnorhinus cyanocephalus*, Johnson 1988; Harris' sparrows, Watt 1986; king penguins *Aptenodytes patagonicus*, Viera et al. 2008), and very few studies have used experimental techniques to assess how manipulated female ornaments influence behavioral interactions (dusky moorhen *Gallinula tenebrosa*, Crowley and Magrath 2004; European starling *Sturnus vulgaris*, Swaddle and Witter 1995; collared flycatcher *Ficedula albicollis*, Hegyi et al. 2008; streak-backed oriole *Icterus pustulatus* Murphy et al. 2009). To the best of our knowledge, our study represents the first experimental evidence to demonstrate that variation within the natural range of carotenoid-based coloration functions to mediate contests among females over food. Future research on this system should focus on testing how social interactions are mediated by bill color under natural contexts and whether females use this signal during competition for resources associated with mating (implying sexual selection) or just during competition over food resources (implying social selection). Detailed work is needed to assess which aspects of phenotypic condition and quality are signaled by female bill color, as this will help us understand the mechanisms that

maintain signal reliability. Our study demonstrates that carotenoid ornaments can be and are used as signals of status, and that females, like males, can maintain ornaments that mediate intrasexual contests.

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