Animal Behaviour 93 (2014) 121–127

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Same trait, different receiver response: unlike females, male American goldfinches do not signal status with bill colour

Troy G. Murphy [a,*], Joe A. West [a], Tiffany T. Pham [a], Lucy M. Cevallos [a], Richard K. Simpson [a], Keith A. Tarvin [b]

[a] Department of Biology, Trinity University, San Antonio, TX, U.S.A.
[b] Department of Biology, Oberlin College, Oberlin, OH, U.S.A.

ARTICLE INFO

Article history:
Received 1 December 2013
Initial acceptance 7 January 2014
Final acceptance 18 March 2014
Published online
MS. number: A13-00990

Keywords:
American goldfinch
carotenoid ornamentation
elaborate monomorphic ornamentation
genetic correlation
social competition
Spinus tristis
status signal

In species in which both sexes have similar ornamentation, the ornaments often function as sexual or social signals in both sexes. However, males and females may use ornaments in different signalling contexts. We previously demonstrated that carotenoid-based bill colour of female American goldfinches, *Spinus tristis*, functions as a signal of status during intrasexual, but not intersexual, competition. Here we test whether male bill colour functions as a competitive status signal during both intra- and intersexual contests. We tested whether focal males and females avoided feeding adjacent to taxidermic male models as a function of the models' experimentally altered bill colour. We additionally tested whether male bill colour functions as a mate choice signal by presenting females with a choice of two live males with experimentally altered bill colour. In the status signal experiment, neither focal males nor females avoided male models with more colourful bills, as was predicted by the status-signalling hypothesis. These results indicate that male bill coloration does not function as a signal of competitive status and that the signal function of male bill colour does not parallel that of female bill colour. In our mate choice experiment, females showed no preference for male bill colour, suggesting that male bill colour may have some yet untested signalling function or that male bill colour may no longer be under selection. Our findings suggest that selection can lead to different signalling strategies in males and females, even in species that express mutual ornamentation.

Many species express elaborate ornamental traits in both sexes, and theoretical models and empirical research have supported the role of sexual or social selection in maintaining elaborate monomorphic ornamentation when competition for mates or other resources occurs in both sexes (reviewed in: Amundsen & Pärn, 2006; Tarvin & Murphy, 2012; Tobias, Montgomerie, & Lyon, 2012). Although the mutual selection and social selection hypotheses have gained much attention in recent years (Amundsen, 2000; Clutton-Brock, 2007; Lyon & Montgomerie, 2012), many studies have failed to find evidence that ornamentation functions as a social signal in both males and females (reviewed in Kraaijeveld, Kraaijeveld-Smit, & Komdeur, 2007). As such, there is growing acknowledgment that a complex interplay of selective processes may account for elaborate traits when expressed in both sexes (LeBas, 2006). Some research has revealed that male and female ornamental traits may function in different selective contexts; for example, an elaborate trait may have sexually or socially selected ornamental function in one sex, while in the other sex, the trait may have evolved in response to natural selection for viability (e.g. for antipredation: Heinsohn, Legge, & Endler, 2005; Montgomerie, Lyon, & Holder, 2001; Murphy, 2006, 2007; Packer, 1983) . In addition, studies have found that elaborate traits may be functional in males, yet be expressed in females as nonadaptive by-products of genetic correlation (Cuervo, de Lope, & Møller, 1996; Lande, 1980; Muma & Weatherhead, 1991; Murphy & Pham, 2012; Wolf, Casto, Nolan, & Ketterson, 2004). As such, knowledge of the ornamental function in one sex does not necessarily describe the function of a similarly expressed trait in the other sex. We should thus expect that sex-specific selective forces may act to maintain elaborate traits, even in species in which both sexes are similarly ornamented.

Ornamental traits generally fall into two signalling categories: they function during mate assessment and are assessed by opposite-sex members to evaluate potential mates, or they function as signals of status that convey information about fighting ability or resource-holding potential (Andersson, 1994). Among species in

* Correspondence: T. G. Murphy, Department of Biology, Trinity University, San Antonio, TX 78212, U.S.A.
E-mail address: troy.murphy@trinity.edu (T. G. Murphy).

http://dx.doi.org/10.1016/j.anbehav.2014.04.034
0003-3472/

which both sexes are similarly ornamented to some degree (i.e. mutually ornamented species), many studies have tested for a mate choice function to male and female signals, but the potential for status signalling has received less attention (but see Kraaijeveld, Gregurke, Hall, Komdeur, & Mulder, 2004; Rohwer, Ewald, & Rohwer, 1981; Vedder, Korsten, Magrath, & Komdeur, 2008). Status signals provide a means for competitors to assess the fighting abilities of their opponents and allow individuals of unequal fighting ability to avoid wasting time and energy fighting and to avoid injury (Rohwer, 1975, 1985). This form of signalling is thought to be favoured in flocking or highly social species where agonistic encounters are common (West-Eberhard, 1983). Selection can shape status signals when they influence access to mates among same-sex individuals (sexual selection), or access to other resources not directly tied to mating success (between same-sex or opposite-sex opponents; i.e. social selection; West-Eberhard, 1979, 1983). Although much research has supported the role of signals of status among males (Griggio, Serra, Licheri, Monti, & Pilastro, 2007; Møller, 1987; Pryke & Andersson, 2003; Senar & Camerino, 1998), few examples of status signalling in females have been described (but see Coady & Dawson, 2013; Crowhurst, Zanollo, Griggio, Robertson, & Kleindorfer, 2012; Crowley & Magrath, 2004; Murphy, Hernández-Muciño, Osorio-Beristain, Montgomerie, & Omland, 2009; Murphy, Rosenthal, Montgomerie, & Tarvin, 2009; Swaddle & Witter, 1995). This male bias in research results is surprising given that both males and females of many species compete for access to mates or other resources (Tobias et al., 2012). As such, in species in which both sexes engage in inter- or intrasexual competition for resources, both males and females may evolve status signals that convey information on competitive ability.

Both male and female American goldfinches, *Spinus tristis* (hereafter goldfinches) have a colourful carotenoid-based orange bill during the breeding season. In previous research, we found that bill colour of female goldfinches mediates competitive interactions with other females during the breeding season (Murphy, Rosenthal, et al., 2009). However, it is unknown whether male bill colour also functions as a competitive status signal. Here we test whether male bill colour functions as a competitive signal during contests over food. We follow methods of Murphy, Rosenthal, et al. (2009) (also see Senar & Camerino, 1998), wherein we presented captive individuals (both males and females, separately) with a choice of two feeders from which to feed; above each feeder we placed a taxidermic model of a male goldfinch with either experimentally augmented or dulled bill colour. If bill colour signals competitive ability, we predicted that focal individuals would avoid feeding next to the model with the more colourful bill. By testing for status signal function of male bill colour, we were able to test whether the signal function of bill colour differs between males and females. We additionally tested whether male bill colour functions as a mate choice signal. To test the mate choice hypothesis, we gave females a choice between two live males whose bills were either experimentally augmented or dulled. By testing for both status signal and mate choice function of male bill colour, we were able to assess whether selection for signalling phenotype differs between the sexes.

METHODS

American goldfinches are socially monogamous with biparental care. Individuals spend the nonbreeding months in mixed-sex social flocks (McGraw & Middleton, 2009) and frequently engage in brief competitive interactions while foraging communally in both the nonbreeding and breeding seasons (T. G. Murphy, personal observation). Aviary-based experiments have demonstrated that competition for access to food and other agonistic interactions occur both within and between sexes (Coultlee, 1967; Popp, 1987a). Although both males and females defend nest sites during the nesting season (Coutlee, 1967; Middleton, 1979; Stokes, 1950), neither sex defends all-purpose territories, and instead individuals of both sexes forage communally in temporally and spatially ephemeral food patches. As a consequence, they regularly compete with both familiar and unfamiliar individuals for food. Females appear to be more aggressive than males during the nesting period (Coutlee, 1967).

Approximately 2–3 months prior to nesting, bill colour changes from drab brown to rich orange in both sexes. During the breeding season, male and female bill colour is similar in orange coloration, with only moderate male-biased sexual dichromatism (mean ± SE: bill brightness: males: 0.266 ± 0.007; females: 0.222 ± 0.008; bill saturation: males: 0.248 ± 0.001; females: 0.246 ± 0.002; bill hue: males: 550.1 ± 0.957 nm; females: 546.2 ± 1.085 nm; Kelly, Murphy, Tarvin, & Burness, 2012). Orange bill coloration is in part carotenoid-based (Hill, Hood, & Huggins, 2009) and has been shown to reflect stress and to respond to a short-term immune challenge in both sexes (Kelly et al., 2012; Rosenthal, Murphy, Darling, & Tarvin, 2012) and to coccidiosis in males (McGraw & Hill, 2000; as yet untested in females). Bill colour is correlated with immunoglobulin and natural antibody levels in females, but not in males (Kelly et al., 2012).

We captured birds at traps baited with niger seed. Sex and age class were determined based on plumage (Pyle, 1997). Upon capture, we measured basic morphometrics, colour of the upper mandible and throat plumage. All measures were taken by T.G.M. Colour measures were taken with an Ocean Optics USB2000+ spectrometer and PX-2 pulsed xenon lamp (Ocean Optics Inc, Dunedin, FL, U.S.A.) with the probe held 90° to the colour patch. The probe was mounted in a holder that minimized ambient light and positioned the tip of the probe approximately 7 mm from the substrate. We quantified reflectance (R) as the percentage of light reflected off the bill compared with a Spectralon white standard (Labsphere, Inc., North Sutton, NH, U.S.A.), at 1 nm intervals across the avian visual range (320–700 nm). The white standard was kept in a housing that ensured that the probe tip did not touch the surface of the standard, thus preventing the transfer of oil and dirt from the substrate to the standard. The spectrometer was calibrated to the standard prior to measuring each patch. We calculated the mean reflectance of five measures, which were taken at haphazardly chosen locations on the colour patch. All measures of bill colour were taken within 1 h of capture because bill colour can change rapidly (Rosen & Tarvin, 2006; Rosenthal et al., 2012). Using mean reflectance curves, we calculated mean brightness ('luminance'; mean R from 320 to 700 nm), hue (wavelength where $R = (R\text{max} + R\text{min})/2$) and yellow saturation ((sum of R from 550 to 625 nm)/total R from 320 to 700) using the program RCLR v0.9.33 (Montgomerie, 2010); see Table 3.2 in Montgomerie (2006) for further details.

General Procedures

To conduct male aviary-based dominance experiments, we followed methods of Murphy, Rosenthal, et al. (2009), which tested whether female bill colour signals competitive status. In the present study, we replicated the methods of Murphy, Rosenthal, et al. (2009) by conducting this study at the same site, using the same aviaries and the same experimental protocol. Our studies were conducted in southern Ontario, Canada, at the Queens University Biological Station (44°33′N, 76°19′W) from 6 to 27 July 2010 (the previous study on females was conducted 2 years previous, from 12 to 28 July 2008). Goldfinches in southern Ontario begin nesting in early July with peak breeding occurring during late July (McGraw &

Middleton, 2009 and references therein); hence, our study was conducted from early to peak breeding season. This study was approved by the Institutional Animal Care and Use Committee of Trinity University (82009-TM3).

We prepared 10 taxidermic models of adult males in a lifelike posture, with glass eyes, and with their heads forward in a feeding posture. To ensure that models were unfamiliar to focal birds, we collected models at sites more than 5 km from where focal birds were captured. Before assigning models to treatment groups, we ranked them based on yellow saturation of their bill, and then sequentially assigned models to different treatments, thus balancing the treatment groups for natural bill colour. Birds that were used as models in the two treatments ($N = 5$ models per treatment) did not differ significantly in size (Wilcoxon two-sample tests: mass: $W = 25.0, P = 0.63$; bill length: $W = 23.5, P = 0.46$; tarsus: $W = 27.0$, $P = 0.97$), throat coloration (hue: $W = 25.0$, $P = 0.64$; yellow saturation: $W = 27.0$, $P = 0.97$; mean brightness: $W = 26.0$, $P = 0.84$) or bill coloration (hue: $W = 25.5, P = 0.71$; yellow saturation: $W = 27.0$, $P = 0.97$; mean brightness: $W = 27.9$, $P = 1.0$).

We used a mix of nontoxic felt-tipped art markers (Prismacolor, Oak Brook, IL, U.S.A.) to alter bill coloration of models. To make bills more orange, we applied a mix of PM-14 Pale Vermillion and PM-19 Canary Yellow. To dull bill colour, we applied PM-100 Warm Grey. Because saturation is thought to be a good indicator of carotenoid deposition (Saks, McGraw, & Hõrak, 2003), we altered bill colour so that yellow saturation of manipulated bills resembled either the most colourful, or least colourful, birds in the population during the breeding season. We used the same colour manipulation technique as in our previous study of this species (for a comparison of colour spectra of manipulated bills and natural bills, see Table 1 and Figure 1 in Murphy, Rosenthal, et al., 2009). After colour manipulation, augmented model bills were significantly more saturated than dulled-bill models (Wilcoxon two-sample test: $W = 15$, $N = 10$, $P = 0.008$).

Male Intrasexual Status Signal Experiment

Focal males were transported from the capture site and placed individually in an experimental cage ($1.2 \times 1.2 \times 1.2$ m). Each experimental cage was visually isolated from the others, with only one side made of transparent screen (Fig. 1). Within each cage there was a single feeder and water dish, and each focal bird spent the afternoon after it was captured in isolation. During this period all focal birds learned to eat from the feeder, which was confirmed by checking seed level. At dusk on the day of capture, we removed each focal bird from its experimental cage and transferred it to a smaller overnight-holding cage ($0.3 \times 0.3 \times 0.4$ m), which contained water but not food, to increase and standardize hunger. The following morning we returned each focal bird to its experimental cage. Before releasing the bird into the experimental cage, we placed two feeders, separated by approximately 1 m, at opposite ends of the transparent screen wall (the original feeder was removed, but the water dish remained). Adjacent to each feeder we placed a taxidermic male model with its bill positioned approximately 1 cm above the feeder's small trough. The models were placed in a way that the bill colour of both models could be seen from anywhere within the aviary (except from directly below the feeder). In each experimental cage, one model had an augmented bill and the other model had a dulled bill. We randomly selected male models from a pool of five models for each treatment. Models were not paired more than once for each type of focal bird tested (i.e. adult focal males, yearling focal males). Model placement was balanced so that approximately half of the trials had a model with an augmented bill on the left. Focal birds were tested once and then released.

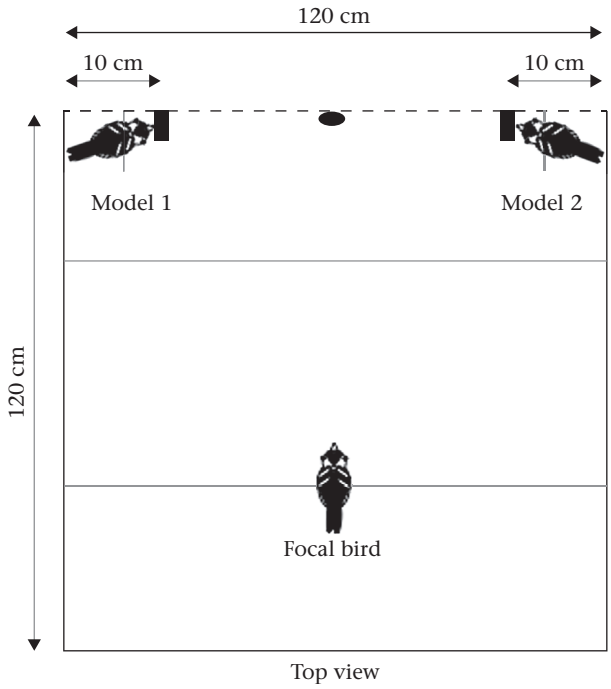

Figure 1. Schematic diagram of aviary used in the inter- and intrasexual status-signalling experiment of American goldfinches. Solid lines are opaque walls; dashed lines are screen walls; thin solid lines are perches. Perches were placed in the front and rear of the male cage. Two feeders (dark rectangles) were placed on the front screen, and water was placed between the two feeders (circle). Above each feeder, we placed a male taxidermic model with either an augmented or dulled bill colour.

We ran up to five trials per day. On the morning of the status signalling experiment, we introduced the focal bird into the experimental cage between 0650 and 0730 hours local time (GMT −5 h), with the exception of one trial that started at 0945 hours because of inclement weather. The behavioural trial began when the focal bird was introduced into the experimental cage. We videorecorded behaviour for 90 min for later analysis. To assess whether focal individuals responded to competitor bill colour when deciding which competitor to interact with, we noted the feeder that was first used. We assessed whether bill colour of the focal bird was related to its own competitive ability by testing for a relationship between the focal bird's bill colour and the likelihood of feeding under the dulled versus augmented model, as well as the latency of the focal bird to feed. We removed one trial because the focal bird did not eat from either feeder within 60 min, resulting in a sample of 40 focal males (23 adults, 17 yearlings).

Male Intersexual Status Signal Experiment

To test whether male bill colour functions as an intersexual status signal directed to females, we followed the protocol described above (again with male models placed above feeders), but instead introduced focal females into the experimental cages. We performed this experiment with 30 focal females (24 adults, 6 yearlings).

Male Mate Choice Signal Experiment

The mate choice experiment was conducted at the same field site described above between 26 June and 28 July 2011. Birds were captured and measured as described above. Males and females were captured from sites separated by more than 5 km to reduce the probability of previous interactions. Only yearling birds were

used in this experiment to avoid age-related variation in mating preference and experience. Birds were captured the day of or the day prior to each trial, and members of each dyad of stimulus males were caught on the same day to standardize capture stress. Before trials, birds were held in individually isolated cages ($38 \times 38 \times 24$ cm) with ad libitum food and water.

To test the hypothesis that male bill colour functions as a mate choice signal, we presented 19 females a choice between a pair of live males. We matched each dyad of males for bill size, and then randomly assigned them to treatment groups (augmented versus dulled-bill) for a total of 19 dyads. Bill coloration was manipulated as specified above. Males that were placed in the two treatments did not differ significantly in size (Wilcoxon signed-ranks test: bill length: $T = 7.5$, $N = 19$, $P = 0.72$; tarsus: $T = -26.5$, $N = 19$, $P = 0.18$; mass: $T = 9$, $N = 19$, $P = 0.71$), breast coloration (hue: $T = -23.0$, $N = 18$, $P = 0.30$; yellow chroma: $T = -20.5$, $N = 18$, $P = 0.39$; mean brightness: $T = 10.5$, $N = 18$, $P = 0.67$) or premanipulated bill coloration (hue: $T = -30$, $N = 18$, $P = 0.10$; yellow chroma: $T = 22.5$, $N = 18$, $P = 0.35$; mean luminance: $T = 22.5$, $N = 18$, $P = 0.35$). For colour measures, $N = 18$ because one dyad was not measured.

We used a Y-shaped aviary divided into three compartments (Fig. 2) to assess female mate preference. A male was placed in each of two small compartments attached to the screen dividing the male from female arm of the aviary. The males were visually isolated from one another by a solid wall between each male compartment. We defined the mate preference zone as the area within 20 cm of the male compartment. When a female was perched near the back of the aviary (distant from the males), she could see both males. When on the perch closest to the male compartments (i.e. within the mate preference zone), the female could see only one male at a time. Treatment side was balanced so that approximately half of the trials had an augmented-bill male on the left. Females were introduced into the female arm of the aviary after males were placed in their compartments. We videorecorded

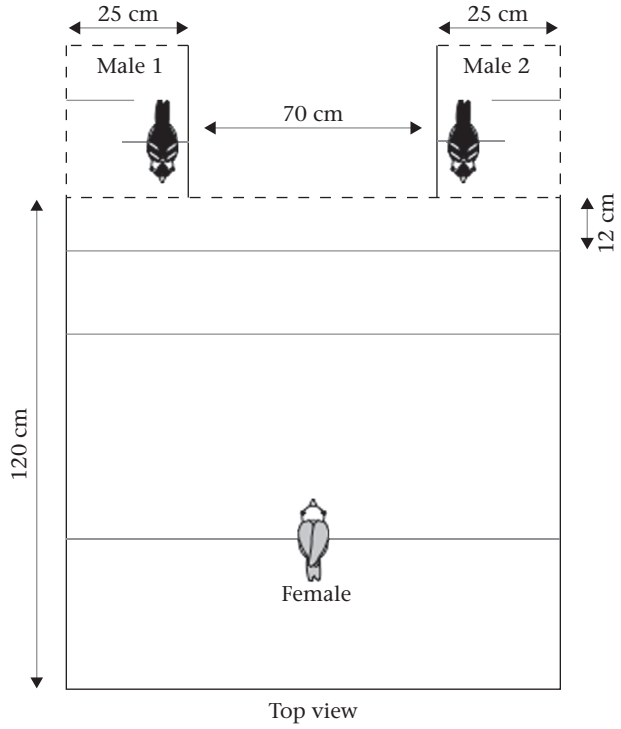

Figure 2. Schematic diagram of the aviary used in the mate choice experiment of American goldfinches. See Fig. 1 for explanation of symbols. Live stimulus males were housed in small compartments and separated from the larger female cage by screen.

female behaviour for later analysis. We began scoring behavioural interactions after the focal female was able to see both stimulus males. We inferred that this occurred when the focal female perched on a central perch from where she could view both males, or when she had entered both choice zones. Trials lasted 30 min, beginning from the time at which the female could see both males. Trials were run in the evening, starting between 1730 and 1810 hours local time (GMT −5 h). Males and females were used once and then released. We removed four trials because the focal female did not associate with a male during the first 30 min of the trial, resulting in a sample of 15 females.

Statistics

All statistical analyses were performed in JMP 10.0.2 (SAS Institute Inc., Cary, NC, U.S.A.). All tests were two tailed. In the status-signalling experiment, we used a binomial test to assess whether focal birds were more likely to first forage at the feeder under the dulled-bill male. We did not assess foraging response over a longer period (e.g. number of visits to each feeder, time spent at each feeder, etc.) because focal birds may habituate to unresponsive models. Sexes were tested separately, and age classes were analysed together and separately. To assess whether a focal bird's bill colour influenced its own competitive decisions, we used generalized linear model with binomial probability distribution and logit link function to test the influence of the focal bird's bill saturation on the decision to forage first under the dulled-bill versus augmented-bill model (i.e. model bill colour was the binomial response variable and focal male bill saturation was the predictor variable). We additionally used standard least squares regression to test whether latency to feed was related to bill yellow saturation of the focal bird. Sexes were tested separately, and age class was included in models if $P < 0.25$.

To compare the response of focal males and females to competitors with different bill colour (i.e. the tendency to feed next to dulled-bill male models versus dulled-bill female models), we combined data on focal males from the present study with data on focal females from Murphy, Rosenthal, et al. (2009). We used generalized linear models with a binomial probability distribution and logit link function, and included sex of the focal bird as a factor to test whether the sex of the focal bird predicted whether it would first feed adjacent to the augmented-bill or the dulled-bill model.

For the mate choice experiment, we used paired t tests to assess whether females spent more time near the augmented-bill model compared to the dulled-bill model.

Ethical Note

Birds were humanely trapped in funnel traps and no birds were injured in the process. Traps were checked within 45 min, and to reduce stress, were not deployed when temperature or weather was extreme. Birds that were to be used as taxidermic models were sacrificed immediately after capture by either thoracic compression or cervical dislocation. At the end of each aviary experiment, focal birds were released near the site of capture. The animal care protocol was approved by Trinity University (IACUC 82009-TM3).

RESULTS

Male Intrasexual Status Signal Experiment

Experimentally altered bill colour of male models did not affect where focal males first foraged (under dulled-bill male model = 23 trials; under augmented-bill male model = 17 trials; binomial test: $N = 40$, $P = 0.43$). The results were not qualitatively different when

we restricted the analysis to adult males ($N = 23$, $P = 0.68$) or yearlings ($N = 17$, $P = 0.63$). Thus, during the initial foraging decision, focal males did not avoid the augmented-bill male model (Fig. 3).

We detected no relationship between a focal male's bill colour and his competitive decisions: the bill colour of a focal male was unrelated to his tendency to forage first under the dull or augmented model ($\chi^2_1 = 2.78$, $P = 0.10$) or to his latency to feed ($F_{1,38} = 1.14$, $P = 0.33$).

Male Intersexual Status Signal Experiment

Experimentally altered bill colour of male models did not affect where focal females first foraged (under dulled-bill male model = 16 trials; under augmented-bill male model = 13 trials; binomial test: $N = 29$, $P = 0.71$). The results were not qualitatively different when we restricted the analysis to adult females ($N = 23$, $P = 1.0$). Thus, during the initial foraging decision, focal females did not avoid the augmented-bill male model (Fig. 3).

We detected no relationship between the focal female's bill colour and her competitive decisions: the bill colour of a focal female was unrelated to her tendency to forage first under the dull or augmented models ($\chi^2_1 = 0.01$, $P = 0.92$) or to her latency to feed ($F_{2,25} = 0.86$, $P = 0.44$).

Difference in Response of Sexes to Model Bill Colour

During intrasexual interactions in our previous study, we found that focal females first foraged under the dulled-bill female model in 17 of 19 trials (Murphy, Rosenthal, et al., 2009). Analysis of data from the female-model study (Murphy, Rosenthal, et al., 2009) combined with the present male-model study revealed a significant effect of sex on the decision to feed under augmented versus dulled-bill models: females avoided augmented female models in most (89.5%) trials, and males avoided augmented male models in little over half of trials (57.5%) (model likelihood comparing the full model to a model without sex: $\chi^2_1 = 6.82$, $P = 0.009$). In treatments in which focal birds were of the opposite sex as model birds, there was no significant difference in the tendency of males and females to respond to model bill colour: females avoided augmented male models in 55.2% of trials and males avoided augmented female models in 47.8% of trials (model likelihood: $\chi^2_1 = 0.277$, $P = 0.60$).

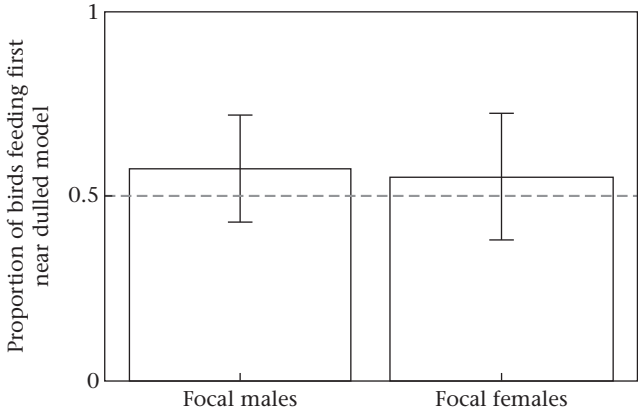

Figure 3. Results of behavioural trials testing intra- and intersexual status-signalling function of male bill colour in the American goldfinch. Focal birds were given a choice of two feeders from which to feed. Bars represent the proportion of trials in which the focal bird (males shown on left; females on right) fed first near the male taxidermic model with dulled-colour bill. Error bars are 95% confidence intervals (likelihood method). Dashed line represents the expected proportion under the null hypothesis that bill colour does not signal status.

Mate Choice Signal Experiment

Male bill colour did not influence female preference in the Y-shaped aviary where females were given a choice of two live males with experimentally altered bill colour. Females spent similar amounts of time in association with the augmented and the dulled males (mean ± SE: augmented-bill male: 258.4 ± 114.2 s; dulled-bill male: 343.9 ± 119.0 s; paired t test: $t_{14} = 0.46$, $P = 0.65$).

DISCUSSION

Our aviary-based social foraging experiments provide evidence that male bill colour does not function during inter- or intrasexual agonistic interactions, suggesting that male bill colour is not used as a signal of status during competition for access to food. We thus conclude that male bill colour lacks a communicative function during these types of social interactions. Although this conclusion is based on lack of evidence for signalling, we previously demonstrated a very strong effect of bill colour on female–female competitive interactions using the same experimental protocol (Murphy, Rosenthal, et al., 2009) and so we have confidence that the methodology that we replicate in the present experiment is biologically relevant and yields meaningful results. Furthermore, our previous experiment with female models had a much smaller sample size and detected a strong effect size (effect size: 89%; 95% CI = 0.71–0.98, with 17 of 19 focal females avoiding female models with augmented bills). The sample size in the present study (intrasexual experiment, $N = 40$) was twice as large as that in the study using female models, and our estimate of the effect size was robust: the confidence intervals in the present study were similarly narrow to those in the previous study and clearly enveloped the null expectation of 50% (intrasexual effect size 57%, 95% CI = 0.42–0.72; intersexual effect size: 55%, 95% CI = 0.37–0.72; Fig. 3). Thus, together these results support the conclusion that male bill colour does not affect receiver response in either sex. Furthermore, the direct comparison of male to female intrasexual response to model bill colour (i.e. comparing focal males from the current study to focal females from the previous study) indicates that the sexes differ significantly in how they respond to the bill colour of same-sex competitors. Our two studies in combination therefore provide strong evidence that bill coloration in the American goldfinch, which is highly similar between the sexes, functions differently in males and females.

The lack of support of status signalling in males indicates that goldfinches use an elaborate monomorphic ornament in a signalling context that is restricted to females. This is in stark contrast with much of the previous work on the function of ornaments similarly expressed in males and females, which has shown that both males and females typically use shared ornaments in the same signalling contexts (reviewed in Amundsen & Pärn, 2006). This includes signals of quality that are assessed by potential mates of either sex (Andersson, Örnborg, & Andersson, 1998; Nolan et al., 2010; Torres & Velando, 2003) and signals of status that communicate fighting ability (Crowley & Magrath, 2004; Kraaijeveld et al., 2004; Viera, Nolan, Côté, Jouventin, & Groscolas, 2008). Likewise, the pattern that male and female ornaments function similarly has also been commonly documented among species in which females have a reduced version of the male-like trait (Amundsen, Forsgren, & Hansen, 1997; Hill, 2002; Jawor, Gray, Beall, & Breitwisch, 2004; Siefferman & Hill, 2005). Among these more dimorphic species, the similarity of the function of ornaments in both sexes suggests that selection for similar forms of communication often operate on both sexes, despite differences in the costs and benefits associated with ornamentation in each sex (see, e.g. Chenoweth, Doughty, & Kokko, 2006; Fitzpatrick, Berglund, & Rosenqvist, 1995).

Our finding that only one sex signals status with bill colour is unexpected given that both male and female goldfinches compete intra- and intersexually over food resources (Popp, 1987b), defend nesting sites (Stokes, 1950) and frequently interact with individuals of both sexes when foraging in large flocks. Signals of status often evolve in species that encounter unfamiliar individuals, as they allow for quick assessment of fighting ability. Given that goldfinches often flock with unfamiliar individuals on ephemeral and widely dispersed patches of flowering plants, it seems likely that selection would favour the evolution of this type of signal in both sexes. One unexplored possibility that could potentially explain why females were found to signal status with bill colour, but males were not, could be that we did not test the appropriate context for male status signalling. In other words, it is possible that males use bill colour as a status signal, but in contexts unrelated to foraging competition. This explanation would require that a male's competitive ability is linked to signal quality in some competitive contexts, but not in others, which seems unlikely given that male goldfinches do not defend mating territories or all-purpose territories at any time of the year. In addition, it is possible that males pay attention to status signals in contexts related to competition over nonforaging resources yet disregard signals of status while foraging because there is little competition among males over food, whereas for females, food may be more valuable during the breeding season to produce eggs. However, this explanation is in contrast to findings of Popp (1987a), who showed that both male and female goldfinches compete over food resources. As a final possibility, males may signal status with other ornaments, such as plumage coloration, or they may signal status with multiple ornaments simultaneously (see Chaine, Tjernell, Shizuka, & Lyon, 2011), and these other ornaments may supersede any information conveyed by bill colour alone. In summary, there are several possible reasons that could explain why male bill colour is not used as a status signal, or why it is not evaluated in foraging contexts, and so further testing is required to assess these possibilities.

In addition to failing to find evidence of a status-signalling function to male bill colour, the results from the present study suggest that female goldfinches do not show systematic mate preference for male bill colour. This is in contrast to a previous correlational study that investigated the mate choice signalling role of ornamental traits in male goldfinches (Johnson, Rosetta, & Burley, 1993). Although the earlier study suggested that male bill colour and plumage colour were each related to female preference, neither bill nor plumage colour was experimentally manipulated, so it is unclear which of these ornaments (or some correlated character such as body size or behaviour) females directly assessed. The lack of support for the mate choice hypothesis in the present study must be interpreted cautiously because we cannot exclude the possibility that our experimental set-up may not have allowed us to detect mate choice. For example, female stress due to recent capture may have prevented them from assessing male bill colour. However, given that similar Y-design aviary-based experimental paradigms have been widely used in studies to assess mate choice (e.g. Amundsen et. al., 1997), it is generally thought that mate choice can be assessed reasonably well in an aviary-based environment. Another potential shortcoming of our mate choice study design is that it was conducted after pair bonding had already occurred for many individuals in the population, and so focal females may not have expressed interest in forming a new pair bond. However, goldfinches breed for extended periods during the summer and experience high nest mortality (McGraw & Middleton, 2009; K. A. Tarvin, personal observation.), and often form new pair bonds for second nesting attempts (McGraw & Middleton, 2009), indicating that mate choice is likely to occur throughout the summer. Moreover, only two females in our data set had brood patches upon capture, indicating that the majority had not initiated a nesting attempt for the year.

The lack of support for the status-signalling hypothesis among males raises the question of how an elaborate ornament that is similarly expressed in males and females can evolve a particular signal function in one sex but not in the other. One possibility is that male bill colour functions as a mate choice signal, and we simply failed to detect this with our experimental design. Alternatively, male bill colour may function in other signalling contexts. It is also possible that male bill colour is expressed as a nonadaptive by-product of selection for signalling in females (i.e. results from genetic correlation between the sexes; Lande, 1980). This hypothesis has generally been put forward in systems in which only the male ornament has been found to have a signal function (e.g. Cuervo et al., 1996; Muma & Weatherhead, 1991; Wolf et al., 2004). The genetic correlation hypothesis requires that selection operates more strongly on one sex, so there is no reason to expect that the sex under stronger sexual or social selection has to be the male. Although this genetic correlation hypothesis represents a reasonable null hypothesis, carotenoid-based coloration is unlikely to be expressed without costs (McGraw, 2006), and so it is unlikely that male goldfinches would be selected to maintain a colourful bill without corresponding benefits. Likewise, given that male bills are somewhat more colourful than female bills (Kelly et al., 2012), it seems unlikely that male colour is a nonadaptive by-product of selection on females. Another alternative explanation for the apparent lack of status signal function to male bill colour is that male bill colour may have been favoured by selection in the past but subsequently lost its signal function (e.g. Ligon & Zwartjes, 1995; Westneat, 2006). Such a scenario could have occurred independently of the selective function of female bill colour, thus leading to the present pattern of a status signal function in females but not in males.

Our results indicate that bill colour of the male American goldfinch does not function as a status signal during competition over food resources. Our results also suggest that bill colour may have a signalling function only in females, but further study is required to better assess alternative signalling functions of male bill colour. Regardless of whether male bill colour functions in a manner that has yet to be identified, we can conclude that male and female goldfinches have diverged in their use of this shared ornament, and we urge future research on signal function of male and female ornamentation to consider the hypothesis that selection for ornamentation can differ between the sexes, even in species in which both sexes express an ornament to a similar degree (Tarvin & Murphy, 2012).

Acknowledgments

For help collecting data, we are grateful to Aaron Rosenblatt, Timothy Knoedler, Alissa Murphy and Caitlin Murphy. For logistic support, we are grateful to Bob Montgomerie and the staff at the Queen's University Biological Station, especially Frank Phelan and Mark Conboy. We are grateful to Taylor Wright for access to his property. T.G.M. was supported by faculty development funds from Trinity University. K.A.T. was supported by a Research Status Appointment from Oberlin College.

References

Amundsen, T. (2000). Why are female birds ornamented? *Trends in Ecology & Evolution, 15*, 149–155.

Amundsen, T., Forsgren, E., & Hansen, L. T. T. (1997). On the function of female ornaments: male bluethroats prefer colourful females. *Proceedings of the Royal Society B: Biological Sciences, 264*, 1579–1586.

Amundsen, T., & Pärn, H. (2006). Female coloration in birds: a review of functional and non-functional hypotheses. In G. E. Hill, & H. J. McGraw (Eds.), *Bird coloration, volume 2: Function and evolution* (pp. 280–345). Cambridge, MA: Harvard University Press.
Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.
Andersson, S., Örnborg, J., & Andersson, M. (1998). Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proceedings of the Royal Society B: Biological Sciences, 265*, 445–450.
Chaine, A. S., Tjernell, K. A., Shizuka, D., & Lyon, B. E. (2011). Sparrows use multiple status signals in winter social flocks. *Animal Behaviour, 81*, 447–453.
Chenoweth, S. F., Doughty, P., & Kokko, H. (2006). Can non-directional male mating preferences facilitate honest female ornamentation? *Ecology Letters, 9*, 179–184.
Clutton-Brock, T. (2007). Sexual selection in males and females. *Science, 318*, 1882–1885.
Coady, C. D., & Dawson, R. D. (2013). Subadult plumage color of female tree swallows (*Tachycineta bicolor*) reduces conspecific aggression during the breeding season. *Wilson Journal of Ornithology, 125*, 348–357.
Coutlee, E. L. (1967). Agonistic behavior in the American goldfinch. *Wilson Bulletin, 79*, 89–109.
Crowhurst, C. J., Zanollo, V., Griggio, M., Robertson, J., & Kleindorfer, S. (2012). White flank spots signal feeding dominance in female diamond firetails, *Stagonopleura guttata*. *Ethology, 118*, 63–75.
Crowley, C. E., & Magrath, R. D. (2004). Shields of offence: signalling competitive ability in the dusky moorhen, *Gallinula tenebrosa*. *Australian Journal of Zoology, 52*, 463–474.
Cuervo, J. J., de Lope, F., & Møller, A. P. (1996). The function of long tails in female barn swallows (*Hirundo rustica*): an experimental study. *Behavioral Ecology, 7*, 132–136.
Fitzpatrick, S., Berglund, A., & Rosenqvist, G. (1995). Ornaments or offspring: costs to reproductive success restrict sexual selection processes. *Biological Journal of the Linnean Society, 55*, 251–260.
Griggio, M., Serra, L., Licheri, D., Monti, A., & Pilastro, A. (2007). Armaments and ornaments in the rock sparrow: a possible dual utility of a carotenoid-based feather signal. *Behavioral Ecology and Sociobiology, 61*, 423–433.
Heinsohn, R., Legge, S., & Endler, J. A. (2005). Extreme reversed sexual dichromatism in a bird without sex role reversal. *Science, 309*, 617–619.
Hill, G. E. (2002). *A red bird in a brown bag: The function and evolution of colorful plumage in the house finch*. New York, NY: Oxford University Press.
Hill, G. E., Hood, W. R., & Huggins, K. (2009). A multifactorial test of the effects of carotenoid access, food intake and parasite load on the production of ornamental feathers and bill coloration in American goldfinches. *Journal of Experimental Biology, 212*, 1225–1233.
Jawor, J. M., Gray, N., Beall, S. M., & Breitwisch, R. (2004). Multiple ornaments correlate with aspects of condition and behaviour in female northern cardinals, *Cardinalis cardinalis*. *Animal Behaviour, 67*, 875–882.
Johnson, K., Rosetta, D., & Burley, N. (1993). Preferences of female American goldfinches (*Carduelis tristis*) for natural and artificial male traits. *Behavioral Ecology, 4*, 138–143.
Kelly, R. J., Murphy, T. G., Tarvin, K. A., & Burness, G. (2012). Carotenoid-based ornaments of female and male American goldfinches (*Spinus tristis*) show sex-specific correlations with immune function and metabolic rate. *Physiological and Biochemical Zoology, 85*, 348–363.
Kraaijeveld, K., Gregurke, J., Hall, C., Komdeur, J., & Mulder, R. A. (2004). Mutual ornamentation, sexual selection, and social dominance in the black swan. *Behavioral Ecology, 15*, 380–389.
Kraaijeveld, K., Kraaijeveld-Smit, F. J. L., & Komdeur, J. (2007). The evolution of mutual ornamentation. *Animal Behaviour, 74*, 657–677.
Lande, R. (1980). Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution, 34*, 292–305.
LeBas, N. R. (2006). Female finery is not for males. *Trends in Ecology and Evolution, 21*, 170–173.
Ligon, J. D., & Zwartjes, P. W. (1995). Ornate plumage of male red junglefowl does not influence mate choice by females. *Animal Behaviour, 49*, 117–125.
Lyon, B. E., & Montgomerie, R. (2012). Sexual selection is a form of social selection. *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*, 2266–2273.
McGraw, K. J. (2006). Mechanics of carotenoid-based coloration. In G. E. Hill, & K. J. McGraw (Eds.), *Bird coloration: Mechanisms and measurements* (Vol. 1, pp. 177–242). Cambridge, MA: Harvard University Press.
McGraw, K. J., & Hill, G. E. (2000). Differential effects of endoparasitism on the expression of carotenoid- and melanin-based ornamental coloration. *Proceedings of the Royal Society B: Biological Sciences, 267*, 1525–1531.
McGraw, K. J., & Middleton, A. L. A. (2009). American goldfinch (*Spinus tristis*). In A. Poole (Ed.), *The birds of North America online. No. 80*. Ithaca, NY: Cornell Lab of Ornithology. Retrieved from http://bna.birds.cornell.edu/bna/species/080/articles/introduction.
Middleton, A. L. A. (1979). Influence of age and habitat on reproduction by the American goldfinch. *Ecology, 60*, 418.
Montgomerie, R. (2006). Analyzing colors. In G. E. Hill, & K. J. McGraw (Eds.), *Bird coloration: Mechanisms and measurements* (Vol. 1, pp. 90–147). Cambridge, MA: Harvard University Press.
Montgomerie, R. (2010). *RCLR: Colour analysis using R*. Version 0.9.33. Kingston, Canada: Queen's University. Retrieved from http://post.queensu.ca/~mont/color/analyze.html.
Montgomerie, R., Lyon, B. E., & Holder, K. (2001). Dirty ptarmigan: behavioral modification of conspicuous male plumage. *Behavioral Ecology, 12*, 429–438.
Muma, K. E., & Weatherhead, P. J. (1991). Plumage variation and dominance in captive female red-winged blackbirds. *Canadian Journal of Zoology, 69*, 49–54.
Murphy, T. G. (2006). Predator-elicited visual signal: why the turquoise-browed motmot wag-displays its racketed tail. *Behavioral Ecology, 17*, 547–553.
Murphy, T. G. (2007). Racketed tail of the male and female turquoise-browed motmot: male but not female tail length correlates with pairing success, performance, and reproductive success. *Behavioral Ecology and Sociobiology, 61*, 911–918.
Murphy, T. G., Hernández-Muciño, D., Osorio-Beristain, M., Montgomerie, R., & Omland, K. E. (2009). Carotenoid-based status signaling by females in the tropical streak-backed oriole. *Behavioral Ecology, 20*, 1000–1006.
Murphy, T. G., & Pham, T. T. (2012). Condition and brightness of structural blue-green: motmot tail-racket brightness is related to speed of feather growth in males, but not in females. *Biological Journal of the Linnean Society, 106*, 673–681.
Murphy, T. G., Rosenthal, M. F., Montgomerie, R., & Tarvin, K. A. (2009). Female American goldfinches use carotenoid-based bill coloration to signal status. *Behavioral Ecology, 20*, 1348–1355.
Møller, A. P. (1987). Variation in badge size in male house sparrows *Passer domesticus*: evidence for status signalling. *Animal Behaviour, 35*, 1637–1644.
Nolan, P. M., Dobson, F. S., Nicolaus, M., Karels, T. J., McGraw, K. J., & Jouventin, P. (2010). Mutual mate choice for colorful traits in king penguins. *Ethology, 116*, 635–644.
Packer, C. (1983). Sexual dimorphism: the horns of African antelopes. *Science, 221*, 1191–1193.
Popp, J. W. (1987a). Choice of opponents during competition for food among American goldfinches. *Ethology, 75*, 31–36.
Popp, J. W. (1987b). Risk and effectiveness in the use of agonistic displays by American goldfinches. *Behaviour, 103*, 141–156.
Pryke, S. R., & Andersson, S. (2003). Carotenoid-based status signalling in red-shouldered widowbirds (*Euplectes axillaris*): epaulet size and redness affect captive and territorial competition. *Behavioral Ecology and Sociobiology, 53*, 393–401.
Pyle, P. (1997). *Identification guide to North American birds*. Bolinas, CA: Slate Creek Press.
Rohwer, S. (1975). The social significance of avian winter plumage variability. *Evolution, 29*, 593–610.
Rohwer, S. (1985). Dyed birds achieve higher social-status than controls in Harris' sparrows. *Animal Behaviour, 33*, 1325–1331.
Rohwer, S., Ewald, P. W., & Rohwer, F. C. (1981). Variation in size, appearance, and dominance within and among the sex and age classes of Harris' sparrows. *Journal of Field Ornithology, 52*, 291–303.
Rosen, R. F., & Tarvin, K. A. (2006). Sexual signals of the male American goldfinch. *Ethology, 112*, 1008–1019.
Rosenthal, M. F., Murphy, T. G., Darling, N., & Tarvin, K. A. (2012). Ornamental bill color rapidly signals changing condition. *Journal of Avian Biology, 43*, 553–564.
Saks, L., McGraw, K., & Hõrak, P. (2003). How feather colour reflects its carotenoid content. *Functional Ecology, 17*, 555–561.
Senar, J. C., & Camerino, M. (1998). Status signalling and the ability to recognize dominants: an experiment with siskins (*Carduelis spinus*). *Proceedings of the Royal Society B: Biological Sciences, 265*, 1515–1520.
Siefferman, L., & Hill, G. E. (2005). Evidence for sexual selection on structural plumage coloration in female eastern bluebirds (*Sialia sialis*). *Evolution, 59*, 1819–1828.
Stokes, A. W. (1950). Breeding behavior of the goldfinch. *Wilson Bulletin, 62*, 107–127.
Swaddle, J. P., & Witter, M. S. (1995). Chest plumage, dominance and fluctuating asymmetry in female starlings. *Proceedings of the Royal Society B: Biological Sciences, 260*, 219–223.
Tarvin, K. A., & Murphy, T. G. (2012). It isn't always sexy when both are bright and shiny: considering alternatives to sexual selection in elaborate monomorphic species. *Ibis, 154*, 439–443.
Tobias, J. A., Montgomerie, R., & Lyon, B. E. (2012). The evolution of female ornaments and weaponry: social selection, sexual selection and ecological competition. *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*, 2274–2293.
Torres, R., & Velando, A. (2003). A dynamic trait affects continuous pair assessment in the blue-footed booby, *Sula nebouxii*. *Behavioral Ecology and Sociobiology, 55*, 65–72.
Vedder, O., Korsten, P., Magrath, M. J. L., & Komdeur, J. (2008). Ultraviolet plumage does not signal social status in free-living blue tits; an experimental test. *Behavioral Ecology, 19*, 410–416.
Viera, V. M., Nolan, P. M., Côté, S. D., Jouventin, P., & Groscolas, R. (2008). Is territory defence related to plumage ornaments in the king penguin *Aptenodytes patagonicus*? *Ethology, 114*, 146–153.
West-Eberhard, M. J. (1979). Sexual selection, social competition, and evolution. *Proceedings of the American Philosophical Society, 123*, 222–234.
West-Eberhard, M. J. (1983). Sexual selection, social competition, and speciation. *Quarterly Review of Biology, 58*, 155–183.
Westneat, D. F. (2006). No evidence of current sexual selection on sexually dimorphic traits in a bird with high variance in mating success. *American Naturalist, 167*, E171–E189.
Wolf, W. L., Casto, J. M., Nolan, V., Jr., & Ketterson, E. D. (2004). Female ornamentation and male mate choice in dark-eyed juncos. *Animal Behaviour, 67*, 93–102.