



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



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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.

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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

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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-Mucio, 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 (Coutlee, 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  $\pm$  SE: bill brightness: males:  $0.266 \pm 0.007$ ; females:  $0.222 \pm 0.008$ ; bill saturation: males:  $0.248 \pm 0.001$ ; females:  $0.246 \pm 0.002$ ; bill hue: males:  $550.1 \pm 0.957$  nm; females:  $546.2 \pm 1.085$  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  $90^\circ$  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  $R = (R_{\max} + R_{\min})/2$ ) 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 ( $44^\circ 33'N$ ,  $76^\circ 19'W$ ) 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 &

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