Winter Plumage Coloration in Male American Goldfinches: Do Reduced Ornaments Serve Signaling Functions in the Non-Breeding Season?

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Abstract

The signaling role of sexual ornaments that are displayed during the mating season is well known for many species, but dimorphisms that occur in the non-breeding season have received much less attention, particularly when individuals only partially express their breeding condition during reproductively inactive periods. I assessed variation in the expression of colorful breeding and non-breeding plumages in male American goldfinches (Carduelis tristis), a species in which males molt out of their colorful breeding ornaments in the fall but still display reduced carotenoid- and melanin-based sexual dichromatism during the winter. I found that variability in the saturation of carotenoid-based plumage pigmentation did not differ significantly between the breeding and non-breeding seasons. Moreover, the area of melanin coloration in the cap was more variable in winter than when it is fully displayed during breeding. I also detected a significant positive correlation between the extent of melanin coloration during the winter and the saturation of non-breeding carotenoid-based plumage. Because of such variation in and correlated expression of these two color ornaments in winter, it is conceivable that male goldfinches display these hints of non-breeding coloration for use as conspecific social or sexual signals. Natural selection pressures like predation and energetic demands are traditionally thought of as factors that restrict sex ornaments to breeding times alone, but this should not preclude animals from simply reducing their exaggerated features during winter and finding an expression optimum that balances signal costs and value. Such ‘remnant’ winter ornaments might be expected to evolve not only in animals that live in large non-breeding groups (e.g. status-signaling systems) but also in those where mates begin associating before breeding onset.

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Introduction

Classic examples of sexually selected traits involve those that are displayed during the mating season only (Andersson 1994). In certain instances, however, reduced forms of secondary sexual characteristics are also expressed in the non-breeding season. Many fishes and lizards with brilliant breeding colors, for example, will retain light washes of color during non-breeding times (Bagnara & Hadley 1973). Although the adaptive significance of non-breeding dimorphisms have been studied in situations where individuals express the same degree of ornamentation throughout the year (e.g. for winter status signals; Rohwer 1975; Senar 1999), virtually no attention has been paid to the variation in or function of less exaggerated non-breeding ornamentation in animals.

The American goldfinch (*Carduelis tristis*) is unique among cardueline finches in that individuals complete two annual molts and acquire their dimorphic nuptial plumage through replacement of their body feathers just prior to the breeding season (Middleton 1977; see Hamilton & Barth 1962 for other examples in North American birds). At this time, males display striking carotenoid-based orange bill coloration, yellow plumage pigmentation on their throat, breast, nape, back and rump, and a melanin-based black cap on the top of their head; in contrast, females are drab olive and yellow in coloration and lack the black cap (Middleton 1993; McGraw et al. 2001). Females prefer to mate with males that have the brightest bills and plumage (Johnson et al. 1993), and bright carotenoid-based pigmentation is an honest indicator of endoparasite load during spring molt (Olson 1996; McGraw & Hill 2000) and of a male’s ability to physiologically process pigments obtained in the diet (McGraw & Hill 2001). Interestingly, melanin ornamentation does not similarly respond to parasitism, and as of yet its function is unknown (McGraw & Hill 2000).

At the end of the breeding season, both sexes lose their orange beak color and molt into a reduced olivaceous appearance, with females displaying only a light wash of yellow on the throat, but with males still displaying a bright yellow throat and a few black feathers on the crown (Middleton 1993). In this study, I describe variation in and relationships among winter and summer plumage characters for groups of male American goldfinches in eastern North America. Specifically, I asked the following two questions: (1) How variable are carotenoid- and melanin-based plumage colors in the non-breeding season compared to the breeding season? and (2) Is the expression of carotenoid-based ornamentation correlated with the expression of melanin coloration within the non-breeding season as well as during the breeding season?

Methods

A total of 87 wintering male goldfinches were captured in hanging basket traps at thistle feeder stations in Auburn, AL between 15 January and 24 January 1999. At capture, males were aged as either hatch-year (n = 48) or
after-hatch-year (n = 39) based on plumage characteristics of the lesser coverts and primaries (Middleton 1974). I estimated the extent of melanin-based plumage pigmentation in the winter as the percent of crown feathers that were black (to the nearest 1%). I objectively quantified carotenoid-based coloration with a Colortron reflectance spectrophotometer (Hill 1998). This unit measures hue, saturation and brightness of colored areas, and for each male I took a single measurement from the center of the pigmented throat patch displayed during winter. I used plumage saturation as my measure of carotenoid-based coloration because it is the lone tristimulus score that is positively correlated with carotenoid concentration in feathers in this species (McGraw & Gregory in press; also see McGraw & Hill 2000, 2001 for justification and repeatability).

To assess variation in the breeding plumage of wild goldfinches, I captured 29 male goldfinches (all after-hatch-year) in Ithaca, NY between 8 May and 15 May 2000. Again, I gathered saturation scores for carotenoid-based plumage, but because much of the body feathers are pigmented during the breeding season I took three ventral and three dorsal measurements and averaged these six values for each male. I measured the diameter (front to back of head) of the melanin-based black cap to the nearest 0.1 mm with calipers.

I compared the expression of and variation in carotenoid- and melanin-based plumage coloration between the breeding and non-breeding seasons using ANOVA and equality-of-variance F-tests, respectively. I used Pearson correlational analyses to determine the degree to which carotenoid and melanin ornaments were linked within seasons. Like previous studies (Olson 1996; McGraw & Hill 2000; MacDougall & Montgomerie 2003), I found no effect of age on the expression of melanin- or carotenoid-based coloration at any time of year (ANOVA and equality-of-variance F-tests; all p > 0.08).

**Results**

**Interseasonal Variation in Carotenoid and Melanin Coloration**

As expected, non-breeding carotenoid-based plumage was significantly less saturated than that of the breeding plumage (ANOVA, $F_{1,114} = 44.3$, $R^2 = 0.28$, $p < 0.0001$). However, the saturation of summer carotenoid-colored plumage was not significantly more variable than that of the winter plumage (equality-of-variance F-test, $F_{28,86} = 1.29$, $p = 0.42$; Fig. 1a). Coefficients of variation for breeding and non-breeding carotenoid plumage saturation were 13.5 and 14.5%, respectively.

Because of the different units of measurement used to quantify melanin pigmentation during summer and winter, I could not statistically compare the average areas of feather melanization between breeding and non-breeding plumages; however, I estimated that less than 10% ($\bar{x} \pm SE = 8.6 \pm 0.95\%$) of the area of the head that is black during the breeding season was black during the winter. Nonetheless, there was remarkable variation in the amount of cap area
covered in black feathers during winter, ranging from 0 to 40% of the top of the head. Variance in the extent of melanin pigmentation during winter significantly exceeded that found for cap area in the nuptial plumage (F\textsubscript{28,86} = 0.02, p < 0.0001; Fig. 1b). Coefficients of variation for summer and winter melanin-based plumage coloration are 8.5 and >100%, respectively.

**Intraseasonal Correlations between Ornament Types**

I found a significant positive relationship between the extent of melanin pigmentation in the winter plumage and winter carotenoid-based plumage saturation (r = 0.25, t = 2.38, df = 85, p = 0.02; Fig. 2a). Interestingly, during the breeding season, there was a positive correlation between the expression of carotenoid and melanin plumage coloration that was very similar in magnitude, though this relationship was not statistically significant because of a smaller sample size (r = 0.26, t = 1.40, df = 27, p = 0.18; Fig. 2b).
I investigated the expression of two forms of color ornaments in the winter plumage of male American goldfinches. If traits are under sexual selection or serve a signaling role, then their expression is thought to be more variable than naturally selected features (Cuervo & Møller 2001) because of stronger directional selection on and the series of costs associated with the development of these features. In the less elaborate but still colorful non-breeding plumage of goldfinches, I found that both carotenoid and melanin colors were no less variable during winter than in summer; in fact, the extent of melanin pigmen-

Fig. 2: Correlations between carotenoid- and melanin-based coloration in (a) non-breeding and (b) breeding plumage

Discussion

I investigated the expression of two forms of color ornaments in the winter plumage of male American goldfinches. If traits are under sexual selection or serve a signaling role, then their expression is thought to be more variable than naturally selected features (Cuervo & Møller 2001) because of stronger directional selection on and the series of costs associated with the development of these features. In the less elaborate but still colorful non-breeding plumage of goldfinches, I found that both carotenoid and melanin colors were no less variable during winter than in summer; in fact, the extent of melanin pigmen-
tation on the ornamental cap was more variable in the non-breeding than the breeding plumage.

To further characterize variation in winter colors, I tested the relationship between carotenoid- and melanin-based ornamentation in the non-breeding plumage. If these traits serve no adaptive purpose, one might suspect no correlation between the expressions of these two types of color. Instead, I found a significant positive association between the area of melanized feathers on the head and carotenoid-based plumage saturation. A relationship of similar magnitude was also detected for carotenoid- and melanin-based breeding plumage.

There is yet another piece of evidence that links winter pigmentation with breeding colors that have a known mating function. In a previous study, I showed a significant positive correlation between the carotenoid-based plumage saturation of males in their winter and summer plumage (McGraw & Hill 2001). As indicated above, male nuptial carotenoid colors serve to attract mates in goldfinches (Johnson et al. 1993).

Because of such variation in and correlated expression of these colors, I hypothesize that male goldfinches display hints of non-breeding coloration for use as conspecific social or sexual signals. To my knowledge, the idea that less-exaggerated, non-breeding ornaments might evolve as a form of intraspecific visual communication has not previously been offered. Biologists have shown an interest in certain sexual dimorphisms that change, and even reverse, during non-breeding times (e.g. beak coloration in red-billed queleas, *Quelea quelea*; Owens & Short 1995), but in these instances the emphasis has been placed on the physiological mechanisms (e.g. steroid-hormone modulation) that govern such seasonal differences in morphology and rarely on their ultimate function. In one of the only analogous hypotheses, Voelker & Museum (1996) supposed that a retained mottled appearance in winter by certain species (e.g. *Sterna* terns) might signal their non-breeding condition to breeding congeners and reduce heterospecific courtship chases and aggression. Eastern North American goldfinches and their *Carduelis* relatives do not suffer from this problem, however, since they share summer breeding seasons.

Clearly, to test my hypothesis, we now need behavioral evidence that these male colors are used either as signals to females of sexual attractiveness and/or as signals to males of competitive ability. Given the social and mating systems of goldfinches, there is ample opportunity and potential need for both modes of visual signaling during non-breeding periods. Goldfinches form large foraging flocks during winter (Middleton 1993), and competitions for scarce food could in fact be mediated by signals of status that reduce intense aggressive escalations (Rohwer 1975). Moreover, mated pairs begin to form in early spring, when birds are still in winter plumage and grouped into these mixed-sex flocks (Coutlee 1967). However, in certain songbirds like the house finch (*Carpodacus mexicanus*) that also start to associate with mates in advance of breeding (Hill 2002), males display their colorful breeding plumage throughout the year, which could aid in early season mate attraction. Different still, many ducks start pair formation in the winter and accordingly molt out of their drab, late summer eclipse plumage.
into breeding coloration at this time (Andersson 1983). Evidently in goldfinches, there has been some selective pressure to replace their set of feathers twice a year and display only a small degree of color during winter.

Why then do birds like goldfinches complete two molts? They are one of the few North American passerines, and one of only two finches in their songbird subfamily (Carduelinae), to undergo two annual molts and grow out of their nuptial plumage after breeding (Hamilton & Barth 1962; Willoughby et al. 2002). Traditionally, when animals restrict sexual displays to the mating season only, it is thought that natural selection pressures (e.g. changes in climate, predation, and energy demands) are the causal factors (Andersson 1994). Middleton (1986) has previously shown that the biomass of body contour feathers is larger in the winter than in the summer plumage of goldfinches and suggested that the post-nuptial (or pre-basic) molt is essential for providing a fresh, thick plumage to aid in thermoregulation and survival during harsh winter conditions. There is also the notion that cryptic colors may reduce predation risk in seasonally group-forming birds (reviewed in Götmark 1999). Ultimately, since carotenoid and melanin pigmentation have been shown to incur costs at some physiological or behavioral level (McGraw & Hill 2000; McGraw et al. 2002; see more below), these aforementioned agents of natural selection during winter might oppose and impair the ability of individuals to simultaneously develop fully exaggerated non-breeding color. The result need not be the complete absence of an ornament in winter, however, but rather a reduced, still functional signal whose expression optimum is set where the benefits of feather growth and color counterbalance the costs.

One last issue to which these results speak is the evolution of multiple signals in animals (e.g. Möller & Pomiankowski 1993; Johnstone 1995). Here, I considered not only the expression of color in two seasons during the year, but also two types of color signals. Melanin and carotenoid colors in birds have previously been considered to communicate different sets of information because they are produced in different ways (Hill & Brawner 1998; Badyeav & Hill 2000; McGraw & Hill 2000; McGraw et al. 2002; Senar et al. 2003). Carotenoid colors are thought to reveal health and communicate a male’s worth to prospective female mates, whereas melanin colors tend to be condition-independent, hormonally mediated, and signals of competitive ability to rival males (Maynard-Smith & Harper 2003). Here, I found that these ornament types are correlated (and equally so) within the breeding and the non-breeding plumages. Since they do not respond similarly to parasitism (McGraw & Hill 2000), this suggests that the most colorful carotenoid- and melanin-pigmented birds may be better able to meet the different sets of challenges associated with developing both types of colors. Alternatively, the possibility remains that these are redundant or unreliable signals during winter (Moller & Pomiankowski 1993). We must now identify the honesty-reinforcing mechanisms and signaling roles of melanin colors at all times of year before we can fully deduce the information content of these winter and summer ornamental traits in goldfinches.
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