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Correlated changes in male plumage coloration and female mate choice in cardueline finches

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The coevolution of extravagant male traits and female mate preferences is a central tenet of sexual selection theory. In lineages in which males have developed more elaborate sexual characters, females favour the most extreme expression of the trait. In some taxa, however, ornamental displays have evolved from more to less exaggerated states. Under these circumstances, it is unclear whether females show preferences for an ancestral male condition or for the current, less elaborate display. Here, we tested female mate preferences relative to male ornamental coloration in two species of cardueline finch (the American goldfinch, *Carduelis tristis*, and pine siskin, *Carduelis pinus*) that have evolved less elaborate carotenoid-based colour displays from more elaborately coloured ancestral states. We presented females of each species with a choice of males having either large patches of red colour (the elaborate, ancestral condition) or with species-typical patches of yellow colour (the less elaborate, derived state). Female goldfinches and siskins showed consistent preferences for the natural colour displays of males, and not for the more elaborate, ancestral colour pattern. Previous research on another cardueline finch taxon (a subspecies of the house finch, *Carpodacus mexicanus griscomi*), however, showed that females prefer more elaborate, ancestral coloration to the current form of reduced colour expression. The lack of congruence between male trait expression and female trait preference in the lineage with the most recently derived reduction in trait expression suggests that there may be evolutionary lags in the correspondence between male traits and female preferences. A shift in the expression of male coloration appears to be the first step towards the evolution of reduced colour displays in these finches.

One of the fundamental predictions of sexual selection theory is that female mate preferences coevolve with the degree of elaboration of male ornamental traits (Fisher 1958; Lande 1981). There is now much empirical support for the correspondence between what males display and what females prefer (reviewed in Andersson 1994). In virtually all of these studies it appears that male traits have become more exaggerated over evolutionary time. Change in ornament expression, however, need not be from less to more elaborate states. In numerous taxa, less elaborate sexual displays have evolved from more elaborate forms (Wiens 2001). These lineages showing reversals in trait elaboration provide an ideal opportunity to test the generality of congruence between preference for and expression of display traits.

Hill's (1994a) work on a southern Mexican subspecies of the house finch, *Carpodacus mexicanus griscomi*, is one of few investigations into how females respond to an historical reduction in male trait expression (see also Houde & Endler 1990; Saetre et al. 1997; Morris 1998). House finches and other cardueline finches display ornamental carotenoid-based plumage coloration that varies within and among species in both the hue (from yellow to red) and the size of coloured patches (from small to large) (Clement et al. 1993). Because of the challenges of acquiring carotenoids in the diet (Grether et al. 1999; Hill et al. 2002) and metabolic demands of manufacturing red pigments from yellow dietary precursors (Hill 1996a, 2000), carotenoid pigmentation is widely considered a condition-dependent trait that becomes more elaborate as colour patches get redder and larger. Males from the house finch subspecies *C. m. griscomi* have small patches of red coloration that evolved from a large-patched ancestral condition, yet females show a clear mating preference for large patches of red colour (Hill 1994a; Fig. 1). This research suggested that female preferences do not

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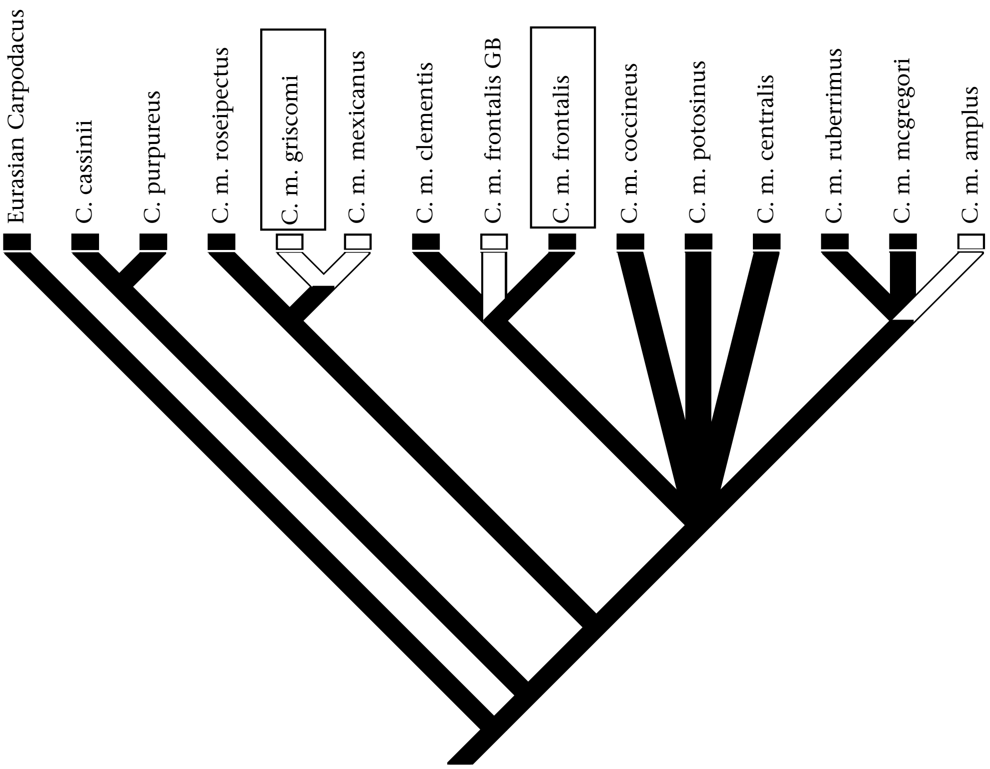


Figure 1. A composite phylogeny of house finch, *Carpodacus mexicanus*, lineages based on a cladistic analysis and biogeographical and morphological evidence (Hill 1996b). Evolution of the extent of ventral carotenoid pigmentation (patch size) was traced on the phylogeny and the states of interior nodes were optimized (Maddison & Maddison 1993). Boxes indicate the two lineages of house finches in which females prefer as mates large (■) versus small (□) patches of colour. In the *C. m. griscomi* lineage, males have small patches of coloured feathers, which are derived from a larger-patched ancestral state, but females still prefer large patches of colour. Note that for this paper the medium- and large-patch categories of Hill (1996b) are combined into a single large-patch category.

always directionally coevolve with male display traits and that changes in the cost to males of producing or displaying an ornament may cause an evolutionary reduction in ornament elaboration (Hill 1994b; Gray 1996).

In this study, we sought to investigate further the degree of congruence between preference for and expression of display traits in cardueline finches (family Fringillidae, subfamily Carduelinae) by focusing on additional taxa that show reduced male trait expression. Specifically, we tested the relationship between female mate choice and male carotenoid display in American goldfinches, *Carduelis tristis*, and pine siskins, *Carduelis pinus*. Male goldfinches have extensive carotenoid-based yellow coloration across most of their body plumage, and this yellow coloration is a sexually selected signal of male condition (Johnson et al. 1993; McGraw & Hill 2000b). Male siskins, in contrast, have small patches of yellow colour only on their wings and tails. Phylogenetic reconstructions indicate that carotenoid pigmentation in both species is derived from a red, large-patched ancestral state (see Results). In this study, we manipulated the plumage colour of male goldfinches and siskins to mimic these ancestral states and examined whether females retain an historical mate preference for the more elaborate colour pattern, as occurs in *C. m. griscomi*.

The work that we present in this paper hinges on the assertion that red carotenoid pigmentation is a fundamentally more elaborate display trait than is yellow carotenoid pigmentation, just as large patches of carotenoid pigmentation are fundamentally more elaborate than small patches of carotenoid pigmentation. Compared to yellow carotenoid pigments, red carotenoid pigments are rare in the foods of most animals, including cardueline finches (Bauernfiend 1981; Goodwin 1984; Slagsvold & Lifjeld 1985; Inouye 1999). To produce red feathers, a male finch must either search for scarce red pigments or metabolically convert yellow pigments to red pigments, and both of these means of acquiring red pigments are costly (Hill 1996a, 1999, 2002; Olson & Owens 1998). Comparative data also support the assertion that red is a more elaborate colour display than yellow in cardueline finches. The degree of sexual dimorphism is greater in red versus yellow species (Hill 1996a; Badyaev & Hill 2000), and when adult males differ in coloration from females and juveniles, in all cases females and juveniles have plumage that is less red (more yellow) than adult males (Hill 1996a). Finally, within house finches, red males are preferred as mates (Hill 1990, 1991, 1994a; Hill et al. 1999), have fewer parasites (Thompson et al. 1997; Brawner et al. 2000), are in better nutritional condition (Hill & Montgomerie 1994; Hill 2000), have access to more dietary carotenoid pigments (Hill et al. 2002), survive better (Hill 1991) and have greater reproductive success (McGraw et al. 2001) than yellow males. Taken together, these observations present a strong case that red carotenoid pigmentation is a fundamentally more elaborate ornamental display than yellow carotenoid pigmentation.

METHODS

Phylogenetic Reconstruction

Deducing the phylogenetic relationships of cardueline finches has been the focus of several studies (Marten & Johnson 1986; Sibley & Ahlquist 1990; Groth 1994; Fehrer 1996; Badyaev 1997; Arnaiz-Villena et al. 2001). Our phylogenetic analysis focused on the relationships within the genus *Carduelis*, which includes both the American goldfinch and pine siskin. Arnaiz-Villena et al. (1998) recently published a phylogeny of genus *Carduelis* based on analysis of mitochondrial cytochrome *b* from 25 of 31 extant members of the genus, and we used Arnaiz-Villena et al.'s tree as our hypothesis for the historical relationships of *Carduelis* species (Fig. 2).

To reconstruct ancestral character states within the genus *Carduelis* we had to have outgroups for comparison, so we included in our phylogeny the other major genera of cardueline finches. For the relationships of these cardueline taxa, we largely followed the groupings of Badyaev (1997), which is the only published phylogeny to include all major genera of cardueline finches. We resolved the *Serinus*/*Carduelis*/*Loxia*/*Carpodacus* polytomy in Badyaev's phylogeny by making *Loxia* the sister group to *Serinus*/*Carduelis* and *Carpodacus* the next most closely related taxa (Marten & Johnson 1986; Arnaiz-Villena et al. 2001; Fig. 2). We also collapsed birds in the genera *Carpodacus*, *Haematospiza*, *Urocynchramus* and *Uragus*, which comprise a monophyletic group in Badyaev's (1997) phylogeny and all of which have large patches of red coloration, into a single taxon that we labelled '*Carpodacus*' (Fig. 2). Because the majority of cardueline finch genera have large red patches of colour, the primary assumption of our paper, that both American goldfinches and pine siskins evolved from a large-patched red ancestor, is supported by any published arrangement of the cardueline finch genera.

We assigned a single character state for colour (red or yellow) and patch size (large or small) to each species within *Carduelis* and to each genus in the outgroup taxa. A species was considered to have a small patch of colour if less than 20% of male plumage, as viewed in profile, had carotenoid coloration. Most genera have characteristic coloration or patch size, and we used the most common character state among species within a genus to characterize that genus. In all cases at least 75% of species displayed the character state that we used to characterize a genus.

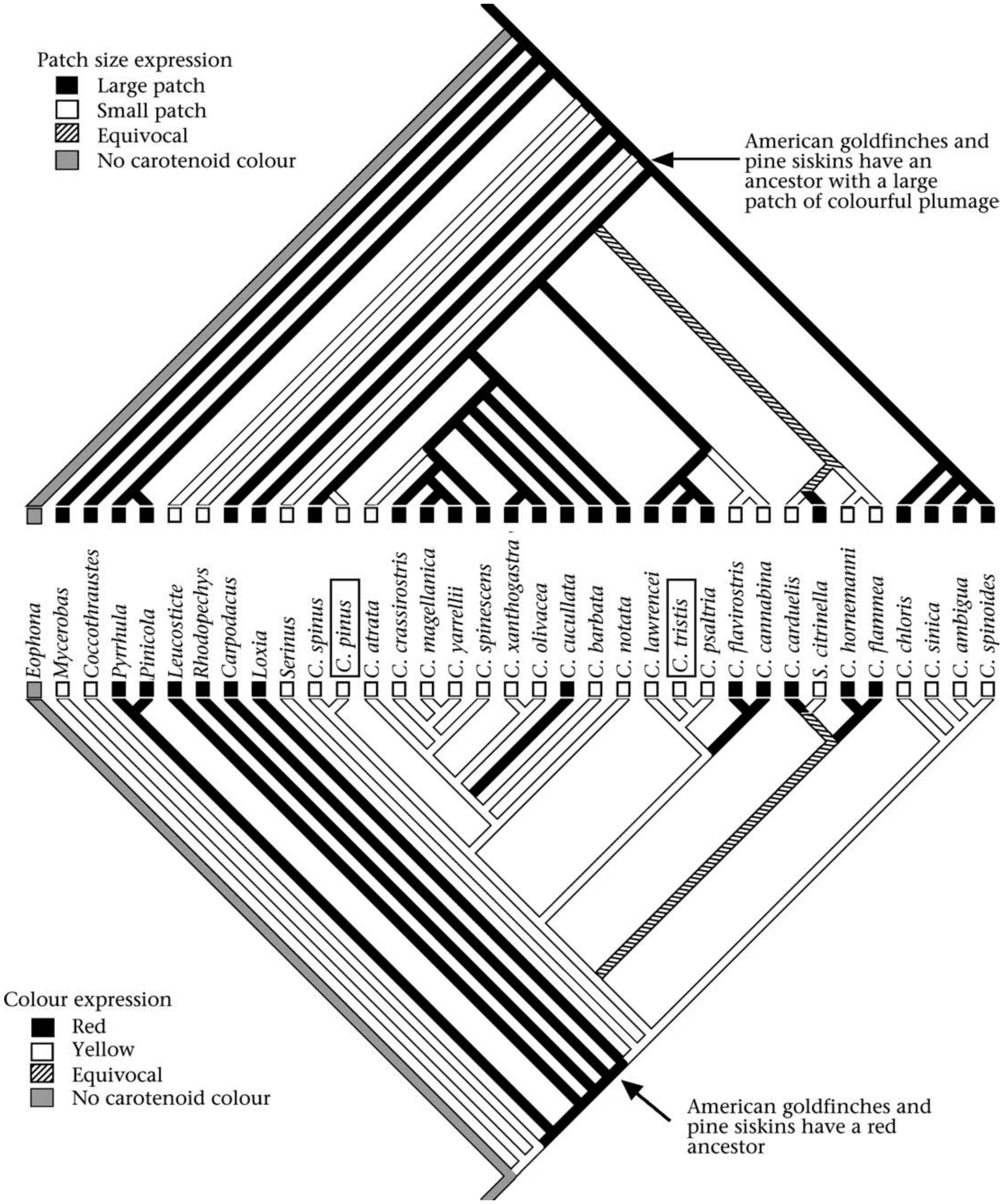
The most influential outgroup in our reconstruction of character states was genus *Serinus*, which is the sister group to *Carduelis*. Expression of patch size is somewhat variable in *Serinus*, so we wanted to be certain that we correctly characterized the primitive condition of colour and patch size in this group. Arnaiz-Villena et al. (1999) have published a detailed phylogeny of the genus *Serinus* based on analysis of mitochondrial cytochrome *b* from 20 of 37 extant species, and we used this phylogeny to determine the likely primitive condition for *Serinus*. We mapped colour and patch size of these canary species and then used the computer program MacClade (Maddison & Maddison 1993) to reconstruct the ancestral states of plumage redness and patch size. The primitive condition for the genus *Serinus* is a large patch of yellow plumage and this is how the genus was entered into the phylogeny used in this study. Once the character states of patch size and plumage hue had been assigned to all extant taxa, we reconstructed the ancestral states of plumage redness and patch size across our entire phylogeny using the computer program MacClade (Maddison & Maddison 1993; Fig. 2).

Mate Choice in American Goldfinches

In January and February 1999, we captured 41 male and 25 female goldfinches in Lee County, Alabama, U.S.A., and housed them outdoors in unisex flocks that were visually isolated. Mate choice trials were conducted between 18 June and 26 July 1999. For each trial, a female was simultaneously presented with a control male (natural yellow coloration) and a treatment male (exaggerated coloration). Male plumage coloration was manipulated using Pantone art markers (McGraw & Hill 2000a). We coloured over all carotenoid-based pigmented feathers on the evening before each trial. In experiment 1, treatment males were coloured with an orange marker (137-T); in experiment 2, treatment males were coloured red (Warm Red 2X-T). In both experiments, we coloured the plumage of control males with a yellow marker (109-T). We used a fibre-optic reflectance spectrophotometer and a UV-visible light source to collect spectral reflectance data for the different marker treatments (McGraw et al. 1999). All marker treatments simulated the natural colour of American goldfinches (yellow) or other cardueline finches (red and orange; Fig. 3). All of the marker treatments caused a relatively small loss of reflectance in the ultraviolet, but because each group was affected equally we assume that uniform loss of UV reflection did not influence the outcome of mate choice trials.

Trials were conducted in an outdoor mate choice arena that consisted of a female association area, a nonchoice area and four adjacent male cages (Tobias & Hill 1998). During trials, we placed stimulus males in the outer two compartments, and we systematically alternated the position of males such that yellow males were on the right for half of the trials. In the evening before the trial in which they were to participate, we placed females in the choice area so that they could acclimate to their new environment. All trials were completed within the first 4 h of morning daylight.

During a trial, a female could associate with stimulus males, one at a time, by landing on perches in front of each cage. Trials began only after females had visited each male cage once, and they lasted for 45 min in experiment 1 and 30 min in experiment 2. We used a unique female in each of 25 trials (14 in experiment 1, 11 in experiment 2). Among the 41 stimulus males, nine participated in two trials and 32 males participated in only one trial. We used the amount of time that females spent associating with individual males as our primary measure of mate preference (Hill 1990; Johnson et al. 1993). Also, in some trials,



American goldfinches and pine siskins have an ancestor with a large patch of colourful plumage

American goldfinches and pine siskins have a red ancestor

Figure 2. A composite phylogeny of cardueline finches. The phylogeny of genus *Carduelis* is from Arnaiz-Villena et al. (1998), which is nested into the genus-level phylogeny of Badyaev (1997) (see text). In this phylogeny the taxon labelled '*Carpodacus*' includes birds in the genera *Carpodacus*, *Haematospiza*, *Urocynchramus* and *Uragus*. Evolution of plumage hue and patch size was traced on the phylogeny and the states of interior nodes were optimized using MacClade (Maddison & Maddison 1993). American goldfinches and pine siskins, the species that were the focus of this study, are indicated by boxes around their names. Both American goldfinches and pine siskins are derived from an ancestor with large patches of red coloration.

females gave quiet feeding calls (Middleton 1993), and we used these courtship behaviours as supplemental indices of female choice. We also quantified the flight displays and song rate of stimulus males.

Mate Choice in Pine Siskins

We captured 45 siskins in Lee County, Alabama, U.S.A., in February 2000. Pine siskins could not be sexed reliably using morphological characteristics, so we determined the sex of each individual using a PCR-based molecular sexing technique (Griffiths et al. 1998). Twenty-seven males and 18 females were then divided into unisex flocks (2 males, 1 female) of 13–16 individuals that were visually isolated.

As in experiments with goldfinches, we manipulated plumage coloration of male siskins with Pantone art markers. In experiment 1, we used the same protocol as above to colour the carotenoid-based tail and wing patches of one male red (Warm Red 2X-T) and one male yellow (109-T). In experiment 2, we coloured the pigment

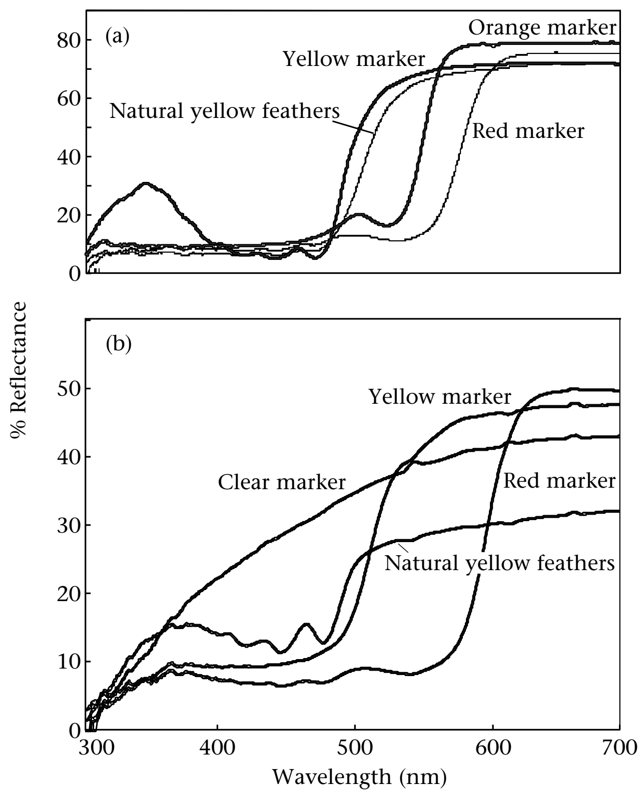


Figure 3. Representative reflectance spectra for the natural and manipulated plumage colours of male American goldfinches (a) and pine siskins (b). See McGraw et al. (1999) for details of methods used to obtain spectral data.

patches of both males yellow and expanded the patch size of one male by colouring his head, breast and nape yellow, while leaving the patch size of control males unchanged. We applied a clear marker (Blender-T) to the same body areas of sham controls.

We ran 11, 60-min trials for experiment 1 between 21 and 29 May 2000 and seven 60-min trials for experiment 2 between 30 May and 2 June 2000. Unique females were used in each of the 18 trials, and all of the males participated in one trial from each experiment. Methodology and data collection for the trials follow those described above for goldfinches, except that we did not measure the vocalizations of male siskins because they sang so infrequently.

RESULTS

Phylogenetic Reconstruction

We found that a large patch of red coloration is the likely ancestral condition for both American goldfinches and for pine siskins (Fig. 2). In the lineage leading to goldfinches and siskins, there was a transition from red to yellow plumage coloration, and in the lineage leading to siskins there was also a transition from a large patch of pigmentation to a small patch. Thus, in both taxa, less elaborate forms of carotenoid display were derived from more elaborate forms.

Mate Choice in American Goldfinches

In experiment 1, in which females were presented with one yellow male and one orange male during a 45-min trial, females spent a mean $\pm$ SE of 77.7 $\pm$ 3.1% (34.1 $\pm$ 3.2 min) of the trial in front of the two male cages and 23.3 $\pm$ 3.1% (10.9 $\pm$ 3.2 min) of the trial in the nonchoice areas (Wilcoxon matched-pairs signed-ranks test: $T = 105$, $N = 14$, $P = 0.0002$). Females showed no significant left/right cage preference ($T = 61$, $P = 0.62$). During the mate assessment periods, females spent 72.0 $\pm$ 6.2% (24.5 $\pm$ 2.9 min) of the trial in front of yellow males and 28.0 $\pm$ 6.2% (9.5 $\pm$ 3.1 min) in front of orange males ($T = 84$, $P = 0.04$; Fig. 4). Females spent more time with yellow males in 12 of 14 trials (binomial test: $P = 0.006$). Females gave significantly more feeding calls to yellow males than to orange males ($T = 100$, $P = 0.001$).

In experiment 2, in which we presented yellow and red males to females during a 30-min trial, females spent 72.4 $\pm$ 6.0% (21.7 $\pm$ 1.8 min) of the trial in front of the two male cages and 27.6 $\pm$ 6.0% (8.3 $\pm$ 1.8 min) in the nonchoice areas ($T = 61.5$, $N = 11$, $P = 0.008$). Females again showed no significant left/right cage preference ($T = 37$, $P = 0.38$). Overall, females spent 64.8 $\pm$ 6.5% of male assessment time (14.5 $\pm$ 2.3 min) in front of yellow males and 35.2 $\pm$ 6.5% (7.2 $\pm$ 1.5 min) in front of red males ($T = 54.5$, $P = 0.05$; Fig. 4). Females spent more time in front of yellow males in nine of 11 trials (two-tailed binomial test: $P = 0.06$). Females gave significantly more feeding calls to yellow males than to red males ($T = 54$, $P = 0.05$).

In neither experiment did females show a significant preference for males who were more active or sang more (all Ts < 40, all NS).

Mate Choice in Pine Siskins

In experiment 1, in which female siskins were presented with males having either small red or small yellow patches of coloration during a 60-min trial, females spent 82.0 $\pm$ 3.2% (49.2 $\pm$ 1.9 min) of the trial in front of the two male compartments and 18.0 $\pm$ 3.2% (10.8 $\pm$ 1.9 min) of the trial in the nonchoice areas ($T = 66$, $N = 11$, $P = 0.001$). Females showed no significant left/right cage preference ($T = 36.5$, $P = 0.79$). Overall, females spent 65.6 $\pm$ 3.5% of mate assessment time (32.5 $\pm$ 2.4 min) in front of yellow males and 34.4 $\pm$ 3.5% (16.7 $\pm$ 1.7 min) in front of red males ($T = 64$, $P = 0.003$; Fig. 5). Females spent more time in front of yellow males during 10 of 11 trials (two-tailed binomial test: $P = 0.01$). Females gave significantly more feeding calls to yellow males than to red males ($T = 57.5$, $P = 0.03$).

In experiment 2, in which female siskins were presented with males having either small yellow or large yellow patches of coloration during a 60-min trial, females spent 85.7 $\pm$ 1.7% (51.4 $\pm$ 1.0 min) of the trial in front of the two male cages and 14.3 $\pm$ 1.7% (8.6 $\pm$ 1.0 min) of the trial in nonchoice areas ($T = 28$, $N = 7$, $P = 0.015$). Females showed no significant left/right cage preference ($T = 21$, $P = 0.30$). Overall, females spent 77.5 $\pm$ 3.9% of

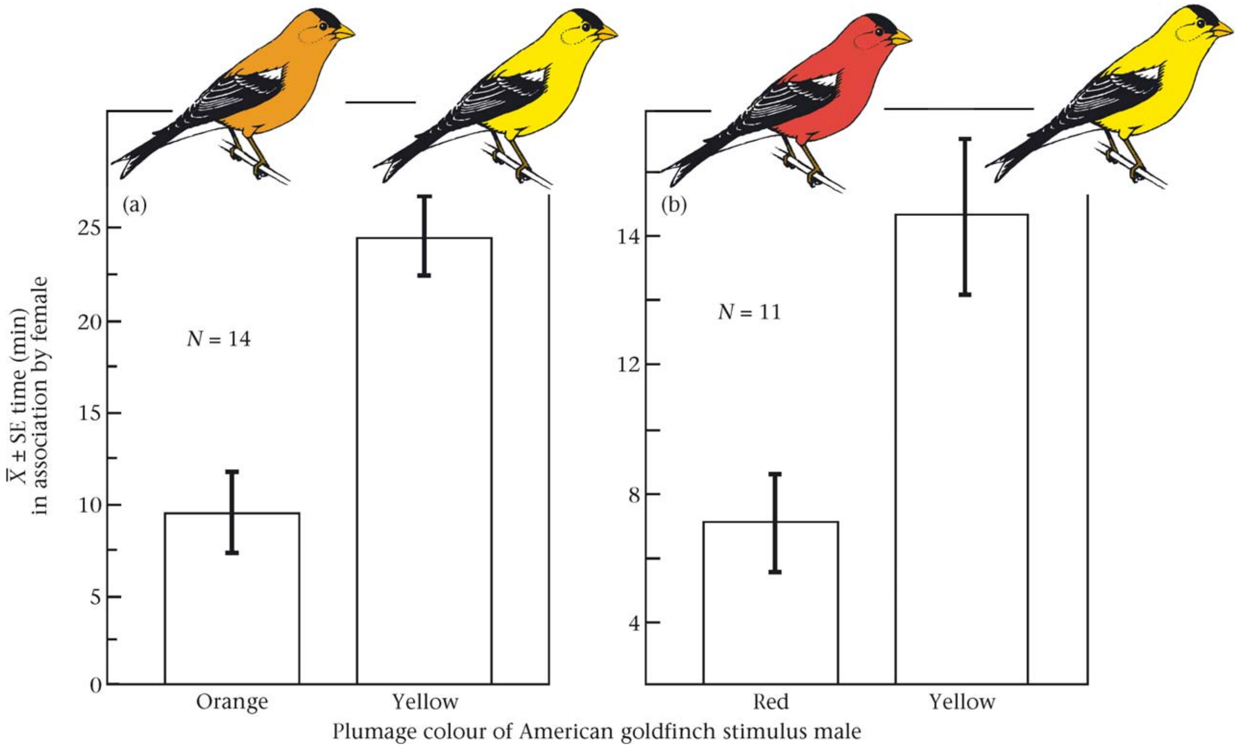


Figure 4. Mate preferences of female American goldfinches presented with males having natural yellow coloration and either orange (a) or (b) red coloration. Red pigmentation is a more elaborate form of colour display and is an ancestral condition for American goldfinches, but female American goldfinches showed a stronger preference for yellow than for orange or red coloration in males.

mate assessment time (39.9 ± 2.1 min) in front of males having normal-sized patches and 22.4 ± 3.9% (11.6 ± 2.1 min) with enlarged-patched males ($T = 28$, $P = 0.015$; Fig. 5). Females spent more time in front of normal-patched males during all seven trials (two-tailed binomial test: $P = 0.02$). There were only three feeding calls by females during these trials, so no statistical analyses were performed on these data.

In both experiments with siskins, male activity pattern was unrelated to the proportion of time that females spent with males in either treatment group (both Ts < 20, both NS).

DISCUSSION

In several cardueline finch taxa, including American goldfinches and pine siskins, expression of carotenoid-based plumage coloration has evolved from a more to a less elaborate state. When female goldfinches and siskins were given a choice of males with the more elaborate ancestral form of ornamentation or the current reduced state, we found congruence between the mate preferences of females and the current colour display of males. Female goldfinches preferred yellow males to males with ancestral red plumage, and female siskins preferred males with small yellow patches of coloration to males with larger or redder ancestral-like patches. These results indicate that the male sexual traits and female mate preferences of cardueline finches coevolve even when ornament expression is reduced over evolutionary time, consistent with recent studies of ornamental coloration in swordtail fish (*Xiphophorus*; Morris 1998). Combining the results from our study with those from previous mate choice tests in the larger-patched subspecies of the house finch, *C. m. frontalis* (Hill 1990, 1994a), we have found congruence between female preference and male ornament display in three cardueline finch taxa.

These patterns of trait preference coevolution differ markedly, however, from those reported for a fourth cardueline finch taxon, *C. m. griscomi* (Hill 1994a) in which males have small patches of red coloration but females prefer as mates males with ancestral, large patches of red. How do we reconcile the differences between these sets of observations from closely related members of the cardueline finch subfamily? The primary difference between these taxa is their age since divergence. The finch taxa that show congruence between female preference and male ornament expression have had the same plumage colour display for millions of years. According to the molecular clock estimates of both Arnaiz-Villena et al. (1998) and Marten & Johnson (1986), the lineage leading to pine siskins split from a large-patched ancestor about 3 million years ago. The lineage leading to most yellow *Carduelis* finches, including the American goldfinch and the pine siskin, split from a red ancestor about 4 million years ago according to Marten & Johnson (1986) or about 9 million years ago according to Arnaiz-Villena et al. (1998). The *frontalis* subspecies of the house finch retained a large patch of red coloration that is ancestral in its genus, dating back millions of years (Hill 1996b, 2002). In contrast, the small-patched subspecies of the house finch evolved from a larger-patched ancestor much more

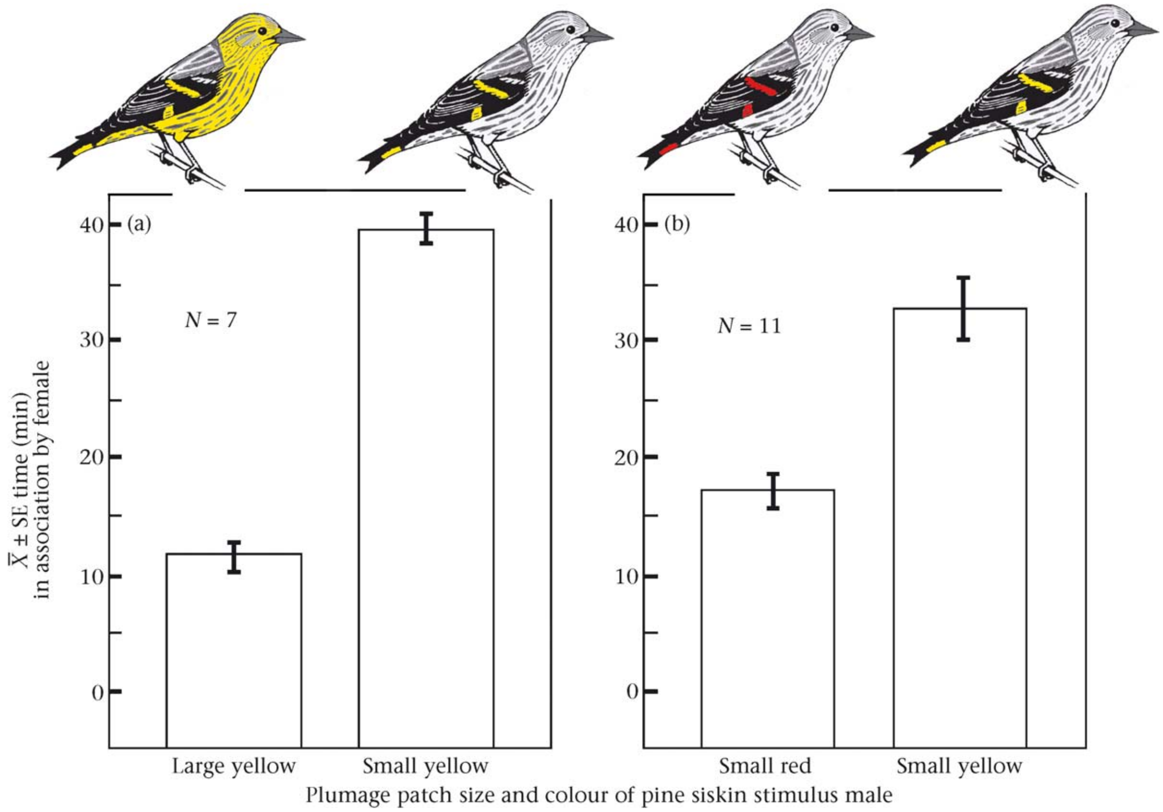


Figure 5. Mate preferences of female pine siskins that were presented with males having natural plumage coloration (small, yellow patches) versus either large patches of yellow colour (a) or small patches of red (b). Large colour patches and red pigmentation are more elaborate forms of colour display and are the ancestral condition for pine siskins, but female siskins showed a stronger preference for males with small yellow patches of coloration.

recently. Based on genetic analysis of *frontalis* and *griscomi* populations and assuming 2% divergence per million years, Wang et al. (in press) estimated that *griscomi* diverged from other house finch populations, and from a large-patched ancestor, about 30 000 years ago. Thus, we may be observing different stages in the coevolutionary process for these different cardueline finch taxa. Traits and preferences have had sufficient time to coevolve in goldfinches, siskins and *frontalis* house finches, but there seems to be an evolutionary lag in the response of female preferences to the change in plumage coloration for the recently diverged, small-patched house finch subspecies.

This proposed shift in male coloration, but not female preference, in *C. m. griscomi* also offers clues into the selective forces that generate evolutionary changes in ornamental traits. Instead of being driven by a change in the costs or benefits of female preferences, plumage colour in male *griscomi* finches is likely to have been reduced by an increase in the cost to males of producing or displaying carotenoid pigments in feathers (Hill 1994a). Carotenoid-based traits are dependent, in part, on the availability of pigments that can be acquired in the diet (Völker 1938; Brush & Power 1976; Hill 1992), and males from the *griscomi* population appear to have limited access to carotenoid pigments compared to other populations of house finches (Hill 1994a, 2002; Hill et al. 2002). Thus, observations of house finches indicate that a decrease in ornamentation independent of any corresponding shift in female preference is likely to be the first step in the evolution of reduced colour expression among these birds.

Given that the elaborateness of carotenoid coloration signals the health and condition of prospective mates (Olson & Owens 1998; Hill 2002), why should females fail to maintain a preference for historical, more costly and exaggerated displays? Clearly, females benefit by confining their preferences to the range of trait expressions displayed by males in their population. By matching their preferences to male colour displays, females may avoid pairing with males from other populations or species (Wallace 1889). Moreover, the visual discrimination of individuals in a species is presumably optimized for the specific portions of the electromagnetic spectrum in which individuals of that species most need fine discrimination (Endler 1991). Birds adapted to discriminate best along one hue axis may do less well in discriminating among others (Peiponen 1992), which would provide selective advantages for females who matched mating preference for ornamental coloration to that displayed by males in their population.

Alternatively, if there was a genetic correlation between male trait expression and female preference, then selection for reduced trait expression in males may have resulted in a change in trait preference in females (Lande 1981, 1987; Arnold 1983). This process would maintain a correlation between female mate preference and male display and would require no direct selection on female preference to maintain such a link. Why such a genetic correlation between expression of carotenoid pigmentation and female preference for colour display exists for *Carduelis* finches but not for house finches remains unknown. Perhaps lack of genetic correlations between female preference and male display in house finches is due to the extreme condition dependence of colour display in house finches (Hill 2002).

Might females in our mate choice trials simply have failed to recognize males with novel coloration as conspecifics? This seems unlikely for a few reasons. All of our colour manipulations left many clues for species recognition including the size and shape of the birds, their species-typical vocalizations, and even most of their natural plumage colour and pattern. In some cases the change in appearance was subtle, such as when the small wing and tail patches of siskins were changed from yellow to red. Recent studies with birds and fish have shown that females sometimes prefer to mate with males having novel or grossly exaggerated secondary sexual traits (Basolo 1990; Burley & Symanski 1998), and that they easily recognize these novel males as conspecifics. In a study with house finches, female *C. m. griscomi* also showed a preference for males with patches of red coloration that were twice as large as those displayed by males of their subspecies (Hill 1994a).

In summary, our observations of the congruence between female mate preference and male trait expression in various cardueline finch taxa support the idea that male traits and female preferences coevolve regardless of the direction of change in male ornamentation over evolutionary time, but that lineage divergence may generate short-term mismatches in male displays and female choice. To test these ideas more thoroughly, additional studies are needed in taxa in which a change in ornamental coloration has occurred relatively recently, like *C. m. griscomi*. Moreover, to extrapolate to condition-dependent ornaments other than carotenoid pigmentation, we will have to identify additional lineages in which traits, such as elongated tail feathers or vocalizations, have evolved towards a less elaborate state.

Acknowledgments

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