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SHORT COMMUNICATION

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Assortative mating by carotenoid-based plumage colour: a quality indicator in American goldfinches, *Carduelis tristis*

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Abstract We investigated the mating patterns in 22 breeding pairs of wild American goldfinches (*Carduelis tristis*) with respect to their body size, condition, and carotenoid-based, yellow plumage colour. Using reflectance spectrometry, we objectively quantified plumage colours across the bird-visible wavelengths, revealing a unexpected UV peak in the reflectance spectrum from yellow feathers. We summarized our colour measurements using a principal components analysis to create a single variable, carotenoid PC1, that represents the intensity of this carotenoid-based yellow colour, a measure of phenotypic quality in this species. We found no evidence of assortative mating with respect to measures of body size or condition but there was positive assortative mating by carotenoid PC1, such that the yellow plumage colours of males and females were significantly correlated within pairs. We argue that the yellow carotenoid coloration of goldfinches may be important in mutual mate choice and, thus, that sexual selection in this species may act upon female ornamentation, as well as the more obvious plumage signals of males. Because assortative mating results in an increase in genetic variance, we suggest that this might be a mechanism that maintains variance in ornamental traits in spite of the variance-eroding effects of sexual selection.

Introduction

Assortative mating, the propensity of phenotypically similar individuals to mate with each other, is one of the most commonly observed mating patterns in animals, particularly with respect to body size (Crespi 1989). Assortative mating by quality-indicating ornamental traits, however, has received much less attention (Jones and Montgomerie 1991; Hill 1993; Kempenaers 1994; Andersson et al. 1998) despite its potential importance as an indicator of mutual mate choice (Burley 1983; Johnstone et al. 1996) and its role in increasing genetic diversity within populations (Partridge 1983). Thus assortative mating might help maintain genetic diversity in quality indicators, such as the carotenoid-based plumage colours of birds (Olson and Owens 1998), which are often highly variable (e.g. Hill 1991) despite the variation-eroding effects of sexual selection.

To assess the likelihood of assortative mating with respect to a quality indicator, we studied breeding pairs of American goldfinches (*Carduelis tristis*), a species in which plumage colour is related to individual condition and health during moulting (McGraw and Hill 2000). Because carotenoids cannot be synthesized by vertebrates, and thus must be ingested, their expression in plumage can be influenced by foraging ability, metabolic processes and general health before and during a moult, which makes them excellent candidates as signals of phenotypic quality (Olson and Owens 1998). Moreover, the intensity of sexual selection on both male and female plumage traits in this species is likely to be high for the following reasons. First, captive mate choice trials have demonstrated female preference for more brightly coloured male goldfinches (Johnson et al. 1993). Second, breeding populations have male-biased adult sex ratios (Middleton 1993), providing females with the opportunity to choose a mate from several unmated males. Third, extrapair paternity is common enough in this socially monogamous species (Gissing et al. 1998) to increase the variance in reproductive success of mated males. Fourth, goldfinches are unique among cardueline finches for their prealternate spring moult whereby males replace their drab, winter plumage with brilliant yellow, carotenoid-pigmented feathers less than 8 weeks before the breeding season begins (Middleton 1993). Females also moult to a brighter yellow plumage in spring, but they remain less bright than the males. Thus the breeding plumage of both sexes could

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serve as an indicator of current phenotypic quality during pair formation. Finally, because both sexes provide nestling care, both may suffer reduced reproductive success if they invest in poor mate choice decisions.

Methods

We studied 22 breeding pairs during June–September 2001 at a field site (44°34–N, 76°19′W) 40 km north of Kingston, Ontario, Canada, where we located most nests during nest-building and incubation. We captured birds using mist nets near their nest a few days following clutch completion, to minimize nest abandonment. We banded each bird with one metal and three colour bands for identification, avoiding yellow, black, orange and blue bands because they might be expected to influence mate choice in this species (Burley et al. 1982; Johnson et al. 1993). At banding, we measured the tarsus length (±0.1 mm), body mass (±0.1 g), wing chord and tail length (±0.5 mm) of each bird, and calculated its body condition (Brown 1996) as the residual from a log–log regression of body mass on tarsus length, for each sex separately. During nestling care, we confirmed the identities of social pairs at each nest.

We objectively measured plumage colour in the field using a portable ST2000 reflectance spectrometer and DT-1000 light source (Ocean Optics, Dunedin, Fla., USA), using methods described by Doucet and Montgomerie (2003). We took five readings from each of four yellow plumage regions (throat, belly, back, rump) and calculated a single mean reflectance curve for each bird's yellow plumage (Fig. 1).

We summarized each bird's plumage colour using three variables (UV amplitude, blue chroma, yellow amplitude) calculated from the UV, blue and yellow segments of the spectrum that correspond to the spectral sensitivities of different cone types in the retinas of passerines (Hart et al. 2000). We use "amplitude" as an index of saturation, or colour richness; objects with flatter reflectance curves have low amplitude and appear more achromatic. Thus yellow and UV amplitudes are the differences in percentage reflectance (*R*) between the short-wave (blue, 435–500 nm) minimum and both long- (yellow, 500–700 nm) and very short-wave (UV, 320–435 nm) maxima, respectively. Blue chroma is the proportion of total reflectance occurring in the blue segment (i.e. $R_{435-500}/R_{320-700}$).

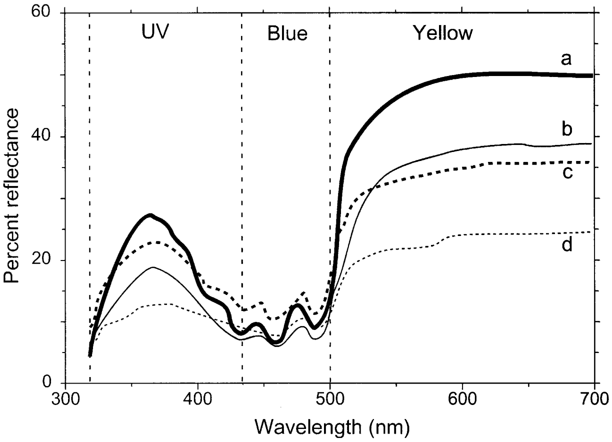

Fig. 1 Sample reflectance spectra from the yellow plumage regions of goldfinches (mean reflectance spectra from 20 measurements per bird): males with (*a*) intense and (*b*) drab, and females with (*c*) intense and (*d*) drab carotenoid coloration. Spectral segments for UV (320–435 nm), blue (435–500 nm), and yellow (500–700 nm) were chosen based on spectral sensitivities of avian cone types and American goldfinch reflectance curves

All three colour variables are expected to be correlated with the carotenoid content of feathers (see also Saks et al. 2003) because the main pigments (canary xanthophylls) in goldfinch plumage absorb light in the blue segment (McGraw et al. 2001). Thus, increased carotenoid concentration results in lower blue chroma and higher UV and yellow amplitudes (S. Andersson, personal communication). Because these variables were significantly correlated with each other ($P<0.0001$), we used principal components analysis ($n=44$ individuals) to calculate a single colour score (carotenoid PC1) to represent the carotenoid colour signal of each bird. PC1 explained 88% of the variation in the colour variables and had high loadings from yellow (0.98) and UV amplitudes (0.94), as well as blue chroma (−0.89). Thus we interpret high carotenoid PC1 to indicate a saturated yellow colour due to the high carotenoid content of the feathers (Saks et al. 2003).

Results

Breeding male goldfinches were significantly larger than their female partners, although females were significantly heavier than males (Table 1). Males had significantly higher mean total reflectance than females, lower blue chroma, and higher yellow and UV amplitudes (Table 1, Fig. 1). Thus the colour of male plumage was a more saturated yellow than that of females and, accordingly, had significantly higher carotenoid PC1 scores (Table 1).

Within pairs there were no significant correlations between the sexes with respect to wing chord ($r=0.20$, $P=0.37$), tail length ($r=0.38$, $P=0.08$), tarsus length ($r=-0.19$, $P=0.41$), mass ($r=-0.20$, $P=0.38$), or body condition ($r=-0.21$, $P=0.36$). There was, however, a significant positive relationship between the carotenoid PC1 scores of paired males and females (Fig. 2).

Pair members tended to be captured on or near the same date, so this apparent assortative mating could simply be a by-product of wear or dirt accumulated daily after moulting. To control for any date effect, we calculated the residuals from regressions of carotenoid PC1 on measurement date, for males and females separately. Residual carotenoid PC1 of males and females

Table 1 Comparison of morphological and colour measurements between mated males and females in 22 breeding pairs of American goldfinches. Values are means±SE; comparisons are two–tailed, paired *t*-tests

Character	Males	Females	Comparison	
			t	*P*
Morphological				
Wing chord (mm)	73.6±0.31	70.4±0.32	8.02	<0.0001
Tail length (mm)	52.3±0.48	50.2±0.52	3.75	0.001
Tarsus length (mm)	14.3±0.07	13.8±0.09	3.67	0.001
Mass (g)	13.1±0.16	14.2±0.20	3.99	0.0007
Colour				
Mean $R_{320-700}$ (%)	29±0.8	20±0.6	10.34	<0.0001
Yellow amplitude (%)	34±1.0	21±0.6	14.81	<0.0001
UV amplitude (%)	16±0.6	9.2±0.3	12.10	<0.0001
Blue chroma	6.8±0.4	9.3±0.3	7.21	<0.0001
Carotenoid PC1	1.3±0.2	−1.3±0.2	9.17	<0.0001

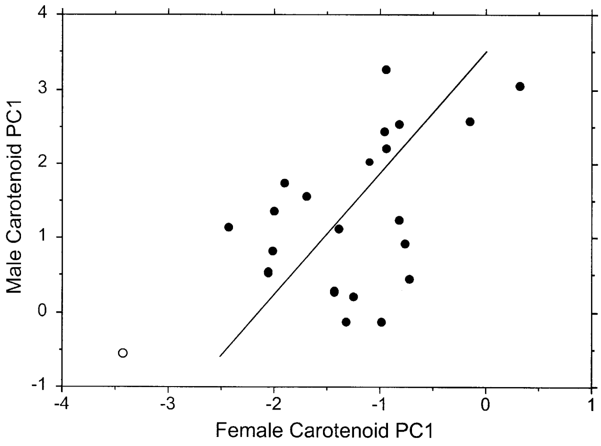

Fig. 2 Relationship between male and female carotenoid PC1 scores within mated pairs of American goldfinches. *Model II regression line* is plotted (y=3.1+1.4x; r=0.55, P=0.008, n=22). Although one female (*open symbol*) had an unusually low carotenoid PC1 score, the relation remains significant with this pair removed from the analysis (r=0.44, P=0.05, n=21)

were also significantly correlated (r=0.47, P=0.03), indicating that males and females with relatively saturated carotenoid coloration tended to be mated to each other, independent of measurement date.

Discussion

In our study population, goldfinches mated assortatively with respect to subtle (to the human eye) variations in their yellow plumage colour, a trait that has been previously shown to be important in mate choice and to correlate with health. We also found an unexpected peak in plumage reflectance in the UV range that is visible to birds but not humans. While it is tempting to speculate that this UV signal might be important in mate choice (Hunt et al. 2001), we have no evidence that it is more strongly correlated between mates or a better predictor of reproductive success than plumage reflectance in the rest of the bird-visible spectrum (A.K. MacDougall and R. Montgomerie, unpublished). Most probably, this UV peak is a simple consequence of carotenoids deposited in white feathers (which reflect in the UV), absorbing wavelengths in the 400–500 nm range (S. Andersson, personal communication).

Apparently very few studies have looked for assortative mating with respect to plumage coloration, despite growing evidence that both male and female colours can often be highly variable among individuals (Andersson et al. 1998; this study), can signal aspects of phenotypic quality (Olson and Owens 1998), and can influence mate choice decisions (Hill 1991, 1993). Thus assortative mating by plumage colour might be expected to be widespread in birds, such as goldfinches, that have these traits. The obvious, and more difficult, question is to determine the mechanism responsible for this pattern.

Our finding that seasonally dichromatic male and female goldfinches mate assortatively with respect to plumage colour suggests that similar selection pressures may act upon both sexes to display brilliant yellow carotenoid-rich feathers during the breeding season. Thus, one potential explanation for the observed assortative mating with respect to signals of carotenoid content in the plumage is mutual mate choice with respect to this trait (Burley 1983; Crespi 1989).

Mutual mate choice is theoretically adaptive to both sexes in species with shared parental care, and the evolution of discriminating males and females is predicted (Johnstone et al. 1996). Male goldfinches invest extensively into each reproductive effort, providing food to both their incubating female and nestlings, vigorous nest defence, and often the majority of the fledgling care (Middleton 1993). Despite natural selection pressure for goldfinch females to be cryptic during incubation, sexual selection may influence their fitness by trading off aspects of plumage crypsis for colours that accrue direct and/or indirect benefits by attracting a high-quality partner. Clearly, males that mate preferentially with females displaying honest indicators of quality could have a selective advantage over males that are not so choosy when male investment into offspring is high, as it is in this species.

Alternatively, correlations between male and female colours could be observed in the absence of male choice, if female colour functions as a signal during intrasexual competition over mates. Interestingly, sexual dominance is reversed in this species from summer to winter, with females dominant to males during the breeding season (Middleton 1993). Clearly, the effects of social dominance and intrasexual competition over both non-sexual (food) and sexual (mates) resources should be further examined in this species.

Assortative mating could also be explained the by the timing of breeding or territory acquisition. If time to reach breeding condition is related to carotenoid coloration, then assortative mating by colour could result from random pairing of birds in breeding condition on a given date. However, this seems unlikely in this short-distance migrant, as both sexes arrive at the breeding grounds in late spring, up to 2 months before relatively synchronous breeding begins in late June (Middleton 1993), so the timing of breeding is not constrained by early spring arrival dates, harsh conditions and low food availability that might influence mate availability.

Thus it seems most likely that assortative mating by carotenoid-based plumage colours in goldfinches is the result of similar mate preferences in male and female goldfinches, although experiments will be needed to confirm this conclusion. Clear examples of such assortative mating in birds are rare, possibly because few studies have looked for it with respect to traits that might be honest signals of mate quality in both males and females. Such signals are thus excellent candidates for further investigation of mutual mate choice in birds. This should be especially true when males and females invest similarly in parental care (Johnstone et al. 1996).

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