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Original Article

Age-dependent relationships between multiple sexual pigments and condition in males and females

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The reliability of sexual signaling may change across age classes due to shifts in resource allocation patterns. Two contrasting hypotheses exist regarding how the condition dependence of ornaments may shift with age, and both have received empirical support. On one hand, ornaments may more reliably reflect condition and quality in older individuals, because younger individuals of high quality invest in survival over signaling effort. On the other hand, the condition dependence of ornaments may decline with age, if older individuals in poor condition terminally invest in ornaments, or if resource constraints decline with age. Further, the expression and condition dependence of different ornaments may shift with age in unique ways, such that multifaceted sexual displays maintain reliable signaling across age classes. In yellow warblers (*Setophaga petechia*) of both sexes, we assessed how relationships between carotenoid- and phaeomelanin-based sexual pigmentation, prenesting body reserves, and condition at molt (reflected by growth bars and feather quality) vary across age classes. Melanin coverage correlated with condition at molt across age classes in males and showed high repeatability in both sexes. In contrast, carotenoid saturation increased longitudinally with age in males and correlated with condition at molt in different age classes in the 2 sexes. Specifically, carotenoid saturation correlated positively with condition at molt in younger, but not older males, whereas in females, the situation was reversed, with a positive correlation present only in older females. Results suggest that age-dependent signaling may promote maintenance of multifaceted sexual displays and that age-dependent signaling dynamics depend on sex.

Key words: **age-dependent sexual signaling, carotenoids, multiple ornaments, phaeomelanin.**

INTRODUCTION

Sexual ornaments represent life-history investments, whose expression varies not only with individual health status and access to resources but also with the proportion of resources invested in ornaments versus other alternatives (Höglund and Sheldon 1998; Badyaev and Qvarnström 2002; Badyaev and Duckworth 2003; Muñez et al. 2008). Age is one important factor that may alter investment in sexual ornaments, thus complicating the relationship between ornamentation and body condition and potentially making ornaments unreliable indicators of individual quality in some age classes (Kokko 1997, 1998; Brooks and Kemp 2001; Proust et al. 2002; Torres and Velando 2007; Evans et al. 2011; Lifjeld et al. 2011). Two contrasting hypotheses have been proposed regarding how the condition dependence of sexual ornamentation shifts with age. First, models by Proust et al. (2002) and Lindström et al. (2009) suggest that younger individuals should signal body condition less reliably than older individuals, because young individuals in good condition maximize fitness by out-surviving rather than out-signaling competitors. Alternatively, a second hypothesis suggests that the association between condition and ornamentation might decline with age, if old individuals in poor condition terminally invest in ornaments or if resource constraints on ornament expression decline with age (Candolin 2000a; Badyaev and Duckworth 2003; Hall et al. 2009; Copeland and Fedorka 2012; Nielson and Holman 2012).

Studies performed to date have yielded support for both of the above hypotheses, with the source of variation in results currently unresolved (Badyaev and Duckworth 2003; Velando et al. 2006; Lindström et al. 2009; Cote et al. 2010; Copeland and Fedorka 2012). For example, in stickleback (*Gasterosteus aculeatus*), the association between carotenoid-based pigmentation and individual condition increases with age across a breeding season (Lindström et al. 2009). However, in crickets (*Allonemobius socius*), experimental infection with parasites reduced calling rate in young males, but

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induced a terminal investment in calling in old males, such that signaling of health status was "dishonest" in old males (Copeland and Fedorka 2012). Further, carotenoid-based pigmentation in house finches (*Haemorhous mexicanus*) varies with condition at molt more strongly in younger males than older males, because foraging efficiency increases with age, reducing the costs and condition dependence of pigmentation in older birds (Badyaev and Duckworth 2003). We aimed to elucidate why varying empirical relationships occur between age and the condition dependence of ornaments. Specifically, we asked whether correlations between different types of pigment-based sexual ornaments and individual condition shift uniquely across age classes and whether age-dependent sexual signaling dynamics depend on an individual's sex.

First, the condition dependence of different types of ornamentation may vary uniquely with age (Freeman-Gallant et al. 2010), and different ornaments may also differentially correlate with age itself (Kokko 1997, 1998; Hegyi et al. 2007; Evans et al. 2010; Laucht and Dale 2012; Saino et al. 2013). In this case, expressing multiple ornaments may promote reliable sexual signaling of individual condition and quality across age classes, suggesting an under-explored mechanism for the maintenance of multifaceted sexual displays (Møller and Pomiankowski 1993; Candolin 2003; Hebets and Papaj 2005; Freeman-Gallant et al. 2010). In birds, the most common types of sexual coloration arise from feather structure, carotenoid-based pigmentation, and melanin-based pigmentation (McGraw 2006a, 2006b; Prum 2006). The condition dependence of different types of coloration might shift in varying ways with age due to dependence on different resources or developmental mechanisms or due to different age-specific costs and benefits of expression (Greene et al. 2000; Badyaev and Duckworth 2003; Freeman-Gallant et al. 2010). As mentioned above, the condition dependence of carotenoid pigmentation appears to decline with age in house finches because carotenoids are dietarily derived, and old birds are more efficient foragers in general and may also selectively forage for carotenoids (Badyaev and Duckworth 2003). In contrast, types of coloration less strongly linked to 1 resource, such as structural or melanin-based coloration, might not show declining condition dependence with age (Prum 2006; McGraw 2008). Further, if a given type of coloration is used in antagonistic interactions, social costs may enforce reliable condition-dependent expression across age classes (Candolin 2000b). Regardless of mechanism, if the relationship between individual condition and different types of coloration shifts uniquely with age, coexpression of multiple types of coloration may allow a more comprehensive assessment of individual quality across age classes (Freeman-Gallant et al. 2010).

Second, how the condition dependence of sexual pigmentation changes with age may depend on sex, because sex may affect allocation of resources toward ornaments (McGraw et al. 2002), and determine age-specific costs and benefits of investing in ornaments. For instance, females may be unlikely to terminally invest in ornaments if benefits of ornamentation are lower than in males, whereas terminal investment in ornaments has been demonstrated in males in a variety of species (Candolin 2000a; Hunt et al. 2004; Hall et al. 2009; Copeland and Fedorka 2012; Nielson and Holman 2012). However, few studies have investigated either how the condition dependence of female ornaments varies with age (but see Bentz and Siefferman 2013) or whether the sexes display different age-dependent patterns of sexual signaling. Importantly, similar factors may underlie between-sex and between-population shifts in age-dependent signaling dynamics. Thus, exploring how age-dependent sexual signaling shifts with sex may elucidate why age-dependent signaling dynamics differ between populations of males, as well as advancing understanding of sexual signaling in females.

We examined age-dependent patterns of sexual signaling across the sexes and multiple types of sexual pigmentation in the yellow warbler (*Setophaga petechia*), a moderately sexually dichromatic passerine bird with carotenoid- and phaeomelanin-based sexual pigmentation in both sexes (Lowther et al. 1999). We explored age-dependent relationships between sexual pigmentation, indirect metrics of condition at molt, and prenesting body mass. Further, to better understand how age and individual quality interact to predict sexual pigmentation, we also assessed the between-year repeatability of pigmentation and whether pigmentation increases longitudinally with age within individuals. We asked whether relationships between carotenoid-based versus melanin-based pigmentation and condition metrics vary differently with age, such that coexpressing these pigment types may maintain reliable signaling of individual quality across age classes. Further, we asked whether age-dependent signaling dynamics differ in the 2 sexes.

METHODS

Study system and field methods

The yellow warbler is a colorful, Neotropical migrant passerine. Yellow coloration across the contour feathers probably derives from lutein, the most common dietarily available carotenoid (McGraw et al. 2003). Yellow warblers also express red-brown ventral streaking (Studd and Robertson 1985a; Lowther et al. 1999). Reflectance properties suggest that red-brown coloration derives from phaeomelanin although we cannot preclude other origins (Toral et al. 2008). Yellow warblers display moderate sexual size dimorphism and dichromatism (Lowther et al. 1999) and vary substantially in pigmentation within both sexes (Figure 1).

From 2010 to 2012, we studied warblers breeding along riparian corridors near the University of California's Sierra Nevada Aquatic Research Laboratory (SNARL; 37°36′51″N/118°49′47″W). Warblers arrived on the breeding grounds in early May and nesting occurred from late May or early June until early July. We lured birds into mist nets using a conspecific decoy and song playback, sexed birds based on distinct differences in pigmentation, and aged birds as second year (SY, in the first breeding season) or after second year (ASY, in subsequent breeding seasons) based on molt limits and tail-feather shape (Pyle 1997). We captured most birds during the preincubation period (including some between-year recaptures, $N = 104$ males [78 ASY, 26 SY, and 88 unique birds], $N = 48$ females [33

Figure 1
Male and female warblers display red-brown phaeomelanin-based pigmentation, largely restricted to the breast, and yellow carotenoid (lutein)-based pigmentation. Breeding males vary highly with respect to coverage of melanin pigmentation (range 4.0–28.4%, mean 15.3 ± 0.427 [SE]) and also show variation in carotenoid pigmentation (a). Females vary highly with respect to both carotenoid and melanin pigmentation but show less overall pigmentation than males (b). From left to right, individuals are an ASY male, 2 SY males, an ASY female, and a SY female.

ASY, 15 SY, and 45 unique birds]) and a smaller number of birds during the nestling stage by placing nets near nests (including some between-year recaptures, $N = 16$ males [7 ASY, 9 SY, and 15 unique birds], $N = 27$ females [18 ASY, 9 SY, and 26 unique birds]). We banded birds with USGS aluminum bands and 3 colored leg bands.

The University of California, Riverside's Animal Care and Use Committee approved all field protocols (Protocol A-20100003E). Sample collection and fieldwork were authorized by a United States Geological Survey (USGS) bird-banding subpermit (23035-G), a California state collecting permit (SC11060), a federal migratory bird collecting permit (MB22669A-0), and the Inyo National Forest (MLD100007P).

Characterizing individual condition

On capturing a bird, we measured unflattened wing chord (±1 mm), tarsus length (±0.01 mm), and body mass (±0.1 g). We also scored feather wear on a scale of 0–4, where 0 corresponds to no wear, 1 to a trace of wear, 3 to moderate wear, and 4 to heavy wear (Ralph et al. 1993). Feather wear indicates the extent to which the tips of primary feathers (main flight feathers) are abraded away and reflects primary feather quality (Ralph et al. 1993; Harper 1999). All birds were measured and scored by A.S.G. or M.L.G., who standardized their scoring criteria and measurement techniques. Further, from birds captured in 2010 and 2011, we collected the first tertial feather (the most distal of the 3 inner most flight feathers). In yellow warblers, tertial feathers are replaced at the prebreeding molt in January to February, when most contour feathers bearing sexual coloration are also replaced. In contrast, warblers replace other flight feathers (including primaries) at the complete postbreeding molt in July to August (Pyle 1997; Lowther et al. 1999). Thus, we used primary feather quality to indirectly assess condition at postbreeding molt and tertial feather quality to indirectly assess condition at prebreeding molt.

To assess primary feather quality, and condition at postbreeding molt, we used primary feather wear and residual wing chord (residuals of a wing chord on tarsus length linear regression; Harper 1999; Dawson et al. 2000; Dawson 2004). We performed regression models used to determine residual wing chord in the 2 sexes separately because body dimensions may differ with sex (see Supplementary Table S1 for models). Feather wear and residual wing chord were correlated, and both relate to primary feather quality. Thus, we performed a principal component analysis (PCA) on these 2 variables to derive a single factor (PC1) (see Table 1 for PCA results), which we term "primary feather quality." SY yellow warblers retain juvenile primary feathers grown during the nestling stage, whereas ASY birds acquire new primaries during the postbreeding molt (Pyle 1997). Thus, primary feather quality reflects postbreeding condition in ASY birds but reflects condition during the nestling stage in SY birds.

To quantify tertial feather quality, and condition at prebreeding molt, we measured tertial feather length (±0.01 mm) using digital calipers and tertial feather weight (±0.0001 g) using a high-precision digital scale. In addition, we used digital calipers to measure the width of 4 central pairs of alternating dark and light growth bars (±0.01 mm), as a metric of feather growth rate (Grubb 2006). Because these measurements were highly correlated, we used PCA to extract a single factor (PC1), which we term "tertial feather quality" (Table 1). For females, we corrected tertial PC1 scores for individual size, by extracting residuals from a regression of PC1 score on tarsus length (male tarsus length was unrelated to tertial PC1 scores, $P = 0.64$, so this correction had no effect; see Supplementary Table S1 for models).

Finally, as a metric of body reserves at time of capture, we calculated residual mass from a mass on body measures regression (Schulte-Hostedde et al. 2005). We initially entered both tarsus length and wing chord as body measures in the model, but tarsus length was not a good predictor of mass either alone or with wing chord also included in the model ($P > 0.20$), so we used only wing chord in the final model (Supplementary Table S1). Birds with higher fat scores (scored on a scale of 1–7; Ralph et al. 1993) had higher residual mass (linear mixed model: $F_{1,173} = 6.77$, $\beta = 0.12 \pm 0.04$, $P = 0.01$), supporting a relationship between this condition metric and body reserves. We analyzed the relationship between residual mass and coloration only among birds caught early in the season because mass varies with breeding stage. Further, because we caught few females early in the season, and some were carrying eggs, we did not analyze the relationship between residual mass and coloration in females.

Table 1

Results from PCAs of primary feather quality, tertial feather quality, carotenoid reflectance, and melanin reflectance

	Primary PC1	Tertial PC1
Feather quality PCAs		
Feather wear	−0.70	—
Residual wing chord	0.70	—
Growth bar width	—	0.51
Tertial length	—	0.60
Tertial weight	—	0.60
Eigenvalue	1.21	2.17
Proportion of variance	0.61	0.72
	Carotenoid PC1	Melanin PC1
Reflectance PCAs		
UV saturation	0.48	—
Carotenoid saturation	0.51	—
Blue saturation	−0.52	—
Total reflectance	−0.06	−0.57
Lambda 50	0.46	0.59
Red saturation	—	0.55
Eigenvalue	3.62	2.27
Proportion of variance	0.72	0.75

Loadings on variables and variance explained.

Measurement of pigmentation

From each bird, we also obtained feather samples and photographs that we used to quantify sexual pigmentation. We collected 5 yellow feathers bearing carotenoid pigmentation and 5 feathers bearing phaeomelanin pigmentation from nonadjacent breast regions. We stored feathers in closed envelopes in a dry, dark location until spectrometric analysis. Further, we used a Stylus 800 Olympus camera to take multiple (2–3) digital photographs of both the front and side of birds. We held a 1-cm grid level to the bird for scale and held the camera perpendicular to the bird at a distance of ~3 cm. We took all pictures outdoors in full shadow to provide a uniform lighting environment and to maximize contrast between yellow and red-brown pigmentation.

For males, we used the threshold color function in the image analysis program ImageJ to extract the percentage coverage of red-brown (phaeomelanin) from photographs (Schneider et al. 2012). We determined percent coverage of melanin in a 2 × 1.5 cm rectangle centered at the top of the breast and in a 2 × 1 cm rectangle centered on the side of the bird, at the top of the wing (Supplementary Figure S1). We averaged percentages derived from 2 photographs from both the front and side of each bird to obtain a final measure of melanin coverage. For females, melanin coverage was generally too low to quantify in ImageJ. Thus, for females, we scored melanin coverage on a scale of 0–4, where 0 corresponded

to no melanin-based streaking, 1 to a trace of streaking, 2 to moderate streaking (~1–2% coverage), and 4 to heavy streaking (~5% coverage). This scoring criterion encompassed the range in melanin coverage observed in females and was 99% repeatable.

To obtain reflectance spectra from feather samples collected in the field, we arranged 5 feathers on a black felt background (with zero reflectance) to mimic natural feather alignment. We then used an USB4000 spectrometer with a xenon light source (range: 200–1100 nm; Ocean Optics Inc., Dunedin, FL) to obtain reflectance spectra between 300 and 725 nm, across the avian visual range. We measured reflectance relative to a white standard and averaged 5 spectra from each feather patch to obtain a final spectrum for each bird. The probe of the spectrometer was enclosed in a black rubber sheath to exclude ambient light, held perpendicular to the sample, and slightly repositioned between each reading (Montgomerie 2006; Hegyi et al. 2007).

To characterize reflectance spectra, we used colorimetric measurements of brightness (reflectance), saturation (chroma or spectral purity), and hue (spectral location). Carotenoid pigmentation displays a bimodal reflectance spectrum, with reflectance peaks for both ultraviolet and yellow (or red) light and high absorbance of blue-green light. Thus, to thoroughly characterize the carotenoid reflectance spectrum, we calculated carotenoid saturation (chroma), blue saturation, ultraviolet saturation, average reflectance, and lambda 50 (see Supplementary Table S2) (Parker et al. 2003; Andersson and Prager 2006; Hegyi et al. 2007). Lambda 50 is the wavelength at which reflectance is halfway between its minimum and maximum value and is a measurement of hue. Previous studies indicate that as the concentration of yellow carotenoids in feathers increases, hue increases (shifts toward orange), average reflectance decreases, and ultraviolet and carotenoid saturation both increase (Andersson and Prager 2006). Melanin pigmentation displays a simpler reflectance spectrum, with reflectance steadily increasing across the visible wavelengths (McGraw et al. 2004; Safran and McGraw 2004). Thus, to characterize melanin spectra, we calculated red saturation, average reflectance, and lambda 50 (Supplementary Table S2). More concentrated melanin-based pigmentation is less reflective and displays greater hue and red saturation (McGraw et al. 2004, 2005; Safran and McGraw 2004; Andersson and Prager 2006; Parejo et al. 2011). Because colorimetric variables were highly correlated, we performed PCAs to derive single factors (PC1) descriptive of variance in reflectance spectra shape (Parker et al. 2003; Andersson and Prager 2006; Montgomerie 2006; Hegyi et al. 2007; Maney et al. 2007) (Table 1). We refer to these variables (PC1 scores) as "carotenoid saturation" and "melanin saturation," due to high positive loadings of carotenoid and melanin (or red) saturation on their respective PC1s.

Before performing analyses, we corrected for year effects on pigmentation by taking residuals of regressions predicting carotenoid PC1 and melanin PC1 from year. Correcting for year effects did not qualitatively alter results but prevents longitudinal age effects on pigmentation arising from year-to-year variation in the mean level of pigmentation expressed in the population. Further, this correction also ensures that year effects do not obscure overall effects of age class on pigmentation (Evans et al. 2013).

Statistical analyses

We performed statistical analyses using R 2.15.2 (R Core Team 2012). We first investigated correlations between pigmentation variables to assess which pigmentation variables might communicate redundant information. We performed Pearson correlations between normally distributed male pigmentation variables and a Spearman correlation between female melanin scores and female carotenoid saturation. Correlations did not indicate high redundancy between pigmentation variables (see Results), so we treated pigmentation variables separately in subsequent statistical tests. Further, to better understand the potential for pigmentation to convey information, we used Bartlett's test, Levine's test, and *F*-tests (depending on the distribution of data) to assess whether variance in pigmentation differed between age and sex classes.

Some birds were caught in multiple years of our study (see Results for sample sizes). Thus, we employed mixed-effects models with individual identity entered as a random effect to investigate the relationship between pigmentation variables and condition metrics. We sequentially reduced models by removing nonsignificant predictors ($\alpha = 0.05$).

To assess the relationship between male melanin pigmentation and condition metrics (primary feather quality, tertial feather quality, residual mass), we used linear mixed-effects models (LMMs). We analyzed whether the interaction between age and each condition metric (in separate models) predicted melanin coverage and saturation (in separate models). To derive final *F*-tests and *P* values for LMMs, we employed a Satterthwaite approximation of degrees of freedom (R package lmerTest; Kuznetsova et al. 2013). In parallel, for females, we tested whether the interaction between age and condition metrics (in separate models) predicted melanin score, but we used generalized linear mixed-effects models (GLMMs) with a Poisson distribution to account for the distribution of melanin scores.

When analyzing the relationship between carotenoid saturation and condition metrics, we entered data from both sexes into the same model. We constructed LMMs to predict carotenoid saturation from the 3-way interaction between age, sex, and condition metrics (primary and tertial feather quality, in separate models). Thus, we could test whether age and condition metrics differentially predicted carotenoid saturation in the 2 sexes. In males alone, we constructed a separate model to assess the relationship between carotenoid saturation and the age-by-residual mass interaction.

Finally, we explored whether pigmentation levels were repeatable between years or increased longitudinally with individual age. We constructed LMMs to predict pigmentation variables from year of capture (1, 2, 3; 1 is assigned at first capture of each bird) and individual identity (the random effect). Where the year covariate was significant and retained in the model, the repeatability estimate is conditional on controlling for the covariate. We used R package rptR (function rpt.remlLMM or rpt.remlLMM.adj, for conditional repeatability) to calculate repeatability with standard error (SE) and 95% confidence intervals (CIs) based on variance components from LMMs (Nakagawa and Schielzeth 2010). *P* values for repeatability estimates derive from log likelihood ratio tests for rpt.remlLMM.adj and permutation tests (which perform better at marginal repeatability; Nakagawa and Schielzeth 2010) for rpt.remlLMM. For pigmentation, we conducted repeatability analyses in the 2 sexes separately to prevent sex effects on pigmentation from confounding results. We square-root transformed female melanin scores to allow estimation of repeatability within the LMM framework. Across both sexes combined, we also assessed repeatability of condition metrics.

RESULTS

Correlations and variances among pigmentation variables

In males, coverage of melanin pigmentation positively correlated with melanin saturation (Pearson correlation: $r = 0.21$, $P = 0.02$,

N = 117), and melanin saturation also positively correlated with carotenoid saturation (Pearson correlation: r = 0.22, P = 0.01, N = 118). However, male melanin coverage did not correlate with carotenoid saturation (Pearson correlation: r = 0.04, P = 0.69, N = 118). In females, melanin score positively correlated with carotenoid saturation (Spearman correlation: r = 0.41, P < 0.001).

Variance in male melanin coverage (F test: $F_{84,34}$ = 1.46, P = 0.21) did not differ significantly between age classes, but melanin saturation varied more in SY males than in ASY males (F test: $F_{82,34}$ = 0.45, P = 0.003). Melanin scores varied more in ASY females than in SY females (Levene's test: $F_{1,73}$ = 6.48, P = 0.01). Further, variance in carotenoid saturation differed between sex and age classes (Bartlett's test: Bartlett's K-squared = 69.98, degrees of freedom [df] = 1, P < 0.001). Carotenoid saturation varied more in females than in males (F-test: $F_{74,118}$ = 5.75, P < 0.001) and more in SY than in ASY males (F-test: $F_{51,22}$ = 0.57, P = 0.04). However, variance in carotenoid saturation did not differ between SY and ASY females (F-test: $F_{51,22}$ = 0.68, P = 0.27; Supplementary Table S3). Despite differences in variances, LMMs did not display heteroscedastic residuals.

Sexual pigmentation and condition at postbreeding molt (primary feather quality)

Melanin pigmentation

Males with greater melanin coverage were in better condition at postbreeding molt (or in better condition as nestlings, for SY birds) than other males, as indicated by primary feather quality (LMM: $F_{1,117}$ = 15.96, β = 1.44 ± 0.36, P < 0.001; N = 120 observations, 101 males, 70 unique ASY birds, and 35 SY birds; Figure 2). SY and ASY males did not differ in melanin coverage (LMM: $F_{1,115}$ = 0.98, β = 1.01 ± 1.02, P = 0.32), and the relationship between melanin coverage and primary feather quality was not age dependent, as indicated by a nonsignificant age-by-feather quality interaction (LMM: $F_{1,115}$ = 0.45, β = 0.52 ± 0.89, P = 0.56; Supplementary Table S4, full model). Indeed, within both SY males (LM: $F_{1,33}$ = 9.46, R^2 = 0.20, β = 2.00 ± 0.65, P = 0.004) and ASY males (LMM: $F_{1,83}$ = 7.84, β = 1.39 ± 0.49, P = 0.006) separately, birds with greater melanin coverage displayed higher primary feather quality.

SY males had lower primary feather quality than ASY males (LMM: $F_{1,105}$ = 31.14, β = −1.01 ± 0.18, P < 0.001). Thus, we reran the analysis to confirm that age remained unrelated to male melanin coverage when excluding primary feather quality from the model. Even when we entered age alone as a predictor of melanin coverage, SY and ASY males did not differ significantly in melanin coverage (LMM: $F_{1,97}$ = 0.88, β = −0.81 ± 0.84, P = 0.33).

Males with greater melanin saturation were also in better condition at post-breeding molt, as indicated by primary feather quality (LMM: $F_{1,116}$ = 6.68, β = 0.20 ± 0.07, P = 0.01, N = 118 observations, 100 males). SY and ASY males did not differ in melanin saturation (LMM: $F_{1,114}$ = 0.51, β = 0.16 ± 0.23, P = 0.47), and the relationship between primary feather quality and melanin saturation was not age-dependent (LMM: $F_{1,114}$ = 0.96, β = 0.19 ± 0.19, P = 0.33, for the interaction term; Online Supplement Table S4, full model). Indeed, the relationship between primary feather quality and melanin saturation was similar in SY males (LM: $F_{1,33}$ = 2.77, R^2 = 0.05, β = 0.35 ± 0.21, P = 0.10) and ASY males (LMM: $F_{1,81}$ = 3.34, β = 0.16 ± 0.08, P = 0.07) separately. SY and ASY males did not differ in melanin saturation even when excluding primary feather quality from the model (LMM: $F_{1,116}$ = 0.69, β = −0.16 ± 0.19, P = 0.41).

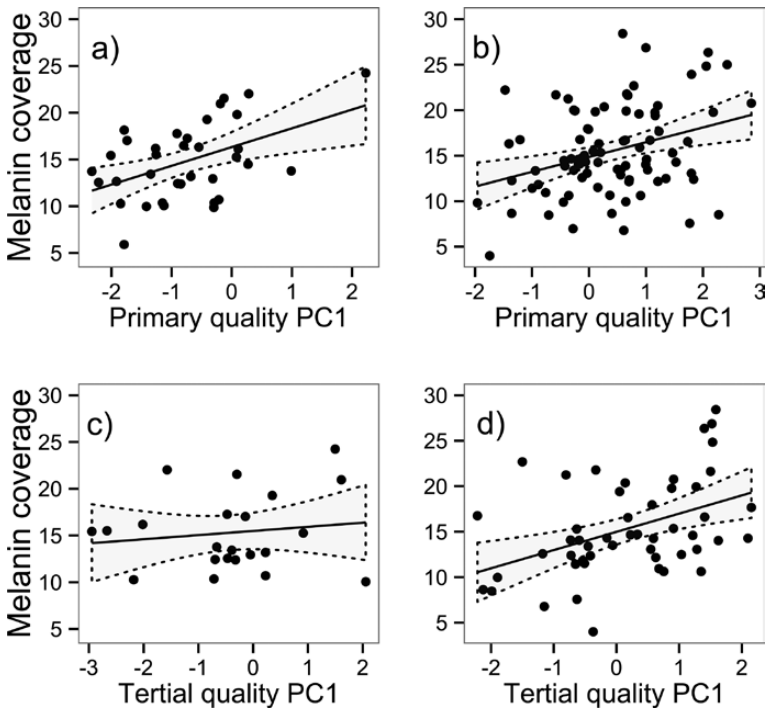

Figure 2
Relationship between coverage of phaeomelanin pigmentation, primary feather quality (condition at postbreeding molt/in the nest), and tertial feather quality (condition at prebreeding molt) in SY males (a and c) and ASY males (b and d). Regions bounded by dashed lines represent 95% CIs.

In females, SY birds had lower melanin scores than ASY birds (GLMM: $\mathcal{Z} = -2.64$, $\beta = -0.92 \pm 0.35$, $P = 0.008$; $N = 75$ observations, 69 birds, 52 unique ASY birds, and 23 SY birds). However, melanin score was unrelated to condition at postbreeding molt, as indicated by primary feather quality (GLMM: $\mathcal{Z} = 0.26$, $\beta = 0.04 \pm 0.15$, $P = 0.78$), and unrelated to the primary feather quality-by-age interaction (GLMM: $\mathcal{Z} = -0.33$, $\beta = -0.10 \pm 0.33$, $P = 0.74$; see Supplementary Table S5, full model). When dropping age from the model, melanin scores remained unrelated to primary feather quality (GLMM: $\mathcal{Z} = 0.83$, $\beta = 0.11 \pm 0.13$, $P = 0.40$).

Carotenoid pigmentation

The relationship between carotenoid saturation and age was sex specific, as indicated by a significant sex-by-age interaction term ($F_{1,186} = 48.89$, $\beta = 2.44 \pm 0.34$, $P < 0.001$; $N = 194$ observations, 169 birds, 70 unique ASY males, 35 SY males, 47 ASY unique females, and 23 SY females; Table 2 and Figure 3). In males alone, carotenoid saturation did not vary with age class ($F_{1,118} = 0.543$, $\beta = -0.09 \pm 0.13$, $P = 0.46$), whereas in females, ASY birds had much higher carotenoid saturation than SY birds ($F_{1,67} = 23.85$, $\beta = 1.67 \pm 0.34$, $P < 0.001$).

Further, the relationship between postbreeding condition (as indicated by primary feather quality) and carotenoid saturation depended on both sex and age class, as indicated by a 3-way interaction between sex, age, and primary feather quality ($F_{1,186} = 21.78$, $\beta = 1.40 \pm 0.30$, $P < 0.001$; Table 2, full model). Testing simple effects within each class of birds (ASY males, SY males, etc.) clarified how correlations between primary feather quality and carotenoid saturation shifted across classes. In males, SY birds in better condition as nestlings, as indicated by primary feather quality, displayed greater carotenoid saturation (LM: $F_{1,33} = 21.79$, $R^2 = 0.37$, $\beta = 0.53 \pm 0.11$, $P < 0.001$), but primary feather quality was unrelated to carotenoid saturation in ASY males (LMM: $F_{1,80} = 1.59$, $\beta = 0.08 \pm 0.06$, $P = 0.21$). In contrast, in females, SY birds in better condition as nestlings displayed lower carotenoid saturation than other members of their cohort (LM: $F_{1,21} = 8.10$, $R^2 = 0.24$, $\beta = -0.73 \pm 0.25$, $P = 0.009$). Primary feather quality and carotenoid saturation were unrelated in ASY females (LMM: $F_{1,44} = 1.09$, $\beta = 0.19 \pm 0.18$, $P = 0.30$).

Sexual pigmentation and condition at prebreeding molt (tertial feather quality)

Relationships between prebreeding condition metrics, age, and pigmentation were in many cases similar to relationships described above involving postbreeding condition metrics. Indeed, birds with greater tertial feather quality also displayed higher primary feather quality, suggesting considerable consistency in individual condition across molts (LMM: $F_{1,109} = 30.65$, $\beta = 0.54 \pm 0.09$, $P < 0.001$, $N = 114$ observations on 101 birds).

Melanin pigmentation

Males with greater melanin coverage were in better condition at prebreeding molt, as indicated by tertial feather quality (LMM: $F_{1,69} = 5.51$, $\beta = 1.07 \pm 0.45$, $P = 0.02$; $N = 72$ observations, 62 males, 41 unique ASY males, and 22 SY males; Figure 2). The relationship between melanin coverage and tertial feather quality did not differ significantly between age classes (LMM: $F_{1,63} = 2.26$, $\beta = -1.40 \pm 0.93$, $P = 0.13$ for the interaction; Supplementary Table S6, full model). However, within age classes separately, ASY males with higher melanin coverage had higher tertial feather quality (LMM: $F_{1,48} = 7.01$, $\beta = 1.65 \pm 0.62$; $P = 0.01$), whereas in SY males, melanin coverage did not correlate with tertial feather quality (LM: $F_{1,20} = 0.39$, $R^2 = 0.01$, $\beta = 0.44 \pm 0.69$, $P = 0.53$). Across age classes, males with greater melanin saturation showed a weak tendency to have higher tertial feather quality (LMM: $F_{1,69} = 1.70$, $\beta = 0.13 \pm 0.10$, $P = 0.19$; Supplementary Table S6, full model).

As for males, females with higher melanin coverage (scores) were in better condition at prebreeding molt (GLMM: $\mathcal{Z} = 2.74$, $\beta = 0.49 \pm 0.18$, $P = 0.006$; $N = 43$ observations, 40 birds, 26 unique ASY birds, and 15 SY birds), as indicated by tertial feather quality, when controlling for a near-significant age effect on pigmentation (GLMM: $\mathcal{Z} = 1.68$, $\beta = 0.76 \pm 0.45$, $P = 0.09$). The relationship between tertial feather quality and melanin score did not differ between age classes (GLMM: $\mathcal{Z} = -0.07$, $\beta = -0.02 \pm 0.40$, $P = 0.94$ for the interaction; see Supplementary Table S5, full model). In ASY females alone, birds with higher melanin scores had higher tertial feather quality (GLMM: $\mathcal{Z} = 2.37$, $\beta = 0.50 \pm 0.21$, $P = 0.01$; $N = 28$ observations, 26 birds). In SY females, the positive relationship between melanin score and tertial feather quality

Table 2

LMM predicting carotenoid saturation (PC1) from the interaction between age, sex, and primary feather quality (condition at postbreeding molt [ASY birds] or during the nestling stage [SY birds])

	Estimate ($\beta \pm$ SE)	F	df (Denom.)[a]	P
Intercept[b]	-1.52 ± 0.13	—	—	<0.001
Sex[c]	2.77 ± 0.18	483.80	169	<0.001
Age[d]	-2.13 ± 0.26	26.96	186	<0.001
Primary quality	0.17 ± 0.13	0.03	184	0.84
Sex × age	2.44 ± 0.34	48.89	186	<0.001
Sex × primary quality	-0.11 ± 0.17	14.84	184	<0.001
Age × primary quality	-0.91 ± 0.22	1.93	186	0.16
Sex × age × primary quality	1.40 ± 0.30	21.78	186	<0.001
	Variance	SD	r_1 [95% CI]	
Random effect (individual)[e]	0.54	0.73	0.55 [0.212, 0.762]	
Residual	0.40	0.63		

$N = 194$ observations, 169 birds; 69 ASY males, 35 SY males, 52 ASY females, and 23 SY females. SD, standard deviation.
[a]Denominator degrees of freedom from Satterthwaite approximation.
[b]P value from initial linear mixed model output.
[c]Males contrasted to females.
[d]SY birds contrasted to ASY birds.
[e]Repeatability estimate from package rptR (rpt.remlLMM.adj function).

was present but nonsignificant (GLM: $\chi = 1.51$, $\beta = 0.47 \pm 0.31$, $P = 0.13$).

Carotenoid pigmentation

As for condition at postbreeding molt, the relationship between condition at prebreeding molt (tertial feather quality) and carotenoid saturation depended on age and sex, as indicated by a 3-way interaction between sex, age, and tertial feather quality (LMM: $F_{1,95} = 17.05$, $\beta = 1.26 \pm 0.30$, $P < 0.001$; $N = 115$ observations, 102 birds, 41 unique ASY males, 22 SY males, 26 unique ASY females, and 15 SY females; Table 3, full model). Again, testing simple effects elucidated how correlations between tertial feather quality and carotenoid saturation varied between classes. In males, SY birds in better condition at prebreeding molt (with higher quality tertials) also had greater carotenoid saturation (LM: $F_{1,20} = 18.36$, $R^2 = 0.45$, $\beta = 0.47 \pm 0.11$, $P < 0.001$), whereas in ASY males, tertial feather quality and carotenoid saturation were unrelated (LMM: $F_{1,45} < 0.01$, $\beta = -0.001 \pm 0.08$, $P = 0.98$) (Figure 4). In contrast, in females, ASY birds in better condition at prebreeding molt showed higher carotenoid saturation (LMM: $F_{1,26} = 8.30$, $\beta = 0.73 \pm 0.25$, $P = 0.004$). In SY females, there was no relationship between condition at prebreeding molt and carotenoid saturation (LM:

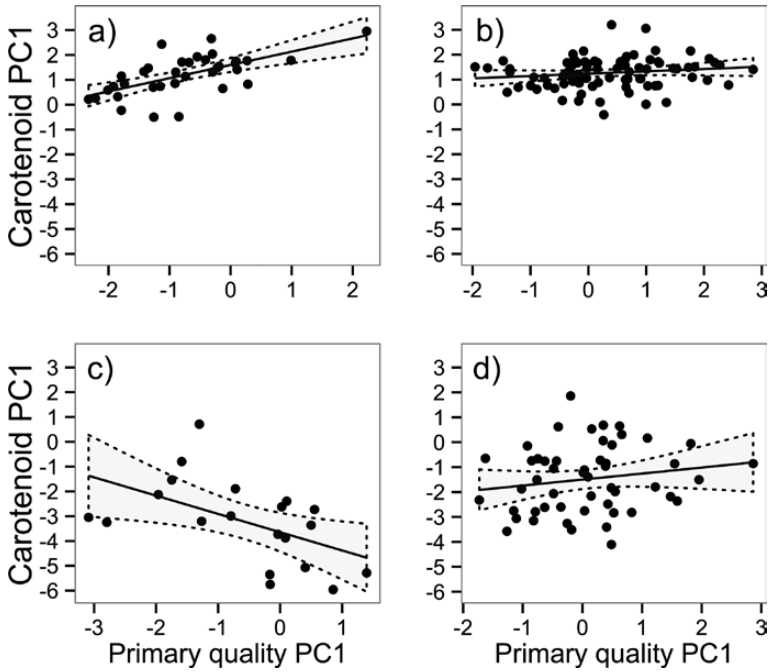

Figure 3
Relationships between primary feather quality (condition at postbreeding molt/in the nest) and carotenoid saturation according to sex and age categories in SY males (a), ASY males (b), SY females (c), and ASY females (d). Regions bounded by dashed lines represent 95% CIs.

Table 3
LMM predicting carotenoid saturation from the interaction between age, sex, and tertial feather quality (condition at prebreeding molt)

	Estimate ($\beta \pm$ SE)	F	df (Denom.)[a]	P
Intercept[b]	-1.80 ± 0.19	—	—	<0.001
Sex[c]	3.06 ± 0.24	348.37	97	<0.001
Age[d]	-1.57 ± 0.32	12.63	100	<0.001
Tertial quality	0.74 ± 0.19	13.66	106	<0.001
Sex × age	1.67 ± 0.47	16.45	100	<0.001
Sex × tertial quality	-0.74 ± 0.22	0.47	106	0.47
Age × tertial quality	-0.78 ± 0.23	1.03	95	0.31
Sex × age × tertial quality	1.26 ± 0.30	17.05	95	<0.001
	Variance	SD	r_1 [95% CI]	
Random effect (individual)[e]	0.61	0.78	0.65 [0.25, 0.872]	
Residual	0.32	0.56		

$N = 115$ observations, 102 birds; 41 ASY males, 22 SY males, 26 ASY females, and 15 SY females.
[a]Denominator degrees of freedom from Satterthwaite approximation.
[b]P value from initial linear mixed model output.
[c]Males contrasted to females.
[d]SY birds contrasted to ASY birds.
[e]Repeatability estimate from package rptR (rpt.remlLMM.adj function).

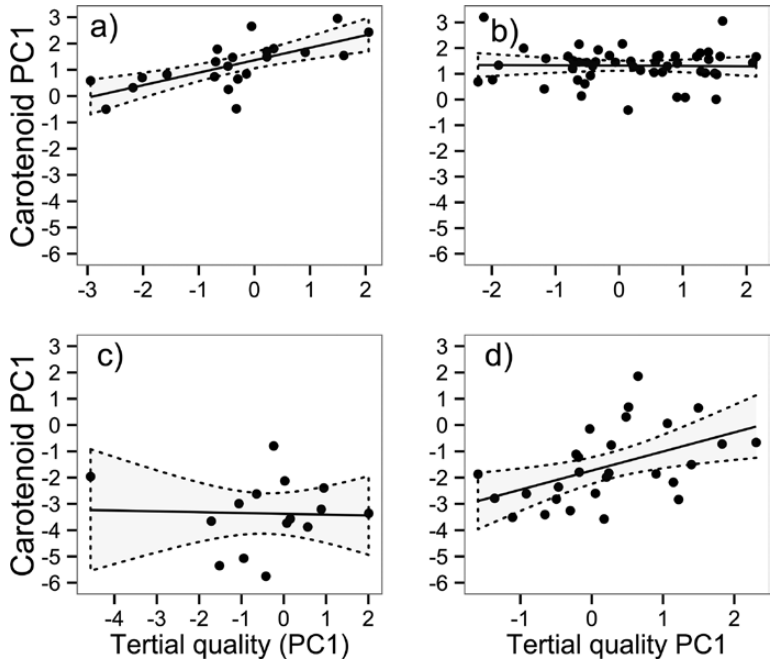

Figure 4
Relationship between tertial feather quality (condition at prebreeding molt) and carotenoid saturation by age and sex categories in SY males (a), ASY males (b), SY females (c), and ASY females (d). Regions bounded by dashed lines represent 95% CIs.

$F_{1,13} = 0.01$, $R^2 < 0.001$, $\beta = -0.03 \pm 0.24$, $P = 0.89$) (Figure 4) although we had low power to test this relationship.

Relationships between sexual pigmentation and indices of condition at postbreeding and prebreeding molt are summarized in Figure 5.

Sexual pigmentation and prenesting body reserves (residual mass)

Among males, sexual pigmentation was unrelated to prenesting body reserves, as measured by residual mass ($P > 0.20$ in all cases, $N = 103$ observations on 87 males, including 79 unique ASY males and 26 SY males, Supplementary Table S7, full model). Further, age did not interact with residual mass to predict pigmentation variables ($P > 0.20$ in all cases, Supplementary Table S7, full model).

Repeatability of coloration and longitudinal age effects

In males, melanin coverage did not increase longitudinally with age (LMM: $F_{1,17} = 0.003$, $\beta = -0.03 \pm 0.64$, $P = 0.95$) but was highly repeatable between years ($r_1 = 0.79$, SE = 0.09, CI = [0.56, 0.91], $P < 0.001$; $N = 36$ observations, 18 males). Melanin saturation neither changed longitudinally with age (LMM: $F_{1,17} = 0.08$, $\beta = 0.08 \pm 0.26$, $P = 0.76$) nor showed repeatability between years ($r_1 < 0.001$, SE = 0.14, CI = [0, 0.45], $P = 0.85$; $N = 35$ observations, 17 males). Carotenoid saturation increased longitudinally with male age (LMM: $F_{1,17} = 10.59$, $\beta = 0.46 \pm 0.14$, $P = 0.004$; $N = 35$ observations, 17 males) and showed repeatability when controlling for the longitudinal age effect ($r_1 = 0.57$, SE = 0.15, CI = [0.23, 0.81], $P = 0.02$). When not controlling for increasing age, repeatability of male carotenoid saturation was marginally nonsignificant ($r_1 = 0.37$, SE = 0.18, CI = [0, 0.72], $P = 0.057$).

In females, we had relatively low power to assess repeatability and longitudinal effects of age on pigmentation ($N = 11$ observations; 5 females). However, female melanin scores showed high repeatability ($r_1 = 0.97$, SE = 0.05, CI = [0.79, 0.99], $P < 0.001$) and did not longitudinally increase with age (LMM: $F_{1,5} = 0.61$, $\beta = 0.04 \pm 0.06$, $P = 0.43$). Female carotenoid saturation showed near-significant repeatability ($r_1 = 0.53$, SE = 0.28, CI = [0, 0.89], $P = 0.06$), with no evidence for a longitudinal increase with age (LMM: $F_{1,5} = 0.69$, $\beta = -0.45 \pm 0.55$, $P = 0.44$).

Lastly, primary feather quality was repeatable between years ($r_1 = 0.58$, SE = 0.13, CI = [0.26, 0.78], $P = 0.001$; $N = 47$ observations, 23 birds), and repeatability of residual mass approached statistical significance ($r_1 = 0.32$, SE = 0.19, CI = [0, 0.67], $P = 0.081$; $N = 36$ observations, 18 birds). Tertial feather quality was not significantly repeatable ($r_1 = 0.10$, SE = 0.18, CI = [0, 0.58], $P = 0.35$), but sample size was small for this analysis ($N = 26$ observations, 13 birds; see Supplementary Table S8 for models).

DISCUSSION

In our study, levels of different sexual pigments most strongly correlated with condition metrics in different age classes, rather than associations between pigmentation and condition changing in a consistent manner with age. In this case, the expression of a multifaceted sexual display may maintain reliable signaling of individual condition and quality as age changes (Møller and Pomiankowski 1993; Freeman-Gallant et al. 2010; Laucht and Dale 2012). First, in males, carotenoid saturation correlated with nestling-stage condition and condition at prebreeding molt (though not prenesting mass) in SY birds but showed low variance and no correlation with condition metrics in ASY males. Further, carotenoid saturation may also indicate male quality by signaling age itself (Kokko and Lindström 1996; Kokko 1998) because carotenoid saturation longitudinally increased with age. In contrast, male melanin coverage positively correlated with condition at both molts among ASY birds

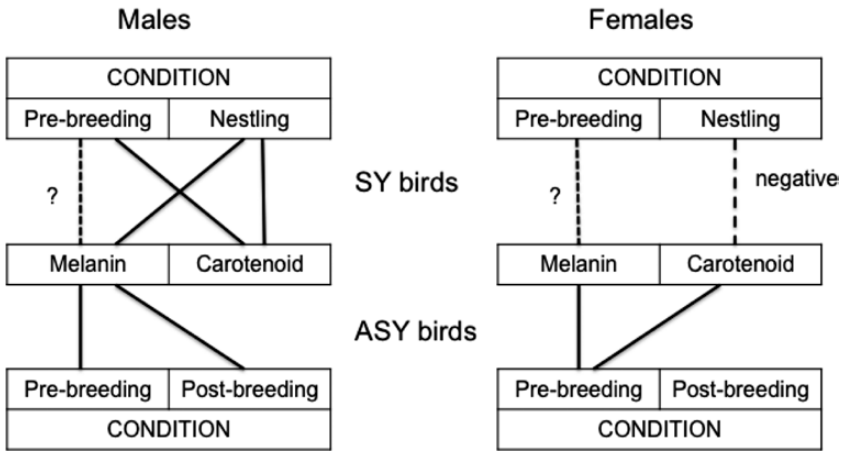

Figure 5
Summary of relationships between pigmentation variables and condition metrics across age and sex categories. Nestling condition in SY birds and postbreeding condition in ASY birds is based on primary feather quality; prebreeding condition is based on tertial feather quality. A question mark indicates that this relationship was not significant within the category but at the same time was not significantly different from that measured in the other age class (as tested by interaction terms).

and correlated positively with the condition of SY males as nestlings. Thus, melanin pigmentation appears associated with male condition and quality in both age classes, but if anything more strongly correlated with condition in ASY males. Further, male melanin coverage was repeatable, rather than increasing longitudinally with age, such that age should not confound relationships between melanin coverage and individual condition. Therefore, in combination, the 2 pigment types may allow accurate assessment of both condition and age-related differences in male quality, across age classes, suggesting an age-dependent mechanism for maintenance of multifaceted sexual displays. Consistent with our results, a previous study in male common yellowthroats (*Geothlypis trichas*) also found that carotenoid- and melanin-based pigmentations both convey information about individual condition and quality but do so differently across age classes (Freeman-Gallant et al. 2010).

Results from females also suggested that expressing multiple sexual pigments may facilitate reliable sexual signaling across age classes, but results were not as clear as for males. Specifically, melanin score was weakly, positively associated with prebreeding condition in SY females ($P = 0.13$), whereas carotenoid saturation negatively correlated with the condition of SY females as nestlings. Therefore, melanin pigmentation, but not carotenoid saturation, may positively reflect condition and quality in SY females, but more data would be needed to solidify this conclusion. Further, both carotenoid- and melanin-based pigmentations were positively associated with condition at prebreeding molt among ASY females, and both increased markedly between female age classes, and thus have potential to communicate differences in female quality associated with age. These results, and the relatively high correlation between female carotenoid saturation and melanin scores ($r = 0.41$), suggest that the redundancy of information associated with pigmentation types is higher in females than in males. Thus, if differences in age-dependent information content selects for maintenance of multiple pigment types, this selection may be acting primarily on males. Indeed, some might argue that selection does not even act directly on female ornaments (Lande 1980; Nordiede et al. 2013). However, we have found evidence that yellow warblers pair assortatively by pigmentation, suggesting that pigmentation may play a sexual signaling function in females as well as in males (Grunst A, unpublished data).

Assuming a signaling function of female pigmentation (even if distinct from that observed in males; Tobias et al. 2013), our results suggest that age-dependent selection on expression of ornaments differs with sex, particularly in the case of carotenoid pigmentation. As described above, carotenoid saturation more strongly correlated with condition at molt in older females, but in males, the opposite pattern occurred, with a stronger association found in SY males. In models of age-dependent sexual signaling, deferred investment in ornaments by young, high-quality individuals leads to lack of reliable signaling in young cohorts (Proust et al. 2002; Lindström et al. 2009) and could thus explain why condition at molt did not positively correlate with carotenoid saturation in young females. Rather, females in high condition as nestlings actually displayed low carotenoid saturation as SY birds. In contrast, the positive correlation between carotenoid saturation and condition metrics in young males, and lack of a clear age structure in male pigmentation, may arise because young, high-quality males do not greatly defer signaling effort. Males may show less deferment of signaling effort than females because pigmentation is essential to male mating success (Yezerinac and Weatherhead 1997; Greene et al. 2000) or because males are socially dominant and have access to more resources, favoring earlier onset of signaling (Stutchbury 1994; Kokko 1997). In contrast to SY males, in older males, age-related increases in signaling effort (Kokko 1997) and relaxed resource constraints (Badyaev and Duckworth 2003) could explain decreased variance in carotenoid saturation and dissociate carotenoid saturation from condition at molt.

Differences in deferment of sexual signaling effort could elucidate population-level differences in age-dependent signaling dynamics, as well as explaining sex differences. In our population, females may defer signaling effort more than males. However, in other populations, young males appear to defer signaling effort, as indicated by distinct delayed plumage maturation in male pigmentation (Greene et al. 2000; Karubian et al. 2008; Hawkins et al. 2012). In populations with deferment of sexual signaling effort in males, sexual pigmentation might be less indicative of condition and quality in SY males (Proust et al. 2002; Lindström et al. 2009), as seen for female carotenoid pigmentation in our population. Indeed, in black-headed grosbeaks (*Pheucticus melanocephalus*), in

which SY males show delayed plumage maturation, no relationship exists between pigmentation in SY males, arrival date on the breeding grounds, or wing chord (Hill 1984; but see Greene et al. 2000). Importantly, delayed expression of ornamentation may be due to resource constraints, rather than a "strategy" of deferred investment in ornaments. Nonetheless, resource constraints and deferred investment in ornaments are not mutually exclusive explanations for delayed plumage maturation (or strong age structure in pigmentation) and could in some cases act in combination to produce lower condition dependence of ornaments in young age classes. Indeed, it may not benefit individuals to commence signaling effort at a young age if young individuals are subject to resource constraints (Kokko 1997; Hawkins et al. 2012).

However, given the correlational nature of our data, explanations of results that do not involve patterns of investment into ornaments are also feasible. First, the fact that the ASY age class encompassed a wider diversity of ages than the SY age class, which represented a single cohort, may have affected results. Specifically, if females suffer greater mortality than males (Greenwood 1980; Gowaty 1993), the ASY group could represent a narrower range of ages in females than in males, causing age to confound relationships between condition and pigmentation in ASY males but not in females (Kokko 1997, 1998). However, low variance in carotenoid saturation in ASY males appeared to contribute to the lack of correlation between carotenoid saturation and condition metrics in this group and is unlikely to reflect a wide age distribution. Further, regardless of causal explanations, carotenoid saturation conveys little information about condition at molt in ASY males, unless females can assess male age more precisely than we could.

Additionally, high mortality among SY males with dull carotenoid pigmentation (Delhey and Kempenaers 2006; Pagani-Núñez and Carlos Senar 2011), rather than differential access to or allocation of carotenoids, could explain the reduced variance in carotenoid saturation and the lack of correlation between carotenoid saturation and condition metrics in ASY males. However, condition as a nestling negatively predicted the carotenoid saturation of SY females, whereas carotenoid saturation positively correlating to prebreeding condition in ASY females. These latter patterns seem unlikely to reflect differential mortality, suggesting that allocation or access to carotenoids may underlie results. Further, regardless of causation, the fact that melanin and carotenoid saturation correlate differently with condition metrics across age classes could favor coexpression of the 2 pigment types. Indeed, male melanin coverage did not show reduced variance in ASY compared with SY birds and correspondingly continued to correlate with male condition at molt in ASY males.

Finally, our results do not support the previous suggestion that carotenoid pigmentation is consistently more strongly condition dependent than melanin pigmentation (Badyaev and Hill 2000; McGraw and Hill 2000; Griffith et al. 2006; Ducrest et al. 2008). Our results corroborated previous studies that have found high repeatability of melanin coverage in yellow warblers, which may initially appear to support substantial genetic influences on pigmentation and limited condition-dependency (Studd and Robertson 1985a, 1985b). However, we also found that certain individuals consistently maintain higher condition than others, as also reported by previous studies in birds (De la Hera et al. 2009). Therefore, melanin pigmentation appears to convey information regarding which individuals are able to consistently maintain superior condition.

It is unclear whether specific properties of carotenoid versus melanin pigmentation can explain why melanin coverage in male warblers appears to correlate with condition at molt more consistently than carotenoid saturation. In a comparative study of serum antioxidant levels, yellow warblers had higher carotenoid levels than any other species (Cohen et al. 2009). Thus, carotenoids may not be highly limited in yellow warblers, as also suggested for some other insectivorous bird species (Parker et al. 2003; Evans et al. 2013). Further, birds may acquire carotenoids with greater efficiency as age increases (Badyaev and Duckworth 2003). In contrast to carotenoid pigmentation, phaeomelanin pigmentation may not be as strongly dependent on the acquisition or allocation of a single resource or may be linked to resources more limited in the diet of warblers (potentially cysteine) (McGraw 2006b, 2008; Galván and Solano 2009). Alternatively, social costs may enforce reliable signaling of condition via melanin pigmentation across age classes (Candolin 2000b). Indeed, male yellow warblers expressing greater coverage of melanin elicit greater aggressive responses in territorial disputes (Studd and Robertson 1985b).

In summary, our study yields 2 main conclusions. First, particularly in males, results suggest that melanin and carotenoid pigmentations correlate with condition in different age classes and also differentially change with age itself. Thus, coexpressing the 2 pigment types may facilitate reliable signaling of condition across age classes, as well as signaling age-related differences in individual quality. Therefore, age-dependent sexual signaling dynamics may help to explain the maintenance of multifaceted sexual displays. Second, age-dependent relationships between carotenoid pigmentation and condition at molt varied with sex. Thus, age-dependent sexual signaling dynamics may shift with sex-specific strategies for allocating resources toward ornaments or with sex-specific resource constraints. Finally, our results also suggest that age-dependent relationships between sexual ornamentation and condition metrics vary with the component of ornamentation quantified, which may help to explain why studies find diverse relationships between age and the condition dependence of ornaments.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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REFERENCES

Andersson M, Prager M. 2006. Quantifying color. In: Hill G, McGraw K, editors. Bird coloration. Volume 1. Mechanisms and measurements. Cambridge (MA): Harvard University Press. p. 90–147.

Badyaev A, Duckworth R. 2003. Context-dependent sexual advertisement: plasticity in the development of sexual ornamentation throughout the lifetime of a passerine bird. J Evol Biol. 16:1065–1076.

Badyaev A, Hill G. 2000. Evolution of sexual dichromatism: contribution of carotenoid- versus melanin-based pigmentation. Biol J Linn Soc. 69:153–172.

Badyaev A, Qvarnström A. 2002. Putting sexual traits into the context of an organism: a life-history perspective in studies of sexual selection. Auk. 119:301–310.

Bentz A, Siefferman L. 2013. Age-dependent relationships between coloration and reproduction in a species exhibiting delayed plumage maturation in females. J Avian Biol. 44:80–88.

Brooks R, Kemp DJ. 2001. Can older males deliver the good genes? Trends Ecol Evol. 16:308–313.

Candolin U. 2000a. Changes in expression and honesty of sexual signaling over the reproductive lifetime of sticklebacks. Proc R Soc Lond B. 267:2425–2430.

Candolin U. 2000b. Male-male competition ensures honest signaling of male parental ability in the three-spined stickleback (*Gasterosteus aculeaus*). Behav Ecol Sociobiol. 49:57–61.

Candolin U. 2003. The use of multiple cues in mate choice. Biol Rev. 78:575–595.

Cohen A, McGraw K, Robinson W. 2009. Serum antioxidants levels in wild birds vary in relation to season, life history strategy, and species. Oecologia. 161:673–683.

Copeland E, Fedorka K. 2012. The influence of male age and simulated pathogenic infection on producing a dishonest signal. Proc R Soc Lond B. 279:4740–4746.

Cote J, Arnoux E, Sorci G, Gaillard M, Faivre B. 2010. Age-dependent allocation of carotenoids to condition versus oxidative defenses. J Exp Biol. 213:271–277.

Dawson A. 2004. The effects of delaying the start of moult on the duration of moult, primary feather growth rates and feather mass in Common Starlings *Sturnus vulgaris*. Ibis. 146:493–500.

Dawson A, Hinsley SA, Ferns PN, Bonser R, Eccleston L. 2000. Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. Proc R Soc Lond B. 267:2093–2098.

Delhey K, Kempenaers B. 2006. Age differences in blue tit *Parus caeruleus* plumage colour: individual changes or colour-biased survival? J Avian Biol. 37:339–348.

Ducrest A-L, Keller L, Roulin A. 2008. Pleiotropy in the melanocortin system, coloration, and behavioral syndromes. Trends Ecol Evol. 29:502–510.

Evans SR, Gustafsson L, Sheldon BC. 2011. Divergent patterns of patterns of age-dependence in ornamental and reproductive traits in the collared flycatcher. Evolution. 65:1623–1636.

Evans SR, Hinks AE, Wilkin TA, Sheldon BC. 2010. Age, sex, and beauty: methodological dependence of age- and sex-dichromatism in the great tit *Parus major*. Biol J Linn Soc. 101:777–796.

Evans SR, Simon R, Sheldon BC. 2013. Pigments versus structure: examining the mechanism of age-dependent change in a carotenoid-based colour. J Anim Ecol. 82:418–428.

Freeman-Gallant C, Taff C, Morin D, Dunn P, Whittingham L, Tsang S. 2010. Sexual selection, multiple male ornaments, and age- and condition-dependent signaling in the common yellowthroat. Evolution. 64:1000–1017.

Galván I, Solano F. 2009. The evolution of eu- and pheomelanic traits may respond to an economy of pigments related to environmental oxidative stress. Pigm Cell Melanoma Res. 22:339–342.

Gowaty P. 1993. Differential dispersal, local resource competition, and sex ratio variation in birds. Am Nat. 141:263–280.

Greene E, Lyon B, Muehter B, Ratcliffe L, Oliver S, Boag P. 2000. Disruptive sexual selection for plumage coloration in a passerine bird. Nature. 407:1000–1003.

Greenwood P. 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim Behav. 28:1140–1162.

Griffith SC, Parker T, Olson V. 2006. Melanin- verses carotenoid-based sexual signals: is the difference really so black and red? Anim Behav. 71:749–763.

Grubb T. 2006. Ptilochronology: feather time and the biology of birds. In: Birkhead T, editor. Oxford ornithology series. Oxford: Oxford University Press.

Hall M, Molles LE, Illes AE, Vehrencamp SE. 2009. Singing in the face of death: male banded wrens *Throphilus pleurostictus* sing more to playback in their last breeding season. J Avian Biol. 40:217–224.

Harper D. 1999. Feather mites, pectoral muscle condition, wing length, and plumage coloration of passerines. Anim Behav. 58:553–562.

Hawkins G, Hill G, Mercadante A. 2012. Delayed plumage maturation and delayed reproductive investment in birds. Biol Rev. 87:257–274.

Hebets E, Papaj D. 2005. Complex signal function: developing a framework of testable hypotheses. Behav Ecol Sociobiol. 57:197–214.

Hegyi G, Szigeti B, Torok J, Eens M. 2007. Melanin, carotenoid, and structural plumage ornaments: information content and role in great tits *Parus major*. J Avian Biol. 38:698–708.

De la Hera I, Perez-Tris J, Telleria J. 2009. Repeatable length and mass but not growth rate of individual feathers between moults in a passerine bird. Acta Ornithol. 44:95–99.

Hill G. 1984. The function of delayed plumage maturation in male black-headed grosbeaks. Auk. 105:1–10.

Höglund J, Sheldon B. 1998. The cost of reproduction and sexual selection. Oikos. 83:478–483.

Hunt J, Brooks R, Jennions M, Smith MJ, Bentsen C, Bussiere L. 2004. High-quality male field crickets invest highly in sexual display but die young. Nature. 432:1024–1027.

Karubian J, Tillet TS, Webster M. 2008. The effects of delayed plumage maturation on aggression and survival in male red-backed fairy wrens. Behav Ecol. 19:508–516.

Kokko H. 1997. Evolutionarily stable strategies of age-dependent sexual advertisement. Behav Ecol Sociobiol. 41:99–107.

Kokko H. 1998. Good genes, old age and life history trade-offs. Evol Ecol. 12:739–750.

Kokko H, Lindström J. 1996. Evolution of female preference for old males. Proc R Soc Lond B. 263:1533–1538.

Kuznetsova A, Brockhoff PB, Christensen RHB. 2013. lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 1.1-0 [cited December 2013]. Available from: http://CRAN.R-project.org/package=lmerTest.

Lande R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution. 34:292–305.

Laucht S, Dale J. 2012. Correlations of condition, testosterone, and age with multiple ornaments in male house sparrows: patterns and implications. Condor. 114:865–873.

Lifjeld J, Kleven O, Jacobsen F, McGraw K, Safran R, Robertson R. 2011. Age before beauty? Relationships between fertilization success and age-dependent ornaments in barn swallows. Behav Ecol Sociobiol. 65:1687–1697.

Lindström J, Pike T, Blount J, Metcalfe N. 2009. Optimization of resource allocation can explain the temporal dynamics and honesty of sexual signals. Am Nat. 174:515–525.

Lowther P, Celada C, Klein N, Rimmer C, Spector D. 1999. Yellow warbler (*Dendroica petechia*). In: Poole A, editor. The birds of North America online. no. 454. Ithaca (NY): Cornell Laboratory of Ornithology.

Maney D, Davis A, Goode C, Reid A, Showalter C. 2007. Carotenoid-based plumage coloration predicts leukocyte parameters during the breeding season in northern cardinals (*Cardinalis cardinalis*). Ethology. 114:369–380.

McGraw K. 2006a. Mechanisms of carotenoid-based coloration. In: Hill G, McGraw K, editors. Bird coloration. Volume 1. Mechanisms and measurements. Cambridge (MA): Harvard University Press. p. 177–242.

McGraw K. 2006b. Mechanisms of melanin-based pigmentation. In: Hill G, McGraw K, editors. Bird coloration. Volume 1. Mechanisms and measurements. Cambridge (MA): Harvard University Press. p. 243–294.

McGraw K. 2008. An update on the honesty of melanin-based color signals in birds. Pigm Cell Melanoma Res. 21:133–138.

McGraw K, Hill G. 2000. Differential effects of endoparasitism on the expression of carotenoid- and melanin-based ornamental coloration. Proc R Soc Lond B. 267:1525–1531.

McGraw K, Hill G, Parker R. 2003. Lutein-based plumage coloration in songbirds is a consequence of selective pigment incorporation into feathers. Comp Biochem Phys B. 135:689–696.

McGraw K, Hill G, Stradi R, Parker R. 2002. The effect of dietary carotenoid access on sexual dichromatism and plumage pigment composition in the American goldfinch. Comp Biochem Phys B. 131:261–269.

McGraw K, Safran R, Evans M, Wakamatsu K. 2004. European barn swallows use melanin pigments to color their feathers brown. Behav Ecol. 15:889–891.
McGraw K, Safran R, Wakamatsu K. 2005. How feather color reflects its melanin content. Funct Ecol. 19:816–821.
Møller A, Pomiankowski A. 1993. Why have birds got multiple sexual ornaments? Behav Ecol Sociobiol. 32:167–176.
Montgomerie R. 2006. Analyzing colors. In: Hill G, McGraw K, editors. Bird coloration. Volume 1. Mechanisms and measurements. Cambridge (MA): Harvard University Press. p. 90–147.
Muñez A, Aparicio J, Bonal R. 2008. Male barn swallows use different resource allocation rules to produce ornamental tail feathers. Behav Ecol. 19:404–409.
Nakagawa S, Schielzeth H. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biol Rev. 85:935–956.
Nielson M, Holman L. 2012. Terminal investment in multiple sexual signals: immune-challenged males produce more attractive pheromones. Funct Ecol. 26:20–28.
Nordiede J, Kekalainen J, Janhunen M, Kortet R. 2013. Female ornaments revisited—are they correlated with offspring quality? J Anim Ecol. 82:26–38.
Pagani-Núñez E, Carlos Senar J. 2011. Changes in carotenoid-based plumage colour in relation to age in European Serins *Serinus serinus*. Ibis. 154:155–160.
Parejo D, Silva N, Danchin E, Avilés J. 2011. Informative content of melanin-based plumage colour in adult Eurasian kestrels. J Avian Biol. 42:49–60.
Parker T, Stansberry B, Becker C, Gipson P. 2003. Do melanin- or carotenoid-pigmented plumage ornaments signal condition and predict pairing success in the Kentucky warbler? Condor. 105:663–671.
Proust S, Day T, Rowe L. 2002. Older males signal more reliably. Proc R Soc Lond B. 269:2291–2299.
Prum R. 2006. Anatomy, physics, and evolution of structural colors. In: Hill G, McGraw K, editors. Bird coloration. Volume 1. Measurements and mechanisms. Cambridge (MA): Harvard University Press. p. 243–294.
Pyle P. 1997. Identification guide to North American birds. Bolinas (CA): Slate Creek Press.
R Core Team. 2012. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing [cited December 2013]. Available from: http://www.R-project.org/
Ralph C, Geupel G, Pyle P, Martin T, DeSante D. 1993. Handbook of field methods for monitoring landbirds. Gen. Tech. Rep. PSW-GTR-144. Albany (CA): U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station.
Safran R, McGraw K. 2004. Plumage coloration, not length or symmetry of tail-streamers, is a sexually selected trait in North American barn swallows. Behav Ecol. 15:455–461.
Saino N, Romano M, Rubolini D, Teplitsky C, Ambrosini R, Caprioli M, Canova L, Wakamatsu K. 2013. Sexual dimorphism in melanin pigmentation, feather coloration and its heritability in the barn swallow (*Hirundo rustica*). PloS One. 8:e58024.
Schneider C, Rasband W, Eliceiri K. 2012. NIH image to ImageJ: 25 years of image analysis. Nat Methods. 9:671–675.
Schulte-Hostedde AI, Zinner B, Millar JS, Hickling GJ. 2005. Restitution of mass-size residuals: validating body condition indices. Ecology. 86:155–163.
Studd M, Robertson R. 1985a. Sexual selection and variation in reproductive strategy in male yellow warblers (*Dendroica petechia*). Behav Ecol Sociobiol. 17:101–109.
Studd M, Robertson R. 1985b. Evidence for reliable badges of status in territorial yellow warblers (*Dendroica petechia*). Anim Behav. 33:1102–1113.
Stutchbury B. 1994. Competition for winter territories in a Neotropical migrant: the role of age, sex and color. Auk. 111:63–69.
Tobias J, Montgomerie R, Lyon B. 2013. The evolution of female ornaments and weaponry: social selection, sexual selection and ecological competition. Phil Trans R Soc B. 367:2274–2293.
Toral GM, Figuerola J, Negro JJ. 2008. Multiple ways to become red: pigment identification in red feathers using spectrometry. Comp Biochem Physiol B. 150:147–152.
Torres R, Velando A. 2007. Male reproductive senescence: the price of immune-induced oxidative damage on sexual attractiveness in the blue-footed booby. J Anim Ecol. 76:1161–1168.
Velando A, Drummond H, Torres R. 2006. Senescent birds facing immune challenge make all-out effort. Proc R Soc Lond B. 273:1443–1448.
Yezerinac S, Weatherhead P. 1997. Extra-pair mating, male plumage coloration and sexual selection in yellow warblers (*Dendroica petechia*). Proc R Soc Lond B. 264:527–532.