

DO MELANIN- OR CAROTENOID-PIGMENTED PLUMAGE ORNAMENTS SIGNAL CONDITION AND PREDICT PAIRING SUCCESS IN THE KENTUCKY WARBLER?

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Abstract. Yellow and red feathers pigmented by carotenoids can signal a bird's condition and are important to both female choice and male-male competition. Melanin-based ornaments are thought to be less effective than carotenoid ornaments as indicators of condition, though their signal function is still relatively unstudied. We examined both carotenoid and melanin-pigmented feather ornaments in a single species, the Kentucky Warbler (*Oporornis formosus*). Both males and females of this species have melanin-pigmented ornamentation (black crown, black face) and carotenoid-pigmented ornamentation (lemon-yellow undersides). Melanin-pigmented plumage patches were larger in males than females, and males had brighter breast plumage, with a larger ultraviolet component, than females. Among males in the wild, individuals in better condition had more extensive black caps and faces, but not brighter-yellow breasts. Males with larger black caps were more likely to attract mates. This work demonstrates that, in a species with both melanin- and carotenoid-pigmented plumage, melanin-pigmented ornaments can signal condition, and that a melanin-based signal can explain variance in mating success.

Key words: *Oporornis formosus*, pairing success, reflectance spectra.

¿Funcionan Como Indicadores de la Condición Física y Predicen del Éxito de Apareamiento los Ornamentos del Plumaje Pigmentados con Melanina o Carotenoides en *Oporornis formosus*?

Resumen. Las plumas amarillas y rojas pigmentadas por carotenoides pueden indicar la condición de un ave y son importantes tanto para la elección de machos por parte de las hembras como para la competencia entre machos. Se cree que los ornamentos a base de melanina son menos efectivos como indicadores de condición que los ornamentos carotenoides, aunque su función como señal ha sido menos estudiada. Examinamos plumas ornamentales pigmentadas con carotenoides y melanina en la especie *Oporornis formosus*. Tanto el macho como la hembra presentan ornamentación pigmentada con melanina (corona negra, rostro negro) y ornamentación pigmentada con carotenoides (flancos inferiores amarillo-limón). Los parches de plumaje pigmentados con melanina fueron mayores en los machos que en las hembras y el plumaje del pecho de los machos fue más brillante y con un componente ultravioleta mayor que el de las hembras. Entre los machos en ambiente natural, los individuos con mejor condición tuvieron coronas y rostros negros más extensos, pero no tuvieron pechos amarillos más brillantes. Los machos con coronas negras más extensas tuvieron una mayor probabilidad de atraer parejas. Este trabajo demuestra que en una especie con plumaje pigmentado con melanina y carotenoides, los ornamentos pigmentados con melanina pueden señalar la condición de los individuos, y que una señal con base en melanina puede explicar la varianza en el éxito reproductivo.

INTRODUCTION

According to indicator models of sexual selection, ornaments are signals of the bearer's qual-

ity. However, some types of ornaments may be more likely than others to be honest signals (Kodric-Brown and Brown 1984). Color ornaments have received much attention in this regard. A number of researchers have distinguished between the reds and yellows produced by carotenoids and the more muted tones typically produced by melanins. In animals, the principal difference between these pigments is that melanins are readily synthesized but carotenoids must be

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derived from the diet (Brush 1990, McGraw and Hill 2000). Thus, ability to display carotenoid-pigmented ornaments might be limited by foraging ability or by a physiological link at some point between foraging and pigment deposition. For instance, infection with intestinal parasites during molt can inhibit expression of carotenoid plumage ornamentation in House Finches (*Carpodacus mexicanus*; Hill and Brawner 1998, Brawner et al. 2000) and American Goldfinches (*Carduelis tristis*; McGraw and Hill 2000). In these same species, however, intestinal parasites did not inhibit melanin deposition in feathers (Hill and Brawner 1998, McGraw and Hill 2000).

Further evidence for the importance of carotenoids as honest signals of sexual ornamentation comes from comparative studies of birds. In North American Passeriformes carotenoid pigmentation was correlated with extent of sexual dimorphism, but melanin pigmentation was not (Gray 1996). Similarly, among cardueline finches, carotenoid pigmentation was closely tied to evolutionary increases in sexual dimorphism while melanins were not (Badyaev and Hill 2000). Also in carduelines, elaboration of song and carotenoid ornamentation are inversely related, suggesting a trade-off between two costly signals (Badyaev et al. 2002). In contrast, song production is unrelated to melanin ornamentation (Badyaev et al. 2002).

Evidence suggests carotenoid-based ornamentation is likely to honestly signal individual quality and has been consistently favored by sexual selection in a variety of taxa. Yet, many apparently sexually selected ornaments are melanin based. Melanin-pigmented ornaments might be effective signals of condition under certain circumstances (Jawor and Breitwisch 2003), although this is still poorly investigated. Understanding the function of melanin-pigmented ornaments demands further study, especially in species with both carotenoid and melanin ornamentation.

We examined both melanin- and carotenoid-pigmented plumage in Kentucky Warblers (*Oporornis formosus*). In this species, melanin-pigmented ornaments vary primarily in area, and the carotenoid-pigmented ornament varies primarily in reflectance spectra. We assessed these variables for these two types of ornaments respectively. First we determined the extent to which these varying pigmented plumage

patches were sexually dimorphic. Then, by measuring and monitoring wild Kentucky Warbler males, we assessed the relative condition-dependence of melanin- and carotenoid-based ornaments and the relative strengths of their correlations with mating success.

METHODS

STUDY SPECIES

Kentucky Warblers are small New World wood warblers that breed in deciduous forests in the southeastern United States and winter in Central and South America (McDonald 1998). Males arrive on our study site at Fort Riley, Kansas (39°15'N, 96°50'W) and begin singing in late April and early May. Signs of pairing with females (most obvious is a decrease in singing) are first noticed one to two weeks later. Males defend a territory from 0.5 to 2 ha with frequent singing and challenges to intruders (McDonald 1998). The song is a simple series of 3–8 paired notes, produced approximately 200 times hr⁻¹ before a female is attracted (Gibbs 1988). Territories are forested, but a wide range of forest ages and structural types are used. Both males and females have olive-green upperparts, bright lemon-yellow undersides and supercilial stripes, black facial patches below the eyes, dividing the green back from the yellow throat, and a black cap (Pyle et al. 1997). Extent of black within the cap varies, and is largely determined by the number of gray-tipped feathers interspersed among those with black tips. The black feathers reflect little light at any wavelength, including ultraviolet (Parker et al., unpubl. data). The feathers in the cap are erected during territorial conflicts (McDonald 1998).

ASSESSMENT OF SEXUAL DIMORPHISM

We examined Kentucky Warbler study skins in the collection of the University of Kansas Natural History Museum and quantified intersexual variation in plumage ornamentation. Only 10 adult female skins were available in the collection. We selected 10 male skins to match these 10 females as closely as possible in year, date, and location of collection. Males were selected by examining a list of specimens rather than the specimens themselves, thus avoiding bias in selecting skins for the comparison. We assessed variation in plumage ornaments in two ways. First, we examined extent of the melanin-based black cap and black face. We took two digital

photos of each specimen: top of head and left side of head. For each photo, the camera was held perpendicular to the ornament. A grid of 25-mm² blocks was positioned adjacent to and in the same plane as the ornament to provide a scale for later image analysis. Images were analyzed using Scion Image (Scion Corporation 2000). We calibrated the measurement of each image by tracing a 5-mm length from the grid adjacent to the ornament in the image. We then traced the outline of the face or the cap (taking care to exclude gray feathers from the cap) with the cursor, and the program calculated its black-feathered area. This process was conducted twice for each bird and the mean ornament value was used in subsequent statistical analyses. Repeatability between measurements was high (cap: $R^2 = 0.98$; face patch: $R^2 = 0.94$).

We assessed variation in the spectral reflectance of the yellow breast using an Ocean Optics S2000 fiberoptic spectrometer with an Ocean Optics PX-2 pulsed xenon light source also directed through fiberoptics (Ocean Optics, Inc., Dunedin, Florida). The spectrometer was calibrated to a Spectralon white standard (Labsphere Inc., North Sutton, New Hampshire) and a black felt standard. The sensor and light source were positioned 6 mm from, and perpendicular to, the feather patch being measured. This measures reflectance over a patch approximately 2 mm across. The spectrometer recorded a spectrum every 0.5 sec and reported the average of five consecutive readings. We took one of these averaged readings from each of four locations on the yellow breast. These locations, at least 5 mm apart from each other, were in areas where no damage to the specimen had disturbed the natural feather positions. We limited our analysis to reflectance between 320 nm and 725 nm, the approximate visible range of passeriform birds (Hart et al. 2000, Örnborg et al. 2002). At each of the 1217 wavelengths in this range at which this spectrometer recorded percent reflectance, we calculated the mean percent reflectance from the readings from the four breast regions. Then, to decrease the number of variables prior to data analysis, we took the median percent reflectance at approximately 10-nm intervals. This produced median percent reflectances at 42 wavelengths between 320 nm and 725 nm. Using medians minimized the impact of anomalous spikes at one or a few wavelengths.

LOCATING AND MONITORING KENTUCKY WARBLERS

We studied wild Kentucky warblers at Fort Riley, a U.S. Army installation at the western edge of the Flint Hills in Riley and Geary Counties, Kansas. Although primarily grassland, there are riparian forests of varying age along perennial and ephemeral streams in the steeply incised terrain. We located singing males through point counts and walks through forested areas in late April and early May as they began to arrive and defend territories. We then attracted males to mist nets with playback of Kentucky Warbler song. Prior to release, we measured mass (to the nearest 0.1 g) and tarsus length (to the nearest 0.1 mm), took digital photos of plumage ornaments, and plucked feathers from the breast for spectral analysis. Finally, each bird was marked with a locally distinct combination of a U.S. Fish and Wildlife Service numbered aluminum leg band and a plastic colored leg band.

To determine pairing status for males, we returned to each of 29 territories for three early-morning 45-min visits spaced approximately two weeks apart. At each visit we recorded the number of songs produced by the banded male, whether a female was observed, and any behavior (e.g., delivering food) that might indicate pairing status. Prior to attracting a female, males sing nearly continuously with few pauses longer than 1 min. For each of the three visits, we made a determination of pairing status (paired or unpaired) for each male. In cases where pair interactions were not observed, we relied on male song rate to infer pair status. After pairing, male song rate declines to approximately 10–20% of its prepairing rate (Gibbs 1988, McDonald 1998). Male song rates were distinctly bimodal (~ 20 songs hr^{-1} vs. ~ 200 songs hr^{-1}), and so pairing status could be unambiguously determined in most cases. However, for the few intermediate cases we made the conservative assumption in light of results presented by Gibbs (1988) that a male was unpaired if he sang more than 60 songs hr^{-1} . The outcomes of analyses reported below did not qualitatively differ when a cut-off of 120 songs hr^{-1} was used instead. Males were classified as either never paired, or paired on at least one visit.

Although a complete picture of reproductive success requires genetic paternity data, in this case, there is reason to believe that a biologically significant portion of the variance in male

reproduction was determined by pairing success. More than 25% (8 of 29) of monitored males never paired. These individuals, though possibly able to copulate with females paired to other males, did not have primary access to a female. Because in many species (Ligon 1999), including Kentucky Warblers (McDonald 1998) and other parulids (Stutchbury et al. 1997, Yezerinac and Weatherhead 1997), males tend to sire the majority of the young in the broods of their social mates, pairing success is likely to be an important determinant of reproductive success.

MEASURES OF WILD-BIRD PLUMAGE ORNAMENTS

In wild males, we focused on three plumage ornaments, the black cap, the black face, and the yellow breast. To assess variability in the cap and face, we took three digital photos of each male in the field: top of head, right side of head, and left side of head. For each photo, the camera was held perpendicular to the ornament and the image was recorded when the bird held its head in its natural, forward-looking position. As with the measurement of study skins, a grid of 25-mm² blocks was held adjacent to and in the same plane as the ornament to provide a scale for image analysis. Analysis of images of live birds was identical to that of study skins described above except that the black face patch value was a mean of four measurements, two from each side. Repeatability of the measurements was high (cap: $R^2 = 0.94$; left side of face: $R^2 = 0.93$; right side of face: $R^2 = 0.95$) as was similarity between right and left sides of the face ($R^2 = 0.62$).

To assess among-individual variability of the yellow breast, we plucked four nonadjacent feathers from the breast of each male for later spectral analysis in the laboratory. The spectrometer was calibrated and positioned as described above for the study skin analysis. Readings were taken from the distal, yellow portion of the feather normally visible on a bird. Individual feathers were placed against a black felt standard background, and one mean reading (from five successive readings, as above) was taken for each of the four feathers. We then averaged the recorded spectra in the same manner as the study skin data.

STATISTICAL ANALYSES

Sexual dimorphism. Prior to comparing plumage ornaments of males ($n = 10$) and females ($n =$

10), we asked whether year of collection (range 1912–1972) influenced extent of the black head ornaments or the reflectance spectra of the yellow breast. There were no significant year effects ($P > 0.1$ for all tests) and including year as a covariate did not qualitatively influence the outcomes of our analyses. Thus we did not statistically account for year of collection in results reported below. Differences between study skins of males and females in extent of the black cap and extent of the black face patch were assessed with a MANOVA (PROC GLM, SAS Institute Inc. 2000).

Because of the complex shape of the reflectance curve (Fig. 1), we first summarized breast-feather reflectance data with a much smaller number of variables using principal components analysis (PROC PRINCOMP, SAS Institute Inc. 2000). We then used MANOVA (PROC GLM, SAS Institute Inc. 2000) to compare breast reflectance between males and females.

Condition. As with the study skin data, reflectance from the yellow feathers plucked from wild males ($n = 29$) were summarized with principal components analysis (PROC PRINCOMP, SAS Institute Inc. 2000) prior to further analysis. To determine whether the ornaments were related to body condition, we used separate multiple regressions (PROC REG, SAS Institute Inc. 2000) for each ornament measurement, with the ornament-expression value as the dependent variable and both mass and tarsus length as independent variables. A significant partial correlation coefficient for mass would indicate that body condition (mass controlled for tarsus length) predicted ornament expression. This analysis was conducted separately for each ornament measurement. For analyses of black head ornaments, we included data for two males whose territories were not monitored, raising the sample size to $n = 31$.

Mating success. If ornament expression influenced male access to females, either through male-male competition or female choice, we might expect correlations between ornament expression and pairing success. Accordingly, we conducted two MANOVAs ($n = 29$ for each, PROC REG, SAS Institute Inc. 2000) comparing ornament expression between males who were paired on at least one visit with males that were never paired (carotenoids in analysis one, melanins in analysis two).

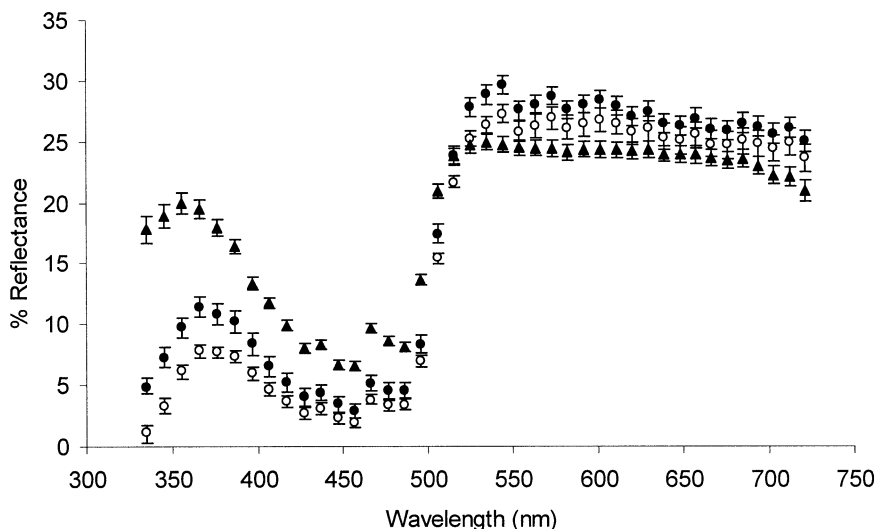


FIGURE 1. Mean \pm SE percent reflectance of Kentucky Warbler yellow breast feathers, reported at approximately 10-nm intervals. Filled circles: study skins of males ($n = 10$) unfilled circles: study skins of females ($n = 10$) filled triangles: feathers plucked from wild males ($n = 29$).

Age. Aspects of the cap and face patch may differ between one-year-old and older males. Both of these black ornaments may be suffused with greenish or olive feathers in one-year-old, but not older, males (Pyle et al. 1997). None of the males we photographed had any greenish or olive feathers in the cap, but five did have such feathers in the face patch. We asked if relationships between head-ornament expression, condition, and pairing success held in the subset of 24 males that appeared to be two years of age or older. Analyses were conducted as described above, but without the five putative first-year males. We also compared mass and head-ornament expression between these two age groups of males with two-tailed Student's *t*-tests.

RESULTS

Sexual dimorphism. The yellow breast feathers showed two peaks of reflectance (Fig. 1), one in the ultraviolet (320–400 nm), and a second, higher and wider peak in the greens, yellows, and reds (520 nm–720 nm). As predicted by Cuthill et al. (1999), the coefficients of the first principal component from the study skin reflectance data were all positive and of similar magnitude, and thus primarily represented variation in percent reflectance (brightness) across the spectrum among individuals. The second principal component was strongly positively repre-

sented by reflectance between 350 and 450 nm and was negatively associated with reflectance above 550 nm. Thus this component represented a relatively high trough between the UV and yellow peaks (Fig. 1) and a relatively weak yellow-red peak. PC3 had strongly negative coefficients below 375 nm and moderately positive coefficients across the rest of the spectrum, and thus characterized a low UV peak relative to the rest of the spectrum. These first three principal components explained 98% of the variation in the data set.

Male ($n = 10$) and female ($n = 10$) Kentucky Warblers showed significant differences in both reflectance of the carotenoid-pigmented breast feathers (Fig. 1, Table 1) and the extent of melanin ornamentation on the cap ($F_{1,18} = 9.7$, $P = 0.006$, Fig. 2a) and face ($F_{1,18} = 12.2$, $P = 0.002$; full MANOVA model of cap and face, $F_{2,27} = 10.5$, $P = 0.001$).

Condition. The shape of the reflectance curve from the yellow breast feathers plucked from wild males was similar to the shape obtained from study skins, although the UV peak was higher and the green-yellow-red peak lower on the plucked feathers (Fig. 1). The basic consistency in shape suggested both methods measured a similar variable, though the differences were great enough to preclude comparisons between plucked and museum feathers. For the

TABLE 1. Results of a MANOVA comparing breast color in male ($n = 10$) and female ($n = 10$) Kentucky Warblers, as measured from study skins and based on principal component (PC) summaries of reflectance spectra (Fig. 1).

	df	<i>F</i>	<i>P</i>	Interpretation of trend
PC1	1,18	4.6	0.05	Males are brighter
PC2	1,18	1.9	0.18	Males have less contrast between reflectance peaks and trough
PC3	1,18	3.4	0.08	Males have greater UV reflectance
Full model	3,16	4.6	0.02	Male breast color differs from female breast color

plucked feathers, coefficients of the first principal component were all positive and of similar magnitude, and thus summarized variation in percent reflectance (brightness) across all wavelengths. Coefficients of the second component were strongly negative below 375 nm, strongly positive between 400 and 500 nm, and moderately negative above 500 nm. Thus a positive association with PC2 indicates a low UV peak and a somewhat low yellow-red peak, but a high trough between peaks. PC3's coefficients were strongly positive below 375 nm and strongly negative between 500 and 600 nm, and thus represented a high UV peak but a low green-yellow peak. These three principal components explained 99% of the variation in the data set.

Two of the principal components summarizing the variation in yellow breast-feather reflectance were unrelated to body condition (mass controlled for tarsus length) of 29 wild males (PC 1: partial $t = 1.1$, partial $R^2 = 0.06$, partial $P = 0.28$; PC 3: partial $t = 0.4$, partial $R^2 = 0.00$, partial $P = 0.72$). There was a weak tendency for males in better condition to have more-distinct reflectance trough and peaks (PC 2: partial $t = -1.8$, partial $R^2 = 0.06$, partial $P = 0.08$). Extent of the black face patches (Table 2) and extent of black in the cap (Fig. 2b, Table 2) were both significantly related to condition in 31 wild males.

Mating success. Two of the principal components summarizing variation in carotenoid ornaments did not predict mating success in 29 wild males (PC 2: $F_{1,27} = 0.0$, $P = 0.91$; PC 3: $F_{1,27} = 0.0$, $P = 0.98$), although there was a weak tendency for paired males to have brighter breast feathers (PC 1, $F_{1,27} = 3.4$, $P = 0.08$; full MANOVA model of PC1, 2, and 3: $F_{3,25} = 1.1$, $P = 0.38$). Melanin ornamentation predicted mating success. Males with less black in the cap tended to remain unpaired throughout the season (Fig. 2c, Table 3).

Age. Within putative second-year or older males ($n = 24$), extent of black in both cap and face patch were positively correlated with condition, though this was significant only for the face patch (partial correlations: cap, $t_1 = 1.7$, $R^2 = 0.11$, $P = 0.10$; face patch, $t_1 = 2.3$, $R^2 = 0.20$, $P = 0.03$). Also within this subset of males, paired individuals had significantly larger caps ($F_{1,22} = 8.8$, $P = 0.007$) but not larger face patches ($F_{1,22} = 0.8$, $P = 0.37$). The putative older males had more black in their caps ($t_{29} = -2.5$, $P = 0.02$) and tended to have more in their face patches ($t_{29} = -1.9$, $P = 0.06$), but did not weigh more ($t_{29} = -1.2$, $P = 0.24$) than younger males. Three of the five males presumed to be one year old went unpaired, in comparison to 5 of the 24 males presumed older. Thus younger males appeared less likely to pair ($\chi^2 = 5.0$, $P = 0.03$).

DISCUSSION

Contrary to the suggestions of some comparative studies (Gray 1996, Badyaev et al. 2002), the correlative evidence we present here supports the hypothesis that melanin-based ornaments can be honest, sexually selected signals. In Kentucky Warblers, melanin-pigmented plumage ornamentation differed in extent between males and females, was lesser in extent for males with poorer body condition, and was lesser in extent for males that did not attract females. Carotenoid ornament reflectance also differed between the sexes. However, the component of carotenoid feather reflectance related to male body condition (trough-peak contrast; PC2) was not the same as the component that was related to pairing success (brightness; PC1), and neither relationship was significant at alpha = 0.05.

Although Kentucky Warblers are sexually dimorphic in both melanin- and carotenoid-based plumage ornaments, this dimorphism is more

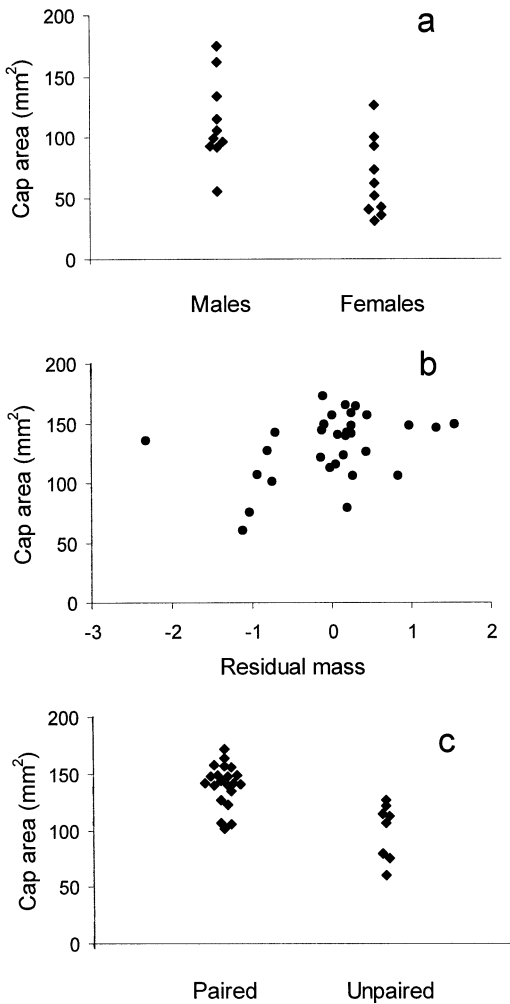


FIGURE 2. Evidence that the black, melanin-pigmented cap of male Kentucky Warblers is a sexually selected indicator of condition. (a) The Kentucky Warbler’s black cap was sexually dimorphic in area on study skins. (b) The area of black in the cap was positively related to male body condition in wild males, here depicted as the residuals of mass on tarsus length (but analyzed as mass with tarsus as a covariate). (c) Cap area predicted pairing success in wild males, with smaller-capped males less likely to pair. In (a) and (c), points are offset horizontally from each other so that individuals can be distinguished.

subtle than in many other species in which plumage signals have been studied. It could be that these ornaments are used by females as well as males in sexual signaling (Jawor and Breitwisch 2003), as appears to be the case for the melanin-pigmented facial patch in the Northern Cardinal (Jawor 2002; Jawor et al., in press).

TABLE 2. Relationships between area of black head ornaments and body condition in territorial male Kentucky Warblers in Kansas ($n = 31$) in two separate multiple regressions. Body condition was indexed using a partial correlation with body mass controlled for tarsus length in a multiple regression.

	Partial t	Partial P	Partial R^2
Cap	2.3	0.03	0.18
Face patch	3.5	0.002	0.32

This possibility remains to be investigated in Kentucky Warblers.

Both yellow, presumably carotenoid-based plumage and melanin-pigmented plumage are common in the Parulidae. The relative importance of these two classes of pigmentation in this group demands further study, especially in light of the limited knowledge we do have about parulid plumage ornaments. For instance in Common Yellowthroats (*Geothlypis trichas*), one of the few other species in this family in which ornament function has been studied, extent of black, melanin-based plumage on the head appears to function in sexual selection (Thusius et al. 2001). The same is true for the rust-colored, presumably melanin-pigmented breast streaks of the Yellow Warbler (*Dendroica petechia*; Yezerinac and Weatherhead 1997). One consideration guiding further research in this group should be the differences in diet between warblers (insectivores) and the better-studied finches (granivores) and the potential implications for access to carotenoid pigments. If certain diets led variation in carotenoid signals to be a poorer correlate of foraging ability or condition, this might lead melanin-based signals to be more important.

Without experimental manipulations we cannot determine whether the male Kentucky Warbler’s black cap directly influences female Kentucky Warbler mate choice, indirectly influences male success by acting in male-male competi-

TABLE 3. Relationship between area of black head ornaments and pairing success in territorial male Kentucky Warblers in Kansas ($n = 29$), as determined by MANOVA.

	df	F	P
Cap	1,27	22.9	<0.001
Face patch	1,27	2.7	0.11
Full model	2,26	11.7	<0.001

tion, or whether the black cap influences social interactions at all. For instance, male condition and female choice could be influenced by factors such as age or territory quality that might correlate with plumage ornamentation.

Based on our rough age-class estimates, older males had more extensive black head ornaments and were more likely to be paired. However, when we limited analyses of condition and pairing success to older males, we still found that black head ornaments correlated with body condition and predicted pairing success. Thus, the melanin-pigmented plumage ornaments appeared to be effective signals within an age class, despite being influenced by age. This is expected if plumage expression is an honest signal of condition and age is one influence on condition. Younger males may tend to be, by some measure, in poorer condition than older males. If females should avoid younger males for this or other reasons, plumage color could help females make adaptive mate choices.

Regardless, the relationship between condition and ornament expression means that melanin ornaments signal condition in this species, and the correlation between male crown area and male pairing success suggests conspecifics may respond to this signal. These results underscore the need for further study of the function of melanin-pigmented ornaments.

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