



EVOLUTION OF SEXUAL DICHROMATISM. 2. CAROTENOIDS AND MELANINS CONTRIBUTE TO SEXUAL DICHROMATISM IN NEW WORLD ORIOLES (*ICTERUS* SPP.)

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ABSTRACT.—Several recent studies have investigated how different proximate mechanisms of color production contribute to sexual dichromatism. These studies suggest that carotenoid pigments—which are frequently subject to sexual selection—are more strongly associated with sexual dichromatism than melanins. This reasoning implicitly assumes that increased male elaboration leads to sexual dichromatism. However, sexual dichromatism can be generated through multiple evolutionary pathways, including decreases in female elaboration. We examined whether evolutionary changes in carotenoid- and melanin-based plumage were correlated within New World orioles (*Icterus* spp.), a genus in which male elaboration is ancestral and only female elaboration varies. We found a significant correlation between evolutionary changes in the degree of carotenoid and eumelanin sexual dichromatism. These findings differ from those of previous comparative studies and suggest the possibility of interesting differences when different evolutionary pathways—such as changes in male versus female coloration—lead to sexual dichromatism. *Received 2 July 2007, accepted 5 February 2008.*

Key words: comparative methods, *Icterus*, independent contrasts, loss of elaboration, sexual dichromatism.

La Evolución del Dicromatismo Sexual. 2. Carotenoides y Melaninas Contribuyen al Dicromatismo Sexual en Especies de *Icterus*

RESUMEN.—Varios estudios recientes han investigado el papel de diferentes mecanismos próximos de producción del color con respecto al dimorfismo sexual. Estos estudios sugieren que los pigmentos carotenoides, que están sujetos frecuentemente a la selección sexual, están más fuertemente asociados con el dimorfismo sexual que las melaninas. Este razonamiento supone implícitamente que es el aumento de rasgos elaborados en los machos lo que conduce al dicromatismo sexual. Sin embargo, el dicromatismo sexual se puede generar por múltiples rutas evolutivas, incluso la disminución de caracteres elaborados en las hembras. Examinamos si estos cambios evolutivos del plumaje basado en carotenoides y melaninas están relacionados en *Icterus*. En este género, el plumaje elaborado es ancestral en el macho, y las hembras varían desde sencillas hasta tan elaboradas como los machos. Encontramos una correlación significativa entre los cambios evolutivos del nivel de dicromatismo de carotenoides y melaninas. Estos resultados difieren de los de estudios comparativos previos y sugieren la posibilidad de diferencias interesantes cuando diferentes rutas evolutivas, tales como cambios en la coloración masculina versus la femenina, resultan en dicromatismo sexual.

SEXUAL DICHROMATISM—a difference in color between the sexes—occurs widely throughout the animal kingdom. Sexual dichromatism may range from subtle color differences that are not readily apparent without quantitative means of scoring color to blatant differences that have sometimes led to the classification of males and females as separate species (Andersson 1994, Amundsen and Pärn 2006). The traditional assumption regarding changes in sexual dimorphism is that sexual selection favors increasing male elaboration, whereas natural selection opposes this elaboration in females. However, sexual dichromatism—and sexual dimorphism in general—is a composite trait that can be

generated through changes in male or female coloration (Hofmann et al. 2008; also see Omland and Hofmann 2006).

In birds, two major groups of pigments—carotenoids and melanins—frequently generate the changes in color that lead to sexual dichromatism (Hofmann et al. 2008). Carotenoid- and melanin-based colors are produced by different proximate mechanisms and, in some cases, may serve different signaling functions (Hill and Brawner 1998, McGraw and Hill 2000, Hill 2006; but see Griffith et al. 2006). Carotenoids cannot be synthesized by animals, and these potentially limited-resource pigments have been demonstrated to indicate condition in a diversity of animal taxa (Hill 2006, McGraw

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2006a). Melanins can be synthesized by animals and have largely been assumed not to indicate condition (Hill 2006, McGraw 2006b). It is worth noting, however, that recent studies suggest that melanins indicate condition in some avian taxa, though the specific mechanisms have yet to be elucidated (McGraw 2006b). These potentially different signaling roles have led to the suggestion that carotenoids and melanins contribute unequally toward sexual dichromatism.

Two previous studies have used comparative methods to investigate how carotenoids and melanins contribute to avian dichromatism. Gray (1996) scored color across the avian lineage as “carotenoid,” “melanin,” or “structural” and used independent contrasts to test for associations between the degree of dichromatism and the degree to which coloration was produced by a particular proximate mechanism. Badyaev and Hill (2000) examined the relationship between carotenoid- and melanin-based plumage and sexual dichromatism in cardueline finches. The combined results from these studies suggested that carotenoids, but not melanins, were associated with or had a greater contribution toward sexual dichromatism. Although neither study explicitly addressed whether sexual dichromatism arose through changes in male or female coloration, both implicitly assumed that dichromatism arose through increased male elaboration. Thus, sexual selection was acting to a greater extent on the putatively condition-dependent carotenoid-based coloration.

However, sexual dichromatism is a composite trait that can be generated through gains or losses of male or female elaboration (Omland and Hofmann 2006, Hofmann et al. 2008). Although losses of elaboration may be widespread throughout the animal kingdom (Wiens 2001), cases of dichromatism involving female change remain relatively poorly studied (but see Burns [1998] and discussions in Badyaev and Hill [2003], Amundsen and Pärn [2006], Omland and Hofmann [2006]). We investigated the contribution of carotenoids and melanins to sexual dichromatism in New World orioles (*Icterus* spp.), a genus in which male elaboration is ancestral and losses of female elaboration lead to gains of dichromatism (Hofmann et al. 2008). First, we examined whether both carotenoids and melanins contributed to sexual dichromatism in orioles. We then tested whether evolutionary changes in the degree of carotenoid- and melanin-based dichromatism were correlated.

METHODS

Color measurements.—We measured plumages of male and female orioles with an Ocean Optics USB2000 spectrometer and pulsed xenon light source following standard methods (Hofmann et al. 2006). We then derived two quantitative, colorimetric characters from spectra that described either carotenoid- or melanin-based plumage. For carotenoid-based plumage, we examined spectral saturation, which corresponds to the perception of chroma or color purity (e.g., pink vs. red). Carotenoid spectral saturation was calculated as the difference between maximum and minimum reflectance in the visible region of the spectrum (400–700 nm), normalized to maximum reflectance (this normalization means that changes in the minimum reflectance have a greater influence on spectral saturation values than changes in maximum reflectance, making this character less sensitive to the influence of small amounts of eumelanin; for a detailed discussion of the subtractive nature of carotenoid colors and further biochemical implications of these reflectance measurements, see Andersson

and Prager 2006). For melanin-based plumage, we calculated achromatic brightness, which corresponds to the perception of lightness (black vs. gray), as the average reflectance from 300 to 700 nm (Andersson and Prager 2006). The carotenoid or eumelanin designation was based on the adult male’s appearance, which is either black (primarily eumelanin) or colored (primarily carotenoid) in the body regions analyzed (to limit these comparisons to carotenoids and eumelanins, we excluded colored body regions that had a predominant phaeomelanin influence; Hofmann et al. 2007). See appendix in Hofmann et al. (2008) for specifics of individual taxa.

Independent contrasts.—We used the Phenotypic Diversity Analysis Programs module (PDTree; Midford et al. 2006) implemented in MESQUITE (Maddison and Maddison 2006) to perform Felsenstein’s independent contrasts across the oriole molecular phylogeny (Felsenstein 1985, Omland et al. 1999). We made two groups of related comparisons. We first compared female carotenoid saturation with female melanin achromatic brightness across body regions. However, because color changed in only one sex, we were able to calculate the difference in carotenoid saturation between males and females and compare it with the difference in melanin achromatic brightness (all male orioles have highly saturated color plumage and dark achromatic plumage; only female plumage varies in saturation and achromatic brightness). Therefore, we also had a direct measure of the magnitude of the difference between males and females for each body region that was not a composite character (see Hofmann et al. [2008] for a more detailed discussion).

Preliminary analyses suggested that changes within each proximate mechanism (carotenoid and melanin) were correlated across body regions (Table 1). To avoid the problems inherent with tests for repeated correlations, we chose representative comparisons from the dorsal and ventral surfaces—the back to the rump, and the throat to the breast—respectively. In addition to the fact that these body regions allowed a large number of taxa to be

TABLE 1. Summary of independent contrast results within and between pigment classes.

	Number of contrasts ^a	<i>r</i>	Significance	Sign test significance ^b
Female				
Within pigment class				
Breast vs. rump	33	0.87	<0.01	<0.01
Back vs. throat	33	0.71	<0.01	<0.01
Between pigment classes				
Throat vs. breast	35	−0.77	<0.01	<0.01
Back vs. rump	27	−0.83	<0.01	<0.01
Male–female difference				
Within pigment class				
Breast vs. rump	29	0.82	<0.01	<0.01
Back vs. throat	33	0.66	<0.01	<0.01
Between pigment classes				
Throat vs. breast	31	0.78	<0.01	0.07
Back vs. rump	25	0.77	<0.01	<0.01

^aPhylogenetic branch lengths were scaled to one to represent a punctuated model of evolution.

^bThe sign test was performed with one axis (x) positized and represents the most conservative estimate of significance.

compared (e.g., most orioles had both a black back and a colored rump; Omland and Lanyon 2000), the compared patches are adjacent to one another in each case.

Model testing suggested that a punctuated mode of evolution best fit the changes we observed in female coloration and sexual dichromatism (Hofmann et al. 2008). Therefore, we scaled all phylogenetic branch lengths to one to better represent a punctuated or speciation process in our independent contrasts. However, we also investigated whether scaling branch lengths according to molecular distance, which is more representative of a Brownian mode of evolution, influenced our results. Before comparing independent contrasts, we examined whether there was a significant relationship between the absolute values of the contrasts and their standard deviations. Such a relationship would imply that some contrasts are contributing disproportionately to the correlation

(Garland et al. 1992). Once we determined that no such relationships were present, we performed independent contrasts of female carotenoid saturation with melanin achromatic brightness and of carotenoid dichromatism with melanin dichromatism across species. We report significance values for both the Pearson product-moment correlation coefficient and the more conservative sign test (two-tailed).

RESULTS

Within pigment classes.—Orioles exhibit dichromatism in both melanin- and carotenoid-based coloration. Males have relatively little variation in their carotenoid saturation and melanin achromatic brightness, whereas females vary considerably across species (Fig. 1). Independent contrasts indicated that there were

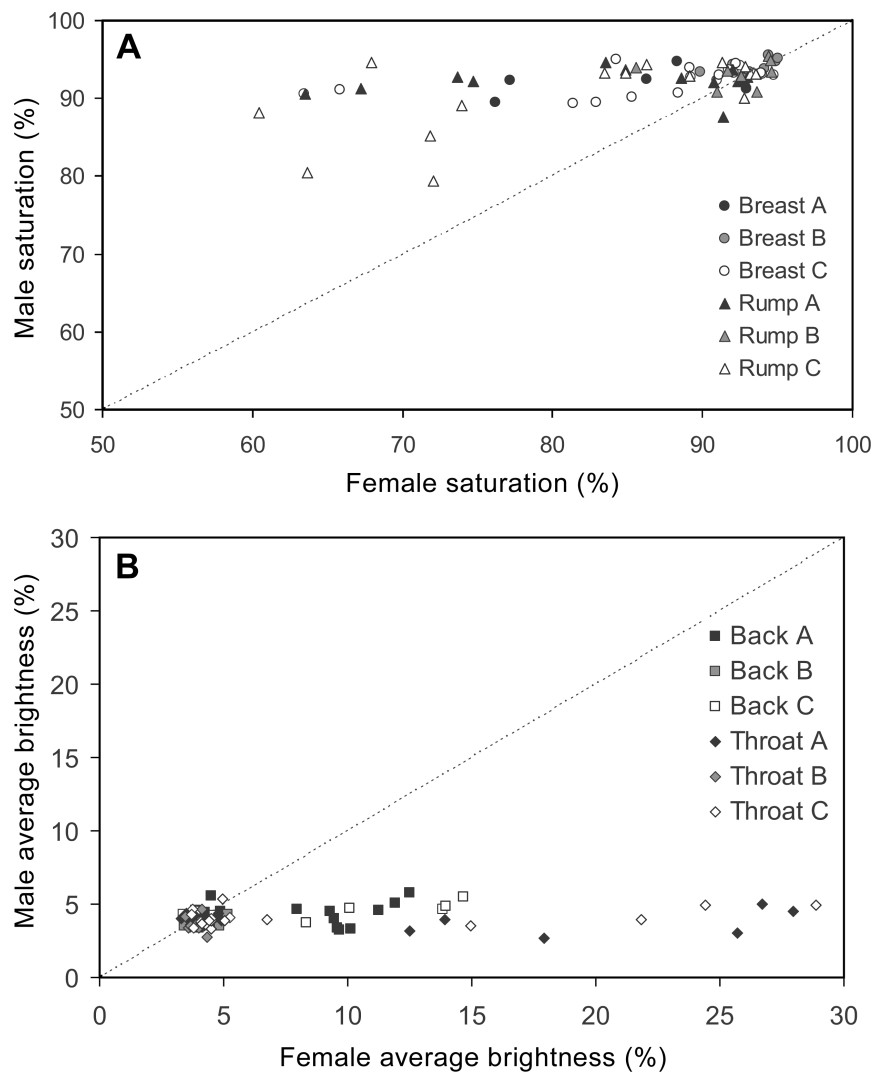


FIG. 1. Male vs. female color measurements. Males vary little in their (A) carotenoid saturation and (B) melanin achromatic brightness, whereas females vary considerably. The dotted line represents a 1:1 relationship. A, B, and C refer to the three major clades of orioles (Omland et al. 1999), showing that female elaboration varies widely both across and within clades. Note that the elaborate “male-like” state is to have high carotenoid saturation but low melanin brightness.

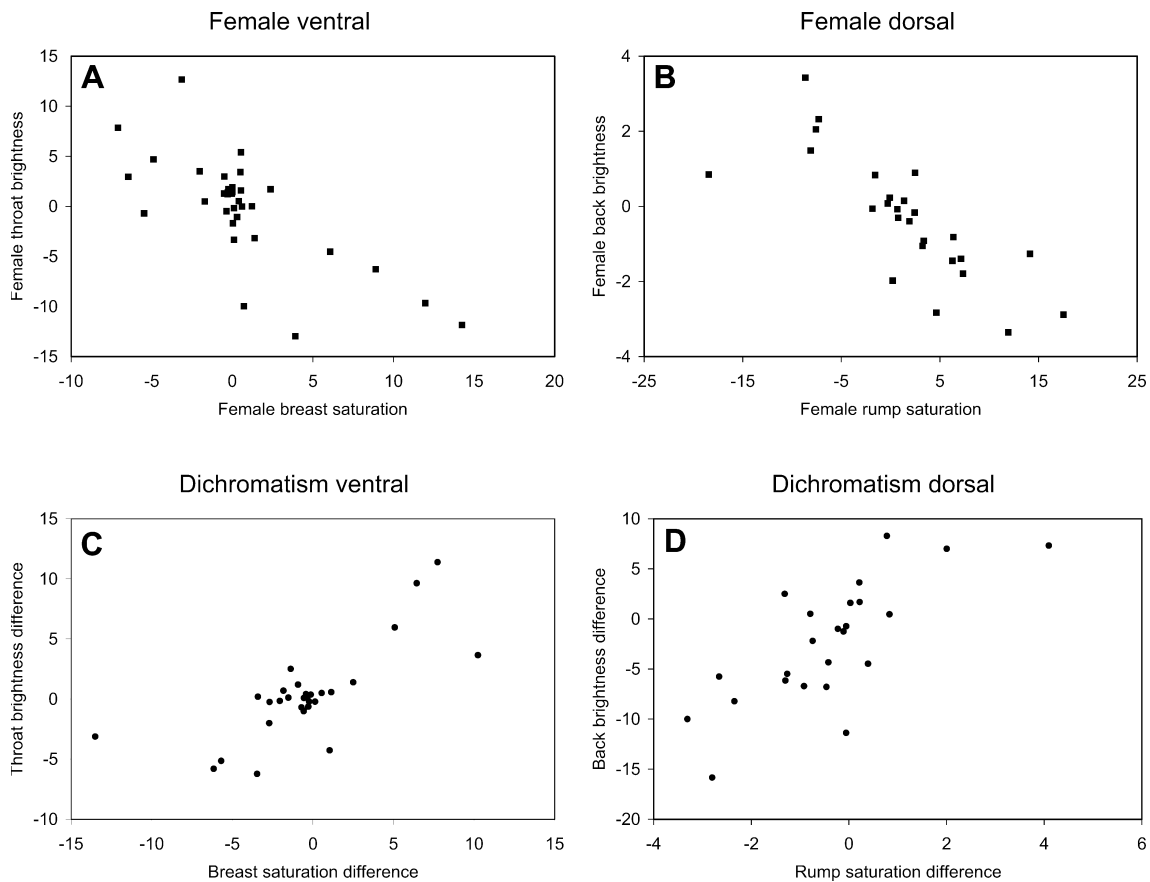


FIG. 2. Standardized independent contrasts corrected for phylogenetic relatedness of female melanin- vs. carotenoid-based plumage and sexual dichromatism in melanin- vs. carotenoid-based plumage. Throat achromatic brightness and breast saturation (A: ventral comparison) are strongly correlated, as are back achromatic brightness and rump saturation (B: dorsal comparison). As female carotenoid saturation increases, female achromatic brightness decreases, resulting in a more contrasting appearance. Differences between males and females in throat achromatic brightness and breast saturation (C) and in back achromatic brightness and rump saturation (D) are strongly correlated. As dichromatism in carotenoid-based plumage increases, so does dichromatism in melanin-based plumage.

significant correlations between body regions that had plumage produced by the same proximate mechanism. Within female orioles, there was a significant correlation between rump and breast carotenoid saturation, and throat and back achromatic brightness (Table 1). When we compared the differences between males and females for these same body regions, we found similar correlations (Table 1). These results were also supported by the more conservative sign test and did not change when branch lengths were scaled according to molecular divergence. Thus, sexual dichromatism within a pigment class does not appear to be restricted to one particular body region in orioles. Rather, when males and females differ in color in one body region, they are likely to differ at others that have color produced by the same pigment class.

Between pigment classes.—We found a significant relationship between changes in female carotenoid and melanin coloration. There was a significant negative correlation between female breast carotenoid saturation and throat eumelanin achromatic brightness (ventral color; Fig. 2A), as well as rump saturation and female back achromatic brightness (dorsal color; Fig. 2B). These

findings suggest that changes in female carotenoid saturation are correlated with changes in melanin brightness (Table 1).

When we compared the differences in carotenoid saturation between males and females with the differences in eumelanin achromatic brightness, there were also strong correlations (Fig. 2C, D and Table 1). The relationship between rump and back was unchanged when the more conservative sign test was used and when branches were scaled by molecular divergence. However, the more conservative sign test failed to find a significant relationship between the throat and breast, even though the Pearson correlation was highly significant (Table 1). This inconsistency may be attributable to the fact that the throat is the most discretely changing of all body regions. A dark throat patch is still present in several orioles that are “slightly dichromatic” but is absent in all orioles that are “strongly dichromatic” (Hofmann et al. 2008). When taken together, our overall findings indicate a strong correlation between differences in carotenoid saturation and melanin achromatic brightness between males and females.

DISCUSSION

Both carotenoid and melanin plumage elements contribute to sexual dichromatism in New World orioles, and evolutionary changes in the degree of dichromatism in carotenoid- and melanin-based plumage are correlated. Females that had more saturated carotenoid colors also tended to have darker-black melanin-based plumage, with the overall result being a highly contrasting, elaborate appearance (Fig. 2). Similarly, females that had less saturated carotenoid colors also tended to have lighter melanin-based plumage, in this case with the overall result being a less contrasting, drab appearance (Fig. 2). Thus, as the difference between male and female carotenoid saturation increased, so did the difference in melanin brightness. Comparing the magnitude of the difference between males and females provides a more direct and intuitive measure of the degree of dichromatism (although this dichromatism is clearly driven by—and dependent on—changes in females).

Our results suggest that evolutionary changes in carotenoid- and melanin-based plumage patches from different body regions are not independent. However, even though evolutionary changes in one body region may correlate with evolutionary changes in other body regions, distinct differences between body regions remain at the level of a single taxon. These differences justify treating body regions as separate characters when reconstructing ancestral states. Lumping these variable body regions together would create a composite character.

Our results differ from those of previous comparative studies that found a relationship between carotenoids—but not melanins—and sexual dichromatism. One intriguing explanation for the differences between these studies is that in New World orioles, strong sexual dichromatism appears to be gained through repeated losses of elaborate female plumage (see Hofmann et al. 2008). Thus, the evolutionary pathway leading to sexual dichromatism in orioles differs from the one traditionally assumed by sexual-selection theory (Martin and Badyaev 1996, Badyaev and Hill 2003, Andersson and Pärn 2006, Omland and Hofmann 2006). There is no strong *a-priori* reason to expect that similar correlations would be observed when dichromatism is generated via these two different evolutionary pathways. Rather, the opposite might be expected, given that these two different directions of change (gains of male vs. losses of female elaboration) are likely to be driven by different selective pressures. Increased male elaboration leading to sexual dichromatism is thought to be driven by increased strength of sexual selection (Andersson 1994). By contrast, it has been suggested that decreases in female elaboration may be driven by predation pressure and may facilitate rapid formation of pair bonds in migratory species with short breeding seasons (Badyaev and Hill 2003, Amundsen and Pärn 2006). In addition, reduced social selection pressure may also result in the loss of female elaboration (West-Eberhard 1983, Irwin 1994). Thus, our findings emphasize that different ultimate mechanisms are likely driving these different evolutionary pathways. Elucidation of these mechanisms presents interesting avenues for future research.

Alternatively, these differences between studies might be explained by the fact that we used rigorous quantitative measurements taken directly from museum specimens or by differences

in taxonomic level (within the genus *Icterus* vs. all extant carduline finches in one case, and across >70 genera from the entire avian lineage in another). They might also be explained by biological differences among the taxa studied—perhaps plumage color does not play the same role in oriole mate choice or social interactions (but see Enstrom 1993). However, at present, there are few studies that have rigorously reconstructed the evolution of sexual dimorphism among closely related species (Omland and Hofmann 2006). To our knowledge, the present study is the first to examine the contribution of carotenoids and melanins to sexual dichromatism in a group of birds where the direction of evolutionary change leading to dichromatism has been reconstructed. Because sexual dichromatism—in orioles and in many avian taxa—appears to be considerably labile (Price and Birch 1996, Omland 1997, Burns 1998, Hofmann et al. 2008), studies among closely related species that have well-resolved phylogenies are likely to be the most informative. Future studies in other genera with well-resolved phylogenies will provide interesting comparisons.

Our findings also emphasize that diverse examples of sexual dichromatism—or any characters that can arise from multiple evolutionary pathways—should not be lumped together in comparative studies (McLennan and Brooks 1993). For example, many previous studies have used sexual dimorphism as an index for the strength of sexual selection (e.g., Owens and Hartley 1998, Phillimore et al. 2006), implicitly assuming that increases in male elaboration have occurred. Yet when male elaboration is ancestral and decreased female elaboration leads to dichromatism, the degree of dichromatism is a poor predictor of male elaboration. Furthermore, other crucial differences may be present when dichromatism arises through these different pathways. However, when careful attention is paid to character coding and the direction of evolutionary change, studies using phylogenetically controlled comparative methods can provide important new insights.

Finally, our results suggest several interesting directions for future ecological and evolutionary studies. For example, how do different ecological or life-history traits contribute to carotenoid and melanin dichromatism in orioles? Is there anything unique about individuals that have particularly high degrees of carotenoid or melanin dichromatism (i.e., the residuals in Fig. 2)? Does the pattern of change exhibited by orioles hold true for other taxa that have lost elaboration? It would be particularly interesting to compare taxa where females have lost elaboration to ones where males have lost elaboration, as seen in some ducks and tanagers (Omland 1997, Burns 1998).

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