



EVOLUTION OF SEXUAL DICHROMATISM. 1. CONVERGENT LOSSES OF ELABORATE FEMALE COLORATION IN NEW WORLD ORIOLES (*ICTERUS* SPP.)

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ABSTRACT.—Studies of sexual dimorphism often focus on the evolution of elaborate male traits, whereas the evolution of elaborate females has been largely ignored. Yet a phylogenetic perspective suggests that changes in either male or female traits may lead to the evolution of sexual dimorphism. Furthermore, changes in the degree of sexual dichromatism can be caused by gains or losses of elaboration. One common form of elaboration found throughout the animal kingdom is the use of highly saturated and contrasting colors. To investigate further the evolution of female elaboration and sexual dichromatism, we took quantitative measurements of color from New World orioles (*Icterus* spp.) and then used ancestral-state reconstruction to infer evolutionary changes in male and female elaboration. Our findings suggest that male elaboration is ancestral and strongly conserved but that female elaboration has changed repeatedly, especially through the loss of saturation and contrast. Thus, changes in female—rather than male—color appear to lead to the evolution of sexual dichromatism in orioles. These repeated gains of strong sexual dichromatism through the loss of female elaboration were supported using multiple methods of character coding and reconstruction. Our phylogenetic results suggest that studies of sexual dichromatism cannot assume that color dimorphism arises through increased male elaboration. These findings have important implications for future studies investigating the ultimate causes of sexual dichromatism. Received 2 July 2007, accepted 5 February 2008.

Key words: ancestral-state reconstruction, color, *Icterus*, orioles, reflectance spectrometry, sexual dimorphism.

La Evolución del Dicromatismo Sexual. 1. Pérdidas Convergentes del Color Elaborado en las Hembras de Especies de *Icterus*

RESUMEN.—Los estudios de dimorfismo sexual frecuentemente se enfocan en la evolución de rasgos elaborados en los machos, mientras que la evolución de la coloración elaborada en las hembras ha sido en gran medida ignorada. Sin embargo, una perspectiva filogenética sugiere que los cambios en los rasgos masculinos o femeninos pueden conducir a la evolución de dimorfismo sexual. Además, los cambios en el nivel de dicromatismo pueden ser causados por la adquisición o la pérdida de rasgos elaborados. Un tipo común de rasgo elaborado encontrado por todo el reino animal es el uso de colores saturados y contrastantes. Para investigar más profundamente la evolución de rasgos elaborados en las hembras y el dicromatismo sexual, medimos cuantitativamente el color en varias especies de *Icterus* y luego usamos una reconstrucción de estados ancestrales para inferir cambios evolutivos del plumaje elaborado en machos y hembras. Nuestros resultados sugieren que el color del plumaje elaborado en los machos es ancestral y se mantiene altamente conservado, pero que en las hembras ha cambiado repetidamente, especialmente por la disminución de la saturación y el contraste. Por eso, son los cambios de la coloración femenina, y no de la masculina, los que parecen generar la evolución de dicromatismo sexual en *Icterus*. Estas adquisiciones repetidas de fuerte dicromatismo sexual por la pérdida de plumaje elaborado en las hembras fueron apoyadas por múltiples métodos de codificación de caracteres y de reconstrucción. Nuestros resultados filogenéticos sugieren que los estudios de dicromatismo sexual no pueden suponer que el dimorfismo de color surge por el aumento de rasgos elaborados en los machos. Estas conclusiones tienen implicaciones importantes para futuras investigaciones sobre las causas fundamentales del dicromatismo sexual.

DIMORPHISM IN COLOR, or sexual dichromatism, is a common form of sexual dimorphism that is found in many animals, including birds, fish, and lizards. The traditional explanation for the evolution of sexual dimorphism is that sexual selection leads to increased

male elaboration, whereas natural selection opposes this elaboration in females (Darwin 1871, Andersson 1994). Therefore, researchers often implicitly assume a dull ancestral species, with increases in male elaboration leading to sexual dimorphism (Fig. 1). In addition,

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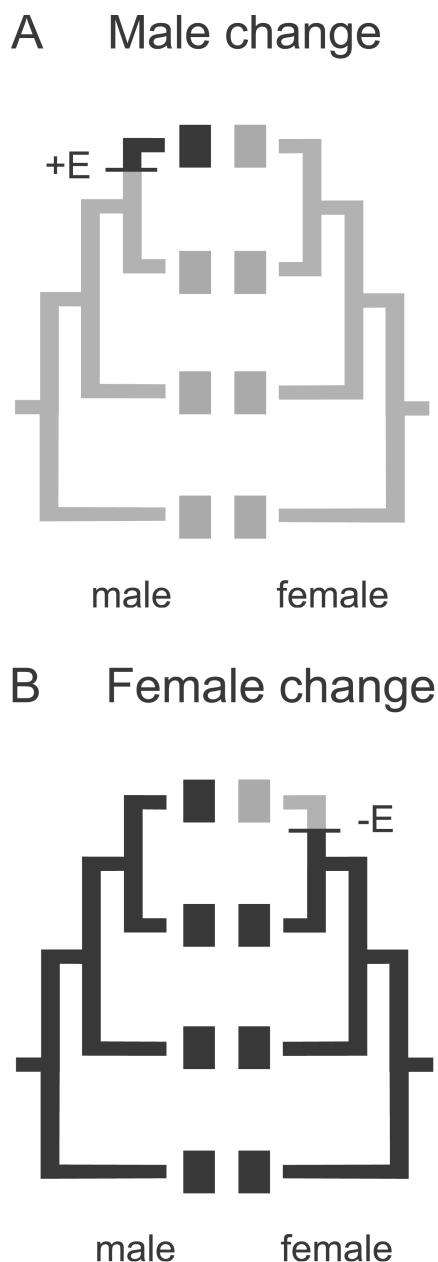


FIG. 1. Two different evolutionary pathways that can lead to sexual dichromatism. Either (A) a gain of male or (B) a loss of female elaboration can generate sexual dichromatism. Dull species are shown as gray, and elaborate species are shown as black. “+E” indicates a gain of elaboration, and “-E” indicates a loss (redrawn from Omland and Hofmann 2006).

researchers also often assume that species with greater degrees of sexual dimorphism have experienced stronger sexual selection than closely related monomorphic species (e.g., Barraclough et al. 1995, Owens and Hartley 1998).

However, there are many species, throughout the animal kingdom, in which male and female traits are equally elaborate (i.e., elaborate monomorphism; Amundsen 2000, Amundsen and Pärn 2006). Furthermore, a phylogenetic perspective suggests that

female elaboration may be ancestral (both sexes are monomorphic bright) and that a decrease in female elaboration—rather than an increase in male elaboration—may lead to sexual dichromatism (Fig. 1; Burns 1998, Wiens 2001, Omland and Hofmann 2006). Thus, sexual dichromatism is a composite character that can be generated through multiple independent pathways (McLennan and Brooks 1993, Coddington et al. 1997). From a dull ancestor, a gain in male elaboration may generate dichromatism. From an elaborate ancestor, a loss of female elaboration may also generate dichromatism (Fig. 1; Omland and Hofmann 2006). Alternatively, ancestral females may lack elaborate coloration, and subsequent gains of female elaboration may lead to sexual monomorphism (again with both sexes monomorphic bright; e.g., Irwin 1994, Burns 1998, Omland and Hofmann 2006). This complexity suggests that detailed phylogenetic studies are necessary to determine which pathway has led to dichromatism in a taxon of interest.

New World orioles (genus *Icterus*) are an ideal system for investigating the evolution of sexual dichromatism. All male orioles appear to have elaborate, highly contrasting plumage patterns that are produced predominantly by carotenoids and eumelanins (in a few orioles, phaeomelanins also produce color; Hofmann et al. 2007a, c). By contrast, female elaboration appears to vary considerably between species. These observations suggest that changes in female color have perhaps led to evolutionary changes in sexual dichromatism in orioles. New World orioles also vary considerably in their degree of sexual dichromatism. In some species, males and females appear to be sexually monochromatic and are indistinguishable to the human eye, whereas others are blatantly dichromatic (Fig. 2). Finally, New World orioles have a well-resolved molecular phylogeny that is supported by both mitochondrial DNA and nuclear introns (Omland et al. 1999, Allen and Omland 2003). This phylogeny has been used to investigate both male pattern (Omland and Lanyon 2000) and male color evolution in orioles (Hofmann et al. 2006, 2007a).

To investigate the evolution of female color and sexual dichromatism, we measured oriole coloration using a spectrometer and reconstructed changes in female color across the molecular phylogeny. We then compared our reconstructions of female color changes to similar reconstructions of male coloration. These methods allowed us to quantify differences between males and females and then reconstruct these measures of dichromatism directly, without creating a composite character. We hypothesized that orioles have evolved dichromatism through the loss of elaborate female coloration.

METHODS

Color scoring.—We measured adult female oriole specimens from the Smithsonian National Museum of Natural History, Delaware Museum of Natural History, and Field Museum of Natural History. Whenever sample size allowed, we measured five females from each of the 43 taxa for which phylogenetic branch-length information is available (Omland et al. 1999) and chose specimens that were in good condition (e.g., collected recently, preserved and stored properly). Many orioles have delayed plumage maturation, and the differences between adult and subadult plumage can be subtle in females, especially in species that lack elaborate plumage. Therefore, we used the presence of achromatic black plumage,

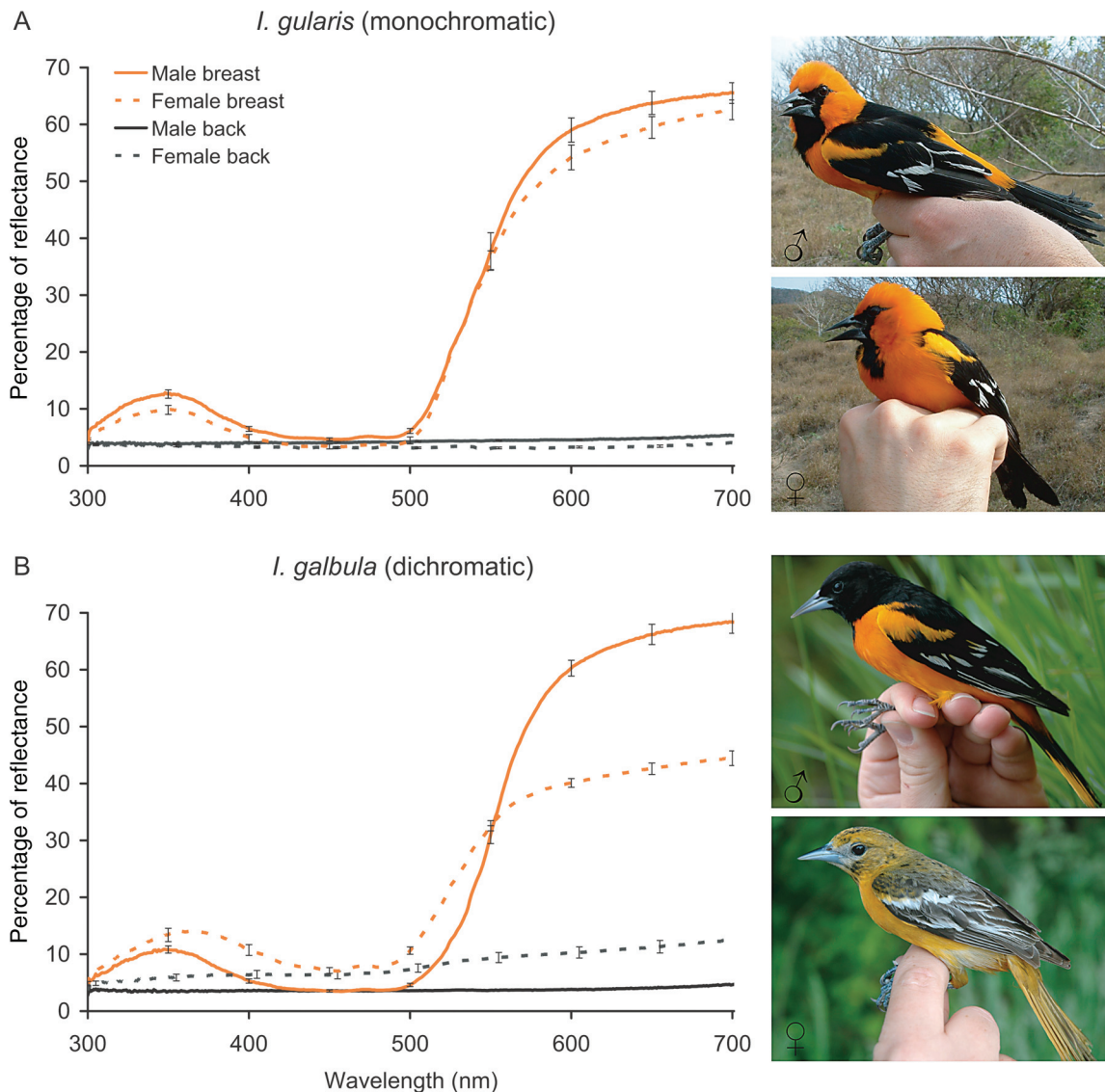


FIG. 2. Reflectance spectra and photographs from (A) monochromatic *Icterus gularis* and (B) dichromatic *I. galbula*. Monochromatic males and females are almost identical, both spectrally and visually, for carotenoid- and eumelanin-based plumage. Dichromatic species differ considerably, spectrally and visually, on both the back and the breast.

published descriptions of adult female coloration, molt limits, and the date of collection to exclude subadult females (Pyle 1997, Jaramillo and Burke 1999).

We measured the plumage of female orioles with an Ocean Optics (Dunedin, Florida) USB2000 spectrometer and a pulsed xenon light source following the same methods that we had used earlier to measure male coloration (Hofmann et al. 2006; also see Andersson and Prager 2006). Reflectance spectra were measured from 300 to 700 nm (near ultraviolet and visible regions) and were relative to a Spectralon (Labsphere, North Sutton, New Hampshire) diffuse white standard and the dark. Measurements were taken from seven different body regions: breast, belly, crown, rump, throat, back, and epaulet. All measurements were taken

in triplicate, perpendicular to the feather surface, and, whenever possible, from non-overlapping portions of each body region.

We derived two quantitative, colorimetric characters from reflectance spectra: spectral saturation and average brightness. Spectral saturation was used to describe chromatic (colorful yellow or orange) carotenoid-based plumage. Spectral saturation generally corresponds to the perception of color purity or chroma (e.g., pink vs. red) and was calculated as the difference between maximum and minimum reflectance in the visible region of the spectrum (400–700 nm). Average brightness was used to describe achromatic (black or dark brown), melanin-based plumage. Average brightness corresponds to the perception of lightness (e.g., black vs. gray) and was defined as the average reflectance across

the entire spectrum (300–700 nm; for detailed descriptions of these and other color attributes, see Andersson and Prager 2006, Montgomerie 2006). Our designation of “chromatic” versus “achromatic” for a given body region was based on the adult male plumage.

Ancestral-state reconstruction.—We reconstructed female saturation and achromatic brightness as continuous characters following methods described previously for reconstructing changes in male coloration (Hofmann et al. 2006; also see Omland and Hofmann 2006). We used the model-testing program COMET (Continuous-character Model Evaluation and Testing) to examine which model of evolution best fits our female colorimetric characters (Oakley et al. 2005, Lee et al. 2006). COMET uses maximum likelihood and Akaike’s information criterion (AIC) to determine which model of evolution best fits a character given a particular tree topology. COMET favored a punctuated model of evolution, which is best represented by linear parsimony, for both colorimetric variables (Oakley et al. 2005, Lee et al. 2006). Therefore, we reconstructed female saturation and achromatic brightness using linear parsimony in MESQUITE (Maddison and Maddison 2006). We then compared these reconstructions of female colorimetric characters with reconstructions of the same characters in males.

We also wanted to test whether our results were robust to different assumptions of character coding and reconstruction (Omland 1999, Hofmann et al. 2006, Omland and Hofmann 2006). We discretized the differences between males and females into three character states: strongly dichromatic, moderately to slightly dichromatic, and monochromatic. We examined our measurements for each body region and chose a break point based on the distribution of values (Price and Lanyon 2002). This approach carries its own assumptions, because in some body regions there appeared to be discrete differences (e.g., Fig. 3A, B), whereas in other body regions the change from slight and moderate dichromatism appeared to be continuous (e.g., Fig. 3C). We then used ordered parsimony, and unordered maximum likelihood (one parameter Markov k state; Schluter et al. 1997) in MESQUITE, to reconstruct changes in sexual dichromatism.

RESULTS

Carotenoid saturation.—Female orioles varied considerably in carotenoid saturation across species. In some taxa, female orioles had carotenoid-based plumage that was highly saturated and visually indistinguishable from that of males (e.g., Altamira Oriole, *I. gularis*; Fig. 2A). In other taxa, females had moderately saturated plumage, often with some variation across body regions. Females of a few taxa had extremely unsaturated carotenoid-based plumage (e.g., Baltimore Oriole, *I. galbula*; Fig. 2B). By contrast, males tended generally to have highly saturated carotenoid coloration (typically $\geq 90\%$; see Appendix). When we quantitatively compared male and female saturation, we found that the absolute saturation differences ranged from 0 to 37% (Appendix).

In both sexes, most oriole taxa had carotenoid-based (colorful) plumage on their breast, belly, and rump (32, 36, and 38 out of 43 taxa, respectively), and we focused our reconstructions of saturation on these body regions. Ancestral-state reconstruction suggested that there had been multiple evolutionary decreases—as

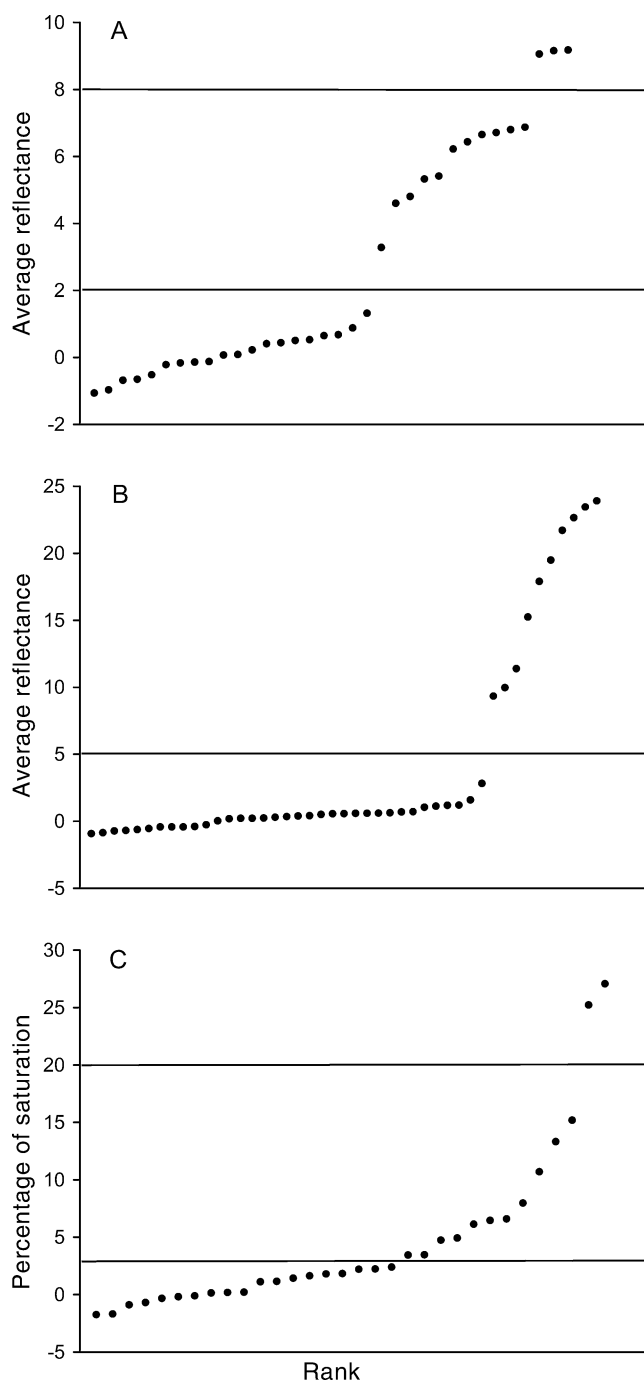


FIG. 3. Rank plots of (A) back and (B) throat achromatic brightness differences and (C) breast saturation differences for each taxon. Horizontal lines represent the cutoff points for the discrete character states. Although all the other choices of cutoff point were straightforward (data gaps), the lower cutoff for the breast was arbitrary.

well as a few increases—in female carotenoid saturation. Comparing the ancestral-state reconstructions of female saturation with reconstructions of male saturation in the same body regions suggested that changes in female saturation were responsible for

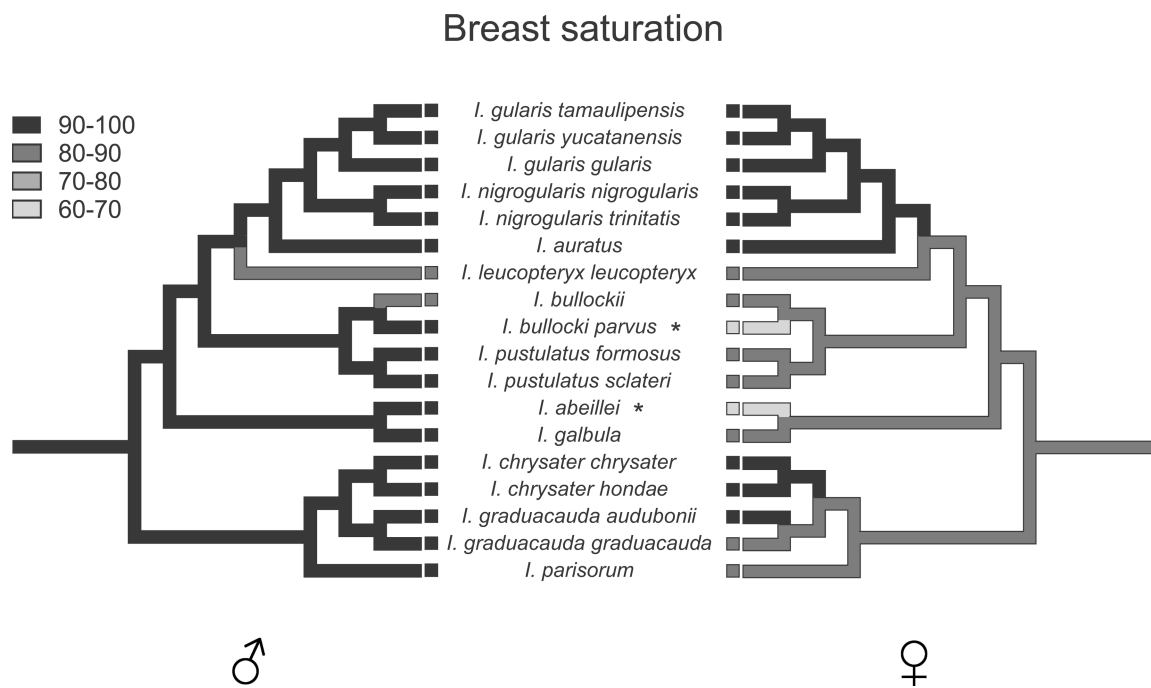


FIG. 4. Reconstruction of male and female breast saturation (%) for one (of three) major oriole clades. All males have highly saturated carotenoid coloration, and only changes in female saturation appear to lead to dimorphism. Two of the taxa that have evolved the strongest dichromatism in saturation are highlighted (*). Character states were reconstructed as continuous characters using linear parsimony and are discretized for illustrative purposes only. Phylogenetic relationships are from Omland et al. (1999).

generating dimorphism (Fig. 4). Because changes were occurring only in one sex, we were able to reconstruct differences in saturation between males and females for each body region without creating a composite character. These continuous reconstructions suggested that male and female saturation differed by approximately 5–10% (4.9–13.3%) in the ancestral oriole (Table 1). However, strong dimorphism in saturation appears to have arisen multiple times independently (Fig. 5).

Melanin achromatic brightness.—All male orioles had black or dark-brown achromatic plumage with low reflectance across their achromatic body regions (typically $\leq 5\%$). By contrast, female orioles varied considerably in achromatic brightness between species (Appendix). Thus, for achromatic plumage, the

elaborate state is less reflectance (dark achromatic plumage adjacent to saturated chromatic plumage creates a highly contrasting pattern). Some female orioles had melanin-based achromatic plumage that was just as dark (had equally low reflectance) as that of males (Fig. 2A). In other taxa, females had lighter (brownish) plumage, and females of a few taxa had grayish-white or unsaturated carotenoid plumage in the same regions where males had black plumage. When we quantitatively compared male and female achromatic brightness, we found that the differences in absolute brightness within taxa ranged from 0 to 24% (Appendix).

Most oriole taxa had achromatic (black) plumage on their backs and throats (34 and 43 out of 43 taxa, respectively), and

TABLE 1. Reconstructed ancestral values for colorimetric characters within males and females and the difference between males and females. Because both male and female spectral locations were changing, we did not reconstruct the difference between male and female spectral location.

	Achromatic brightness (percent reflectance)			Saturation (nm)			Spectral location (nm)	
	Male	Female	Difference	Male	Female	Difference	Male	Female
Breast	—	—	—	92.4	85.3–86.3	4.9–6.1	531	516–518
Rump	—	—	—	92.3–92.7	74.0–84.8	4.0–13.3	523–530	519–521
Belly	—	—	—	91.5–92.1	79.0–86.6	0.9–9.8	519–520	515–516
Crown	3.8–4.2	5.6	1.5–2.1	91.7–92	87.7–88.2	3.2–3.5	538–549	535–538
Throat	3.9	4.4–4.7	0.6–0.7	—	—	—	—	—
Back	4.0–4.7	9.5–10.1	5.3	—	—	—	—	—

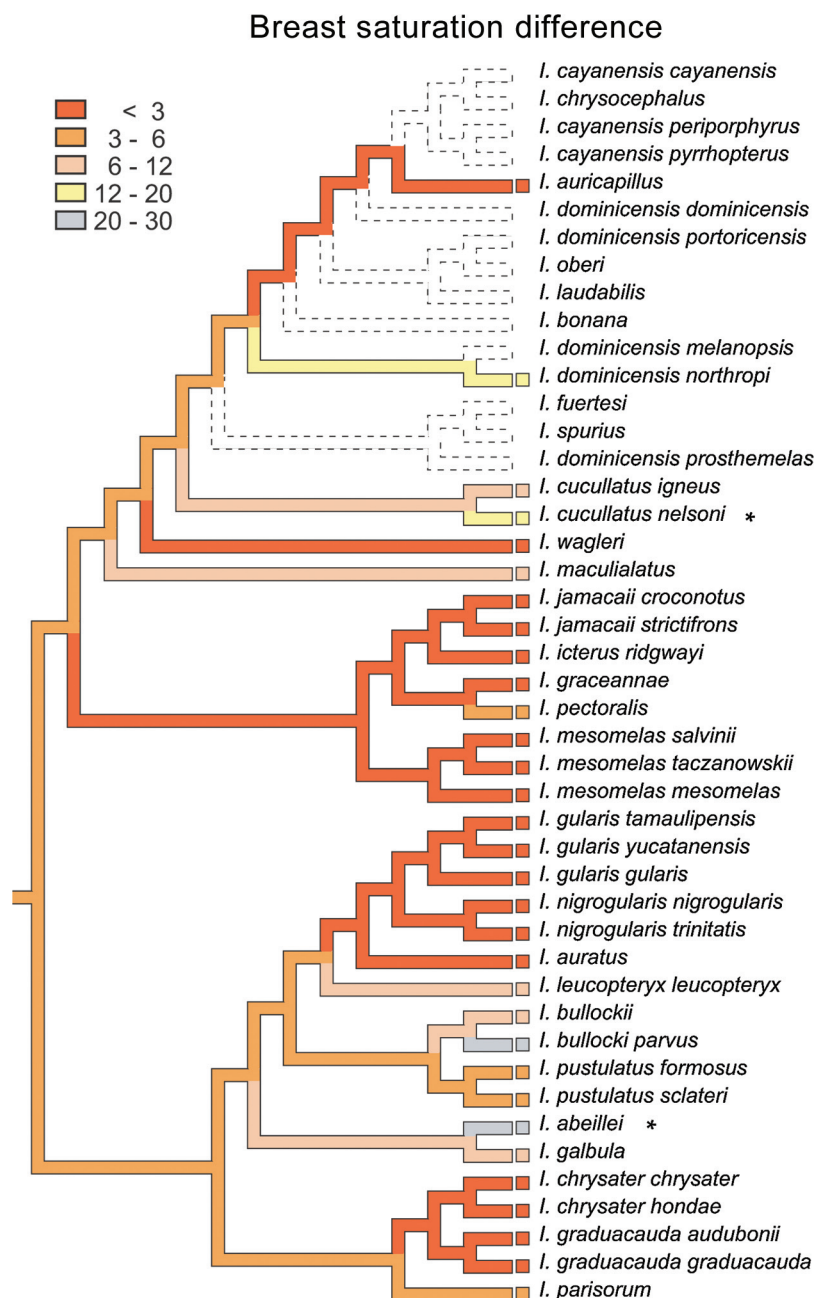


FIG. 5. Reconstruction of the difference between male and female breast saturation. Multiple increases and a few decreases in saturation dimorphism can be found throughout the phylogeny. Two examples of strong sexual dichromatism that have evolved in divergent lineages are marked (*). Difference values were obtained by subtracting the less-saturated females from the more-saturated males. Character states were reconstructed as continuous characters and are discretized for illustrative purposes only. When a range of values was possible, only the minimum values are shown. Dotted lines represent taxa that did not have carotenoid-based breasts in both males and females. Molecular phylogeny is from Omland et al. (1999).

we focused our reconstruction of average brightness on these two body regions. Ancestral-state reconstruction suggested that there had been multiple increases—as well as a few decreases—in female achromatic brightness. Comparing the ancestral-state reconstructions of the achromatic brightness of female throat and back with the reconstructions of male achromatic brightness in the same body regions suggested that changes in female

brightness were responsible for generating the differences between the sexes. As with saturation, changes occurred only in one sex, and we were able to reconstruct differences in male and female achromatic brightness for the throat and back. Our results suggested that in the ancestral oriole, male and female achromatic brightness differed by ~4.5% reflectance in the back and by <1% in the throat (Table 1). Once again, strong dimorphism in

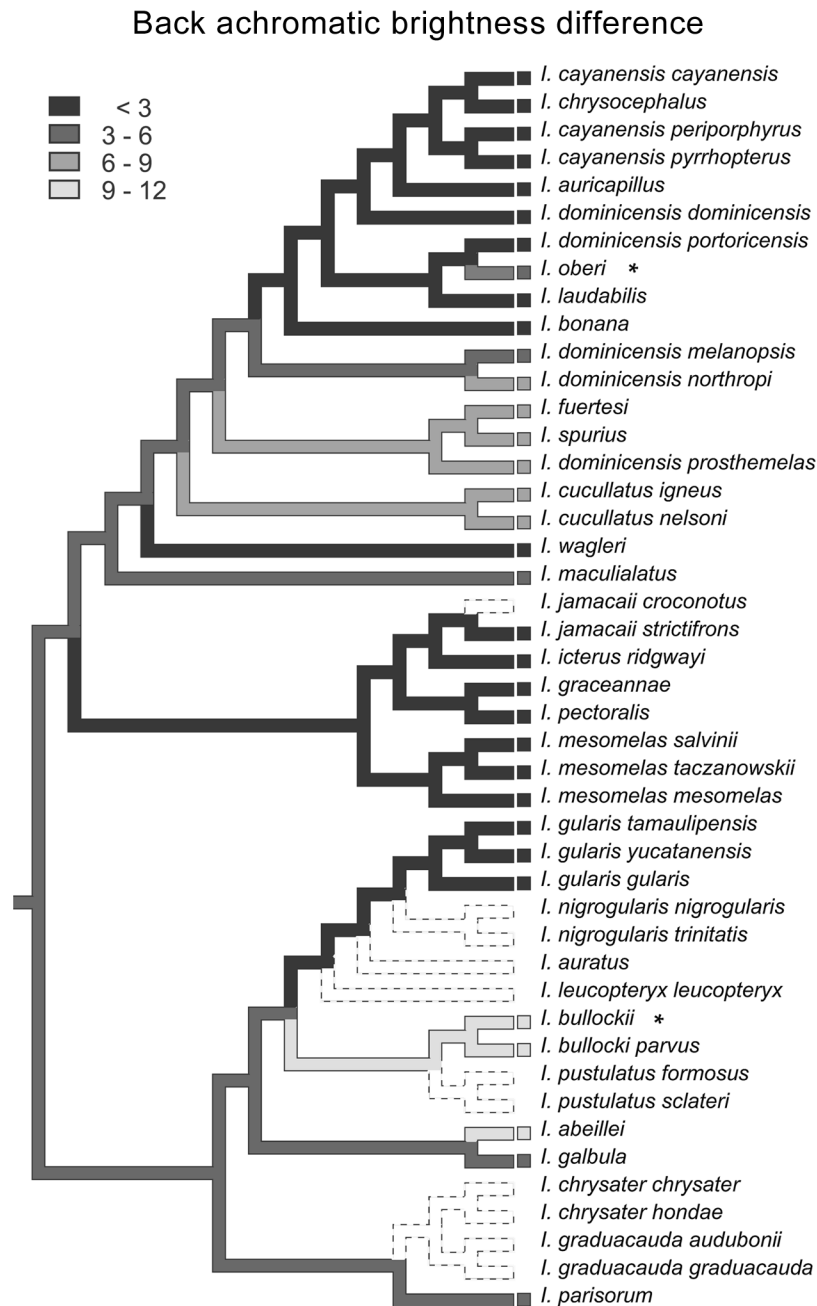


FIG. 6. Reconstruction of the difference between male and female back achromatic brightness as a continuous character. Multiple increases and a few decreases in achromatic brightness dimorphism can also be found throughout the phylogeny. Note that taxa in two clades appear to have evolved strong dichromatism; two of these species are highlighted (*). Differences were obtained by subtracting the darker (less reflective) males from the lighter (more reflective) females. See Figure 5 caption for methods of reconstruction.

achromatic brightness appears to have arisen multiple times independently (Fig. 6).

Discrete changes.—Our reconstructions of discrete chromatic and achromatic color characters also suggested that multiple independent gains of strong sexual dichromatism had occurred. Because the throat patch appeared to vary much more discretely (Fig. 3B), we reconstructed throat difference as a

binary character that was either dimorphic or elaborate monomorphic. Both maximum likelihood and ordered parsimony suggested that there were multiple gains of dimorphism in throat brightness (Fig. 7). The multistate reconstructions across other body regions varied in whether they favored a monochromatic or a moderately dichromatic ancestor. The breast maximum-likelihood reconstruction very slightly favored an ancestor with

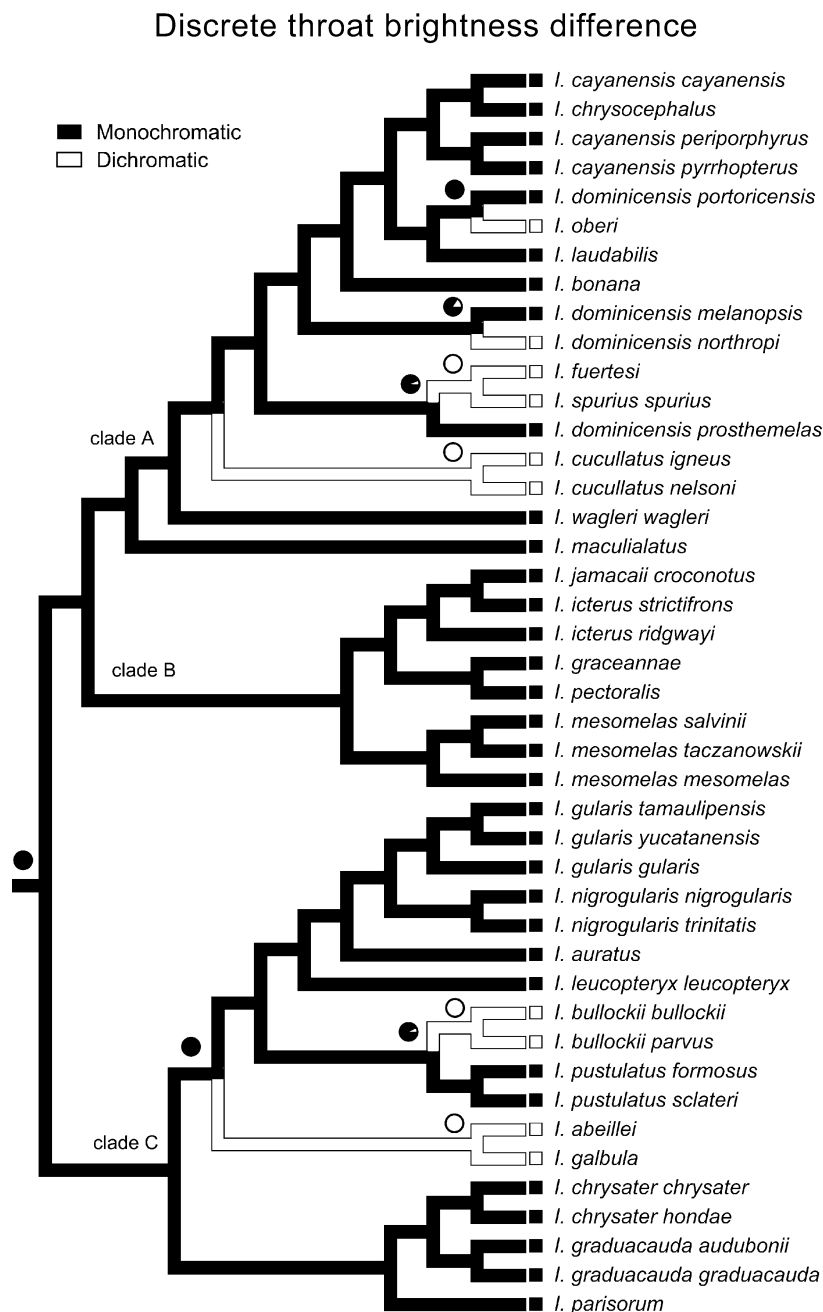


FIG. 7. Reconstruction of the difference between male and female throat achromatic brightness as a discrete binary character demonstrating that different methods of character coding and reconstruction support multiple gains of sexual dichromatism through the loss of female elaboration. Elaborate monomorphism is reconstructed as the ancestral state. Dichromatic throat coloration appears to have evolved as many as six times. Branch colors represent the most parsimonious reconstruction, and pie charts represent proportional likelihoods. Although not shown to scale, branch lengths from Omland et al. (1999) were included in the likelihood reconstructions.

moderate dimorphism in saturation (Table 2). However, both the rump-saturation and back-achromatic-brightness likelihood reconstructions favored monomorphism (Table 2). By contrast, all of the ordered-parsimony reconstructions favored a moderately dimorphic ancestor except for the rump, where moderate dimorphism and monomorphism were equally parsimonious (Table 2).

DISCUSSION

Our results demonstrate that changes in female—rather than male—coloration have led to the evolution of sexual dichromatism in New World orioles. We found multiple losses of female elaboration leading to independent gains of strong sexual dichromatism across multiple body regions. This dichromatism involved

TABLE 2. Proportional likelihood values and most-parsimonious ancestral states for discretized colorimetric characters. The three states were monochromatic (Mono), slightly or moderately dichromatic (Mod), and strongly dichromatic (Strong; see Fig. 3).

	Likelihood			Parsimony
	Mono	Mod	Strong	
Throat ^a	99.2	—	0.8	Mono
Back ^a	50.3	42.6	7.1	Mod
Breast ^b	42.5	54.3	3.2	Mod
Rump ^b	71.7	22.4	5.8	Mono/Mod ^c

^aAchromatic.

^bChromatic.

^cBoth states were equally parsimonious.

both chromatic (colorful) and achromatic (black) plumage (see Hofmann et al. [2008] for more detailed analyses). The repeated evolution of strong dichromatism because of changes in female coloration was supported by all the phylogenetic approaches that we used. Interestingly, although not as strongly supported, our reconstructions of quantitative color measurements suggested that the ancestral oriole may have been slightly dichromatic and that several independent increases in female elaboration may also have occurred (although the magnitudes of these changes are not as great as those when strong dichromatism is gained). Thus, to understand changes in dichromatism in orioles, and perhaps in many other taxa, it is important to measure, quantitatively, female as well as male coloration.

When we discretized our data to test the robustness of our findings to different methods of character coding and reconstruction, we obtained slightly different results. Maximum likelihood tended to favor a monomorphic ancestor, whereas ordered parsimony favored moderate dimorphism (differences that are most likely attributable to the assumption of ordered vs. unordered change; Cunningham et al. 1998, Omland 1999.) This ambiguity in the discrete ancestral-state reconstructions suggests that the inferred continuous ancestral state of slight dichromatism—and, thus, changes toward increased monochromatism—should be interpreted cautiously. Despite this caveat, we favor the continuous reconstructions because there appears to be relatively continuous variation in dichromatism—especially between monochromatic and slightly dichromatic taxa—for most body regions. In these cases, discretizing data will tend to overemphasize some changes and underemphasize others, because of the lumping of slightly to moderately dichromatic taxa into one of two character states (Hofmann et al. 2006). Regardless, all methods of reconstruction suggested that gains of strong sexual dichromatism, resulting from losses of female elaboration, had occurred multiple times.

A phylogenetic perspective suggests that both increases and decreases in female elaboration can occur (Omland and Hofmann 2006). Ancestrally elaborate females may lose their elaboration, and ancestrally drab females may gain elaborate coloration. In the former case, dichromatism increases, whereas in the latter, dichromatism decreases (provided that male elaboration remains constant). Several hypotheses have been proposed to explain evolutionary changes in female elaboration. Decreases

in female elaboration can result from ecological or environmental factors, especially predation, which may select for reduced elaboration in females of some species but not others (Wallace 1889, Wiens 1999, Badyaev and Hill 2003, Amundsen and Pärn 2006). Alternatively, sexual dichromatism may decrease male aggression or facilitate the formation of rapid pair bonds in migratory species with short breeding seasons (Hamilton 1961, Badyaev and Hill 2003). There are also several hypotheses to explain why increases in female elaboration may be favored. One is that sexual selection may act on both sexes—especially in species that form long-term pair bonds (e.g., Irwin 1994, Amundsen and Forsgren 2001). However, other social factors may also drive female elaboration—for example, females may play a role in territorial defense or compete for resources (West-Eberhard 1983, Badyaev and Hill 2003, Amundsen and Pärn 2006). Our ancestral-state reconstructions suggest that the evolution of dichromatism may be more complex than simply “gaining” or “losing” “dichromatism” or “monochromatism.” Thus, these different hypotheses need not be mutually exclusive. Rather, from a slightly to moderately dichromatic ancestor, selection may act to decrease female elaboration repeatedly in some taxa and to increase elaboration in others (but see the cautionary note in the previous paragraph).

Several recent studies that have used similar quantitative methods to score sexual dichromatism suggest that subtle color differences between the sexes are widespread across the avian lineage (e.g., Mennill et al. 2003, Mays et al. 2004, Eaton 2005, Hofmann et al. 2007b). Our finding that many orioles have slight sexual dichromatism in carotenoid- and melanin-based plumage, and that the ancestral oriole may have been slightly dichromatic, fits well in the context of these studies. Whether these subtle, but quantifiable, differences are biologically meaningful in orioles remains to be seen. However, many recent studies have documented the importance of subtle color differences in other taxa (e.g., Andersson et al. 1998, Hunt et al. 1998, Mennill et al. 2003, Doucet et al. 2005). In addition, the multiple changes toward both increased and decreased levels of dichromatism indirectly suggest that there may be important distinctions between slight and strong sexual dichromatism.

Finally, our results illustrate that the different pathways predicted by phylogenetic approaches are not simply theoretical; they may be found within many avian—and other animal—lineages (Coddington et al. 1997, Wiens 2001, Omland and Hofmann 2006). Our findings differ from the traditional paradigm that increased male elaboration leads to sexual dimorphism (Darwin 1871, Andersson 1994). They also differ from previous studies investigating the evolution of elaborate female traits (e.g., Irwin 1994), which suggested that monochromatism was gained from a dichromatic ancestor. Although the slight increases in female elaboration—and, thus, gains of strong monochromatism—that we observed agree with the results of those studies, the large decreases in female elaboration—resulting in multiple independent gains of strong sexual dichromatism—appear to be novel and present an interesting avenue for future research. Therefore, our results provide a basis for framing and testing hypotheses about the ecological and evolutionary forces, such as changes in breeding latitude or migratory behavior, that have driven the repeated gains and losses of plumage elaboration in disparate species.

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LITERATURE CITED

- ALLEN, E. S., AND K. E. OMLAND. 2003. Novel intron phylogeny supports plumage convergence in orioles (*Icterus*). *Auk* 120:961–969.
- AMUNDSEN, T. 2000. Why are female birds ornamented? *Trends in Ecology and Evolution* 15:149–155.
- AMUNDSEN, T., AND E. FORSGREN. 2001. Male mate choice selects for female coloration in a fish. *Proceedings of the National Academy of Sciences USA* 98:13155–13160.
- AMUNDSEN, T., AND H. PÄRN. 2006. Female coloration: Review of functional and nonfunctional hypotheses. Pages 280–345 in *Bird Coloration*, vol. 2: Function and Evolution (G. E. Hill and K. J. McGraw, Eds.). Harvard University Press, Cambridge, Massachusetts.
- ANDERSSON, M. 1994. *Sexual Selection*. Princeton University Press, Princeton, New Jersey.
- ANDERSSON, S., J. ÖRNBORG, AND M. ANDERSSON. 1998. Ultraviolet sexual dimorphism and assortative mating in Blue Tits. *Proceedings of the Royal Society of London, Series B* 265:445–450.
- ANDERSSON, S., AND M. PRAGER. 2006. Quantifying colors. Pages 41–89 in *Bird Coloration*, vol. 1: Mechanisms and Measurements (G. E. Hill and K. J. McGraw, Eds.). Harvard University Press, Cambridge, Massachusetts.
- BADYAEV, A. V., AND G. E. HILL. 2003. Avian sexual dichromatism in relation to phylogeny and ecology. *Annual Review of Ecology, Evolution, and Systematics* 34:27–49.
- BARRACLOUGH, T. G., P. H. HARVEY, AND S. NEE. 1995. Sexual selection and taxonomic diversity in passerine birds. *Proceedings of the Royal Society of London, Series B* 259:211–215.
- BURNS, K. J. 1998. A phylogenetic perspective on the evolution of sexual dichromatism in tanagers (Thraupidae): The role of female versus male plumage. *Evolution* 52:1219–1224.
- CODDINGTON, J. A., G. HORMIGA, AND N. SCHARFF. 1997. Giant female or dwarf male spiders? *Nature* 385:687–688.
- CUNNINGHAM, C. W., K. E. OMLAND, AND T. H. OAKLEY. 1998. Reconstructing ancestral character states: A critical reappraisal. *Trends in Ecology and Evolution* 13:361–366.
- DARWIN, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. John Murray, London.
- DOUCET, S. M., D. J. MENNILL, R. MONTGOMERIE, P. T. BOAG, AND L. M. RATCLIFFE. 2005. Achromatic plumage reflectance predicts reproductive success in male Black-capped Chickadees. *Behavioral Ecology* 16:218–222.
- EATON, M. D. 2005. Human vision fails to distinguish widespread sexual dichromatism among sexually “monochromatic” birds. *Proceedings of the National Academy of Sciences USA* 102:10942–10946.
- HAMILTON, T. H. 1961. On the functions and causes of sexual dimorphism in breeding plumage characters of North American species of warblers and orioles. *American Naturalist* 95:121–123.
- HOFMANN, C. M., T. W. CRONIN, AND K. E. OMLAND. 2006. Using spectral data to reconstruct evolutionary changes in coloration: Carotenoid color evolution in New World orioles. *Evolution* 60:1680–1691.
- HOFMANN, C. M., T. W. CRONIN, AND K. E. OMLAND. 2007a. Melanin coloration in New World orioles II: Ancestral state reconstruction reveals lability in the use of carotenoids and pheomelanins. *Journal of Avian Biology* 38:172–181.
- HOFMANN, C. M., T. W. CRONIN, AND K. E. OMLAND. 2008. Evolution of sexual dichromatism. 2. Carotenoids and melanins contribute to sexual dichromatism in New World orioles (*Icterus* spp.). *Auk* 125:790–795.
- HOFMANN, C. [M.], W.-S. LO, C.-T. YAO, AND S.-H. LI. 2007b. Cryptic sexual dichromatism occurs across multiple types of plumage in the Green-backed Tit *Parus monticolus*. *Ibis* 149:264–270.
- HOFMANN, C. M., K. J. MCGRAW, T. W. CRONIN, AND K. E. OMLAND. 2007c. Melanin coloration in New World orioles I: Carotenoid masking and pigment dichromatism in the orchard oriole complex. *Journal of Avian Biology* 38:163–171.
- HUNT, S., A. T. D. BENNETT, I. C. CUTHILL, AND R. GRIFFITHS. 1998. Blue Tits are ultraviolet tits. *Proceedings of the Royal Society of London, Series B* 265:451–455.
- IRWIN, R. E. 1994. The evolution of plumage dichromatism in the New World blackbirds: Social selection on female brightness? *American Naturalist* 144:890–907.
- JARAMILLO, A., AND P. BURKE. 1999. *New World Blackbirds: The Icterids*. Princeton University Press, Princeton, New Jersey.
- LEE, C., S. BLAY, A. Ø. MOOERS, A. SINGH, AND T. H. OAKLEY. 2006. CoMET: A MESQUITE package for comparing models of continuous character evolution on phylogenies. *Evolutionary Bioinformatics Online* 2:193–196.
- MADDISON, W. P., AND D. R. MADDISON. 2006. MESQUITE: A modular system for evolutionary analysis, version 1.2. Available at mesquiteproject.org.
- MAYS, H. L., JR., K. J. MCGRAW, G. RITCHISON, S. COOPER, V. RUSH, AND R. S. PARKER. 2004. Sexual dichromatism in the Yellow-breasted Chat *Icteria virens*: Spectrophotometric analysis and biochemical basis. *Journal of Avian Biology* 35:125–134.
- MCLENNAN, D. A., AND D. R. BROOKS. 1993. The phylogenetic component of cooperative breeding in perching birds: A commentary. *American Naturalist* 141:790–795.
- MENNILL, D. J., S. M. DOUCET, R. MONTGOMERIE, AND L. M. RATCLIFFE. 2003. Achromatic color variation in Black-capped Chickadees, *Parus atricapilla*: Black and white signals of sex and rank. *Behavioral Ecology and Sociobiology* 53:350–357.
- MONTGOMERIE, R. 2006. Analyzing colors. Pages 90–147 in *Bird Coloration*, vol. 1: Mechanisms and Measurements (G. E. Hill and K. J. McGraw, Eds.). Harvard University Press, Cambridge, Massachusetts.
- OAKLEY, T. H., Z. GU, E. ABOUHEIF, N. H. PATEL, AND W.-H. LI. 2005. Comparative methods for the analysis of gene-expression evolution: An example using yeast functional genomic data. *Molecular Biology and Evolution* 22:40–50.
- OMLAND, K. E. 1999. The assumptions and challenges of ancestral state reconstructions. *Systematic Biology* 48:604–611.
- OMLAND, K. E., AND C. M. HOFMANN. 2006. Adding color to the past: Ancestral-state reconstruction of coloration. Pages 417–454

- in Bird Coloration, vol. 2: Function and Evolution (G. E. Hill and K. J. McGraw, Eds.). Harvard University Press, Cambridge, Massachusetts.
- OMLAND, K. E., AND S. M. LANYON. 2000. Reconstructing plumage evolution in orioles (*Icterus*): Repeated convergence and reversal in patterns. *Evolution* 54:2119–2133.
- OMLAND, K. E., S. M. LANYON, AND S. J. FRITZ. 1999. A molecular phylogeny of the New World orioles (*Icterus*): The importance of dense taxon sampling. *Molecular Phylogenetics and Evolution* 12:224–239.
- OWENS, I. P. F., AND I. R. HARTLEY. 1998. Sexual dimorphism in birds: Why are there so many different forms of dimorphism? *Proceedings of the Royal Society of London, Series B* 265:397–407.
- PRICE, J. J., AND S. M. LANYON. 2002. Reconstructing the evolution of complex bird song in the oropendolas. *Evolution* 56:1514–1529.
- PYLE, P. 1997. Identification Guide to North American Birds, part I: Columbidae to Ploceidae. Slate Creek Press, Bolinas, California.
- SCHLUTER, D., T. PRICE, A. Ø. MOOERS, AND D. LUDWIG. 1997. Likelihood of ancestor states in adaptive radiation. *Evolution* 51:1699–1711.
- WALLACE, A. R. 1889. *Darwinism*. Macmillan, London.
- WEST-EBERHARD, M. J. 1983. Sexual selection, social competition, and speciation. *Quarterly Review of Biology* 58:155–183.
- WIENS, J. J. 1999. Phylogenetic evidence for multiple losses of a sexually selected character in phrynosomatid lizards. *Proceedings of the Royal Society of London, Series B* 266:1529–1535.
- WIENS, J. J. 2001. Widespread loss of sexually selected traits: How the peacock lost its spots. *Trends in Ecology and Evolution* 16:517–523.
- Associate Editor: D. B. McDonald

APPENDIX. Achromatic brightness and saturation values of male and female orioles (means \pm SE). Dashes indicate taxa that do not have the type of plumage for the measurement reported (e.g., a carotenoid back, or a eumelanin rump). Taxa with phaeomelanin-based plumage that were excluded from the chromatic color analyses are designated “P.”

	<i>n</i>	Brightness		Saturation		
		Back	Throat	Breast	Rump	Belly
		Males				
<i>Icterus abeillei</i>	5	4.7 ± 0.3	3.9 ± 0.1	91.1 ± 0.7	—	85.7 ± 1.3
<i>I. auratus</i>	5	—	4.1 ± 0.1	92.4 ± 0.7	93.2 ± 0.2	93.4 ± 0.3
<i>I. auricapillus</i>	5	4.2 ± 0.3	4.0 ± 0.3	91.2 ± 0.8	92.7 ± 0.9	92.1 ± 0.5
<i>I. bonana</i>	5	3.8 ± 0.3	3.5 ± 0.2	P	P	P
<i>I. bullockii</i>	5	4.9 ± 0.2	4.9 ± 0.3	89.4 ± 1.2	88.1 ± 1.5	89.3 ± 1.2
<i>I. bullockii parvus</i>	5	5.5 ± 0.5	4.9 ± 0.6	90.6 ± 1.3	84.8 ± 2.3	81.7 ± 5.9
<i>I. cayanensis cayanensis</i>	5	3.8 ± 0.3	3.4 ± 0.3	—	—	—
<i>I. cayanensis periporphyrus</i>	2	3.4 ± 0.2	3.5 ± 0.5	—	—	—
<i>I. cayanensis pyrrhopterus</i>	5	4.5 ± 0.3	4.0 ± 0.1	—	—	—
<i>I. chrysater chrysater</i>	5	—	3.4 ± 0.1	93.6 ± 0.3	92.8 ± 0.6	92.9 ± 0.3
<i>I. chrysater hondae</i>	3	—	3.6 ± 0.4	94.2 ± 0.9	94.6 ± 0.9	94.7 ± 0.5
<i>I. chryscephalus</i>	5	4.3 ± 0.1	3.8 ± 0.2	—	92.2 ± 0.6	—
<i>I. cucullatus igneus</i>	5	3.3 ± 0.1	2.7 ± 0.1	94.8 ± 0.1	94.6 ± 0.2	92.6 ± 0.4
<i>I. cucullatus nelsoni</i>	5	5.0 ± 0.7	4.5 ± 0.6	92.4 ± 1.0	90.6 ± 1.9	89.4 ± 1.0
<i>I. dominicensis dominicensis</i>	5	4.5 ± 0.4	4.3 ± 0.3	—	87.6 ± 2.8	87.0 ± 1.3
<i>I. dominicensis melanopsis</i>	5	4.5 ± 0.2	4.1 ± 0.2	—	93.6 ± 0.2	—
<i>I. dominicensis northropi</i>	2	4.6 ± 0.3	3.1 ± 0.0	89.5 ± 0.9	92.3 ± 1.0	90.8 ± 0.4
<i>I. dominicensis portoricensis</i>	5	4.6 ± 0.2	4.0 ± 0.2	—	93.6 ± 0.9	—
<i>I. dominicensis prothemelas</i>	5	3.2 ± 0.2	3.6 ± 0.2	—	92.6 ± 0.5	91.5 ± 0.7
<i>I. galbula</i>	5	3.7 ± 0.1	3.6 ± 0.2	95.0 ± 0.4	94.6 ± 0.5	93.9 ± 0.5
<i>I. graceannae</i>	5	3.8 ± 0.1	3.4 ± 0.2	93.8 ± 0.4	93.4 ± 0.4	92.0 ± 0.4
<i>I. graduacauda audubonii</i>	5	—	3.3 ± 0.1	93.0 ± 0.6	85.1 ± 2.7	92.9 ± 0.4
<i>I. graduacauda graduacauda</i>	5	—	3.9 ± 0.2	90.8 ± 1.1	80.5 ± 3.2	89.0 ± 1.0
<i>I. gularis gularis</i>	5	4.2 ± 0.2	5.3 ± 0.2	93.2 ± 0.5	93.2 ± 0.7	92.1 ± 1.1
<i>I. gularis tamaulipensis</i>	5	4.3 ± 0.1	4.7 ± 0.1	93.0 ± 0.4	93.1 ± 0.5	92.3 ± 0.4
<i>I. gularis yucatanensis</i>	5	4.5 ± 0.3	4.0 ± 0.2	93.1 ± 0.7	94.1 ± 0.2	94.1 ± 0.2
<i>I. icterus ridgwayi</i>	5	3.5 ± 0.1	3.5 ± 0.1	94.8 ± 0.5	95.4 ± 0.3	94.3 ± 0.3
<i>I. jamaicaii strictifrons</i>	4	3.5 ± 0.1	2.7 ± 0.2	94.3 ± 0.4	93.6 ± 1.3	94.3 ± 0.5
<i>I. jamaicaii croconotus</i>	5	—	3.4 ± 0.2	95.6 ± 0.4	94.9 ± 0.5	95.1 ± 0.5
<i>I. laudabilis</i>	5	3.5 ± 0.2	3.9 ± 0.2	—	92.1 ± 0.9	90.9 ± 0.9
<i>I. leucopteryx leucopteryx</i>	5	—	3.8 ± 0.6	89.5 ± 1.7	79.3 ± 1.7	87.9 ± 1.8
<i>I. maculialatus</i>	5	4.0 ± 0.4	3.9 ± 0.3	92.4 ± 0.6	92.7 ± 1.0	91.2 ± 0.6
<i>I. mesomelas mesomelas</i>	5	3.7 ± 0.3	4.1 ± 0.2	93.3 ± 0.2	90.9 ± 1.7	92.1 ± 0.4
<i>I. mesomelas salvinii</i>	5	4.3 ± 0.2	4.7 ± 0.2	92.6 ± 0.4	90.8 ± 1.4	92.0 ± 0.6
<i>I. mesomelas taczanowskii</i>	1	3.7	3.7	95.2	92.9	94.2
<i>I. nigrogularis nigrogularis</i>	5	—	4.3 ± 0.3	93.2 ± 0.6	93.2 ± 0.5	93.4 ± 0.3
<i>I. nigrogularis trinitatis</i>	1	—	3.7	94.4	90.1	92.0

(Continued)

APPENDIX. Continued.

	<i>n</i>	Brightness		Saturation		
		Back	Throat	Breast	Rump	Belly
Males						
<i>I. oberi</i>	5	4.7 ± 0.3	3.9 ± 0.2	—	91.2 ± 0.6	89.0 ± 1.3
<i>I. parisorum</i>	5	4.8 ± 0.4	3.9 ± 0.2	90.2 ± 0.8	89.1 ± 1.4	89.9 ± 0.2
<i>I. pectoralis pectoralis</i>	5	4.3 ± 0.1	3.7 ± 0.2	93.3 ± 0.6	94.0 ± 0.3	93.2 ± 0.7
<i>I. pustulatus formosus</i>	5	—	3.9 ± 0.4	92.7 ± 0.2	94.3 ± 0.2	92.1 ± 0.8
<i>I. pustulatus sclateri</i>	5	—	3.9 ± 0.2	93.9 ± 0.4	93.2 ± 1.0	92.9 ± 0.6
<i>I. spurius fuertesi</i>	5	5.8 ± 0.4	5.0 ± 0.5	P	P	P
<i>I. spurius</i>	5	3.4 ± 0.3	3.0 ± 0.3	P	P	P
<i>I. wagleri</i>	5	5.6 ± 0.2	4.4 ± 0.2	93.0 ± 0.4	92.1 ± 0.3	91.5 ± 0.8
Females						
<i>I. abeillei</i>	5	13.8 ± 2.4	21.8 ± 1.9	65.9 ± 7.4	—	—
<i>I. auratus</i>	5	—	5.3 ± 0.4	90.9 ± 1.5	83.5 ± 1.8	88.6 ± 1.4
<i>I. auricapillus</i>	5	4.0 ± 0.1	3.3 ± 0.2	92.9 ± 0.6	93.0 ± 0.2	91.6 ± 1.3
<i>I. bonana</i>	4	4.5 ± 0.2	4.2 ± 0.3	P	P	P
<i>I. bullockii</i>	5	13.9 ± 1.3	24.4 ± 3.7	81.4 ± 2.6	60.4 ± 7.5	52.0 ± 3.6
<i>I. bullockii parvus</i>	5	14.6 ± 0.5	28.9 ± 2.0	63.5 ± 2.5	—	—
<i>I. cayanensis cayanensis</i>	5	4.3 ± 0.6	3.6 ± 0.4	—	—	—
<i>I. cayanensis pyrrhopterus</i>	4	4.9 ± 0.6	4.8 ± 0.5	—	—	—
<i>I. chrysater chrysater</i>	5	—	3.8 ± 0.3	91.8 ± 0.7	89.1 ± 1.8	91.3 ± 0.8
<i>I. chrysater hondae</i>	5	—	4.3 ± 0.1	92.5 ± 0.4	91.3 ± 0.9	92.9 ± 0.5
<i>I. chrysocephalus</i>	3	4.1 ± 0.3	4.3 ± 0.2	—	92.8 ± 0.9	—
<i>I. cucullatus igneus</i>	3	10.1 ± 0.6	17.9 ± 0.9	88.3 ± 2.0	83.5 ± 1.6	86.6 ± 1.8
<i>I. cucullatus nelsoni</i>	5	11.9 ± 0.8	28 ± 2.6	77.2 ± 3.5	63.5 ± 3.7	70.7 ± 3.5
<i>I. dominicensis dominicensis</i>	5	4.2 ± 0.2	3.8 ± 0.2	—	91.4 ± 0.6	87.4 ± 0.7
<i>I. dominicensis melanopsis</i>	5	9.3 ± 0.3	4.7 ± 0.2	—	84.8 ± 1.2	—
<i>I. dominicensis northropi</i>	3	11.3 ± 0.6	12.5 ± 0.8	76.2 ± 2.8	74.7 ± 1.6	79.3 ± 1.9
<i>I. dominicensis portoricensis</i>	5	3.9 ± 0.1	3.6 ± 0.3	—	92.0 ± 1.4	85.9 ± 1.9
<i>I. dominicensis prosthemelas</i>	5	9.7 ± 1.5	3.7 ± 0.1	91.6 ± 0.2	88.6 ± 1.1	90.6 ± 0.8
<i>I. galbula</i>	5	8.3 ± 0.8	14.9 ± 1.8	84.3 ± 1.2	67.9 ± 8.1	70.3 ± 5.7
<i>I. graceannae</i>	2	4.0 ± 0.3	3.6 ± 1.3	94.1 ± 0.2	94.6 ± 0.8	91.8 ± 1.2
<i>I. graduacauda audubonii</i>	5	—	4.5 ± 0.1	91.1 ± 0.8	71.9 ± 5.6	90.5 ± 1.2
<i>I. graduacauda graduacauda</i>	5	—	4.5 ± 0.2	88.4 ± 1.2	63.6 ± 7.0	85.9 ± 3.1
<i>I. gularis gularis</i>	4	4.6 ± 0.2	5.0 ± 0.3	92.1 ± 0.3	93.5 ± 0.5	90.8 ± 1.8
<i>I. gularis tamaulipensis</i>	5	3.4 ± 0.2	3.8 ± 0.2	94.7 ± 0.6	93.2 ± 0.6	93.6 ± 0.4
<i>I. gularis yucatanensis</i>	5	3.9 ± 0.2	4.5 ± 0.4	94.0 ± 0.4	92.9 ± 0.8	92.3 ± 1.0
<i>I. icterus ridgwayi</i>	5	3.4 ± 0	3.7 ± 0.1	94.9 ± 0.2	94.4 ± 0.5	93.8 ± 0.5
<i>I. jamacaii strictifrons</i>	3	4.9 ± 0.7	4.3 ± 0.7	92.0 ± 1.8	91.7 ± 0.5	91.4 ± 0.9
<i>I. jamacaii croconotus</i>	5	—	4.0 ± 0.3	94.4 ± 0.5	94.5 ± 0.5	94.0 ± 0.6
<i>I. laudabilis</i>	4	3.6 ± 0.2	3.6 ± 0.3	—	92.4 ± 0.6	90.2 ± 0.5
<i>I. leucopteryx leucopteryx</i>	2	—	4.1 ± 0.3	82.9 ± 3.0	72.1 ± 5.8	78.1 ± 2.0
<i>I. maculialatus</i>	2	9.5 ± 0.2	4.9 ± 0.7	86.3 ± 0.9	73.7 ± 0.8	83.2 ± 4.3
<i>I. mesomelas mesomelas</i>	5	3.7 ± 0.2	3.4 ± 0.1	93.1 ± 0.6	91.0 ± 1.5	92.3 ± 1.0
<i>I. mesomelas salvinii</i>	5	3.8 ± 0.1	4.1 ± 0.2	92.7 ± 0.3	93.7 ± 0.2	92.4 ± 0.4
<i>I. mesomelas taczanowskii</i>	2	4.2 ± 0.0	4.1 ± 0.4	95.1 ± 0.3	92.6 ± 0.6	92.0 ± 0.1
<i>I. nigrogularis nigrogularis</i>	5	—	3.7 ± 0.2	93.9 ± 0.7	93.5 ± 0.5	94.0 ± 0.3
<i>I. nigrogularis trinitatis</i>	1	—	4.1	92.2	92.8	89.4
<i>I. oberi</i>	4	8.0 ± 0.3	13.9 ± 1.4	80.4 ± 1.4	67.2 ± 1.5	79.3 ± 1.3
<i>I. parisorum</i>	4	9.3	3.4	85.3 ± 0.6	74.0 ± 1.4	79.0 ± 1.0
<i>I. pectoralis pectoralis</i>	5	5.2 ± 0.5	4.3 ± 0.1	89.9 ± 0.8	85.6 ± 1.6	87.0 ± 1.3
<i>I. pustulatus formosus</i>	5	—	6.8 ± 1.0	89.2 ± 1.2	86.3 ± 2.4	86.0 ± 2.1
<i>I. pustulatus sclateri</i>	3	—	5.0 ± 0.2	89.2 ± 1.2	84.9 ± 3.4	87.6 ± 2.0
<i>I. spurius fuertesi</i>	5	12.5 ± 1.4	26.7 ± 2.4	65.8 ± 7.2	54.1 ± 7.1	64.7 ± 4.4
<i>I. spurius</i>	5	9.6 ± 0.2	25.7 ± 1.7	79.9 ± 1.2	64.8 ± 1.5	74.3 ± 2.3
<i>I. wagleri</i>	5	4.5 ± 0.1	3.5 ± 0.2	92.8 ± 0.5	90.8 ± 1.2	91.8 ± 0.8