

CORRELATED EVOLUTION OF MIGRATION AND SEXUAL DICHROMATISM IN THE NEW WORLD ORIOLES (*ICTERUS*)

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The evolution of sexual dimorphism has long been attributed to sexual selection, specifically as it would drive repeated gains of elaborate male traits. In contrast to this pattern, New World oriole species all exhibit elaborate male plumage, and the repeated gains of sexual dichromatism observed in the genus are due to losses of female elaboration. Interestingly, most sexually dichromatic orioles belong to migratory or temperate-breeding clades. Using character scoring and ancestral state reconstructions from two recent studies in *Icterus*, we tested a hypothesis of correlated evolution between migration and sexual dichromatism. We employed two discrete phylogenetic comparative approaches: the concentrated changes test and Pagel's discrete likelihood test. Our results show that the evolution of these traits is significantly correlated (CCT: uncorrected $P < 0.05$; ML: LRT = 12.470, $P < 0.005$). Indeed, our best model of character evolution suggests that gains of sexual dichromatism are 23 times more likely to occur in migratory taxa. This study demonstrates that a life-history trait with no direct relationship with sexual selection has a strong influence on the evolution of sexual dichromatism. We recommend that researchers further investigate the role of selection on elaborate female traits in the evolution of sexual dimorphism.

KEY WORDS: Bird coloration, comparative method, female ornaments, sexual dimorphism, sexual selection.

Darwin's *Descent of Man and Selection in Relation to Sex* (1871) is filled with descriptions of the many cases of sexual dimorphism, and their relevance to his concept of sexual selection. Over the past three decades, understanding the causes of these phenomena has been a major goal in the study of evolution. Most of the research in this field has taken a microevolutionary perspective, and focused on understanding why elaborate male ornaments have been favored by sexual selection (reviewed in Andersson 1994). Such a research program implicitly assumes that dimorphic species have evolved from a cryptic monomorphic ancestor. However,

considering this issue from a phylogenetic perspective provides several possible historic pathways that can lead to the gain or loss of sexual dimorphism (Omland and Hofmann 2006, their figure 10.8).

Avian genera that inhabit both temperate and tropical zones provide a unique opportunity to investigate the gain and loss of sexual color dimorphism (dichromatism). In many groups, there is a tendency for tropical-breeding resident species to be monochromatic and temperate-breeding migratory species to be dichromatic (Hamilton 1961; Price and Birch 1996). In these birds, tropical

species often have elaborate coloration in both females and males (monochromatic elaborate), whereas temperate species tend to have cryptically colored females and elaborately colored males (dichromatic). Such patterns are found in a range of taxa including warblers (Parulidae), tanagers (Thraupidae), and blackbirds (Icteridae) (Hamilton 1961).

Dichromatism has been gained or lost repeatedly in many avian groups (Mayr 1963; Price and Birch 1996; Omland 1997; Burns 1998a,b; Amundsen 2000). Repeated gain and loss of sexually dimorphic ornaments has also been reported in many other taxa (reviewed in Wiens 2001), including swordtail fish (*Xiphophorus*, Basolo 1990; Wiens and Morris 1996) and *Sceloporus* lizards (Wiens 1999; Wiens et al. 1999). However, more work is needed to understand the causes of these gains and losses, especially by focusing on previously neglected elaborate female traits.

The genus *Icterus* is ideally suited to studying evolutionary changes in sexual dichromatism. *Icterus* is the most species-rich genus in the blackbird family (Icteridae) and includes a mix of dichromatic and monochromatic species (although all species are socially monogamous; Jaramillo and Burke 1999). Recent studies by Hofmann et al. (2008a,b) describe and reconstruct the evolution of plumage differences between male and female orioles in *Icterus*. Changes in female rather than male elaboration are responsible for many of the transitions between sexual monochromatism and dichromatism during avian evolution.

An earlier study (Irwin 1994) of plumage evolution in *Icteridae* also observed that most occurrences of sexual dichromatism in this clade were due to losses of female elaboration, and found such losses to be correlated with changes in mating system. However, that study was based on a sparse and uneven sampling of the blackbird family. In contrast, studies of the complete oriole genus provide a robust and unbiased set of taxa with which to test hypotheses about evolution. Moreover, as all New World orioles share a socially monogamous mating system (Jaramillo and Burke 1999), the striking variation in their extent of sexual dichromatism eludes conventional explanations.

In orioles, as in many other bird genera, the migratory temperate-breeding species are frequently dichromatic, whereas the sedentary tropical-breeding species are generally monochromatic (Jaramillo and Burke 1999). Males in all *Icterus* species have elaborate coloration (Omland and Lanyon 2000; Hofmann et al. 2006, 2007, 2008a). Although the apparent correlation between migration and sexual dichromatism seems strong (Hamilton 1961; Hamilton and Barth 1962), this correlation has never been tested using comparative methods to correct for phylogenetic history. Differences in migratory behavior (and breeding latitude) are likely to be correlated with differences in social behavior, which could result in different selection pressures on female coloration. Tropical-breeding, sedentary species tend to stay near

breeding sites year-round, so both males and females may participate in and benefit from territorial establishment and defense (see Stutchbury and Morton 2001). Year-round territoriality is supported by observations of tropical Icterids (Whittingham et al. 1992), and color-banded orioles remaining paired and on territory during the nonbreeding season (*I. pustulatus*; Murphy et al. 2009). Female territoriality may lead to selection for elaborate female plumage (Trail 1990; Whittingham et al. 1992; Murphy et al. 2009). In contrast, males of migratory species generally arrive first on the breeding grounds, and defend their territories from conspecific males. In this context, there may be relaxed selection for elaborate female plumage, or increased selection for cryptic plumage due to predation on the female or the nest (Martin and Badyaev 1996). Elaborate female traits are being studied increasingly in a wide range of taxa, but reasons for the gain and loss of these colors and ornaments are still poorly understood (reviewed in Amundsen and Pärn 2006). Our study represents the first attempt to test adaptive hypotheses concerning migratory behavior's influence on elaborate signal traits using a phylogenetic perspective.

Methods

CHARACTER SCORING

We used character data from two recent studies of oriole evolution: Kondo and Omland's (2007) work reconstructing migratory behavior, and Hofmann et al.'s (2008a,b) quantitative color measurements. For the purposes of our research, we define migration as the presence of any seasonal movement between a breeding and wintering range (Kondo and Omland 2007). However, we acknowledge that migration as a phenomenon represents a suite of characteristics (e.g., Zink 2002), not all of which have been measured for the taxa used in this study. We considered migration simply as a binary character whose presence or absence on a branch might influence the evolution of other characters. Kondo and Omland (2007) used published migration distances and range maps to reconstruct the evolution of migration in this manner (Fig. 1), and it is their binary scoring and reconstruction that we used in our study.

We used two methods to determine whether taxa were sexually monochromatic or dichromatic. The first was a single female character, throat brightness, which appeared to vary discretely and was correlated with other measures of dichromatism (Hofmann et al. 2008a,b; Figure S1). The second used data from the appendix of Hofmann et al. (2008a) to derive by cluster analysis composite characters describing overall female elaboration and the degree of sexual dichromatism (Figures S2 and S3). All characters are based on reflectance spectra that spanned the full avian visual range, including the UV (300–400 nm) and visible (400–700 nm) regions. All taxa were consistently assigned to a character state

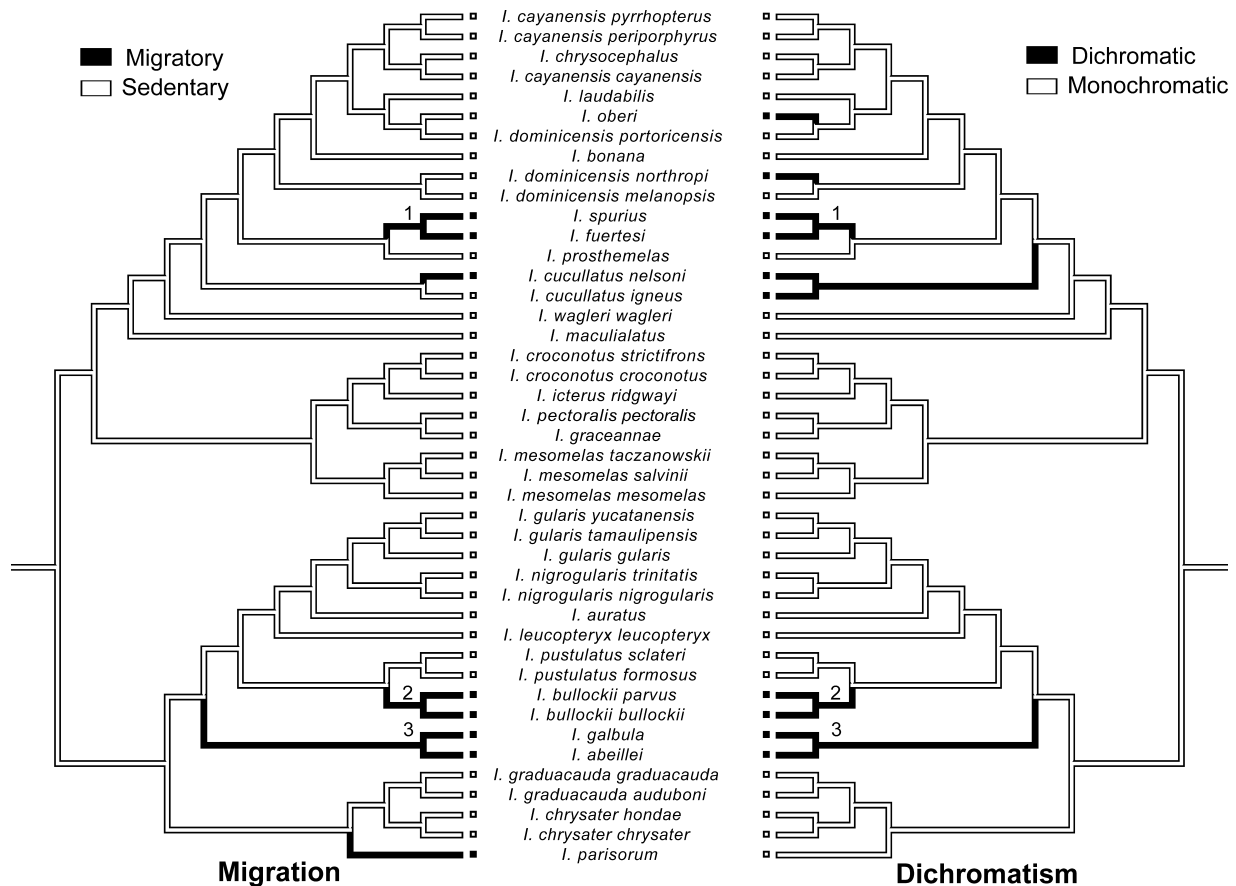


Figure 1. Ancestral state reconstruction of migration (left, from Kondo and Omland 2007) and sexual dichromatism (right, female throat brightness from Hofmann et al. 2008a). All states were reconstructed unambiguously using simple parsimony, and concordance was observed with maximum likelihood reconstructions. Changes in dichromatism reflect changes in female elaboration, as males of all oriole species are elaborate (Hofmann et al. 2008a). Taxon names follow Clements (2007).

across these methods, with the exception of two (*I. cucullatus igneus* and *I. dominicensis melanops*; see Figures S1–S3). Both the previous studies of migration and dichromatism used Omland et al.'s (1999) well-supported phylogeny of the New World orioles. This tree is also supported by data from multiple nuclear introns (Allen and Omland 2003; F. Jacobsen and K. Omland, unpublished data).

PHYLOGENETIC COMPARATIVE METHODS

The concentrated changes test (CCT; Maddison 1990) is a parsimony-based comparative method that is used to test associations between characters as they are gained or lost on a phylogeny (e.g., Johnson 1999; Johnson and Lanyon 2000).

When trees are symmetrical in topology and unbiased in their set of included taxa, this has been shown to be a statistically robust approach (Lorch and Eadie 1999). We performed a CCT in MacClade 4.0 (Maddison and Maddison 2000) using migration as the independent character. Our phylogeny included too many taxa to allow an exact count of possible patterns of gains and losses, so these were estimated from 10^7 simulations.

We also used Pagel's (1994) discrete method to test models of independent and dependent evolution between migration and dichromatism. This maximum likelihood (ML) method provides the unique opportunity to study evolutionary pathways through the estimation of transition rates between pairs of binary character states, and has been used successfully to this end (e.g., Hibbet and Donoghue 2001). We employed the analysis as implemented in *Mesquite* (Pagel 1994; Maddison and Maddison 2009) with 100 ML replicates over at least 1000 repeated simulations, and using branch lengths corrected using the HKY model of sequence evolution as in Hofmann et al. (2008a) (see Omland et al. 1999).

Results

Of the six independent losses of female elaboration observed in *Icterus* (in each case a gain of dichromatism; Hofmann et al. 2008a,b), three of these occur concurrently with gains of migration (see labeled nodes in Fig. 1). Using this evolutionary pattern, the concentrated changes test showed a significant association between these two characters (uncorrected $P < 0.05$). Significant

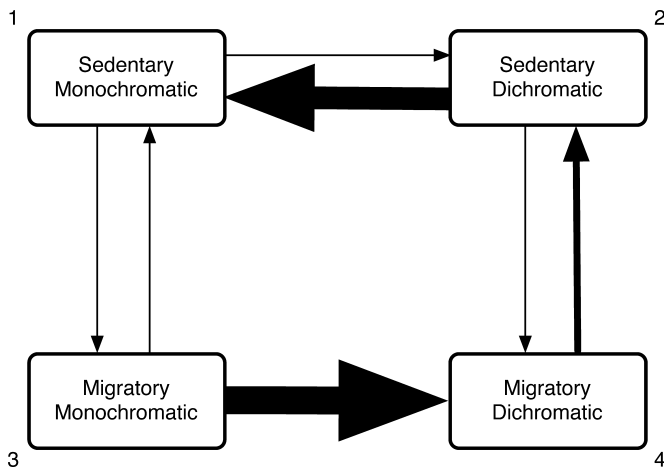


Figure 2. Illustration of the best-fitting model generated by Pagel's discrete method. Arrow widths indicate relative transition rates between pairs of character states. The rate of transition from state 1 to state 2 (q_{12}) is 8.09; $q_{13} = 7.41$, $q_{21} = 160.36$, $q_{24} = 2.85$, $q_{31} = 0.76$, $q_{34} = 189.87$, $q_{42} = 40.06$, $q_{43} = 0.00$.

associations were also observed between migration and both overall female elaboration (uncorrected $P < 0.005$; See Figure S2) and overall dichromatism (uncorrected $P < 0.05$; See Figure S3).

The discrete model test reported a greater $-\log$ likelihood for the best dependent model than that for the independent model (likelihood ratio test = 12.468, $P < 0.005$). This indicates strong evidence in favor of a hypothesis of correlated evolution between migration and dichromatism in the New World orioles. The best model generated (Fig. 2; log likelihood = -25.398) strongly suggests migration as the independent character, supporting a scenario in which changes in migration influenced changes in dichromatism. The rate parameter describing the probability of gaining dichromatism on any branch was far greater in migratory taxa ($q_{34} = 189.87$) than in sedentary taxa ($q_{12} = 8.09$). Models favored in analyses of overall plumage characteristics exhibited similar patterns (female elaboration: LRT = 15.134, $P < 0.001$; dichromatism: LRT = 13.928, $P < 0.005$).

Discussion

Both comparative approaches and all methods used to score dichromatism in this study showed a significant correlation between the evolution of migration and of sexual dichromatism. This relationship has previously been hypothesized (Hamilton 1961; Hamilton and Barth 1962), but has not been tested using phylogenetic comparative methods until now. The best model generated by the ML method indicates that dichromatism is 23 times more likely to be gained in migratory taxa than in sedentary ones (Fig. 2). This finding suggests that the evolution of sexual dichromatism in the New World orioles has largely been contingent on the evolution of migration. Because changes in dichromatism are

the result of losses of female elaboration, our results imply that elaborate female plumage may be adaptive in sedentary species, and/or maladaptive in migratory species.

Female plumage elaboration need not be maintained by selection, as genetic correlation with male traits or phyletic inertia could also maintain this trait (Amundsen 2000). However, our observation of repeated losses of female elaboration in migratory clades suggests that selection can mold this trait in at least one context. Several functional hypotheses have been proposed to explain the presence of elaborate female coloration (reviewed in Amundsen 2000; Amundsen and Pärn 2006), including sexual selection (e.g., mutual choice) or social selection (e.g., female aggression/territoriality; West-Eberhard 1983). Female territory defense may provide an explanation for maintenance of female elaboration in sedentary orioles. A recent field study of *I. pustulatus* demonstrated that females play a crucial role in territorial defense, and experimental manipulation indicated a strong role for color in territoriality (Murphy et al. 2009). Indeed, species accounts have reported that several other sedentary oriole taxa exhibit female territory defense (*I. bonana* and *I. wagleri*; Jaramillo and Burke 1999). Another characteristic of female territoriality, female song, is lost concurrently with nearly every loss of female plumage elaboration in *Icterus* (Price et al. 2009). These findings suggest that either social selection or sexual selection may be acting on both traits in a similar fashion. Female elaboration could also be maintained by sexual selection through mutual mate choice. Year-round pairing has been observed in several oriole species (*I. chrysater*, *I. nigrogularis*, *I. gularis*, and *I. wagleri*; Jaramillo and Burke 1999), a possible source of selection for mutual mate choice (Trail 1990; Whittingham et al. 1992; Murphy et al. 2009). These selection pressures could be reduced or absent in migratory species, and/or increased predation in migratory species may cause natural selection against female elaboration.

As an interesting exception to the pattern we observed, the endangered Montserrat oriole (*I. oberi*) represents a Caribbean island population that is clearly sedentary but exhibits strong sexual dichromatism (Jaramillo and Burke 1999; Hofmann et al. 2008a). Furthermore, some orioles display intermediate degrees of migration or sexual dichromatism (e.g., *I. parisorum* and *I. cucullatus igneus*, respectively). As our approach used discrete binary character scoring, we were not able to incorporate this more subtle variation into our analyses. However, when we used two additional characters derived from overall plumage coloration that differed in how these taxa were scored, our results remained significant. Thus, we emphasize that the correlation we observed is significant *despite* these exceptions and intermediate cases, which should have biased our methods against observing such a correlation. Future case studies investigating the behavioral ecology of intermediate and outlier taxa would likely reveal much about the selection pressures influencing sexual dichromatism.

Furthermore, future studies should assess color from an avian visual perspective (see Cuthill 2006; Hastad and Odeen 2008).

The correlation we observe in orioles suggests an alternative scenario to be tested in other cases of sexual dimorphism: that ornaments are gained in both sexes by sexual or social selection, then lost in females by natural selection. This scenario contrasts with the conventional assumption that sexual dimorphism arises due to sexual selection on males. As all oriole species are reported to be socially monogamous, we consider the hypothesis that the mating system drives the evolution of sexual dimorphism (Emlen and Oring 1977; Irwin 1994; Dunn et al. 2001) to be inconsistent with our results. This hypothesis predicts that extra-pair matings or polygyny should increase male elaboration, but it is not sufficient to explain repeated losses of female elaboration.

Our findings show that a life-history trait with no direct relationship with sexual selection has a strong influence on the evolution of sexual dichromatism due to changes in female elaboration. Therefore, we caution researchers against using measures of sexual dichromatism as an index of sexual selection (e.g., Barrowclough et al. 1995; Nadeau et al. 2007), for we consider our findings an example of how selection on female elaboration might confound such an assumption. We urge researchers to investigate the behavioral functions of female ornaments and coloration, so that the evolutionary distinction between sexually dichromatic, elaborate monochromatic, and cryptic monochromatic species becomes more apparent.

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Supporting Information

The following supporting information is available for this article:

Figure S1. Rank plot female throat brightness (Hofmann et al. 2008a).

Figure S2. Analysis of female elaboration using average saturation (across carotenoid-colored body regions) and average brightness (across eumelanin-colored body regions).

Figure S3. Analysis of sexual dichromatism using male–female difference in average saturation (across carotenoid-colored body regions) and difference in average brightness (across eumelanin-colored body regions).

Table S1. Characters and characters states for each of the three measures of dichromatism.

Supporting Information may be found in the online version of this article.

(This link will take you to the article abstract).

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