

EVOLUTION OF COLORFUL DISPLAY

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How the displays of bowerbirds have evolved has attracted widespread interest. Endler et al. (2005) analyzed color use in display in a subset of bowerbird species and generalized their results to all bowerbirds. Here we discuss problems with their analysis that calls into question their conclusions. For example, they state that bowerbirds do not use decorations that match their background, but this is not supported by their results. They reconstruct historical patterns of sexual dimorphism in plumage display using questionable methodology. The high lability of these display traits makes these reconstructions unreliable and, using accepted methods and acknowledging the lability problem, we were unable to support their conclusions. Their claim that plumage differences between sympatric species are due to character displacement is not supported by the available data. Their focus is on visual contrast as the cause for display color and we offer additional hypotheses that may contribute to explaining color use. We support studies of spectral analysis of display traits but urge greater care in using this information to reach conclusions about how colorful displays have evolved.

KEY WORDS: Character displacement, character-state reconstruction, mate recognition, rapid evolution, sexual selection.

Bowerbirds are widely known for their multifaceted sexual displays including a bower, bower decorations, and dancing and vocal elements. They have become an important model for the study of how multiple components are integrated into a complex sexual display (e.g., Patricelli et al. 2004). Endler et al. (2005) provide a highly detailed analysis of color patterns of plumage and bower decorations for bowerbird species. They measure color spectra to test the hypothesis that plumage and decoration colors of bowerbirds have evolved as signals that visually contrast with their background. They also claim that male plumage had diverged in sympatry with other bowerbird species and that they "... observed character displacement ..." (p. 1795) that enables species recognition. Using phylogenetic information they assign bowerbird species to groups representing "stages" in the evolution of plumage color and decoration use based on the number of nodes between a lineage and the base of their tree. They report that "least derived" species showed no sexual dimorphism in plumage, "intermediate derived" species evolved a high level of plumage dimorphism, and "most derived" species show a loss of dimorphism, and use this to suggest a sequence of stages of trait evolution. Endler et al. (2005) state that "... the data and the phy-

logeny suggest the following sequence of events: (1) increase of contrast under sexual selection; (2) onset of increased predation pressure with increased conspicuousness; (3) evolution of dimorphism to reduce predation on females; (4) transfer of conspicuousness to bower ornaments; and (5) reduction of conspicuous plumage components to parts of the males used in displays and consequent reduction of sexual plumage dimorphism" (p. 1814).

We question whether the methodology and analysis of Endler et al. (2005) can support these major conclusions. Their proposed sequence of stages of trait evolution in bowerbirds conflicts with evidence showing rapid change in bowerbird displays, including reversals. Their analysis relies on information on plumage and decorations from only a subset of bowerbird species (40%) from two different major clades. Their explanations for why these stages occur are often unclear, and commonly they do not consider relevant alternative hypotheses. Their claim that visual contrast with background has been the basis for selecting bower decorations is inconsistent with their results showing that color spectra of decorations used on bowers often match their background (their fig. 4). Male plumage is suggested to show character displacement, but there is no difference in plumage between allopatric and sympatric

populations of species in which character displacement is claimed to occur. We elaborate on these concerns below.

Recent evidence from bowerbirds (Kusmierski et al. 1997; Uy and Borgia 2000; Borgia and Coleman 2000) and other species with nonresource based mating systems (e.g., Prum 1997; Sturmbauer et al. 1996; Omland and Lanyon 2000; Wiens 2001) show rapid evolution of display traits at the tips of the phylogeny. Large differences in character states between sister groups suggest high lability of displays both within and between lineages. This lability limits effective character state reconstruction because it adds to uncertainty in resolving earlier evolved character states (Kusmierski et al. 1997). While noting the occurrence of this rapid evolution, Endler et al. (2005) do not use it to inform their analysis. Their method of ancestor character state reconstruction and proposed stages in bowerbird evolution requires that, once species diverge from sister groups, their displays remain relatively unchanged, which is unlikely if there is rapid display trait evolution. With rapid trait evolution the available historical information on trait phenotypes is too limited to confidently test hypotheses about character state changes that have occurred between the time that a lineage diverged from other bowerbirds and the present. For example, Endler et al. (2005) claim to have identified transference of conspicuousness from plumage traits to bower decorations at a particular stage (4) in bowerbird evolution, but the information available from currently existing phenotypes is insufficient to show if there were multiple transfers of conspicuousness from plumage to decorations, or transfers in the opposite direction as might be expected with highly labile trait evolution. We do not know if past gains in bower decorations were contemporaneous with loss of plumage elaboration as expected under the transference hypothesis (Gilliard 1969), or if these changes occurred as temporally separate events. Also, because our ability to accurately reconstruct past character states is limited we do not know if male plumage preceding the hypothesized transference was conspicuously bright and suited to be transferred. Thus, both the method of reconstruction and the information on which it is based are inadequate to show if a transfer of display occurred or is limited to a particular stage in bowerbird evolution.

Models of ancestor trait reconstruction emphasize the need for inclusion of as many species as possible (Cunningham et al. 1998; Losos 1999), but their reconstruction includes information from only eight of 20 bowerbird species. The qualitative information they (Endler et al. 2005) use for describing display traits defining stages of bowerbird evolution (e.g., sexual dimorphism) does not depend on spectral measurements and is available for all bowerbird species (e.g., Gilliard 1969; Forshaw and Cooper 1977; Frith and Frith 2004). In some cases, information from these missing species does not support their key conclusions. For example, they suggest that the last stage (5) in bowerbird evolution involves a “reduction of conspicuous plumage components to parts of the

males used in displays . . .” (p. 1814). However, among the excluded *Amblyornis* bowerbirds, limitation of plumage coloration to head crests occurs in both the early diverged streaked bowerbirds and in Macgregor’s bowerbird that occupies an intermediate position in their phylogeny; there is an absence of crests in the last diverged Vogelkop bowerbirds. In the *Chlamydera* species, whose relatives are in the “most derived” grouping, two species (fawn [an included species] and yellow breasted [excluded]) do not have colorful head crests, and two other excluded species (western and yellow breasted) have bright yellow breast plumage. Also, there is no pattern of restriction of plumage coloration among the *Sericulus* bowerbirds in which all four species are brightly colored over their bodies. Among *Sericulus*, there also is no clear pattern of change in plumage related to time of divergence that would support their hypothesis. Applying their hypotheses across a more complete set of species does not provide consistent support for their proposed sequence of stages of display trait evolution in bowerbirds. Additionally, for most bowerbird species there is little information on the extent to which particular conspicuous plumage elements function in courtship display, so it is unclear how Endler et al. (2005) could, for example, determine if the conspicuous breast plumage of some *Chlamydera* species is used in sexual display or for some other function.

Their method of character state reconstruction and the associated stages of bowerbird trait evolution that they propose raise several additional issues. First, Endler et al. (2005) mix species from different clades and, as a result, their sequence does not reflect the actual evolutionary history of the bowerbirds. All but two of the bower building species in their sequence are members of the avenue building bowerbird clade. The golden bowerbirds are unambiguously members of the other major (maypole) clade in all recent bowerbird reconstructions including the one of Endler et al. (2005) (their fig. 2). A reanalysis of their data places Toothbilled bowerbirds (TBBBs) in the maypole building clade (see below). Mixing of species from different clades to produce a common sequence of stages of bowerbird display evolution might be tenable if it could be shown that similar evolutionary patterns have occurred in both major clades. Their sample of two species from the maypole clade is too small to test this assumption and the examples we present (e.g., patterns of crest development in *Amblyornis* discussed above) suggest that there are different patterns of display trait evolution in the maypole and avenue building clades. Because some species from these clades appear to have evolved in different environments (e.g., the genus *Chlamydera* has the only arid zone bowerbird species) with different backgrounds, the hypothesis that Endler et al. (2005) favor, that display traits evolve to contrast with backgrounds, supports the suggestion that there should be different patterns of display coloration in each clade. This does not support the mixing of species of different clades for this analysis, nor justify making conclusions

about trait evolution in all bowerbirds using their limited set of species.

Second, their placement of TBBBs as the only member of the “least derived” stage of Endler et al. (2005) is critical for their proposed sequence of trait evolution. When we reconstructed their dataset and performed a more thorough analysis our results do not support placement of this species with the majority of other species in their analysis that belong to the avenue building clade. As they point out, their placement of this species at the base of the avenue building clade only has weak support (63% bootstrap value) in their mt-DNA based phylogenetic analysis. This differs from other recent molecular phylogenies that use more reliable parsimony and maximum likelihood approaches (Kusmierski et al. 1997) that place TBBBs with the maypole builders. We reconstructed the dataset of Endler et al. (2005) in a similar manner using CLUSTALW and performed a more thorough phylogenetic analysis. We estimated models of nucleotide substitution under AIC in Modeltest version 3.6 (Posada and Crandall 1998). The most likely tree, from 10 random starts, was found through a heuristic search using PAUP* v4.0b10 (Altevec) (Swofford 2001). A likelihood bootstrap value of 74 was obtained from 500 replicates with data replacement supporting the TBBBs as the basal maypole builder. More convincingly, a Bayesian analysis using MrBayes version 3.0 (Ronquist and Heulsenbeck 2003) showed a 99% posterior probability of the TBBBs as the basal maypole builders. This placement of TBBBs with maypole building bowerbirds suggests that they are not ancestors of most of the species in the analysis of Endler et al. (2005). Moreover, the very unique display behavior of the dull monomorphic TBBBs may be derived (see Borgia 1995a and below) and thus may not accurately represent the ancestral condition of court clearing bowerbirds as suggested by their analysis.

Third, the analysis of Endler et al. (2005) does not consider character states at nearby nodes as is typical of more standard trait reconstruction methods (e.g., Schluter et al. 1998; Maddison and Maddison 2005). This is important because averaging trait values across nearby nodes reduces the impact of rapid evolutionary change in a single species on the predicted ancestor's character states. The discussion of Endler et al. (2005) of early display trait evolution relies heavily on the display traits of a single species (TBBB) to represent their least derived category. We reconstructed ancestral character states for dimorphism and plumage brightness mapped onto their phylogeny (with TBBBs placed in the maypole building clade following the results from above) using the program MESQUITE version 1.4 (Maddison and Maddison 2004). A species scored 0 for monomorphism and a 1 for dimorphism. The program, using a likelihood reconstruction criterion, estimated an intermediate value of 0.54 at the node that joins the TBBB lineage to the other maypole builders, and 0.75 at the node that joins the two clades of bower builders. For plumage

brightness (0 for dull and 1 for bright) the likelihood estimate was 0.42 at the node joining the TBBB lineage with the other maypole builders and 0.58 at the node joining the two clades of bower builders. Although recognizing the important limitations of these reconstructions (Cunningham et al. 1998; Losos 1999), particularly when there has been rapid trait evolution, these estimates suggest a weak bias toward dimorphism and bright plumage at the time of the split of the two major clades of bower building bowerbirds. Thus, the hypothesis that the least derived bower building bowerbirds had dull plumage is less definitive than suggested by Endler et al. (2005) and the proposed series of trait changes they suggest across stages of bowerbird evolution may not be correct.

Fourth, Endler et al. (2005) use the trait, sexual dimorphism, to define stages of bowerbird evolution and then argue that these different stages show differing patterns of dimorphism. They separate evolutionary stages in bowerbirds by the “degree of derivation and the switches to and from sexual dimorphism” (p. 1797). Endler et al. (2005) then claim that sexual monomorphism is ancestral, sexual dimorphism “appears in the intermediately derived species, and then disappears in the most derived species . . .” (p. 1812). This use of the same trait to delineate stages and then to later claim that that trait differs between these stages seriously confounds their methodology with their results. A more acceptable approach would have been to define their stages independent of dimorphism. Such an approach would more effectively measure the relationship between derivation and change in dimorphism.

Fifth, the attention of Endler et al. (2005) to display trait dimorphism is puzzling given their paper's focus on the signal value of male display traits and not male–female differences per se. In two of the three *Chlamydera* monomorphic species they place in their most derived category, both sexes have distinctive lilac neck crests. During sexual display males in these species turn their head or bow repeatedly showing their erected crest to females (Borgia 1985). In the remaining species neither males nor females have crests. Thus, these monomorphic species differ greatly in the extent to which bright plumage is used in sexual display. Endler et al. (2005) suggest that plumage brightness and dimorphism show similar patterns, but among *Chlamydera* species (counting species included and excluded from their analysis), three of five have crests, but all are scored as monomorphic because females share crests with males in species where crests are present. These patterns suggest that the role of plumage in male display in these species is more complicated than suggested by the degree of dimorphism and that the presence of bright male plumage would seem a more useful trait than dimorphism for identifying overall patterns of plumage expression in males.

Endler et al. (2005) claim that predation increased as a result of the evolution of bright plumage (stage 2) and that this in turn led to the evolution of sexual dimorphism to reduce predation pressure on females (stage 3). Alternatively, bright male plumage

may have increased with decreased predation pressure. There is no historical information on predation in bowerbirds that allows us to discriminate between these hypotheses. The only long-term study of predation in bowerbirds suggests that in a species they consider to have bright plumage, there is only a low level of predation on mature males (Borgia 1993, 1995, 1997). Their suggestion that after conspicuous plumage evolved, sexual dimorphism evolved to reduce predation on females is also difficult to test because of the absence of any information from bowerbird species with brightly colored plumage that is consistently exposed in males and females. Without this information we do not know if, as they suggest, bright plumage evolved in both sexes and later evolved to be sex-limited, as they propose, or if bright plumage only evolved in males and never developed in females.

A key hypothesis Endler et al. (2005) test using spectral information is that background color contrasts with bower decorations. They state that “Rather than being a narrow preference for some colors, the birds do not take objects that have colors similar to that of the background” (p. 1812). Both parts of this claim are mistaken. Numerous studies of bowerbirds have shown strong preferences for particular colors. Male satin bowerbirds show a strong preference for blue decorations and an aversion to red in choice tests (see Borgia et al. 1987; Borgia and Keagy 2006). Males also preferentially steal blue decorations (Borgia and Gore 1986; Hunter and Dwyer 1997) and females mate with males with more blue on their bowers (Borgia 1985; Coleman et al. 2004; Patricelli et al. 2004). Thus, satin bowerbirds and probably other bowerbirds have specific color preferences. Also, in response to the second part of their claim, their results show that males in four (satin, spotted, great, and regent) of seven species use decorations that match background color spectra peaks (their fig. 4). For three of these species, contours showing visual background color are obscured by numerous decoration data points, indicating that males commonly collect objects that match the measured background color. This lack of support for their hypothesis could occur because their plots (near and far) of background color for each species may not have sufficient detail to show contrasting backgrounds for particular decorations (and male plumage) that are displayed at specific locations around the bower. In spotted and great bowerbirds, males place red objects and display with their lilac crests near areas with contrasting green objects. This specificity in locating contrasting bower decorations and decorations that complement male plumage may not be shown in their bower wide measures of contrast. An alternative hypothesis not considered by Endler et al. (2005) is that local backgrounds are constructed because they enhance the display of prized decorations initially selected for other reasons. For example, male and female satin bowerbirds prefer rare blue feathers, flowers, and berries, and male ability to collect and retain these rare items is suggested to be an indicator of male quality (Borgia et al. 1987;

see also Madden 2002 for a similar argument for spotted bowerbirds). Males may have evolved to enhance the visibility of these relatively low reflectance decorations by constructing a bright yellow straw/leaf background on the platform where decorations are arrayed and blue–black plumed males display.

Endler et al. (2005) suggest that some bowerbirds use plumage in species recognition, but there is little support for this claim. They state that the plumage color “. . . distributions of GO [golden] and RG [regent] extend outside the background in the same direction, indicating the use of similar colors in allopatry and similar divergence from ST [satin] in sympatry. This suggests that the plumage may be used as a species recognition character and has diverged in sympatry.” (p. 1813). For these and other bowerbird species Endler et al. (2005) provide no example of intraspecific differences in plumage or other traits that differ between areas of allopatry and sympatry with another bowerbird species. This kind of evidence would, if present, provide a more convincing case for plumage color divergence in sympatry and character displacement (e.g., Endler 1986; Alatalo et al. 1994). The claim of Endler et al. (2005) that the yellow of the Australian regent bowerbird, a member of the genus *Sericulus*, is a result of character divergence in sympatry with satin bowerbirds is particularly weak because three other *Sericulus* species in New Guinea (not included in their analysis), where the satin bowerbird does not (and likely never did) occur, also have evolved similar but still strikingly distinctive yellow/orange plumage on a black background. Thus, the kinds of plumage differences that Endler et al. (2005) attribute to character displacement occur in both sympatric and allopatric pairings of *Sericulus* species with satin bowerbirds suggesting that there was no character displacement nor that these plumage differences evolved to enable species recognition. Their claim that plumage in golden and satin bowerbirds diverged in sympatry to enable species recognition also seems unlikely. These species have large (i.e., tall maypole spires vs. short two-walled avenue bowers) and ancient (they belong to different major clades) differences in display traits that would seem to be sufficient to allow species recognition and obviate the need for character displacement in other traits. The plumage differences they describe may evolve for many different reasons. For example, golden and regent bowerbirds have bright yellow or orange in their plumage and commonly court females away from decorated courts (G. Borgia, pers. comm.). The blue–black satin bowerbirds typically display on a court carpeted with yellow decorations (Borgia 1985) that may provide contrast with the male’s dark plumage. Thus, differences in species plumage may have evolved in response to differences in conditions under which display occurs (e.g., Endler and Thery 1995; Endler et al. 2005) and the presence of other display traits rather than to enable species recognition. Bowerbirds are known for their fine scale intraspecific mate discrimination based on multiple courtship elements (Coleman et al. 2004; Patricelli

et al. 2004). Thus, female bowerbirds may accomplish species recognition by using their precise intraspecific mate choice abilities to exclude heterospecific males whose trait values for display elements typically fall outside of the range females' favor in mate choice (Uy and Borgia 2000; Ryan et al. 2003) thus making character divergence unnecessary for species recognition (K. Shaw, Pers. Comm.) in bowerbirds.

Perhaps the most interesting result of Endler et al. (2005) is that man-made objects used by bowerbirds often occupy different color space than natural objects. This suggests that objects of preferred colors may often be rare in the natural habitat. The assessment of color use by Endler et al. (2005) on bowers provides some insights into decoration color preferences but a full description of color preferences will require experiments that make available a large palate of colors for males to choose from, so as to exclude the possibility that colors missing on bowers are not scarce because of their limited availability in the habitat.

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