

# PLUMAGE EVOLUTION IN THE OROPENDOLAS AND CACIQUES: DIFFERENT DIVERGENCE RATES IN POLYGYNOUS AND MONOGAMOUS TAXA

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Avian plumage colors are frequently used in studies of sexual selection, yet surprisingly little is known about how these traits evolve under different mating systems. We compared historical rates of divergence in male color patterns among the oropendolas and caciques (genera *Cacicus*, *Gymnostinops*, *Ocyalus*, and *Psarocolius*), a group with both polygynous and monogamous representatives. Reconstructing the evolution of individual color patches on a molecular phylogeny showed that overall color patterns have changed much more rapidly in oropendolas, which comprise two groups that evolved polygyny independently, than in caciques, which are predominantly monogamous. None of these taxa are notably sexually dichromatic, however, suggesting that higher rates of plumage evolution occurred in both sexes rather than just males. Despite high rates of change, color patterns show few examples of convergence among taxa, similar to the lack of homoplasy in male song among oropendolas but in a stark contrast to the repeated convergence in both plumage and song patterns found in a closely related, monogamous clade, the New World orioles (*Icterus*). Our results support previous suggestions that display traits evolve more rapidly and with less homoplasy in polygynous mating systems, and we provide surprising evidence that these patterns may occur in both sexes.

**KEY WORDS:** Ancestral state reconstruction, avian plumage coloration, convergent evolution, dimorphism, phylogeny, sexual selection.

Birds exhibit a remarkable diversity of color patterns across species. Indeed, even among closely related taxa, avian plumage colors often differ much more dramatically than do other aspects of morphology, suggesting that these traits can diverge relatively rapidly (e.g., Omland and Lanyon 2000; Kondo et al. 2004; Yeh 2004; Milá et al. 2007; Kiere et al. 2009). Such rapid evolutionary changes can result from differences in habitat, including differences in environmental light conditions, levels of predation, or available pigments in the diet (Endler 1992; Endler and Théry 1996; Badyaev and Hill 2003; Price 2008). Rapid trait divergence can also result from sexual selection (West-Eberhard

1983; Schluter and Price 1993; Andersson 1994; Prum 1997; Cuervo and Møller 1999a,b), and such mechanisms might be especially important during early speciation, given the importance of display traits in mate recognition and reproductive isolation (Price 2008).

Multiple evolutionary forces may interact in complex ways during character evolution (e.g., Irwin et al. 2008). However, in general, traits involved in mate choice and/or intrasexual competition are expected to change more rapidly when operational sex ratios are more highly skewed, causing these characteristics to be more elaborate and divergent in polygynous than in monogamous

taxa (Andersson 1994). Comparative studies using a wide range of taxonomic groups have provided indirect support for such differences in evolutionary rates by comparing sexual dimorphism in traits across taxa in relation to mating system (e.g., Lindenfors and Tullberg 1998; Baker and Wilkinson 2001; Dunn et al. 2001; Ord et al. 2001; Thorén et al. 2006). However, to our knowledge, no previous studies have tested this assumption explicitly by comparing historical rates of change in male traits among closely related lineages with different mating systems.

The oropendolas (genera *Gymnostinops*, *Ocyalus*, *Psarocolius*) and caciques (*Cacicus*) provide an excellent model clade for testing hypotheses about trait evolution under different social mating systems. Taxa in this group exhibit a wide range of breeding behaviors and levels of sexual size dimorphism, from species that are monogamous and monomorphic (e.g., *Cacicus solitarius*: Jaramillo and Burke 1999) to some of the most extreme examples of polygyny and sexual size dimorphism known in birds (e.g., *Gymnostinops montezuma*: Webster 1994, 1997). The polygynous oropendolas and the predominantly monogamous caciques together constitute a monophyletic group, but they are not reciprocally monophyletic based on DNA sequence data (Price and Lanyon 2002a, 2004a). Oropendolas are polyphyletic, comprising two distinct subclades, whereas caciques are paraphyletic, with some species more closely related to oropendola taxa than to other caciques. Furthermore, at least two cacique species (*Cacicus cela* and *C. haemorrhous*) are known to breed polygynously (Feeles 1981; Robinson 1986; Webster 1992). Thus, based on phylogenetic relationships, polygyny appears to have evolved from monogamy multiple times in this clade (Searcy et al. 1999; Price and Lanyon 2004a).

Size dimorphism in oropendolas and caciques is positively correlated with intensity of sexual selection, as measured by mean harem size (Webster 1992). However, despite such large differences in mating systems, no taxa in this group are notably sexually dichromatic (Jaramillo and Burke 1999). Female coloration is often only slightly duller than that of males, so male coloration is not an obvious target of sexual selection. Furthermore, although the males of many polygynous species perform elaborate visual displays to females (Jaramillo and Burke 1999), the role of plumage colors in mating is unknown. Nevertheless, this lack of dichromatism does not necessarily indicate the absence of sexual selection in any form, because sexually selected traits are not always dimorphic between the sexes (Amundsen 2000), especially in regard to avian color patterns (Amundsen and Pärn 2006). Female traits could change as a genetically correlated response to selection on males, assuming that these traits do not carry substantial costs for females (Lande 1980). Female colors could also be influenced by selection directly, perhaps as a result of intrasexual competition over resources (West-Eberhard 1983; LeBas 2006). Even in the

absence of sexual selection based on color, it is possible that visual signals in females are influenced by different selection pressures in polygynous and monogamous mating systems.

Reconstructing the evolution of plumage coloration in the oropendolas and caciques is especially interesting in light of recent phylogenetic comparative studies of another display trait, male song, in the oropendola–cacique clade, and in a closely related clade, the orioles (*Icterus*). Both groups are members of the New World blackbird family (Icteridae) and are closely related (Lanyon and Omland 1999; Price et al. 2009). In the oropendola–cacique group, songs have changed more frequently in lineages that are more sexually dimorphic in size, which suggests that vocal evolution has occurred relatively rapidly under stronger levels of sexual selection (Price and Lanyon 2004a). Yet, despite such rapid changes, oropendola song features have accumulated with almost no convergence among taxa (Price and Lanyon 2002b), such that songs reflect phylogenetic relationships in this group surprisingly well (Price and Lanyon 2004b). Conversely, in the orioles, these same song features show repeated convergence and reversals when mapped onto the oriole phylogeny, with many distantly related taxa having songs that are nearly identical in overall pattern (Price et al. 2007). Unlike the highly polygynous oropendolas, orioles are socially monogamous with biparental care (Robinson 1986; Jaramillo and Burke 1999). Such striking differences in levels of convergence might indicate that oropendola and oriole songs are influenced by different predominant mechanisms of selection (Prum 1997; Price et al. 2007).

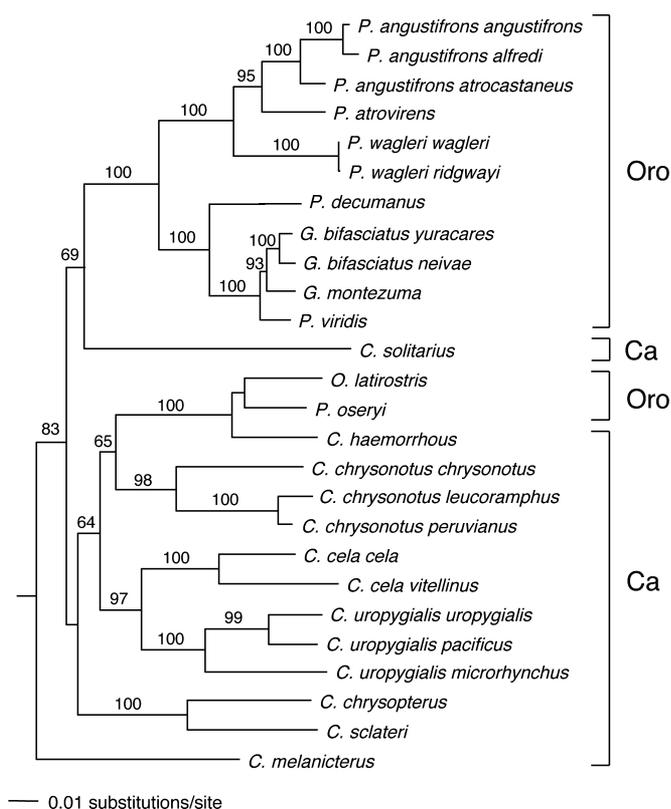
In a previous study of plumage evolution in orioles, Omland and Lanyon (2000) found high levels of homoplasy in oriole plumage similar to those found in oriole song (Price et al. 2007). Indeed, as with song, overall plumage patterns in orioles provide remarkable examples of convergent evolution between distantly related taxa (Omland and Lanyon 2000; Allen and Omland 2003; Hoekstra and Price 2004; Hofmann et al. 2006). Whether plumage patterns in oropendolas and caciques have evolved like oriole plumage, with repeated convergence and reversals, or like oropendola song, with almost no convergence and high phylogenetic signal, has not been previously investigated.

Here, we reconstruct the evolution of male color patterns in the oropendola–cacique clade with two main objectives. First, we compare evolutionary patterns among the oropendolas and caciques to investigate whether plumage coloration shows different rates of divergence in polygynous and monogamous taxa. Second, because we use methods similar to those used in previous reconstructions of character evolution in oropendolas and in orioles (Omland and Lanyon 2000; Price and Lanyon 2002b; Price et al. 2007), we are able to compare the evolution of two display traits, male plumage and song, both within and between these clades.

## Methods

### STUDY TAXA

We used a published molecular phylogeny of the oropendolas and caciques for our study (Fig. 1; Price and Lanyon 2004a). This tree is based on DNA sequence data from two mitochondrial genes, cytochrome *b* and ND2, and was used previously for reconstructing the evolution of song in these birds (Price and Lanyon 2002b, 2004a,b). Recent analyses including multiple nuclear intron markers have provided strong additional support for these relationships (Price et al. 2009; S. M. Lanyon, pers. comm.). Oropendola taxa are divided into two distinct clades on the phylogeny: a group including the *Gymnostinops* genus and all but one member of *Psarocolius* (hereafter referred to as the “true oropendolas”) and



**Figure 1.** Molecular phylogeny used in reconstructing plumage evolution in the oropendola and cacique clade (from Price and Lanyon 2004a). Neither the oropendolas (Oro) nor the caciques (Ca) are monophyletic, with the oropendola group divided into the “true oropendola” clade (genera *Gymnostinops* and *Psarocolius*, excluding *P. oseryi*) and the species *P. oseryi* and *Ocyalus latirostris* nested within the caciques. We considered *O. latirostris* together with the cacique group in our analyses based on a variety of similarities between these taxa, including relatively low levels of sexual size dimorphism. Branch lengths reflect number of nucleotide substitutions and numbers above branches show nodal support in bootstrap analyses of mitochondrial DNA sequence data. Genus abbreviations: C = *Cacicus*; G = *Gymnostinops*; O = *Ocyalus*; P = *Psarocolius*.

a group including only the casqued oropendola (*Psarocolius oseryi*) and the band-tailed oropendola (*Ocyalus latirostris*). Both groups are more closely related to cacique species than they are to each other (Fig. 1). Because *O. latirostris* shares more characteristics with caciques than with other oropendolas (see below), and for the ease of discussion, we included this species in the cacique group in our phylogenetic analyses of color evolution.

Sexual size dimorphism is closely associated with social mating system in the oropendolas and caciques, with polygynous species having greater differences in body size between the sexes than monogamous species, as measured by male–female differences in tarsus length (Webster 1992; Price and Lanyon 2004a). Because mating systems have not been described for all of our study taxa, we used sexual size dimorphism as an approximate indicator of social mating system in our study. We categorized taxa with size differences >15% as polygynous and those with differences <15% as monogamous based on evidence from behavioral observations that this is an appropriate dividing point (Robinson 1986; Webster 1992; Jaramillo and Burke 1999; Price and Lanyon 2004a).

Both behavioral data and measurements of sexual size dimorphism suggest that oropendolas and caciques differ considerably in their general mating systems. True oropendola taxa exhibit female-defense polygyny, based on descriptions of many species in the field (Robinson 1986; Webster 1997; Jaramillo and Burke 1999; Fraga and Kreft 2007) and a molecular analysis of paternity in one species (*G. montezuma*; Webster 1994). On average, male oropendolas are 21.1% larger than females, as measured by differences in tarsus length (SE = 0.7%; range = 17.6–24.1%;  $N = 9$ ; data from Price and Lanyon 2004a). This difference is significantly greater than the 9.0% mean difference between male and female caciques (SE = 1.4%; range = 0.4–18.8%;  $N = 14$ ;  $t$ -test,  $P < 0.0001$ ), which appear to breed mostly as monogamous, territorial pairs (Robinson 1986; Jaramillo and Burke 1999). Two exceptions are the polygynous yellow-rumped cacique (*C. cela*) and red-rumped cacique (*C. haemorrhous*), although male mating success in these species is not nearly as skewed as in true oropendolas (Feekes 1981; Robinson 1986; Webster 1992; Webster and Robinson 1999). These two caciques are the most sexually size dimorphic representatives of their genus, with male–female tarsus differences of 15.6% and 18.8%, respectively (Price and Lanyon 2004a).

*Psarocolius oseryi* exhibits a variety of characteristics that are convergent with true oropendolas, including polygynous mating (Leak and Robinson 1989), high levels of size dimorphism (male–female tarsus difference = 19.4%), similar song features (e.g., long continuous sounds and relatively low frequency notes; Price and Lanyon 2004a; Price et al. 2006), and similarities in overall appearance (Ridgely and Tudor 1989; Jaramillo and Burke 1999). Indeed, these factors presumably explain why this species

was previously placed in the genus *Psarocolius* (Blake 1968; Sibley and Monroe 1990). *Ocyalus latirostris*, on the other hand, is relatively monomorphic with one of the lowest male–female tarsus differences in the clade (5.5%). Little is known about its mating system; however, it is similar to cacique species in its overall appearance (Ridgely and Tudor 1989; Jaramillo and Burke 1999) and vocalizations (Price and Lanyon 2004a). Because of these similarities, we considered *O. latirostris* together with the caciques in our study rather than with the oropendolas.

Neither oropendolas nor caciques are reported to be notably sexually dichromatic. In oropendolas and in the two polygynous cacique species, females are generally described as having color patterns that are similar to but slightly duller than conspecific males, whereas in socially monogamous caciques, the sexes are often described as identical (see plates and descriptions in Jaramillo and Burke 1999). Thus, sexual dichromatism may vary with mating system in this clade, but not markedly so. The combination of high size dimorphism and low levels of apparent dichromatism, as occurs in the oropendolas, is not uncommon among socially polygynous birds (Owens and Hartley 1998). Moreover, dichromatism is known to occur in ultraviolet colors outside our visible spectrum (Eaton and Lanyon 2003). In our phylogenetic analysis comparing evolutionary rates among taxa, we focused only on adult male coloration and ignored any variation between the sexes.

### PLUMAGE SCORING

We scored male color patterns by examining museum skins at the Smithsonian National Museum of Natural History and the American Museum of Natural History. We also looked at color plates in Jaramillo and Burke (1999) to score wing patterns and other body regions not easily examined in museum specimens. We scored all 26 oropendola and cacique taxa included in the phylogeny of Price and Lanyon (2004a), which included 17 of the 20 recognized species (Sibley and Monroe 1990) and nine additional subspecies (Blake 1968). We also sampled multiple male representatives of taxa that have wide geographic ranges to ensure that male colors did not vary enough within taxa to affect our scores.

Our methods for choosing and scoring plumage characters followed those of Omland and Lanyon (2000). We scored the entire external appearance of male oropendolas and caciques by dividing each bird into discrete color patches that varied among taxa, and we defined a color patch as a continuous region of feathers or other integumentary structures with a similar coloration. Our methods differed from those of Omland and Lanyon (2000) in two ways. First, we did not divide adjacent feather regions that differed structurally, such as primary and secondary flight feathers, into different patches if these regions had the same color in all taxa. We felt this was an appropriate decision because large color patches on the wings of oropendolas and caciques often

include multiple feather types, unlike the more complex wing color patterns of orioles (Ridgely and Tudor 1989; Howell and Webb 1995; Jaramillo and Burke 1999). Second, some of our character states differed from those used by Omland and Lanyon (2000). Most color patches in oropendolas and caciques were scored as either black/brown (b), carotenoid (c), green (g), or russet (r) (Table 1), whereas most oriole feather patches were scored as black, carotenoid, or white (Omland and Lanyon 2000). Like Omland and Lanyon (2000), we also scored several additional integumentary features in our study taxa, such as patches of bare skin, coloration of the beak, and the presence of a crest or a wattle. We refer to all of these integumentary features as plumage characters in our study, despite the fact that some did not include feathers.

We selected color character states based on gross differences in coloration among taxa. Like the color scores used by Omland and Lanyon (2000), each of our scores was a discrete category that encompassed a continuous range of colors. Although the genetic basis and biochemistry of coloration in oropendolas and caciques has not been studied, we used what is known from other species to define discrete color states that are likely to be heritable and to be produced via different mechanisms. Patches scored as black/brown in our study included a range of shades from soot black to light chestnut, and these colors are generally a product of melanin pigmentation in birds (McGraw 2006b). The black feathers of many adult male oropendolas and caciques are chestnut in the juvenile molt (Jaramillo and Burke 1999), providing further evidence that black is simply a more melanin-saturated form of brown in this group. Bright yellows, oranges, and reds are typically products of carotenoid pigmentation in birds (Hofmann et al. 2006; McGraw 2006a; but see McGraw et al. 2004), so we combined these colors into one character state in our analysis, as was done by Omland and Lanyon (2000). Carotenoid color patches have switched rapidly between yellows and reds during the evolutionary history of the caciques (Kiere et al. 2009), which strongly indicates that these colors are products of similar mechanisms. Patches scored as green in our study included various shades of olive plumage as well as the light green coloration on the beak of *Psarocolius viridis*. Green is usually a product of structural colors in combination with color pigments (Prum 2006), and appears to be restricted to the oropendolas within the Icteridae family (Jaramillo and Burke 1999). Finally, russet is a distinctive burnt-orange color exhibited by only a few closely related taxa (*Psarocolius atrovirens* and subspecies of *P. angustifrons*). Although its origin is unknown, we felt that this color differed enough from brown and carotenoid to be categorized as a separate character state.

In all, we scored 39 color patches, 38 of which varied in coloration across the 26 taxa (Table 1). Only one color patch, proximal remiges, was invariant and dark brown in all taxa. We scored fewer color patches in our study than were scored in orioles

**Table 1.** Matrix of male plumage coloration characters for oropendola and cacique species (genera *Cacicus*, *Gymnostinops*, *Ocyalus*, and *Psarocolius*). Character descriptions are listed in Table 2.

Taxon	Character																																							
	Wing						Body						Head						Tail																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38		
<i>Psarocolius oseryi</i>	b	b	c	b	b	b	b	b	b	b	b	b	b	b	b	b	b	g	g	b	b	b	b	b	b	g	g	b	g	g	g	g	u	u	g	A	A	b	c	b
<i>Psarocolius decumanus</i>	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	u	u	b	A	P	c	c	c	
<i>Psarocolius viridis</i>	b	g	g	b	g	b	b	b	b	b	g	g	b	b	b	b	b	s	s	s	g	g	g	g	g	g	g	g	g	g	g	c	g	A	P	c	c	g		
<i>Psarocolius atrovirens</i>	g	g	g	g	g	g	r	r	g	g	r	r	g	g	g	g	g	g	g	g	g	g	g	g	g	g	g	g	g	g	u	u	g	A	P	g	c	g		
<i>Psarocolius a. angustifrons</i>	b	b	b	b	g	b	b	r	r	b	b	b	b	b	b	b	r	s	s	g	g	g	g	g	g	g	g	g	g	g	b	g	A	P	b	c	b			
<i>Psarocolius a. alfredi</i>	b	g	g	b	g	b	r	r	b	b	b	b	b	b	b	b	r	s	s	c	g	g	g	g	g	g	g	g	g	c	u	u	c	A	P	b	c	b		
<i>Psarocolius a. atrocastaneus</i>	b	b	b	b	b	b	r	r	r	b	b	b	b	b	b	b	r	b	b	c	c	b	b	b	b	b	b	b	b	c	u	u	c	A	P	g	c	g		
<i>Psarocolius w. wagleri</i>	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	u	u	b	A	P	c	c	b		
<i>Psarocolius w. ridgwayi</i>	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	u	u	b	A	P	c	c	b		
<i>Gymnostinops montezuma</i>	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	s	s	b	b	b	b	b	b	b	b	b	b	b	b	c	s	P	A	c	c	c		
<i>Gymnostinops b. yuracares</i>	b	b	b	b	b	g	b	b	b	b	b	b	b	b	b	b	b	g	g	g	g	g	g	g	g	g	g	g	g	g	b	c	s	A	P	c	c	c		
<i>Gymnostinops b. neivae</i>	b	b	b	b	b	g	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	c	s	A	P	c	c	c		
<i>Ocyalus latirostris</i>	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	u	u	b	A	A	b	c	b			
<i>Cacicus cela cela</i>	b	b	c	b	b	b	b	b	c	c	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	u	u	b	A	A	b	b	b			
<i>Cacicus cela vitellinus</i>	b	b	c	b	b	b	b	b	c	c	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	u	u	b	A	A	b	b	b			
<i>Cacicus haemorhous</i>	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	u	u	b	A	A	b	b	b			
<i>Cacicus u. uropygialis</i>	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	u	u	b	A	A	b	b	b			
<i>Cacicus u. pacificus</i>	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	u	u	b	A	A	b	b	b			
<i>Cacicus u. microhynchus</i>	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	u	u	b	A	A	b	b	b			
<i>Cacicus chrysopterus</i>	b	b	c	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	u	u	b	A	A	b	b	b				
<i>Cacicus c. chrysonotus</i>	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	u	u	b	A	A	b	b	b				
<i>Cacicus c. leucoramphus</i>	b	b	c	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	u	u	b	A	A	b	b	b				
<i>Cacicus c. peruvianus</i>	b	b	c	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	u	u	b	A	A	b	b	b				
<i>Cacicus sclateri</i>	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	u	u	b	A	A	b	b	b				
<i>Cacicus solitarius</i>	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	u	u	b	A	A	b	b	b				
<i>Cacicus melanicterus</i>	b	b	c	b	b	b	b	b	c	c	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	u	u	b	A	P	c	c	b				

General color character state definitions: b, black or brown; c, carotenoid; g, green; r, russet; s, bare skin of any color; u, unpigmented beak. Other character state definitions indicate the presence or absence of a morphological feature: A, absence; P, presence.

(44 color patches: Omland and Lanyon 2000), which makes sense given that we defined these characters using fewer taxa (26 rather than 45 taxa). However, the mean number of states per character in our study (2.49, SE = 0.09) was very similar to that used in reconstructing plumage evolution in the orioles (2.47, SE = 0.10: calculated from data in Omland and Lanyon 2000).

### ANCESTRAL STATE RECONSTRUCTION

We reconstructed ancestral states for our plumage characters on the molecular phylogeny using MacClade 4.06 (Maddison and Maddison 2003). We examined the degree to which our plumage data were congruent with the phylogeny by calculating the overall consistency index (CI) and overall retention index (RI) for all characters together, as well as the CI and RI for each character individually, reconstructed onto the tree. These values were calculated for characters on the entire oropendola–cacique phylogeny, on just the true oropendola clade (genera *Gymnostinops* and *Psarocolius*, excluding *P. oseryi*) and on just cacique taxa (*Cacicus* plus *O. latirostris*). For both the CI and RI, a score of 1.0 represents perfect congruence with phylogeny, with no convergence or evolutionary reversals, whereas a score approaching 0.0 indicates high levels of homoplasy. Characters that do not vary at all among taxa have CI and RI scores of 0.0. Calculating these scores allowed us to compare the levels of homoplasy in our characters mapped onto different groups of taxa in the oropendola–cacique clade, and the scores additionally allowed comparisons to CI and RI values calculated for plumage patterns in orioles (Omland and Lanyon 2000) and song characters in oropendolas (Price and Lanyon 2002b). Such scores are strongly affected by number of taxa sampled (Sanderson and Donoghue 1989), however, so comparisons between clades were interpreted with caution.

We tested for an association between evolutionary changes in color patterns and levels of sexual size dimorphism using the concentrated changes test in MacClade (Maddison 1990). Lineages with male–female size differences >15% were used as our independent character in this analysis to test the hypothesis that changes in multiple color patches are concentrated in highly size-dimorphic lineages. Ancestral levels of sexual size dimorphism were taken from Price and Lanyon (2004a).

We further investigated evolutionary patterns in oropendola and cacique coloration by plotting “plumage distance” between all possible pairs of taxa as a function of mitochondrial DNA sequence divergence (uncorrected *p* distances; from Price and Lanyon 2004a). We calculated plumage distance as the number of plumage characters with different states, and we assumed that pairs of taxa with greater plumage distances relative to their molecular distances had diverged more rapidly in overall plumage coloration. Similar plots have been produced using oriole plumage (Omland and Lanyon 2000), oriole song (Price et al. 2007), and

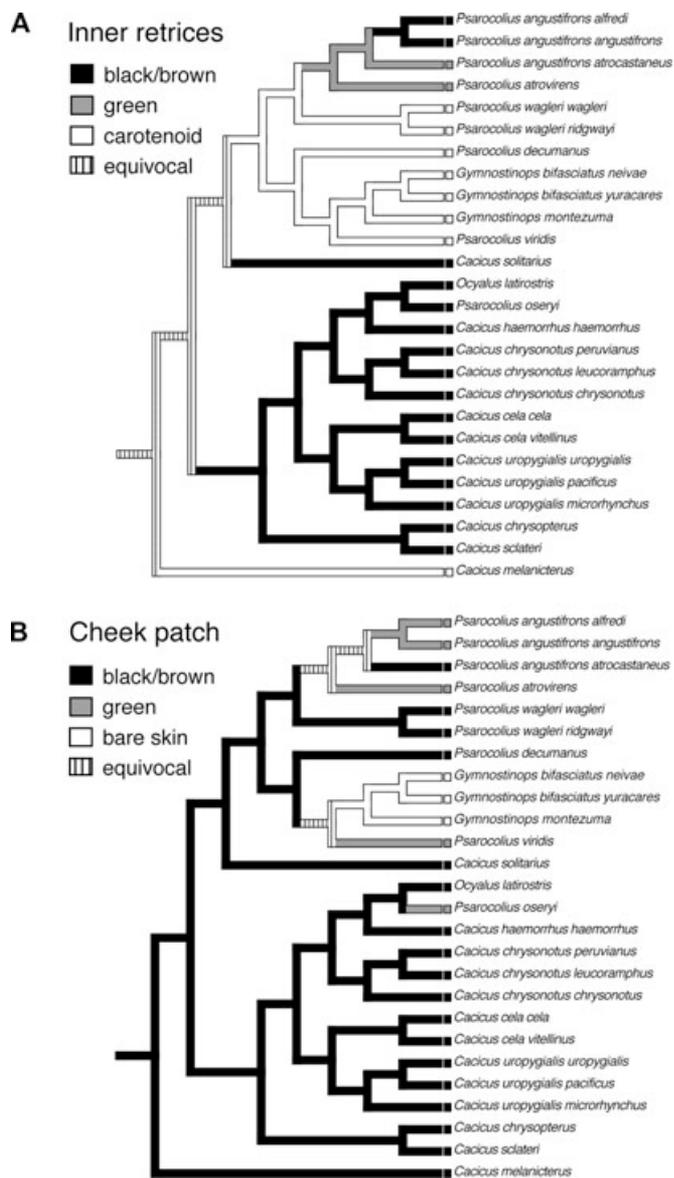
oropendola song (Price and Lanyon 2002b), and these plots show that maximum phenotypic differences tend to increase linearly with increasing molecular divergence. This upper bound presumably represents the upper limit for rates of evolutionary divergence in a trait.

To characterize the upper limit for plumage divergence rates in the oropendolas and caciques, we calculated an upper-bound regression by binning molecular divergence values into 1% increments, selecting the maximal plumage distance in each bin, and then calculating a linear regression through these points (Blackburn et al. 1992; Price et al. 2007). We then determined the relative level of plumage divergence for each taxon pair by calculating their “evolutionary deviation” from this upper-bound regression, which was the minimum orthogonal distance from a point in our plot to the regression line (Podos 2001). Taxa that were highly divergent in their plumage patterns, given their molecular divergence, were represented by points close to the upper limit for the clade and so had low evolutionary deviation scores, whereas minimally divergent taxa had points farther from this line and so had higher deviation scores. We calculated mean evolutionary deviations for taxa relative to the upper limit for the oropendola–cacique clade as a whole, and we also calculated separate upper-bound regressions for the true oropendolas and for the caciques (including *O. latirostris* but excluding *P. oseryi*) to compare their upper limits of plumage divergence. Although the values used in these analyses were not phylogenetically independent (Felsenstein 1985), they still provided a useful means for comparing general evolutionary divergence rates among different taxa within the clade.

## Results

Tracing our 38 characters onto the molecular phylogeny revealed multiple examples of homoplasy, with 34 characters showing convergent states or evolutionary reversals on the tree (Fig. 2). Seven characters, however, included at least one shared derived state that clearly reflected relationships among taxa, such as russet plumage in the tail regions of some oropendolas (characters 9, 10, and 17) and bare skin patches on the heads of *Gymnostinops* species (characters 25, 26, and 33; Fig. 2B). One character, distal beak (character 32), exhibited no homoplasy at all, with orange beaks defining a clade including *Gymnostinops* and *P. viridis*. Three characters (1, 12, and 34) included only autapomorphic states, which were uniquely derived in taxa and thus provided no phylogenetic information.

Although many individual color patches showed convergent states on the tree, few pairs of taxa were convergent in multiple color patches. Instead, our reconstructions showed that overall similarities between taxa were generally the result of shared ancestral characteristics. For example, in at least 30 of our character



**Figure 2.** Ancestral reconstructions of two plumage characters with typical patterns of variation among taxa. (A) Inner retrices (character 36) shows evidence of convergence and reversal between black/brown, green, and carotenoid plumage (CI = 0.5, RI = 0.75), while the ancestral state at the base of the clade is unresolved. (B) Cheek patch (character 26) also shows evidence of homoplasy (CI = 0.4, RI = 0.5), with at least three independent gains of green plumage and one potential reversal to black/brown, but it also includes one character state, bare skin, that defines the genus *Gymnostinops*.

reconstructions, the black or dark brown plumage of many oropendolas and caciques was also found to occur in the ancestor of the clade (this ancestral node was unresolved for seven characters). The one notable example of convergence in multiple plumage characters was between *P. oseryi* and the true oropendola clade, which independently evolved a variety of features including green

coloration and yellow tail feathers. Both *P. oseryi* and the true oropendolas differ markedly from closely related cacique species in their overall appearance (Ridgely and Tudor 1989; Jaramillo and Burke 1999).

Our plumage characters had an overall CI of 0.42 and overall RI of 0.50 when mapped onto the oropendola–cacique phylogeny, with individual CIs ranging from 0.2 to 1.0 and RIs ranging from 0.0 to 1.0 (Table 2). These values did not change appreciably when characters were reconstructed onto just the true oropendola clade: overall indices were similar (CI = 0.47; RI = 0.42) and half of the characters (19 of 38) maintained the same individual CI and RI scores. However, when our plumage characters were mapped onto just cacique taxa (*Cacicus* and *Ocyalus*), most characters (27 of 38) became invariant among taxa, with CIs and RIs of 0.0. Thirty-two characters were phylogenetically informative in the true oropendolas, whereas only eight were informative in caciques. Thus, in general, our characters showed much more variation among the oropendolas than among the caciques.

Accordingly, color patches have changed much more often in the two oropendola groups than in the caciques (Fig. 3). Branches with multiple character changes occurred throughout the true oropendola clade and in the recent ancestors of *P. oseryi*, whereas many cacique lineages showed no changes at all. Among the caciques, only the lineage leading to the relatively dimorphic species *C. cela* showed more than one change in plumage color. Of the 13 branches of the tree showing multiple changes in color patches, 12 were lineages that also exhibited high levels of size dimorphism (males >15% larger than females in tarsus length; Price and Lanyon 2004a), which is an association unlikely to have occurred by chance (concentrated changes test:  $P = 0.0013$ ).

Larger numbers of ancestral changes in oropendolas are reflected in significantly higher plumage distances between true oropendola taxa on average (mean number of character differences = 16.5; SE = 1.0;  $N = 55$ ) than between caciques (mean = 3.8; SE = 0.3;  $N = 91$ ;  $t$ -test:  $P < 0.0001$ ), despite significantly lower DNA sequence divergences among true oropendolas (mean = 5.4%; SE = 0.3%) than among caciques (mean = 8.4%; SE = 0.2%;  $P < 0.0001$ ). Plumage distances between *P. oseryi* and cacique taxa (mean = 13.1; SE = 0.7;  $N = 14$ ) were higher on average than mean plumage distances between pairs of caciques ( $t$ -test:  $P < 0.0001$ ), but tended to be lower than the mean plumage difference between pairs of true oropendolas ( $P = 0.09$ ).

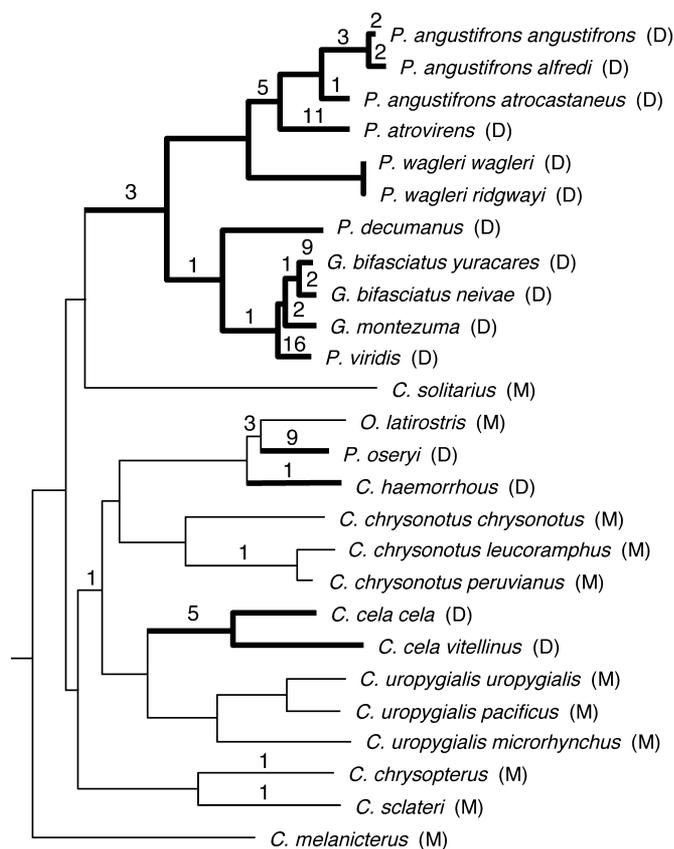
Plots showing plumage distances as a function of molecular sequence divergence (Fig. 4) also revealed very different patterns in the oropendolas and caciques. True oropendolas (Fig. 4B) showed much higher plumage divergence rates than did caciques (Fig. 4C: black circles), as evidenced by their significantly different mean deviations from the upper bound for the oropendola–cacique clade as a whole (mean deviation score for oropendolas = 4.2, SE = 0.4; mean deviation score for caciques = 12.6,

**Table 2.** Measures of homoplasy for plumage characters in male oropendolas and caciques. Consistency indices (CI) and retention indices (RI) are for characters mapped onto the entire oropendola–cacique phylogeny, just the true oropendolas (genera *Gymnostinops* and *Psarocolius*, excluding *P. oseeryi*) or just the caciques (*Cacicus* and *Ocyalus latirostris*).

Character (Overall index)	All taxa included		True oropendolas		Caciques		
	CI (0.42)	RI (0.50)	CI (0.47)	RI (0.42)	CI (0.48)	RI (0.37)	
1	Proximal coverts	1.00	0.00	1.00	0.00	0.00	0.00
2	Distal coverts	0.33	0.00	0.33	0.00	0.00	0.00
3	Distal remiges	0.50	0.00	0.33	0.00	0.00	0.00
4	Epaulet	0.40	0.40	1.00	0.00	0.25	0.40
5	Scapulars	0.50	0.00	0.50	0.00	0.00	0.00
6	Thigh	0.50	0.50	0.50	0.50	0.00	0.00
7	Breast	0.33	0.33	0.33	0.33	0.00	0.00
8	Belly	0.33	0.33	0.33	0.33	0.00	0.00
9	Crissum	0.67	0.80	1.00	1.00	0.50	0.50
10	Under tail coverts	0.67	0.80	1.00	1.00	0.50	0.50
11	Posterior flank	0.50	0.33	0.50	0.00	0.50	0.50
12	Anterior flank	1.00	0.00	1.00	0.00	0.00	0.00
13	Upper back	0.33	0.00	0.33	0.00	0.00	0.00
14	Lower back	0.50	0.00	0.33	0.00	1.00	0.00
15	Upper rump	0.40	0.70	0.50	0.00	0.33	0.33
16	Lower rump	0.40	0.73	0.50	0.00	0.33	0.00
17	Upper tail coverts	0.67	0.80	1.00	1.00	0.50	0.50
18	Superior eye-ring	0.33	0.20	0.40	0.25	0.00	0.00
19	Inferior eye-ring	0.33	0.20	0.40	0.25	0.00	0.00
20	Lores	0.50	0.00	0.50	0.00	0.00	0.00
21	Anterior supercilium	0.33	0.20	0.40	0.25	0.00	0.00
22	Posterior supercilium	0.50	0.50	0.50	0.50	0.00	0.00
23	Auricular	0.25	0.25	0.25	0.25	0.00	0.00
24	Crown	0.25	0.25	0.25	0.25	0.00	0.00
25	Malar	0.40	0.40	0.50	0.50	0.00	0.00
26	Cheek patch	0.40	0.50	0.50	0.60	0.00	0.00
27	Medial nape	0.25	0.25	0.25	0.25	0.00	0.00
28	Lateral nape	0.20	0.20	0.25	0.25	0.00	0.00
29	Throat	0.20	0.20	0.25	0.25	0.00	0.00
30	Forehead	0.33	0.20	0.40	0.25	0.00	0.00
31	Proximal beak	0.67	0.67	0.67	0.67	0.00	0.00
32	Distal beak	1.00	1.00	1.00	1.00	0.00	0.00
33	Culmen patch	0.50	0.50	0.60	0.60	0.00	0.00
34	Wattle	1.00	0.00	1.00	0.00	0.00	0.00
35	Crest	0.33	0.80	1.00	0.00	1.00	0.00
36	Inner retrices	0.50	0.75	1.00	1.00	1.00	0.00
37	Outer retrices	0.33	0.83	0.00	0.00	0.50	0.00
38	Edges retrices	0.50	0.60	0.50	0.60	0.00	0.00

SE = 0.2; *t*-test:  $P < 0.0001$ ). Plumage divergence rates between *P. oseeryi* and caciques (Fig. 4C: gray circles) were also significantly closer to this upper bound (mean deviation score = 7.9, SE = 0.5) than were divergence rates among caciques ( $P < 0.0001$ ). For each of these groups, the maximum number of plumage differences between taxa increased linearly with increasing molecular divergence, suggesting an upper limit to their

rates of plumage divergence. The upper bound regression line for plumage divergence among only the true oropendolas was nearly identical to the upper bound for the oropendola–cacique clade as a whole (Fig. 4B), whereas the upper bound for caciques was considerably lower (Fig. 4C). Interestingly, within the caciques, comparisons between *C. cela* subspecies and other cacique taxa were closer to the upper bound of the clade (mean deviation



**Figure 3.** Numbers of unambiguous changes in plumage characters (indicated above branches) reconstructed on the molecular tree. Branches with no numbers had no unambiguous changes. Letters in parentheses indicate taxa that are relatively sexually size dimorphic (D) or monomorphic (M), based on whether males are >15% or <15% larger than females, respectively, and thicker branches on the tree indicate ancestral lineages that are relatively size dimorphic (from Price and Lanyon 2004a). Multiple changes in color occurred in dimorphic taxa more often than expected by chance (concentrated changes test:  $P = 0.0013$ ).

score = 11.6, SE = 0.2,  $N = 25$ ) than were comparisons between other pairs of caciques ( $P = 0.001$ ). The plot for the entire oropendola–cacique clade (Fig. 4A) was very similar in overall shape to that calculated previously for orioles (Fig. 4D; Omland and Lanyon 2000).

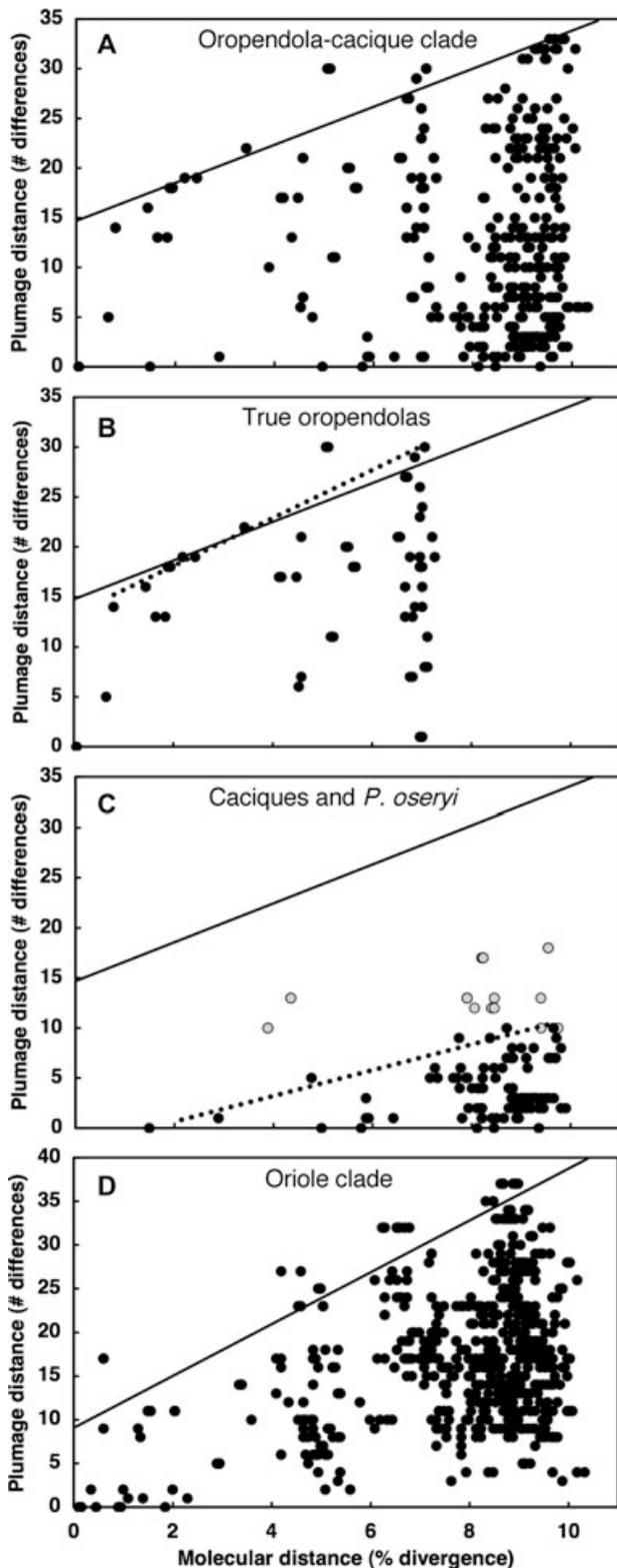
## Discussion

Reconstructions of male plumage evolution in the oropendolas and caciques provide strong support for the idea that color patterns have diverged more rapidly in polygynous than in monogamous taxa. More color changes have accumulated in the oropendolas, which comprise two groups that evolved polygyny independently (Price and Lanyon 2004a), in comparison to the caciques, which are predominantly monogamous (Jaramillo and Burke 1999). Multiple color changes were strongly associated with high levels

of size dimorphism (males >15% larger than females), including in at least one relatively dimorphic cacique (*C. cela*), and sexual size dimorphism is positively associated with degree of polygyny in these birds (Webster 1992). Different rates of plumage evolution were not related to any obvious differences in habitat, because oropendolas and caciques occupy many of the same areas throughout the Neotropics (Ridgely and Tudor 1989; Howell and Webb 1995; Jaramillo and Burke 1999). Different evolutionary rates are also not easily explained by rates of speciation, because each group included similar numbers of taxa in our study (12 oropendolas and 14 caciques, including *O. latirostris*). Rather, rates of plumage evolution appear to have increased in association with the evolution of polygyny at least three separate times in this clade.

Most previous comparisons between mating system and plumage evolution in birds have focused on levels of sexual dichromatism (reviewed in Badyaev and Hill 2003) or on plumage features that are sexually dimorphic in size (e.g., Cuervo and Møller 1999a,b; Dunn et al. 2001). Trait dimorphism in relation to mating system has been studied in a variety of other taxonomic groups as well (e.g., Baker and Wilkinson 2001; Ord et al. 2001; Thorén et al. 2006). In general, dimorphism between the sexes is positively associated with higher variance in male reproductive success, such as in polygynous mating systems (Andersson 1994; Owens and Hartley 1998; Dunn et al. 2001). Our findings compliment this previous work by showing that polygynous breeding may also be associated with increased rates of trait divergence among taxa, rather than just between the sexes. But our study raises new questions as well, because visible color patterns in the oropendolas and caciques do not differ notably between the sexes (Jaramillo and Burke 1999). Thus, rates of color evolution have increased in both sexes rather than just males.

If rates of plumage evolution are influenced by sexual selection acting on male color patterns, why have female colors changed at similar rates? In a previous comparative study of secondary sexual characteristics in birds, Cuervo and Møller (1999a) also found similar evolutionary rates in males and females, and they proposed that this lack of difference could be due to genetic correlation between the sexes, such that selection on one sex results in a correlated response to selection in the other (also see Lande 1980; Amundsen 2000). If this is the case in oropendolas and caciques, it would suggest that natural selection against the appearance of new color patterns in females is relatively weak. Alternatively, these correlated changes could be the result of direct selection on females (Amundsen 2000; Amundsen and Pärn 2006). Previous phylogenetic studies have found that female traits can change even more rapidly than male traits, despite the fact that sexual selection is presumably acting primarily on males, as shown in male and female plumage colors (Irwin 1994; Burns 1998; Hofmann et al. 2008) and male and female songs (Price



**Figure 4.** Plots showing pairwise plumage distances as a function of molecular sequence divergence between (A) all oropendola and cacique taxa, (B) just true oropendola taxa, (C) just cacique taxa (black circles) and *Psarocolius oseryi* versus cacique taxa (gray circles), and (D) all oriole taxa (*Icterus*; from Price et al. 2007). Deviations from the upper-bound regression representing the upper

et al. 2009). Indeed, color patterns in oropendolas and caciques may have little to do with mate choice at all, by either sex, and instead may play an important role in social competition (West-Eberhard 1983; Amundsen 2000; LeBas 2006), which in turn may differ according to mating system. For example, polygynous members of this clade tend to nest colonially, whereas monogamous species generally nest as dispersed, territorial pairs (Feekees 1981; Robinson 1986; Jaramillo and Burke 1999; Fraga and Kreft 2007). Whether such differences play a role in color evolution, however, remains to be investigated.

#### COMPARISONS TO SONG EVOLUTION

In many respects, the evolution of plumage coloration in the oropendolas and caciques resembles the evolution of song in this group. Song features, like plumage patterns, have changed much more dramatically in true oropendolas and in *P. oseryi* than in the monogamous caciques (Price and Lanyon 2004a). Both plumage and song also appear to have evolved convergently between *P. oseryi* and the true oropendolas. These birds share a variety of morphological traits, including olive coloration, yellow tail feathers, and high levels of sexual size dimorphism (Ridgely and Tudor 1989; Jaramillo and Burke 1999), and their songs share several unusual features not found in the songs of any cacique (Price and Lanyon 2004a). Yet, molecular data confirm that *P. oseryi* and the true oropendolas are distantly related and that these attributes are almost certainly independently derived (Price and Lanyon 2002a, 2004a).

Other than the similarities between *P. oseryi* and true oropendolas, however, both plumage and song show few other examples of convergence in overall patterns among taxa. Within the true oropendolas, changes in plumage characters have accumulated almost linearly with increasing genetic divergence between taxa (Fig. 4B), similar to how changes have accumulated in oropendola song (Price and Lanyon 2002b). Our 38 plumage characters exhibited more homoplasy on the true oropendola phylogeny than did 29 song characters mapped onto the same tree, reflected in lower overall CI and RI scores for plumage (CI = 0.47; RI = 0.42;

limit for rates of plumage divergence in the oropendola-cacique clade (solid lines in A-C;  $y = 1.9x + 14.8$ ,  $N = 11$ ,  $r^2 = 0.85$ ) show that plumage divergence rates of true oropendolas and of *P. oseryi* were significantly higher than divergence rates of caciques. Upper-bound regressions for true oropendolas (dotted line in B;  $y = 2.5x + 12.8$ ,  $N = 8$ ,  $r^2 = 0.87$ ), for caciques (dotted line in C;  $y = 1.3x - 2.9$ ,  $N = 8$ ,  $r^2 = 0.74$ ), and for the oriole clade (solid line in D;  $y = 2.9x + 9.2$ ,  $N = 10$ ,  $r^2 = 0.80$ ) are also shown for comparison. Regressions were not evaluated for statistical significance because datapoints were not phylogenetically independent. Molecular divergence values were uncorrected *p* distances based on mitochondrial DNA.

Table 2) than for song (CI = 0.78; RI = 0.88; Price and Lanyon 2002b). Furthermore, in a study of carotenoid color evolution in caciques, Kiere et al. (2009) showed that red plumage patches have appeared in this group multiple times convergently. Yet, in overall patterns, neither plumage nor song shows any evidence of convergence among true oropendola taxa. Both traits, in fact, provide reasonably accurate indicators of phylogenetic relationships among taxa (e.g., Price and Lanyon 2004b). Overall, then, plumage evolution appears to have occurred largely in parallel with song evolution in the oropendolas and caciques.

Traits influenced by sexual selection, such as male plumage and song, are expected to evolve in concert in the absence of constraining ecological factors (Shutler and Weatherhead 1990) or other significant costs (Badyaev et al. 2002). Costly traits, in contrast, such as secondary sexual features that are condition dependent, should exhibit evolutionary trade-offs in which the elaboration of one trait occurs at the expense of another based on such factors as their relative costs, detectability in particular environments, or reliability as indicators (Schluter and Price 1993; Badyaev et al. 2002). In the oropendolas and caciques, such trade-offs would have manifested as increased plumage evolution in some lineages and increased song evolution in others, but not necessarily both traits together. Correlated rate increases in these two display traits along multiple polygynous lineages, as shown here, are consistent with models of selection in which traits are relatively inexpensive and novel character changes are not strongly constrained by natural selection (Møller and Pomiankowski 1993; Prum 1997).

### COMPARISONS TO PLUMAGE AND SONG EVOLUTION IN ORIOLES

Patterns of both plumage and song evolution in the orioles are strikingly different from what we found in the oropendolas and caciques. Plumage patterns and song features have converged repeatedly among oriole taxa, and not always between the same taxa, resulting in many distantly related oriole species that are strikingly similar in plumage or in song, or both (Omland and Lanyon 2000; Allen and Omland 2003; Hoekstra and Price 2004; Hofmann et al. 2006; Price et al. 2007). Both plumage and song show high levels of homoplasy in the orioles, reflected in low overall CI and RI scores (plumage: CI = 0.31, RI = 0.63; song: CI = 0.27, RI = 0.35; Omland and Lanyon 2000; Price et al. 2007). Unlike in the oropendolas, neither color patterns nor song features in the orioles provide much reliable information about phylogenetic relationships among taxa.

Thus, overall patterns of character change in the oropendola–cacique clade and in the oriole clade present an interesting contrast. In both groups, plotting plumage distance against molecular sequence divergence results in triangular plots that are remarkably similar in overall shape (compare Fig. 4A,D). Each shows a nearly

identical linear upper bound to plumage distance that increases with molecular distance, suggesting similar upper limits to the rate of character divergence in each clade. Both plots also include many points in their lower right portions indicating little apparent relationship between plumage distance and molecular distance. The plots for each clade differ, however, in the evolutionary histories behind those lower right points. In the oropendolas and caciques, similar color patterns in distantly related taxa are most frequently the result of shared ancestral traits (e.g., points in the lower right of Fig. 4B represent comparisons between taxa that are almost entirely black/brown, similar to their common ancestor), whereas in the orioles such similarities are frequently the result of evolutionary convergence in multiple characters (Omland and Lanyon 2000; Allen and Omland 2003; Price et al. 2007). Furthermore, points in the oropendola–cacique graph are distributed according to mating system, with those along the upper limit representing polygynous oropendolas (Fig. 4B) and those in the lower right representing the predominantly monogamous caciques (Fig. 4C), whereas all points in the oriole graph represent taxa that are socially monogamous and exhibit little sexual size dimorphism (Fig. 4D; Jaramillo and Burke 1999). Plots of song differences versus molecular divergence show a similar contrast between these clades, with almost no convergence in song features among oropendolas (Price and Lanyon 2002b) but repeated convergence in orioles (Price et al. 2007).

Previous studies (Omland and Lanyon 2000; Price and Lanyon 2002b; Price et al. 2007) used methods for scoring characters similar to those used here, with similar mean ( $\pm$  SE) numbers of states/character (oropendola–cacique plumage:  $2.49 \pm 0.09$ ; oriole plumage:  $2.47 \pm 0.10$ ; oropendola song:  $2.34 \pm 0.12$ ; oriole song:  $2.38 \pm 0.24$ ), so it seems unlikely that differences in homoplasy were due to the methods we used. Both clades also have similar maximum levels of molecular sequence divergence (10.32% in the oropendola–cacique clade; 10.32% in the orioles; uncorrected *p* distances; Omland et al. 1999; Price and Lanyon 2004a), so different levels of homoplasy are also not easily explained by differences in time scale. Orioles are a more speciose group (Sibley and Monroe 1990), with 25 recognized species in comparison to the 17 oropendola and cacique species included in our study, and more speciation events could have provided more opportunities for convergence among taxa given a limited number of potential character states (Sanderson and Donoghue 1989; Price et al. 2007). However, such moderate differences in speciation and/or extinction rates seem insufficient to fully explain the stark contrast between these clades in their patterns of evolutionary convergence.

### MECHANISMS OF SELECTION

The underlying mechanisms of selection causing color changes in oropendolas and caciques remain unclear, especially given the

lack of obvious sexual dichromatism in these birds. The mechanisms behind color changes in orioles are also poorly understood, although it has been shown that dichromatism in this clade has resulted from changes in female coloration rather than changes in males (Irwin 1994; Hofmann et al. 2008; also see Price et al. 2009). Nevertheless, the strikingly different patterns of trait convergence in these two clades provide intriguing evidence suggesting that different predominant mechanisms are involved.

For example, alternative models of sexual selection (reviewed in Andersson 1994) are expected to yield distinct macroevolutionary patterns that conform well to the patterns revealed here (Prum 1997). In Fisherian models, for instance, male traits are genetically correlated with female mating preferences, resulting in a "runaway process" in which traits can evolve in arbitrary directions of elaboration that have little relationship with viability or condition (Fisher 1958; Lande 1981; Kirkpatrick 1982). At the macroevolutionary level, Fisherian selection should cause rapid, arbitrary divergence of traits with little convergence among lineages, such that new traits may accumulate to yield a historically nested distribution of homologous character states reflecting phylogenetic relationships among taxa (Prum 1997). Conversely, in "honest indicator" models of sexual selection, in which secondary sexual traits provide reliable information about a signaler's condition or quality (Zahavi 1975; Hamilton and Zuk 1982; Kodric-Brown and Brown 1984; Grafen 1990), character traits should not evolve in such a cumulative way because they are relatively costly, and thus former traits should be selected against when new indicators evolve (Schluter and Price 1993; Badyaev et al. 2002). Furthermore, because the number of potential indicator traits is limited, indicator selection should result in more frequent convergence in traits among lineages (Prum 1997).

In a previous phylogenetic test of alternative sexual selection mechanisms, Prum (1997) showed that macroevolutionary patterns in male plumage and display traits in the lek-breeding manakins (Pipridae) were more consistent with the Fisherian model of sexual selection than with other models, including honest indicator mechanisms. Manakin traits have evolved in an unconstrained, cumulative way, resulting in an explosive pattern of trait diversity in which character states are hierarchically distributed across taxa and thus reflect phylogenetic relationships (Prum 1990, 1997). Similar evolutionary patterns are found in the highly polygynous birds of paradise (Paradisaeidae), in which plumage features and behavioral displays are extremely elaborate and diverse yet show little convergence among taxa (Scholes 2008). These patterns contrast strongly with the relatively constrained pattern of plumage and display evolution in the predominantly monogamous tyrant flycatchers (Tyrannidae; Prum 1997).

Macroevolutionary patterns in the polygynous oropendolas and the monogamous orioles present a similar contrast. As in the manakins, plumage and vocal display elements in the oropendolas

have changed rapidly with surprisingly little convergence among taxa, suggesting unconstrained evolution in which new features have accumulated without many concurrent losses of earlier ones (Price and Lanyon 2002b; also see Møller and Pomiankowski 1993). As a result, oropendolas exhibit a variety of derived morphological and behavioral features that are unusual in New World blackbirds, if not songbirds in general, including various integumentary facial ornaments and extremely extravagant and diverse songs (Jaramillo and Burke 1999; Price and Lanyon 2002b, 2004a). Furthermore, assuming that male color patterns are under sexual selection, the apparent lack of natural selection against correlated changes in female oropendolas is consistent with the idea that these features have little to do with viability or condition, conforming well to the predictions of arbitrary Fisherian selection (Fisher 1958; Lande 1981; Kirkpatrick 1982; Prum 1997). In contrast, plumage and song in the socially monogamous orioles exhibit a much more constrained evolutionary pattern, in which nearly identical color patterns and song features have appeared repeatedly among different lineages throughout the clade (Omland and Lanyon 2000; Allen and Omland 2003; Hoekstra and Price 2004; Price et al. 2007). This pattern is more consistent with indicator models of sexual selection, which predict diversification through successive switching to new traits (Schluter and Price 1993), but which also predict evolutionary trade-offs and the loss of previous costly traits through natural selection (Badyaev et al. 2002). Successive switching among a limited array of potential traits should result in repeated patterns of evolutionary convergence (Prum 1997), as we see in the oriole clade.

Costs that constrain the evolution of novel display traits may be relatively low in highly polygynous species that have no paternal investment, whereas costly indicator mechanisms may predominate in taxa that have lengthy pair bonds and parental investment by both sexes (Prum 1997). Our results should not imply, however, that Fisherian and indicator selection mechanisms have been solely responsible for historical changes in oropendola and oriole traits, respectively. These models represent ends of a continuum and both presumably contribute in various degrees during character evolution (Kokko et al. 2006). Indeed, oropendola traits presumably do have some functions as indicator mechanisms (e.g., Price et al. 2006) and oriole traits may evolve in part through Fisherian selection. Our results simply suggest differences in the predominant mechanisms of evolutionary change in each group, which may correspond with their predominant mating systems.

Altogether, our study provides empirical support for two ideas: (1) that male color patterns diverge more rapidly in polygynous than in monogamous taxa and, (2) that different modes of selection may predominate under different mating systems. But our results raise new questions as well. For instance, why have female color patterns changed so rapidly in polygynous species, in concert with males? Is this due to sexual selection, or something

else? Furthermore, given the general lack of character convergence in the oropendolas and caciques, why have plumage and song traits converged so strikingly between *P. oseryi* and the true oropendola clade? Are there particular attributes (e.g., green colors and low frequency sounds) that are especially favored among highly polygynous taxa in this group? And finally, what are the relative contributions of different selection mechanisms to the various plumage and display patterns we see today? Different plumage colors (e.g., carotenoid-based vs. melanin-based colors) and different song features can have very different potential utilities as indicators of quality (Badyaev et al. 2002; McGraw 2006a,b; Price and Lanyon 2004a; Price et al. 2006), and such factors may have played important evolutionary roles in the historical patterns shown here. We know little about how colors and songs function in male–male competition and in female mate choice in these birds, and it will be interesting to investigate these questions through detailed studies of individual species in the field.

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