SONG AND PLUMAGE EVOLUTION IN THE NEW WORLD ORIOLES (*ICTERUS*) SHOW SIMILAR LABILITY AND CONVERGENCE IN PATTERNS

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Both song and color patterns in birds are thought to evolve rapidly and exhibit high levels of homoplasy, yet few previous studies have compared the evolution of these traits systematically using the same taxa. Here we reconstruct the evolution of song in the New World orioles (*Icterus*) and compare patterns of vocal evolution to previously reconstructed patterns of change in plumage evolution in this clade. Individual vocal characters exhibit high levels of homoplasy, reflected in a low overall consistency index (CI = 0.27) and retention index (RI = 0.35). Levels of lability in song are comparable to those found for oriole plumage patterns using the same taxa (CI = 0.31, RI = 0.63), but are strikingly dissimilar to the conservative patterns of change seen in the songs of oropendolas (*Psarocolius, Ocyalus*; CI = 0.82, RI = 0.87), a group closely related to the orioles. Oriole song is also similar to oriole plumage in exhibiting repeated convergence in overall patterns, with some distantly related taxa sounding remarkably similar. Thus, both song and plumage in orioles show repeated convergence in individual elements and in overall patterns across the clade, suggesting that both of these character classes are highly labile between taxa yet highly conserved within the genus. Our results provide new insights into the tempo and mode of evolution in sexually selected traits within and across clades.

KEY WORDS: Ancestral state reconstruction, animal signals, bird song, concerted homoplasy, convergent evolution, evolutionary constraint, sexual selection.

The elaborate songs and color patterns of birds are influenced by sexual selection (Andersson 1994), and thus both of these traits are thought to evolve rapidly (Schutler and Weatherhead 1990; Read and Weary 1992; Burns 1998; Omland and Hofmann 2006). Behavioral characters such as song and integumentary features such as plumage are generally assumed to provide little information about relationships among taxa, primarily because both are presumed to exhibit high levels of evolutionary lability and homoplasy (e.g., Atz 1970; Chu 1998; Omland and Lanyon 2000;

Blomberg et al. 2003; but see de Queiroz and Wimberger 1993). Indeed, taxa that are very closely related genetically can exhibit large differences in both song features and plumage (e.g., Irwin et al. 2001; Kondo et al. 2004; Zink et al. 2005; Hofmann et al. 2006), strongly indicating that changes in these traits have occurred recently and relatively rapidly. Studies using ancestral state reconstruction methods have investigated the evolutionary histories of song features (reviewed in ten Cate 2004) and plumage patterns (reviewed in Omland and Hofmann 2006) in various groups

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of passerine birds. Yet, no previous studies have compared the evolutionary lability of these traits in a systematic and rigorous way by reconstructing both song and plumage evolution in the same taxa.

Recent phylogenetic comparative studies of two closely related avian groups, the oropendolas (*Psarocolius, Ocyalus*) and the orioles (*Icterus*), suggest that song features and color patterns have very different levels of evolutionary lability. Both groups are members of the New World blackbirds (Icterini) and are closely related to each other based on mitochondrial DNA (mtDNA) sequence data (Lanyon and Omland 1999; Klicka et al. 2000). Price and Lanyon (2002b) reconstructed the evolution of song in the oropendolas by mapping vocal features onto an mtDNA-based phylogeny. This analysis revealed that many aspects of oropendola song are evolutionarily conservative and exhibit a remarkable lack of homoplasy on the tree. Song features can even be used for assessing relationships among oropendola taxa with surprising accuracy (Price and Lanyon 2004a). In contrast, a similar study by Omland and Lanyon (2000), which reconstructed the evolution of plumage patterns in 45 oriole taxa, found comparatively high levels of homoplasy. Individual plumage patches in orioles show repeated examples of reversal and convergence during evolutionary history, which has resulted in some distantly related species that are remarkably similar in overall plumage pattern (e.g., *Icterus galbula* and *Icterus spurius*; see Hoekstra and Price 2004). These dramatic examples of overall plumage convergence have since been confirmed using independent trees based on several nuclear introns (Allen and Omland 2003; unpubl. data). Whether the different levels of evolutionary lability seen in oropendola song and oriole plumage patterns can be explained by differences in how these character classes generally evolve, or by other factors, has not been previously tested.

Here, we reconstruct the evolutionary history of song in the New World orioles, using vocal characters that were used previously in reconstructing song evolution in oropendolas (Price and Lanyon 2002b) and a molecular phylogeny used in previous reconstructions of plumage evolution in orioles (Omland et al. 1999; Omland and Lanyon 2000; Hofmann et al. 2006, 2007). The orioles comprise the most speciose genus in the blackbird family and exhibit a wide diversity of both song and plumage patterns (Howell and Webb 1995; Hardy et al. 1998; Jaramillo and Burke 1999). Thus, they are an ideal group for addressing questions about how acoustic and visual signals evolve. Moreover, because the characters we use for reconstructing song evolution in orioles were also used previously in examining song evolution in oropendolas (Price and Lanyon 2002b, 2004a,b), our study also allows us to directly compare patterns of vocal evolution in two closely related yet phylogenetically independent groups of birds. Has oriole song evolved in a conservative manner, as found in the songs of oropendolas (Price and Lanyon 2002b), or with re-

peated convergence and reversals, as in the color patterns of orioles (Omland and Lanyon 2000)? This was the primary question our study addressed.

Methods
SONG MEASUREMENTS

Recordings of oriole vocalizations were obtained in the field by the authors, from the Macaulay Library of Natural Sounds at Cornell University, and from several commercially available cassette tapes (Coffey and Coffey 1989; Peterson 1990; Hardy et al. 1998; source details available from the authors). Multiple recordings from different geographical areas and by different recordists were available for most species. We generated spectrograms of songs using Raven sound analysis software (version 1.2; Cornell Laboratory of Ornithology, Ithaca, NY; sampling frequency = 44.1 kHz; frequency resolution = 124 Hz; time resolution = 11.6 msec). Orioles produce a variety of different types of sounds in addition to what are generally considered songs (Hardy et al. 1998; Jaramillo and Burke 1999). Therefore, in our study we defined a "song" as any vocalization that included tonal elements, was longer than 0.5 sec in duration, and was preceded and followed by intervals greater than 1 sec. This definition allowed us to include the complex whistled vocalizations of many species while excluding broadband chatters and short calls. To maximize the independence of our samples, we analyzed only one relatively undistorted example of song from each recording. Recordings made at different geographic locations were assumed to be of different individual birds, and recordings that did not include a clear song example were discarded. In all we measured 276 songs, each presumably from a different bird, with one to 45 songs representing each of 35 different oriole taxa (mean = 7.9, SE = 1.8 songs/taxon).

In many oriole species both males and females are known to sing (Beletsky 1982; Jaramillo and Burke 1999), so when possible we used recordists' notes in an attempt to measure only the songs of males. Such information was often not available, however, primarily because many oriole taxa are monochromatic and thus males and females are difficult to distinguish in the field (Howell and Webb 1995; Jaramillo and Burke 1999). Female song has been described as very similar to male song in previously studied oriole taxa (Miller 1931; Howell 1972; Beletsky 1982; Flood 1990; Scharf and Kren 1996; Skutch 1996; Rising and Flood 1998; Jaramillo and Burke 1999; Pleasants and Albano 2001). Furthermore, preliminary inspections of recordings in this study suggested that any differences between the sexes within taxa would be relatively small in comparison to differences between taxa. For these reasons, we assumed that any variation in our song measures caused by combining male and female song within taxa was unlikely to influence our reconstructions of evolutionary change.

Table 1. Descriptions of the 26 oriole song characters and their character states.

(1) Click: Short pulse of broadband sound less than 15 msec long. Produced singly (i.e., not as part of a trill [see 2]). 0: absent, 1: present.

(2) Trill: Rapid series of identical note patterns repeated at least 5 times/second. 0: absent, 1: present.

(3) Broadband: Harsh, broadband sound more than 15 msec long. 0: absent, 1: present.

(4) Squawk: Rapidly frequency modulated tone. 0: absent, 1: present.

(5) Whine: Harmonically rich sound more than 15 msec long, with no clear fundamental frequency. 0: absent, 1: present.

(6) Song duration: Time from the beginning to the end of a song.. 0: less than 1.4 sec, 1: 1.4 sec to 1.6 sec, 2: greater than 1.6 sec.

(7) Note percentage: Summed duration of all notes in a song divided by the song duration. 0: could not be parsed into more than one character state.

(8) Tone percentage: Summed duration of tones (i.e., not broadband notes) in a song divided by the song duration. 0: could not be parsed into more than one character state.

(9) Note overlap: Summed duration of overlapping notes (indicating production of two different sounds by the syrinx simultaneously) divided by the song duration. Notes were counted as overlapping only if their frequencies were not integer multiples of each other and/or they appeared to have different frequency slopes in spectrograms. 0: less than 2%, 1: greater than 2%.

(10) Longest note: Longest continuous sound measured in a song. 0: less than 0.12 sec, 1: greater than 0.12 sec.

(11) Longest pause: Longest interval between notes in a song. 0: could not be parsed into more than one character state.

(12) Average note duration: Summed pause duration divided by the number of pauses in a song. 0: less than 0.28 sec, 1: greater than 0.28 sec.

(13) Average pause duration: Summed pause duration divided by the number of pauses in a song. 0: less than 0.29 sec, 1: greater than 0.29 sec.

(14) Pause rate: Number of pauses in a song divided by the song duration. 0: less than 1.95/second, 1: greater than 1.95/second.

(15) Trill rate: Number of notes per second during a trill (see 2). 0: less than 2.5/second, 1: 2.5/second to 5.75/second, 2: 5.75/second to 7.75/second, 3: 7.75/second to 12.35/second, 4: greater than 12.35/second.

(16) Overall peak frequency: Frequency with highest amplitude in entire song. 0: could not be parsed into more than one character state.

(17) Highest frequency: Highest emphasized frequency occurring in a song. 0: less than 2.9 kHz, 1: 2.9 kHz to 6 kHz, 2: 6 to 6.75 kHz, 3: greater than 6.75 kHz.

(18) Lowest frequency: Lowest emphasized frequency occurring at any point in a song. 0: less than 1 kHz, 1: greater than 1 kHz.

(19) Frequency range: Difference between the highest and lowest frequencies (see 18 and 19) in a song. 0: less than 1.7 kHz, 1: 1.7 kHz to 3.1 kHz, 2: 3.1 to 3.6 kHz, 3: 3.6 kHz to 5.3 kHz, 4: greater than 5.3 kHz.

(20) Frequency shift rate: Number of frequency shifts in a song divided by the song duration. A frequency shift was defined as a change in frequency greater than 1 kHz in less than 20 msec. 0: less than 0.75/second, 1: 0.75/second to 1.25/second, 2: 1.25/second to 1.65/second, 3: greater than 1.65/second.

(21) Maximum frequency shift: The largest frequency shift measured in a song. 0: less than 1 kHz, 1: 1 kHz to 2.5 kHz, 2: greater than 2.5 kHz.

(22) Note frequency range: The average frequency range of notes within a song. 0: less than 1.6 kHz, 1: greater than 1.6 kHz.

(23) Frequency slope: Reflects the overall frequency pattern of a song. Scored by first measuring the temporal positions (first, second, third, or fourth quarter of the song) of the highest and lowest frequencies (see 18 and 19), and then subtracting the quarter with the lowest frequency from the quarter with the highest frequency. 0: could not be parsed into more than one character state.

(24) Amplitude peak: Reflects the overall amplitude pattern of a song, based on the temporal position of the overall peak amplitude (first, second, third, or fourth quarter of the song). 0: less than -1, 1: greater than -1.

(25) Note diversity: Number of distinct note "types" in a song divided by the total number of notes. 0: less than 19%, 1: 19% to 99%, greater than 99%.

(26) Note count: Total number of notes in a song. 0: less than 5, 1: 5 to 27, 2: greater than 27.

We used Raven to measure 26 different components of each song (Table 1), 21 of which corresponded to characters used by Price and Lanyon (2002b) in their study of song evolution in oropendolas. Five of our characters (characters 1–5) were chosen to reflect the presence or absence of a particular type of sound in a taxon's song. We classified sounds into types based on consistent patterns in frequency and duration (e.g., tonal or broadband, shorter or longer than 15 msec), and we scored characters as "present" if they appeared in any of a taxon's songs and "absent" if they never appeared. Twenty-one characters (characters 6–26) were based on measurements of continuous variables in songs, reflecting aspects of temporal and frequency structure.

Several characters from Price and Lanyon (2002b) could not be used in our analysis because they reflected components of oropendola songs that do not appear to occur in oriole song (e.g., rattles, bow displays, and wingflaps), or because our recordings were not long enough to accurately measure the characters (e.g., song type versatility). Five characters were included in our study that were not included in that of Price and Lanyon (2002b): whines (character 5), average note duration (character 12), note frequency range (character 22), note diversity (character 25), and note count (character 26).

ANCESTRAL STATE RECONSTRUCTION

We reconstructed evolutionary changes in song in MacClade 4.06 (Maddison and Maddison 2003) using a published mtDNA phylogeny for the orioles (Omland et al. 1999; also see Allen and Omland 2003). This phylogeny was used previously to reconstruct changes in plumage evolution in orioles (Omland and Lanyon 2000; Hofmann et al. 2006, 2007). We used Google Earth (version 3; http://earth.google.com/index.html) and published range maps (Howell and Webb 1995; Jaramillo and Burke 1999) to confirm that song-recording locations corresponded to the subspecies sampled in the molecular studies.

To identify consistent vocal differences between taxa that might indicate historical changes in song, we converted our measurements of continuous song features (characters 6–26 in Table 1) into discrete characters before mapping them onto the molecular tree. We parsed each continuous character into discrete, unordered character states by plotting means and standard errors for taxa and then dividing these measures into states in which error bars did not overlap (see Price and Lanyon 2002b, 2004b for more detailed explanations of this technique). Divisions between states were positioned equidistant from nearest error bars. This method allowed us to detect statistically discontinuous evolutionary changes while controlling for within-taxon variability in song patterns. Only taxa that had a minimum of three song samples (20 of the 35 taxa) were used in the defining of character states to ensure a minimal degree of accuracy in the placement of error bars, and error bar size was not significantly influenced by sample size (ANOVA using mean bar sizes: $F_{1,18} = 0.33$, $r^2 = 0.018$, $P = 0.57$). Five characters could not be parsed into more than one character state and thus were scored as constant across taxa: note percentage (character 7), tone percentage (character 8), longest pause (character 11), overall peak frequency (character 16), and frequency slope (character 23) (see Table 1). We scored the remaining 21 characters for all oriole taxa, including those with fewer than three representative songs, based on mean measurements of song features. We did not require a minimum number of measurements for scoring characters (in contrast to our criteria for defining character states) to maximize the number of taxa we were able to include. All mean measurements based on fewer than three songs fell within the character

states calculated using other taxa, so these measurements would not have generated additional character states.

We calculated the consistency index (CI) and retention index (RI) for all of the song characters reconstructed onto the tree using MacClade to assess the degree to which our song data were congruent with the molecular phylogeny. For both the CI and RI, a score of 1 represents perfect congruence with phylogeny (i.e., no evolutionary convergence or reversals), whereas a score approaching 0 indicates high levels of homoplasy and thus evolutionary lability in our song characters. We compared the scores calculated for oriole song to those calculated for color patterns in orioles (Omland and Lanyon 2000) and for song in oropendolas (Price and Lanyon 2002b) to assess the relative levels of homoplasy of both character types in these two closely related groups. We recalculated values for oriole plumage characters using the same 35 oriole taxa included in the present study and recalculated overall values for song evolution in oropendolas using the same song characters used here to make our results directly comparable.

To further explore how well our song characters reflected molecular relationships, as well as the congruence among song characters, we performed parsimony searches using the song dataset in PAUP* (Swofford 2002; heuristic searches, equally weighted). We also used the Incongruence Length Difference (ILD) test in PAUP* to assess levels of incongruence between different datasets, specifically song versus mtDNA and song versus plumage (1000 replicates, heuristic parsimony searches, random addition). These analyses also allowed us to examine the possibility that vocal characters support relationships different than those indicated by molecular data. Given that molecular relationships among most oriole taxa are now well supported by both mtDNA (Omland et al. 1999) and multiple nuclear introns (Allen and Omland 2003; unpubl. data), such a conflict between the song data and molecular data would provide strong evidence for homoplasy in our vocal characters.

In their previous study of plumage evolution in orioles, Omland and Lanyon (2000) examined convergence in overall plumage pattern by plotting pairwise differences in plumage characters as a function of mtDNA sequence divergence. This graph had a triangular shape with a positive upper bound limit to plumage divergence, which increased linearly with increased molecular distance (see Omland and Lanyon 2000, fig. 8). The minimum number of plumage differences in this graph, however, did not change with molecular distance, showing that distantly related taxa could be just as similar in their overall plumage pattern as could closely related taxa. Points on this graph representing few plumage differences but large molecular divergences indicated some extreme examples of evolutionary convergence in overall plumage patterns. To investigate the possibility of similar convergence in oriole song features, and to examine the relationship between song distance and molecular distance, we constructed a graph in which pairwise

differences in song characters were plotted against molecular sequence divergence. We also replotted the graph from Omland and Lanyon (2000) using only the 35 taxa included in the present study for comparison.

Results

EVOLUTIONARY LABILITY IN INDIVIDUAL SONG CHARACTERS

Twenty-one of the 26 vocal characters examined in our study varied across oriole taxa (Table 2) and thus allowed us to reconstruct historical changes in song. Tracing these 21 characters (13 binary and eight multistate) onto the molecular tree revealed high levels of homoplasy, with every character exhibiting at least some convergence on the tree and many showing evidence of evolutionary reversals. Only three characters had any states that were uniquely derived in taxa (i.e., autapomorphic): longest note (character 10), trill rate (character 15), and highest frequency (character 17). Song characters had an overall CI of 0.27 and an overall RI of 0.35 (Table 3), with phylogenetically uninformative characters excluded from the analysis. Individual CIs ranged from 0.11 to 1.00 and RIs ranged from 0.00 to 0.67, with the majority of characters having CIs and RIs less than 0.50. Figure 1 shows ancestral state reconstructions of two characters that showed high (click:

Table 2. Matrix of song character scores for oriole taxa (*Icterus*). Character descriptions are listed in Table 1. *N* indicates number of individuals sampled.

Taxon	N	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
I. cayanensis cayanensis	10	1	1	1	0	1	2	0	0	1	1	0	0	0	1	4	0	1	1	3	1	1	0	0	1	1	1
I. cayanensis periporphyrus	2	0	1	0	0	0	2	0	0	0	1	0	0	1	0	4	0	1	1	1	0	0	0	0	1	1	1
I. cayanensis pyrrhopterus	2	1	1	0	0	0	2	0	0	0	1	0	1	0	1	3	0	1	1	3	1	1	0	0	1	1	1
I. chrysocephalus	2	1	1	0	0	0	2	0	0	0	1	0	0	0	1	3	0	1	1	3	1	1	0	0	1	1	1
I. dominicensis portoricensis	2	1	0	0	0	0	2	0	0	0	1	0	0	0	1	0	0	1	1	3	1	2	0	0	1	2	1
I. oberi	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	1	3	1	1	0	0	2	0
I. laudabilis	1	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	1	1	0	0	0	0	1	2	1
I. dominicensis melanopsis	3	0	0	0	0	0	2	0	0	0	1	0	0	0	1	0	0	1	1	1	0	0	0	0	0	2	1
I. spurius spurius	40	1	1	1	1	0	2	0	0	1	1	0	0	0	1	4	0	2	1	3	4	2	0	0	1	1	1
I. cucullatus nelsoni	9	1	0	0	1	1	2	0	0	1	1	0	0	0	1	0	0	3	1	4	3	2	1	0	1	1	1
I. cucullatus cucullatus	2	1	0	0	0	1	2	0	0	1	1	0	0	0	1	0	0	3	0	4	4	2	1	0	1	1	1
I. wagleri wagleri	1	1	0	1	0	1	2	0	0	1	1	0	0	0	1	0	0	1	1	2	1	1	0	0	1	2	1
I. maculialatus	1	0	0	0	0	0	2	0	0	1	1	0	0	1	0	0	0	1	1	1	1	1	0	0	1	2	1
I. jamacaii croconotus	6	0	0	0	0	0	2	0	0	0	1	0	1	1	0	0	0	1	1	1	0	0	0	0	1	1	1
I. icterus ridgwayi	2	0	0	0	0	0	2	0	0	0	1	0	0	0	1	0	0	0	1	1	0	2	0	0	1	1	1
I. graceannae	4	0	0	0	0	0	2	0	0	1	1	0	0	0	1	0	0	1	1	1	0	0	0	0	1	1	1
I. pectoralis	9	0	0	1	0	1	2	0	0	1	1	0	0	0	1	0	0	1	1	1	0	0	0	0	1	1	1
I. mesomelas mesomelas	8	0	0	0	0	0	2	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1	0	0	1	0	2
I. mesomelas taczanowskii	3	0	0	0	0	0	2	0	0	0	1	0	0	0	1	0	0	1	1	1	1	2	0	0	0	1	1
I. mesomelas salvinii	2	0	0	0	0	0	2	0	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	0	1	0	1
I. gularis gularis	2	0	0	1	0	1	2	0	0	0	1	0	0	0	1	0	0	1	1	1	0	0	0	0	1	1	1
I. gularis yucatanensis	1	0	1	1	0	1	2	0	0	0	1	0	0	0	1	2	0	1	1	1	0	0	0	0	1	1	2
I. gularis tamaulipensis	3	0	1	1	0	1	2	0	0	0	1	0	0	0	1	2	0	1	1	1	1	1	0	0	1	1	1
I. nigrogularis nigrogularis	6	1	1	1	1	0	2	0	0	0	1	0	0	0	1	1	0	1	0	1	0	0	0	0	1	1	1
I. leucopteryx leucopteryx	3	0	0	0	0	0	2	0	0	0	1	0	0	0	1	0	0	1	1	1	0	0	0	0	1	1	1
I. pustulatus microstictus	23	1	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	1	1	1	1	1	0	0	1	2	1
I. pustulatus pustulatus	22	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	2	1	1	0	0	1	1	0
I. bullockii	13	1	0	1	0	0	2	0	0	1	1	0	0	0	1	0	0	1	0	3	2	2	1	0	1	1	1
I. galbula	29	1	1	1	0	1	2	0	0	0	1	0	0	0	1	3	0	1	1	1	1	1	0	0	1	1	1
I. abeillei	1	0	0	1	0	1	2	0	0	0	1	0	0	0	1	0	0	1	1	3	2	1	0	0	1	1	2
I. parisorum	45	0	0	0	0	1	2	0	0	1	1	0	0	0	1	0	0	1	1	1	1	1	0	0	1	1	1
I. chrysater giraudii	6	1	0	0	0	0	2	0	0	1	1	0	0	0	1	0	0	1	1	1	1	1	0	0	1	1	1
I. chrysater chrysater	5	0	0	0	0	1	2	0	0	1	1	0	0	0	1	0	0	1	1	1	1	1	0	0	1	2	1
I. graduacauda audubonii	5	0	0	0	0	0	2	0	0	1	1	0	1	1	0	0	0	0	1	0	0	0	0	0	1	2	1
I. graduacauda graduacauda	2	0	0	0	0	0	2	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1

Table 3. Measures of homoplasy for song characters mapped onto the oriole phylogeny and these same characters reconstructed in oropendolas (from Price and Lanyon 2002b). Consistency index (CI) and retention index (RI) values are for individual characters, with overall scores in parentheses.[1]

Character (overall index)		Oriole songs		Oropendola songs	
		CI (.27)	RI (.35)	CI (.82)	RI (.87)
1	Click	.11	.38	1.00	1.00
2	Trill	.20	.50	1.00	1.00
3	Broadband	.11	.33	.50	.50
4	Squawk	.33	.00	1.00	1.00
5	Whine	.13	.36	NA	NA
6	Song duration	.50	.00	1.00	1.00
7	Note percentage	.00	.00	1.00	1.00
8	Tone percentage	.00	.00	1.00	1.00
9	Note overlap	.17	.67	1.00	1.00
10	Longest note	1.00	.00	1.00	1.00
11	Longest pause	.00	.00	.67	.00
12	Average note duration	.33	.00	NA	NA
13	Average pause duration	.25	.00	.67	.00
14	Pause rate	.25	.25	1.00	1.00
15	Trill rate	.57	.40	1.00	1.00
16	Overall peak frequency	.00	.00	.00	.00
17	Highest frequency	.60	.50	1.00	.00
18	Lowest frequency	.17	.00	.00	.00
19	Frequency range	.40	.33	1.00	.00
20	Frequency shift rate	.29	.38	1.00	.00
21	Maximum frequency shift	.14	.33	1.00	.00
22	Note frequency range	.33	.33	NA	NA
23	Frequency slope	.00	.00	1.00	1.00
24	Amplitude peak	.33	.00	.00	.00
25	Note diversity	.22	.30	NA	NA
26	Note count	.40	.00	NA	NA

[1]Overall values for oropendolas were recalculated using only the characters shown. NA indicates characters not included in Price and Lanyon (2002b).

character 1) and average (note diversity: character 25) levels of homoplasy. These and most other characters showed repeated independent gains as well as evidence of one or more evolutionary reversals.

Tracing unambiguous changes in oriole song features on the tree (Fig. 2) provided strong evidence that song has changed rapidly in this group. Only 10% of reconstructed changes (nine of 83) occurred on branches of the oriole phylogeny above the species level, whereas 77% occurred on terminal branches. All of the changes on deeper branches were either convergent with other changes on the tree, were reversed on later branches, or both. The presence of multiple, recent changes is a strong indicator of rapid evolutionary change. This pattern of rapid change is especially evident in song differences among closely related species and subspecies. For example, the Baltimore oriole (*I. galbula*) and black-backed oriole (*Icterus abeillei*) are very close to each other genetically (Omland et al. 1999; Allen and Omland

2003; Kondo et al. 2004; Kondo 2006), but these species differ consistently in six of the 21 informative vocal characters we measured (Fig. 2, Table 2). Likewise, subspecies of the streak-backed oriole (*Icterus pustulatus pustulatus* and *I. p. microstictus*) are indistinguishable based on mitochondrial cytochrome-*b* sequence data (M. N. Cortes-Rodriguez and K. E. Omland, unpubl. data) yet their songs differ in five vocal characters.

No single feature of oriole song tracked the molecular phylogeny, and few character states unambiguously defined relationships above the species level. Heuristic parsimony searches of the song data alone resulted in 1970 equally parsimonious trees (length 92 steps; CI = 0.39, RI = 0.61; 100 random additions), indicating little congruence among song characters. There was also significant incongruence between the song and mtDNA data, as well as between oriole song and plumage (ILD tests, $P < 0.001$). However, despite such extensive homoplasy, some conspecific relationships on the molecular tree were consistently supported
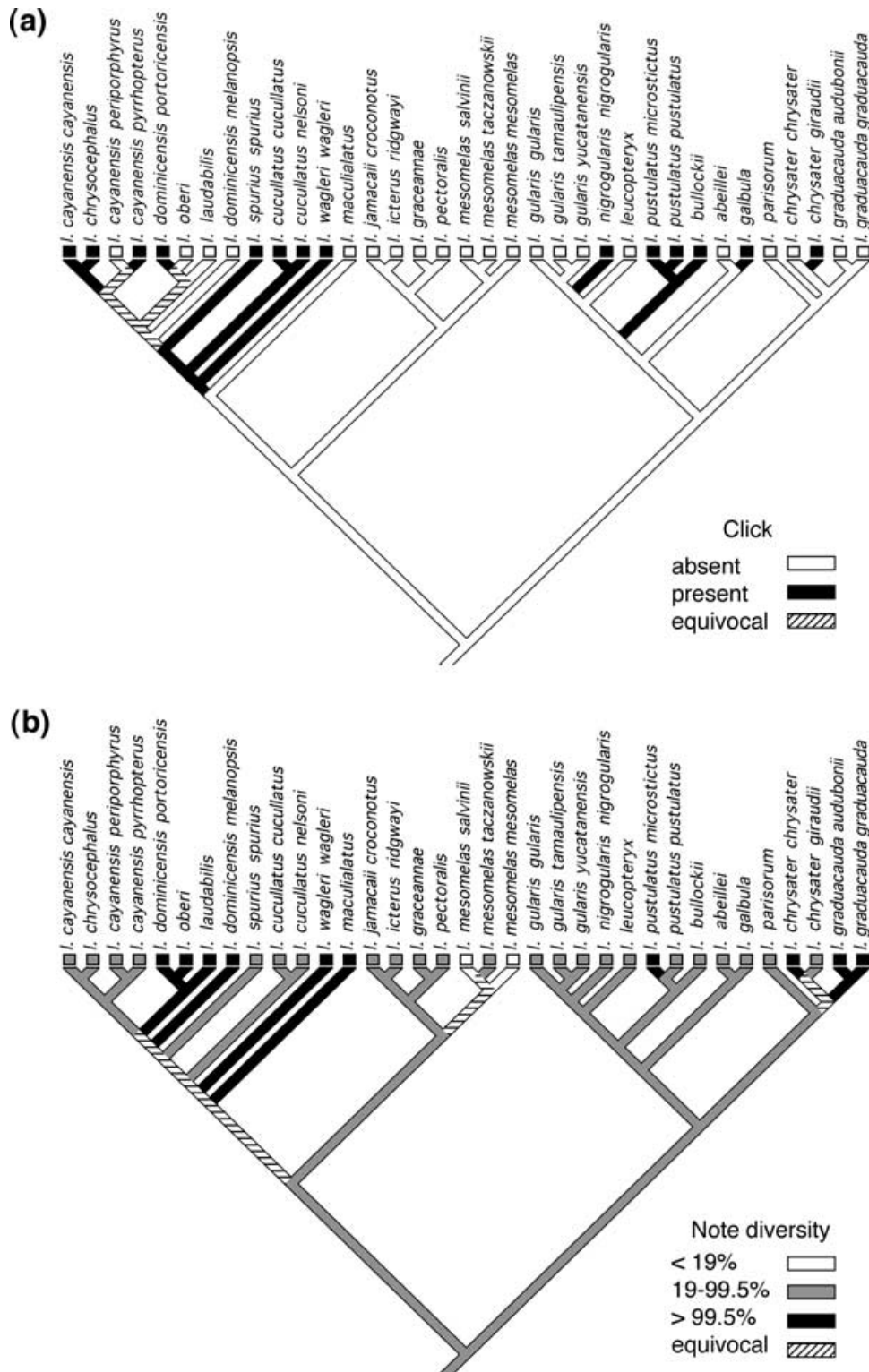
Figure 1. Ancestral state reconstruction of two typical song characters. (a) Click presence or absence has the highest level of homoplasy (CI = 0.11, character 1) and shows at least five independent gains. (b) Note diversity has close to average homoplasy (CI = 0.22, character 25) and shows multiple examples of both increases and decreases in note diversity, as well as potential reversals. Character descriptions are in Table 1. (MacClade 4.06; ancestral state reconstructions using unordered simple parsimony.)
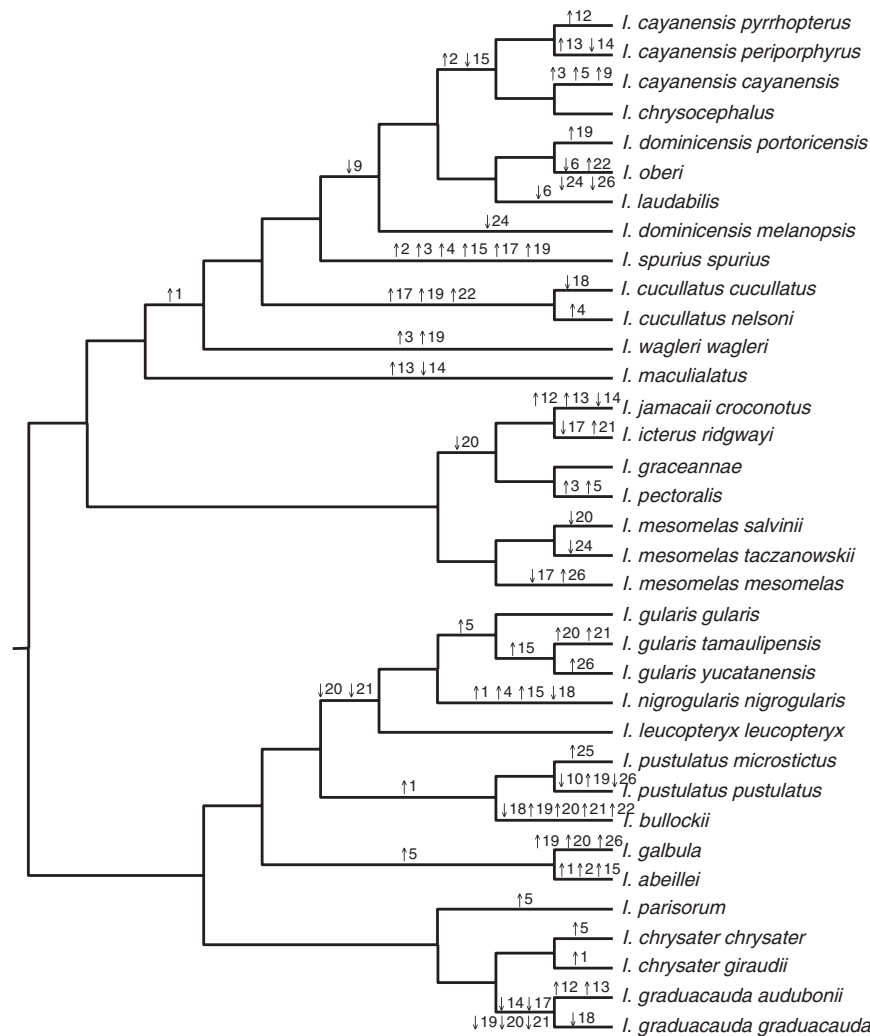
Figure 2. Unambiguous evolutionary changes in oriole song reconstructed on the molecular tree. Arrows and character numbers on branches show the gain/increase (up arrows) or loss/decrease (down arrows) in characters. Note the predominance of changes on terminal and other recent branches of the phylogeny.

by song. The relationship between subspecies of the hooded oriole (*Icterus cucullatus igneus* and *I. c. nelsoni*) was supported by shared derived states (i.e., synapomorphies) in at least three different song characters: highest frequency (character 17), frequency range (character 19), and note frequency range (character 22). A bootstrap analysis of the song data resolved these subspecies as sister taxa in 72% of bootstrap psuedoreplicates. Likewise, subspecies of Audubon's oriole (*I. graduacauda graduacauda* and *Icterus graduacauda audubonii*) were resolved in 52% of bootstrap pseudoreplicates and were supported by synapomorphies in at least five song characters: pause rate (character 14), highest frequency (character 17), frequency range (character 19), frequency shift rate (character 20), and maximum frequency shift (character 21). No other nodes were supported in >50% of the bootstrap pseudoreplicates.

COMPARISONS TO OROPENDOLA SONG AND ORIOLE PLUMAGE CHARACTERS

Comparing homoplasy indices for oriole song characters to scores calculated for oropendola song (Price and Lanyon 2002b) revealed very different levels of evolutionary lability (Table 3). Using just the 21 characters included in both studies, oropendola songs had an overall CI of 0.82 and RI of 0.87, much higher than the values for oriole song using these same characters (CI = 0.28, RI = 0.36). Most characters (61% of those that varied among taxa) showed no evidence of convergence or reversal on the oropendola phylogeny, and only 44% of reconstructed changes in oropendola song occurred on terminal branches (see Price and Lanyon 2002b, fig. 2). Many changes appear to have occurred on deeper branches of the oropendola tree, and these features have since changed little in descendent taxa. Indeed, within one wide ranging oropendola

species, the Crested Oropendola (*Psarocolius decumanus*), in which multiple subspecies were sampled with genetic distances much greater than that between *I. galbula* and *I. abeillei* in the same mtDNA gene regions, no song differences were found at all (1.7% mtDNA divergence on average in *P. decumanus* compared to 0.5% divergence between *I. galbula* and *I. abeillei*; uncorrected p distances; Omland et al. 1999; Price and Lanyon 2002a,b).

We also calculated homoplasy indices for oriole plumage (Omland and Lanyon 2000) using the same subset of 35 taxa that we included in our analysis of oriole song. Plumage patches had an overall CI of 0.31 and overall RI of 0.63 when mapped onto this phylogeny. Like vocal characters, plumage characters provide multiple examples of convergence and reversal. Only 20% of reconstructed changes in plumage pattern (24 of 118) occurred on branches above the species level, suggesting that many changes have occurred relatively recently. Likewise, some closely related taxa that differed in song characters in our study also differ in plumage pattern (e.g., *I. galbula* and *I. abeillei,* Omland and Lanyon 2000).

CONVERGENCE IN OVERALL SONG PATTERNS

Plotting pairwise song differences as a function of molecular sequence divergence in orioles (Fig. 3a) resulted in a point distribution remarkably similar to that shown by plotting plumage differences against molecular divergence (Fig. 3b). Both graphs have a similar upper bound limit to the maximum number of character differences between taxa, which increases nearly linearly with increasing sequence divergence. However, both graphs also show little relationship between the minimum number of character differences and molecular divergence. Distantly related taxa can be just as similar in song or in plumage as can closely related taxa. Thus, although there does appear to be an upper limit on the rate of character divergence between taxa, shown by the absence of points in the upper left portion of each graph, below this limit the number of differences in song or in plumage provides no information about phylogenetic relationships. Oriole song appears to be just as homoplastic as oriole plumage patterns (Omland and Lanyon 2000). This is very different from the evolutionary pattern seen in oropendola song, in which vocal changes have accumulated almost linearly (see Price and Lanyon 2002b, fig. 3) and song distance provides a relatively accurate indicator of molecular distance (Price and Lanyon 2004a).

Points in the lower right portion of Figure 3a provide multiple examples of taxa that are relatively distant genetically but that have very similar overall song patterns. Song spectrograms of three example taxon pairs are shown in Figure 4 to illustrate some of these similarities visually. For example, the spot-breasted oriole (*Icterus pectoralis*) and the Altamira oriole (*icterus gularis gularis*), indicated by the point in the low far right of Figure 3a, are among the most divergent taxa genetically (10.1% divergent) yet
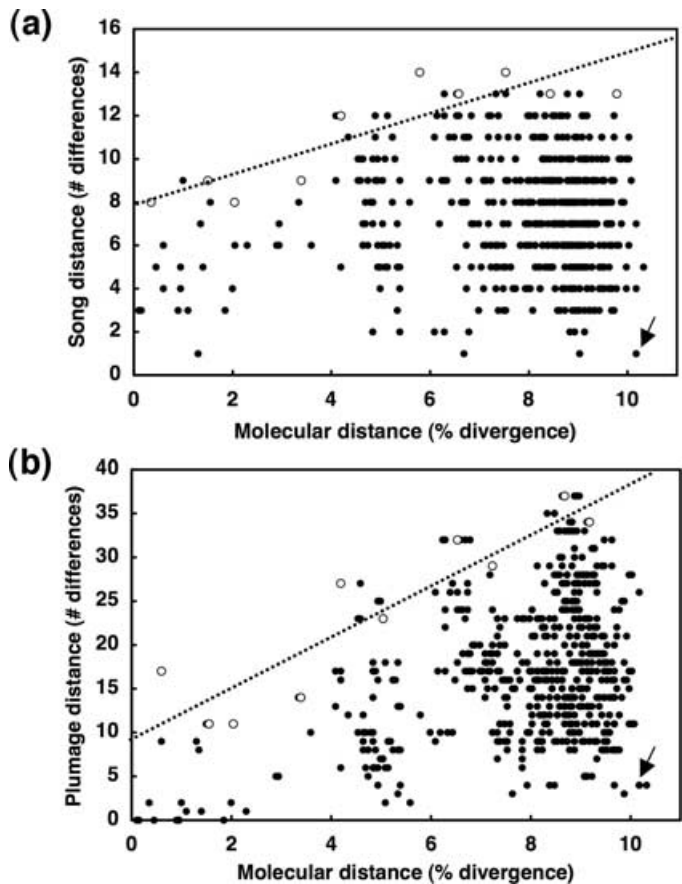

Figure 3. Plots of (a) oriole song distance and (b) oriole plumage distance as a function of molecular distance (uncorrected p distance based on mitochondrial DNA). Dashed lines illustrating the upper bound nature of both plots were calculated by binning molecular divergence values into 1% increments, selecting the greatest song or plumage distance in each bin (open circles), then calculating a linear regression through these maximal values (see Blackburn et al. (1992); song $r^2 = 0.74$, plumage $r^2 = 0.80$; not evaluated for statistical significance due to nonindependence of data points). The points indicated with an arrow in the lower right of both figures show pairwise comparisons between *I. gularis gularis* and *I. pectoralis,* indicating extreme convergence in both overall song pattern and overall plumage pattern. Plumage and molecular divergence values were obtained from Omland and Lanyon (2000) and Omland et al. (1999), respectively.

differ in only one song character (note overlap: character 9). Reconstructions of individual song characters on the tree show that these overall similarities are due at least in part to convergence in independent vocal features. The presence of broadband notes (character 3) and whines (character 5) and similarities in the rates and degrees of frequency shifts (characters 20 and 21) are all features that were independently derived in these two taxa. Likewise, the overall similarity between songs of the hooded oriole (*Icterus cucullatus nelsoni*) and Bullock's oriole (*Icterus bullockii*) is due to convergence in at least five individual song features: presence of
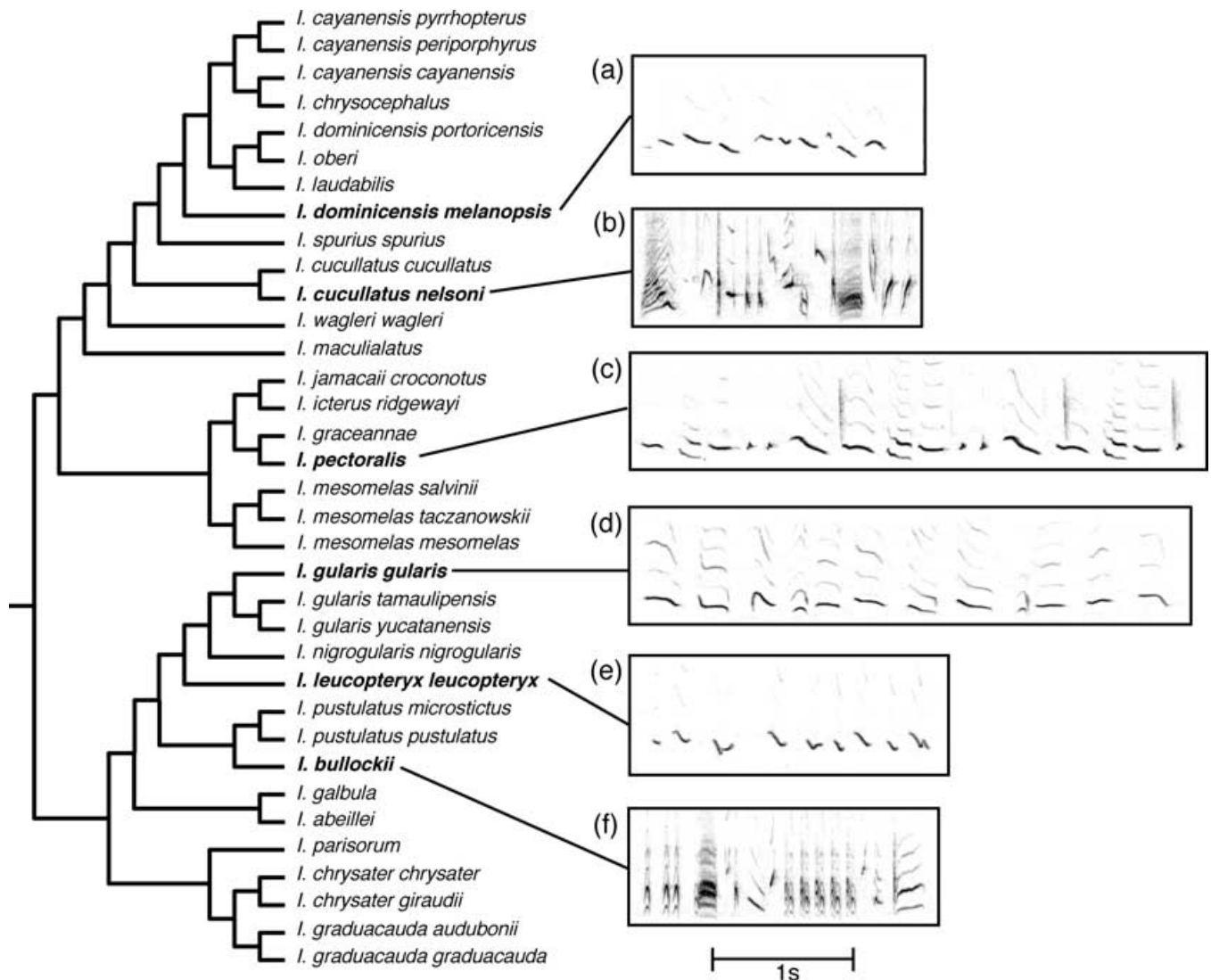
Figure 4. Examples of evolutionary convergence in overall song patterns. Relationships among taxa are shown in the phylogeny on the left. Songs of *I. dominicensis melanopsis*, *I. cucullatus nelsoni*, and *I. pectoralis* (shown as spectrograms a–c on the right) differ from each other in a variety of features, as do the songs of *I. gularis gularis*, *I. leucopteryx leucopteryx*, and *I. bullockii* (spectrograms d–f). Yet each taxon has a song that is very similar to that of a relatively distantly related taxon (a similar to e; b similar to f; c similar to d). Ancestral state reconstructions indicate that these similarities are explained in part by convergent evolution of multiple, independently derived song features.

clicks (character 1), note overlap (character 9), lowest frequency (character 18), maximum frequency shift (character 21), and note frequency range (character 22). The overall similarity of Jamaican oriole (*Icterus leucopteryx*) and Cuban oriole (*Icterus dominicensis melanopsis*) songs is due to convergence in at least four song features (characters 1, 9, 20, and 21). These three pairs of taxa are among the most extreme examples from the nearly continuous distribution of song convergence values shown in Figure 3a.

Overall convergence between these species' songs was also shown in parsimony searches of the song dataset. These analyses placed the songs of *I. pectoralis* and *I. gularis gularis* and the songs of *I. cucullatus* and *I. bullockii* each as each other's closest

relatives in the majority of trees. The songs of *I. leucopteryx* and *I. dominicensis melanopsis* were also consistently closely related. Hooded oriole (*I. cucullatus*) and Bullock's oriole (*I. bullockii*) songs were also both found to be similar to the songs of orchard orioles (*Icterus spurius spurius*), despite large molecular divergences between *I. spurius* and these two species (9.8% divergent from *I. bullockii*; 6.4% divergent from *I. cucullatus nelsoni*; uncorrected p distances; Omland et al. 1999).

Convergence in overall song patterns generally has not occurred between the same oriole taxa as have convergences in plumage pattern (Omland and Lanyon 2000). There was no relationship between song distance and plumage distance, and trees

generated using song or plumage data show little or no agreement in the placement of taxa. The exception was *I. pectoralis* and *I. gularis*, which exhibit extreme convergence in both their overall song patterns and overall plumage patterns (indicated by arrows in both Fig. 3a and b).

Comparisons of multiple pairs of taxa that are distantly related but have similar overall song patterns, including the three examples illustrated in Figure 4, revealed that shared, convergent character states were generally not derived on the same branches of the phylogeny as the shared, convergent states of other characters (i.e., these characters did not change in concert). In fact, no two song characters exhibited identical evolutionary histories in our analyses, and of the 20 characters that changed more than once on the phylogeny (Fig. 2), relatively few changed together on more than one branch, and none changed together more than 75% of the time. The overall vocal similarities we observed between some distantly related orioles are due in large part to convergence in multiple, independently derived features.

Discussion

In many ways the evolutionary history of oriole song is remarkably similar to the evolution of oriole plumage patterns demonstrated by Omland and Lanyon (2000). Both characteristics exhibit high levels of homoplasy, with multiple examples of convergence and reversal in individual characters across the clade. Neither character set reflects phylogeny well, especially above the species level, yet both provide some information about relationships among at least some subspecies. Both song and plumage patterns can evolve rapidly yet can also be remarkably similar among distantly related taxa, with few examples of uniquely derived (autapomorphic) character states. But most surprising of all, overall song patterns appear to have converged repeatedly in the orioles in much the same way as have overall plumage patterns, and not necessarily between the same taxa. Plotting song or plumage against genetic distance results in strikingly similar upper-bound graphs (Fig. 3a and b), with closely related taxa generally being similar in phenotype but distantly related taxa including both similar and divergent phenotypes. As noted by Omland and Lanyon (2000) regarding plumage evolution, these observations reveal a surprising amount of lability at one level but a strong degree of conservatism at another.

Our results agree with those of de Queiroz and Wimberger (1993) in showing that behavioral and morphological characters can have similar levels of evolutionary lability. Traits influenced by learning, such as bird song, might be expected to show higher lability than morphological features such as plumage patterns, because vocal features can vary among conspecifics and are known to change rapidly over time due to cultural evolution (e.g., Price 1998). Vocal learning in songbirds is also thought to play a role

in promoting character divergence during speciation (Slabbekorn and Smith 2001). In our study, however, the particular song components focused on were relatively invariant within taxa in comparison to between taxa, so character differences were probably largely due to genetic changes rather than modifications acquired through learning (Price and Lanyon 2002b). Thus, although song and plumage features might differ in their levels of plasticity within species, our study focused on evolutionary changes in just the species-typical aspects of both of these signal types, and revealed a variety of interesting similarities.

Despite high evolutionary lability in both song and plumage, our data suggest that there are strong evolutionary limits on both. Most oriole song characters involve a restricted number of character states in relation to the number of changes that have occurred, and many changes are reversals to ancestral states or are convergent with states in other oriole taxa. Thus song evolution when considered across the genus as a whole appears to be relatively conserved. Constraints due to development (Wake 1991; Kroodsma 1999), morphology (Ryan and Brenowitz 1985), habitat (Morton 1975; Wiley and Richards 1978), or other factors might have limited the variety of acoustic patterns available within the *Icterus* genus. Limited genetic variation could also have constrained the rate of phenotypic evolution (influenced by the raw mutation rate and rate of recombination), thus contributing to the upper bound nature of divergence plots for oriole phenotypes (Fig. 3). Oriole plumage patterns show similar evidence of constraint (Omland and Lanyon 2000), as do oriole colors and pigments (Hofmann et al. 2006, 2007). However, our results for oriole song are in stark contrast to the less homoplastic evolutionary patterns observed in oropendola song (Price and Lanyon 2002b, 2004b) and in a variety of other types of avian displays (e.g., Livezey 1991; Irwin 1996; Prum 1997; ten Cate 2004).

The difference in homoplasy between oriole song and oropendola song is particularly surprising given the widely held view that traits under stronger sexual selection should evolve more rapidly (Andersson 1994). Orioles are predominantly monogamous with biparental care, whereas most oropendolas are known to be highly polygynous (Webster 1994; Jaramillo and Burke 1999), so sexual selection is expected to be much stronger in oropendola taxa. Indeed, oropendolas provide some of the most extreme examples of sexual size dimorphism known in birds (Webster 1992). Male and female orioles, in contrast, have similar body sizes and more than half of oriole species are monochromatic (Jaramillo and Burke 1999). Song in oropendolas does appear to have changed rapidly in some lineages (e.g., *Psarocolius montezuma*, Price and Lanyon 2002b, 2004b) and thus can show high lability, but it also shows much lower overall homoplasy in individual characters than does oriole song.

Most of the song characters we used in this study were originally chosen to reflect aspects of oropendola song that were

relatively invariant within taxa yet differed between taxa (Price and Lanyon 2002b). Therefore it is possible that the higher levels of homoplasy we observed in orioles could be a result of the fact that these song characters were originally designed for another group of birds with potentially very different song patterns. In other words, variance in our song measurements within taxa relative to between taxa might have been higher in orioles than in oropendolas, which would have resulted in fewer character states per character and thus increased the possibility of convergence and reversals in reconstructions of oriole vocal evolution. However, our methods for parsing continuous song measurements into discrete character states in fact resulted in slightly more character states on average in orioles than in oropendolas (mean = 2.38, SE = 0.24 states/character for orioles; mean = 2.34, SE = 0.12 states/character for oropendolas). Thus, the difference in overall homoplasy between these groups is not likely due to the methods we used in reconstructing historical changes in song.

Orioles and oropendolas have similar maximum levels of molecular sequence divergence between taxa (10.3% in orioles and 9.7% in oropendolas; uncorrected p distances; Omland et al. 1999; Price and Lanyon 2002a), so differences in evolutionary patterns are also not easily explained by differences in time scale. Orioles are a much more speciose group, however, with 25 recognized species in comparison to 11 recognized oropendola species (Sibley and Monroe 1990), so more speciation and/or fewer extinctions have apparently occurred during oriole evolution. More speciation could be correlated with more evolutionary changes in both song and plumage (Slabbekorn and Smith 2001; Omland and Kondo 2006), which in turn could have provided more opportunities for evolutionary convergence and reversal given a limited range of potential character states. Reconstructing the evolution of plumage patterns in oropendolas using methods similar to those used for orioles by Omland and Lanyon (2000) will be needed to see whether the differences we found in song evolution between these clades are found in the evolution of plumage patterns as well.

CONVERGENCE IN OVERALL SONG PATTERN

Why overall song patterns have converged in the orioles is difficult to explain, as is the convergence of oriole plumage patterns (Omland and Lanyon 2000). Theories of sexual selection predict rapid and divergent evolution of sexually selected traits (Andersson 1994), but no current models predict widespread overall convergence as we found here. Furthermore, convergences in both song patterns and plumage patterns have not occurred exclusively, or even primarily, among sympatric taxa, which makes a number of possible adaptive explanations seem unlikely (e.g., interspecific vocal mimicry or similar selection pressures due to shared habitat; Moynihan 1968; Wiley and Richards 1978). In fact, many examples of song convergence are provided by taxa that breed in different geographic regions with few obvious similarities in habitat. For example, the orchard oriole (*I. spurius spurius*) of eastern North America, Bullock's oriole (*I. bullockii*) of western North America, and hooded oriole (*I. cucullatus*) of Mexico and the southwestern United States have largely nonoverlapping breeding and wintering ranges and differ from each other in plumage colors and patterns (Jaramillo and Burke 1999). Yet their complex songs provide one of the most striking examples of convergence in overall pattern (see Fig. 4, *I. spurius* not shown) and differ greatly from the lazy whistles typical of many other oriole species (Hardy et al. 1999). Why each of these species independently converged on a similar, complex song design is not clear.

Although neither song convergence nor plumage convergence in orioles can be generally explained by selection in sympatry, one case is worth mentioning. The Altamira oriole (*I. gularis*) and the spot-breasted oriole (*I. pectoralis*) have widely overlapping ranges in Central America and in fact readily nest alongside each other (Howell and Webb 1995). These species have some of the most similar songs in overall pattern (Fig. 4), with only one different character state between them. They are also among the most similar orioles in plumage, with only four differences between them in overall plumage pattern (Omland and Lanyon 2000; also see plates in Jaramillo and Burke 1999). Yet they are among the most divergent orioles genetically (Omland et al. 1999). Thus these sympatric orioles (indicated in the far lower right of Fig. 3a and Fig. 3b) provide the most dramatic example of evolutionary convergence in both their visual and acoustic signals.

Examples of convergence in both song and morphology can be found outside the orioles as well. For example, in the oropendolas and caciques (*Psarocolius, Ocyalus, Cacicus*), the casqued oropendola (*Psarocolius oseryi*) shares several physical traits with other members of the *Psarocolius* genus including high sexual size dimorphism (Jaramillo and Burke 1999), and also shares a variety of song features including extremely long notes, high levels of note overlap, and a tendency to repeat song types with high redundancy (Price and Lanyon 2004b). But molecular data show that *P. oseryi* is much more closely related to cacique species (*Cacicus*), which lack these characteristics, than to any *Psarocolius* species (Price and Lanyon 2002a, 2004b). Therefore, the overall similarity in both song and appearance between *P. oseryi* and other *Psaracolius* species is almost certainly the result of convergent evolution in a variety of independently derived characteristics (Price and Lanyon 2004b). These similarities probably explain why this species was previously placed in the genus *Psarocolius* (Sibley and Monroe 1990) and provide one of the few examples of convergence in song features among the oropendolas.

The examples of convergence in overall song patterns shown in this study are unlikely due to mistakes in phylogeny. Molecular relationships in orioles have been supported by sequence data from two mtDNA gene regions (Lanyon and Omland 1999; Omland

et al. 1999) and by multiple nuclear intron sequences (Allen and Omland 2003; unpubl. data). Furthermore, convergences in song pattern have generally not occurred in the same taxa as have convergences in plumage pattern, and there is little or no agreement between the song and plumage trees. There also appears to be little congruence among different vocal characters. Cases of convergence in overall song pattern between distantly related species are apparently due to a combination of convergence, reversal, and retained ancestral traits.

Conclusions and Broader Implications

Our study provides clear examples of convergence in individual oriole song characters as well as in overall song design. These results are strikingly similar to results from oriole plumage (Omland and Lanyon 2000), but strikingly different from results based on oropendola song (Price and Lanyon 2002b). Convergence is often interpreted as strong evidence for the role of adaptive evolution in shaping phenotype (e.g., Futuyma 1998), but evolutionary constraint due to genetics, developmental processes, or related mechanistic issues can also lead to convergence (Wake 1991). More functional, theoretical, and comparative research is needed on these and other taxa to more fully understand the causes and generality of these surprising evolutionary patterns.

This and previous studies of song and plumage evolution (Omland and Lanyon 2000; Price and Lanyon 2002b, 2004b; Hoffman et al. 2006, 2007) also provide demonstrations of the utility of ancestral state reconstruction in looking for general evolutionary patterns. By analyzing entire classes of characters we are not forced to rely on the assumptions and accuracy of ancestral state reconstruction for any one character (Omland 1997, 1999; Cunningham et al. 1998; Omland and Lanyon 2000; Maddison and Maddison 2003; Price and Lanyon 2004b). For example, our studies of oriole song and plumage patterns reveal very similar modes of evolution, although the two studies relied on very different types of raw data: discrete color data versus mostly continuous song measurements (see discussions in Omland and Hofmann 2006; Hofmann et al. 2006).

Our methods demonstrate a general quantitative approach to understanding patterns of phenotypic evolution. It will be interesting to apply these methods (especially correlating phenotype with molecular divergence, as in Fig. 3) to other plumage and song data, as well as other morphological and behavioral character sets across a wide range of taxa. Will other character sets generally show constraint and convergence resulting in strong upper bound plots, as in oriole plumage and song? Or will most character sets show linear correlations reflecting steady divergence over time without much homoplasy, as in oropendola song (Price and Lanyon 2002b) and many morphological datasets (Omland 1997)?

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