*Evolution*, 56(7), 2002, pp. 1514–1529

# RECONSTRUCTING THE EVOLUTION OF COMPLEX BIRD SONG IN THE OROPENDOLAS

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*Abstract.*—The elaborate songs of songbirds are frequent models for investigating the evolution of animal signals. However, few previous studies have attempted to reconstruct historical changes in song evolution using a phylogenetic comparative approach. In particular, no comparative studies of bird song have used a large number of vocal characters and a well-supported, independently derived phylogeny. We identified 32 features in the complex vocal displays of male oropendolas (genera *Psarocolius*, *Gymnostinops*, and *Ocyalus*) that are relatively invariant within taxa and mapped these characters onto a robust molecular phylogeny of the group. Our analysis revealed that many aspects of oropendola song are surprisingly evolutionarily conservative and thus are potentially useful characters for reconstructing historical patterns. Of the characters that varied among taxa, nearly two thirds (19 of 29) showed no evidence of evolutionary convergence or reversal when mapped onto the tree, which was reflected in a high overall consistency index (CI = 0.78) and retention index (RI = 0.88). Some reconstructed patterns provided evidence of selection on these signals. For example, rapid divergence of the songs of the Montezuma oropendola, *Gymnostinops montezuma*, from those of closely related taxa suggests the recent influence of strong sexual selection. In general, our results provide insights into the mode of vocal evolution in songbirds and suggest that complex vocalizations can provide information about phylogeny. Based on this evidence, we use song characters to estimate the phylogenetic affinities of three oropendola taxa for which molecular data are not yet available.

*Key words.*—Behavioral evolution, bird song, courtship display, Icteridae, phylogenetic comparative methods, phylogeny, sexual selection.

Received January 29, 2002. Accepted April 29, 2002.

Ethologists have long recognized that avian displays are evolutionarily conservative traits, and thus retain information about evolutionary history (Lorenz 1941; Tinbergen 1959; Van Tets 1965; McKinney 1965). Recent analyses have supported these claims by showing that many of the stereotyped movements performed by birds during courtship map consistently onto phylogenies derived from morphological or molecular data (Wood 1984; Prum 1990; Paterson et al. 1995; Foster et al. 1996; Irwin 1996; Kennedy et al. 1996; Slikas 1998; Johnson et al. 2000). This generalization can be extended to the vocalizations of suboscine and nonpasserine birds, which also appear to contain conservative elements that are consistent with phylogeny (Lanyon 1969; Miller 1996; McCracken and Sheldon 1997; Slabbekoorn et al. 1999). In contrast, the songs of oscine songbirds are generally much more variable and complex, and it is unclear what aspects of these displays, if any, are evolutionarily conserved. Although oscine songs are among the most well studied of all animal displays (e.g., Baptista and Kroodsma 2001), our knowledge of vocal evolution in songbirds is surprisingly poor. Most notably, few researchers have applied a rigorous phylogenetic comparative approach to reconstruct historical patterns in oscine song evolution.

Oscine bird song is widely presumed to be too variable to be studied in a comparative phylogenetic context. Songs are usually modified by learning during development (reviewed in Baptista 1996), thus certain acoustic features can vary dramatically among individuals within a population. Many species also develop song repertoires of several to many distinctly different song types, so acoustic patterns can vary within individuals as well. Furthermore, bird song plays a role in mate attraction and male-male competition (Catchpole and Slater 1995; Searcy and Yasukawa 1996) and is therefore likely to evolve relatively rapidly in response to sexual selection (e.g., Irwin 2000). Aspects of song design are also thought to evolve rapidly, and often convergently, in response to the environment in which signaling takes place (Wiley and Richards 1978; Ryan and Brenowitz 1985; Wiley 1991; McCracken and Sheldon 1997). For example, forest birds tend to use a lower and narrower range of sound frequencies than birds of more open habitats, because these frequencies tend to travel best through these particular environments (Morton 1975; Hunter and Krebs 1979). Such selection can cause distantly related species in similar habitats to have vocalizations more similar than closely related taxa in different habitats.

Evidence has shown, however, that aspects of song have a strong genetic basis (e.g., Marler and Pickert 1984; Kroodsma and Canady 1985; Baptista 1996). Furthermore, a variety of previous comparative studies of songbirds conducted without the benefit of phylogenies (Kroodsma 1977; Catchpole 1980; Catchpole and McGregor 1985; Irwin 1990; Shutler and Weatherhead 1990; Read and Weary 1992; Spector 1992; Podos 1997; Van Buskirk 1997), or using phylogenies that were not strongly supported (Payne 1986; Irwin 1988; Podos 2001), have indicated components of song that are relatively invariant within and across species, and that are therefore likely to be evolutionarily conserved. Components most often focused on in these studies include the patterning of song types during display and the size and complexity of vocal repertoires. Only a few previous comparative studies (e.g., Payne 1986; Van Buskirk 1997; Podos 1997, 2001) have

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included measurements of internal acoustic features of bird song in their comparisons.

We initially conducted the present study to investigate whether or not the comparative approach can be used to reconstruct detailed patterns of change in the evolution of complex vocalizations. As subjects, we selected an oscine group with particularly elaborate song, the oropendolas (genera *Psarocolius*, *Gymnostinops*, and *Ocyalus* [Sibley and Monroe 1990]). Several factors make oropendolas well suited for this sort of investigation. First, the songs of most species are highly stereotyped, both within and between individuals, and are highly acoustically complex. These displays therefore provide a diversity of relatively invariant, potentially homologous acoustic and behavioral characters for comparisons among taxa. Second, unlike the long-distance, territorial songs of most other oscines, oropendola songs appear to be used primarily as short-distance signals by males near or within groups of colonial-nesting females (Jaramillo and Burke 1999). As a consequence, many of the constraints on signal design imposed by the sound transmission properties of the habitat should have relatively little influence on the structure of these vocalizations. Third, a robust molecular phylogeny for the oropendolas is available (Price and Lanyon 2002) which resolves relationships among most described subspecies and geographic variants. This well-supported tree provides an ideal phylogenetic framework for reconstructing song evolution in these birds.

We had three main objectives in this analysis. Our principal goal was to reconstruct historical patterns of change in song characteristics, including nonvocal elements of these displays, during song evolution. Reconstructing such changes is an important first step toward identifying the selective forces driving the evolution of bird song. Second, by measuring levels of homoplasy, we were able to assess the relative degrees to which these song components are consistent with the molecular data, and thus how well these songs reflect phylogeny. Finally, using the molecular tree as a topological constraint, we used patterns of shared song features to estimate phylogenetic relationships in several taxa for which molecular data are not yet available.

## METHODS

### *Taxa Sampled*

Oropendolas are large, colonial-nesting members of the New World blackbird family (Icteridae), found from Mexico to Argentina (Ridgely and Tudor 1989; Howell and Webb 2000). They are closely related to the caciques (*Cacicus*; Freeman and Zink 1995; Lanyon and Omland 1999; Price and Lanyon 2002), which have a similar geographic range. Most, if not all, oropendolas are polygynous to some degree, with one dominant male defending a harem of several to many females at a colony (Robinson 1986; Webster 1994; Jaramillo and Burke 1999). Males produce loud, elaborate vocal displays while defending these harems, and these vocalizations are often accompanied by a stereotyped visual display in which the male bows forward on the branch, often until hanging nearly upside down. Some species also produce a stereotyped wing flap during the display, which is clearly audible from a distance (Jaramillo and Burke 1999). We use the term ''song'' in this study to refer to all components of this display, including both visual and acoustic elements.

We obtained tape recordings of oropendola songs from the Macaulay Library of Natural Sounds, Cornell University, and from several commercially available tapes (Coffey and Coffey 1984; Moore 1993, 1994, 1997; Hardy et al. 1998). These song recordings included representatives from 10 of the 11 species of oropendola recognized by Sibley and Monroe (1990). To sample for potential within-species geographic variation and to obtain the widest possible diversity of song patterns in each taxon, we included songs from multiple subspecies and geographically distant recording locations whenever possible. Throughout this paper, we follow the genus and species nomenclature of Sibley and Monroe (1990), because it is the most comprehensive and widely available recent checklist. For subspecies, however, we use the nomenclature of Blake (1968) because few subspecies are listed in Sibley and Monroe (1990). We divided the songs of one recognized subspecies, *Psarocolius decumanus maculosus*, into two groups, those from Peru (P) and those from Bolivia and Argentina (B), based on molecular evidence that birds from these locations are not each other's closest relatives (Price and Lanyon 2002). In all, we include songs from 17 distinct oropendola taxa in this study.

To maximize the independence of our samples, we made an attempt to use only one representative song from each individual tape-recorded male in our study. We generated spectrograms of all songs (more than 1300 total) using Canary sound analysis software (vers. 1.2.4, Cornell Laboratory of Ornithology, Ithaca, NY; sampling frequency 22.05 kHz, frequency resolution 349.7 Hz, temporal resolution 11.6 msec, 87.5% overlap of frames in successive transforms). In most cases, we selected the single, clearest example from each recording for analysis. Most tape recordings of song were collected at different locations and/or on different dates, so we assumed that each represented a different individual bird. When two or more recordings were collected at the same location and on the same date, however, we chose only one best example from among them because we could not exclude the possibility that they were of the same individual. Alternatively, when field notes by recordists confirmed that more than one bird was present, we selected one song from each individual. Many tape recordings we obtained initially were discarded because they contained no songs that were sufficiently undistorted. Altogether, we included 166 oropendola songs in our analysis, each presumably from a different individual male (mean = 9.8, SE = 1.7 songs/taxon). The source, recordist, location, and date for all of the song recordings used in this study are available from the authors upon request.

A well-supported phylogeny derived from mitochondrial DNA sequence data (Price and Lanyon 2002) indicates that the oropendolas are divided into two reciprocally monophyletic groups: the *Ocyalus* group, which includes *Psarocolius oseryi* and *Ocyalus latirostris*, and the *Psarocolius* group, which includes the rest of the oropendolas (Fig. 1; based on Price and Lanyon 2002, figs. 3 and 4). These two groups are nested within a larger oropendola-cacique clade (Lanyon and Omland 1999). Although *P. oseryi* has been included in the genus *Psarocolius* by Blake (1968) and by Sibley and Monroe

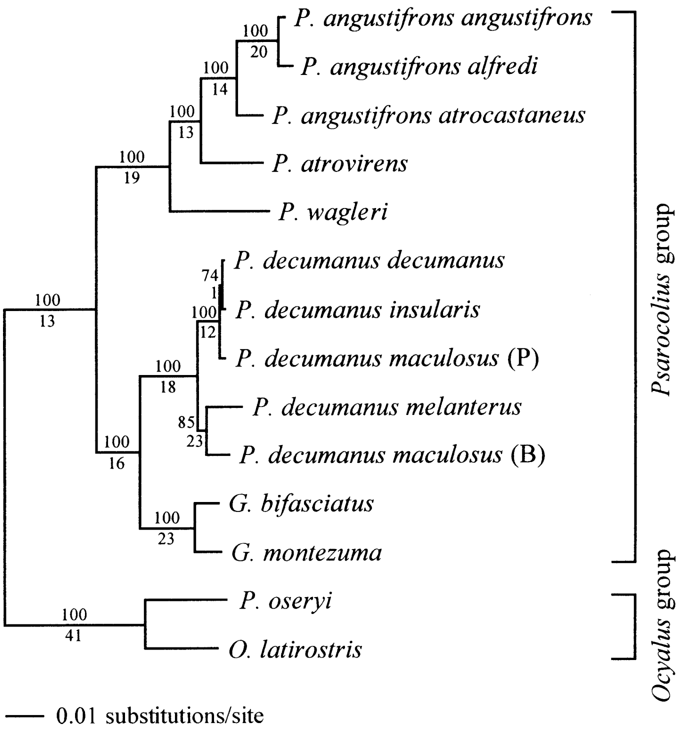

FIG. 1. Molecular phylogeny used in reconstructing song evolution in male oropendolas (from Price and Lanyon 2002). Oropendolas are divided into two clades, the *Psarocolius* group and the *Ocyalus* group, which most likely are not sister taxa. Branch lengths reflect number of nucleotide substitutions, and nodal support values are bootstrap proportions (above branches) and decay index values (below branches) using unweighted sequence data. Genus abbreviations: *P., Psarocolius*; *G., Gymnostinops*; *O., Ocyalus*.

(1990), we refer to it as a member of the *Ocyalus* group here based on this molecular evidence. We analyzed the two oropendola clades separately in this study, based on evidence that they are probably not sister taxa (Price and Lanyon 2002).

### *Measuring Song Features*

Measurements of acoustic features within songs were performed using Canary. We measured most temporal aspects of song directly from on-screen spectrograms, including sounds from the wing flap if present. Many frequency characteristics were measured by generating amplitude spectra, and the temporal locations of amplitude peaks were determined from waveforms. Measurements requiring a series of songs to be analyzed rather than just one (e.g., the mean interval between songs) were performed using SoundEdit 16 (vers. 2, Macromedia, San Francisco, CA), a program that allows spectrograms of relatively long sound recordings to be analyzed. We determined whether aspects of the visual display were present or absent in taxa based on published descriptions (Ridgely and Tudor 1989; Jaramillo and Burke 1999; Howell and Webb 2000) and behavioral observations by recordists (written in field notes or spoken on the tape recordings themselves).

A variety of problems caused by the sound environments in which songs were recorded could have affected the accuracy of our measurements. For instance, reverberation of sounds in forested habitats tends to make notes appear longer in spectrograms and consequently might have made some notes appear to overlap each other when they actually did not. Frequency-dependent attenuation might also have affected our measurements by reducing or eliminating high frequencies, and sounds caused by wind or other animals might have masked some song characteristics. We attempted to minimize these problems by including only relatively undistorted spectrograms in our analysis. Furthermore, although we normally included only one song from each tape-recorded male in the study, we typically examined many more songs to help confirm which patterns were real and which were artifacts. In practice, most tape recordings of taxa were conducted under similar environmental conditions and so were probably equally affected by environmental distortion. Moreover, many forms of signal distortion would have tended to obscure patterns among taxa rather than create false ones.

### *Selecting and Scoring Song Characters*

To identify homologous features in songs, we applied the same criteria used for recognizing homology in morphological traits (Remane 1952; Brooks and McLennan 1991). These criteria are: (1) similarity of relative position, (2) special quality (i.e., similarities in fine structure), and (3) continuity through intermediate forms (Remane 1952). In comparisons of behavioral displays, ''position'' can be interpreted as the temporal position of a sound or movement in a sequence of behaviors (Tinbergen 1959). Thus, by this criterion, displays that are used in the same behavioral context, or components with the same relative position within a display, can be hypothesized to be homologous in different species (Payne 1986; Miller 1996). According to the criterion of ''special quality,'' sounds or behaviors that are highly stereotyped and that share complex details are more likely to be homologous than ones that are variable and relatively simple (Slikas 1998), as such complex features are unlikely to have evolved independently by chance. The presence of ''intermediate forms'' in patterns of vocal evolution is also strongly indicative of homology and can help in identifying display components that are relatively derived or ancestral.

In selecting potentially useful song characters for our study, we specifically focused on aspects of song that are relatively invariant within oropendola taxa. Features that differed notably among the members of a taxon were ignored. We looked for invariant features in acoustic structure by making numerous preliminary sound measurements in Canary, and we supplemented this search by visually comparing spectrogram patterns among conspecifics. Characters reflecting other aspects of singing behavior (e.g., song versatility) were selected after listening to sequences of songs in tape recordings of singing males. Oropendolas in the *Psarocolius* group have courtship songs that are highly stereotyped both within and between individuals, therefore we were able to find a variety of suitable characters based on invariant acoustic features in their songs. Species in the *Ocyalus* group, in contrast, have few such stereotyped song patterns, so many characters based on consistent acoustic features could not be applied in these taxa. The collection of variables selected for inclusion in this study is a subset of a larger number initially considered, several of which were eliminated to reduce redundancy.

Ten characters were chosen to reflect the presence or absence of a particular type of sound or behavior in the courtship display of a taxon. We classified sounds into types based on consistent patterns in frequency and duration. For example, we divided some sounds into different categories based on whether they were tonal or broadband, whether the peak frequency was above or below 1 kHz, and whether the sound duration was shorter or longer than 15 msec. (Divisions were chosen at 1 kHz and at 15 msec based on preliminary measurements of several taxa.) A character was scored as ''present'' if it appeared in any of a taxon's songs and was scored as ''absent'' if it never appeared in a taxon's songs. We scored parts of the visual display as present or absent based on descriptions in the literature and in field notes by recordists.

Twenty-two characters were based on measurements of continuous variables in songs. Using continuous characters in a phylogenetic study can be problematic (e.g., Oakley and Cunningham 2000; Webster and Purvis 2002); consequently, we converted these continuous measures into discrete character states for our analysis. For each character, we first measured the relevant feature in the songs of at least three individuals per taxon. From these measurements, we plotted 95% confidence intervals for taxa and then divided each character into character states based on where these confidence intervals did not overlap (see Appendix). Divisions between categories were positioned approximately equidistant from nearest confidence interval bars. We required a minimum of three measurements to ensure a minimal degree of accuracy in these confidence intervals. Taxa with fewer than three representative song samples (*P. decumanus insularis* and *G. guatimozinus*,) or with fewer than three examples of a particular song feature (e.g., wing flap rate and duration in *G. bifasciatus*) were excluded from this exercise. Species in the *Ocyalus* group (*P. oseryi* and *O. latirostris*) were excluded from analyses of acoustic features within songs because these birds lack any intraspecifically invariant song patterns.

Only three continuous measures could not be parsed into more than one character state using this technique (overall peak frequency, lowest peak frequency, and amplitude peak; see Appendix). In several cases, a character based on an attribute of a song feature (e.g., trill rate) could not be measured because the feature that the attribute describes (i.e., the trill) was absent in a particular taxon. We represented these absent character states as zero in our analyses. How such inapplicable character states are coded in a character matrix can have important consequences when these characters are used in building a phylogenetic tree (Strong and Lipscomb 1999). However, our primary goal in this study was to reconstruct changes in song characters onto an independently derived phylogeny, therefore many of these potential problems do not necessarily apply here.

Using the character states defined in the Appendix, we scored these continuous characters for all oropendola 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, as opposed to defining character states, in order to maximize the information we were able to obtain from the data. All mean measurements based on fewer than three songs fell within the 95% confidence limits calculated for other taxa (i.e., these measurements would not have generated additional character states).

### *Phylogenetic Analysis of Songs*

To reconstruct song evolution, we mapped the song characters onto a molecular phylogeny of the oropendolas (Fig. 1). This phylogeny is based on 2011 base pairs of sequence data from the cytochrome *b* and ND2 regions of the mitochondrial genome, and was generated using a variety of tree-building algorithms, including maximum parsimony, maximum likelihood, and neighbor joining (Price and Lanyon 2002). The tree resolves all relationships among included taxa and is very robust. Most nodes were supported in 100% of bootstrap pseudoreplicates, even under a wide range of parsimony weighting schemes (transversion:transition ratios from 1:1 to 15:1). Fourteen of the 17 taxa included in the present study are included in the molecular tree (Fig. 1); consequently, the three oropendola taxa for which phylogenetic relationships are unknown were not included in this particular analysis.

We reconstructed evolutionary changes in song characters on the molecular phylogeny using simple parsimony in MacClade (vers. 4.0, Maddison and Maddison 2000). Different features of oropendola songs most likely vary in their mutability and thus their potential for providing useful information about evolutionary history. We lacked the necessary a priori knowledge of song evolution to differentially weight these characters, however, thus we weighted our song characters equally in our analyses. For similar reasons we coded all multistate characters as unordered.

We assessed the degree to which our song data are congruent with the molecular phylogeny by calculating the overall consistency index (CI; Kluge and Farris 1969) and overall retention index (RI; Farris 1989) for all of the song characters reconstructed onto the tree, as well as the CIs and RIs for each individual song character on this tree. Both indices measure the amount of homoplasy (i.e., number of evolutionary convergences and reversals) in a character set. The RI provides an advantage in comparative studies because it reflects the observed number of steps in relation to the maximum number possible, and thus is not artificially inflated by autapomorphies. Few previous authors have calculated RIs, however, so we included CI values in this analysis to allow comparisons to other phylogenetic studies. For both the CI and RI, a score of 1 represents perfect congruence with phylogeny (i.e., no homoplasy), whereas a score approaching 0 indicates high levels of homoplasy and thus a lack of fit between the data and the tree. We also explored the degree of conflict between the song and molecular data sets by performing a partition homogeneity test in PAUP* (vers. 4.0b6, Swofford 2001).

### *Using Song Characters to Estimate Relationships*

Three of the oropendola taxa included in our analysis of song characters were not included in the study of molecular relationships by Price and Lanyon (2002), nor in any other

TABLE 1. Descriptions of the 32 oropendola song characters and their character states.

(1) Introductory rattle: presence of a rattle of any type at the beginning of a song. A rattle is defined as a series of short (less than 15 msec long), repeated pulses of sound with most or all energy below 1 kHz. 0: absent, 1: present.

(2) Tonal rattle: a series of short, tonal pulses of sound produced at the beginning of the song. Pulses include a narrow range of frequencies between 0.3 and 1 kHz. 0: absent, 1: present.

(3) Broadband rattle: a series of short, broadband pulses of sound at the beginning of the song. Pulses include a broad range in frequencies, with peak energy below 1 kHz. 0: absent, 1: present.

(4) Rattle-whistle: simultaneous production of a broadband rattle (3) and a continuous high-frequency tone. Often described as sounding like a finger running over the teeth of a comb (Jaramillo and Burke 1999). The whistle can be higher than 8 kHz, and usually descends, although occasionally it ascends, in frequency. 0: absent, 1: present.

(5) Click: short pulse of broadband sound (less than 15 msec long) with peak energy above 1 kHz. Produced individually (i.e., not as part of a trill [see 6]). 0: absent, 1: present.

(6) Trill: rapidly produced series of identical, short, broadband sounds (i.e., clicks [see 5]), with peak energy above 1 kHz. 0: absent, 1: present.

(7) Crash: harsh, broadband sound (more than 15 msec long), with peak energy above 1 kHz. Sounds similar to a stick hitting a snare drum. 0: absent, 1: present.

(8) Squawk: rapidly modulated tone more than 15 msec long. 0: absent, 1: present.

(9) Bow: stereotyped visual display performed during song. The bird bows down, with the bill pointed downwards, the wings raised, and the tail cocked, until hanging nearly upside down. 0: absent, 1: present.

(10) Wing flap: an audible, rapidly repeated wing flap associated with the bow display. Normally given at the end of the display. 0: absent, 1: present.

(11) Song versatility: mean number of distinct song types produced per minute. Songs were considered the same song type if their spectrograms were visually indistinguishable. 0: less than two song types/min., 1: two to four song types/min., 2: more than four song types/min.

(12) Intersong interval: time from the end of a song to the beginning of the next song during a singing bout. Three to seven interval measures were averaged for each individual. 0: less than 10 sec, 1: greater than 10 sec.

(13) Wing flap rate: number of wing flaps per second during a wing flap display (see 10). 0: less than 4/sec, 1: greater than 4/sec.

(14) Wing flap duration: time from beginning to end of a wing flap display (see 10). 0: less than 0.4 sec, 1: 0.4 sec to 1.3 sec, 2: greater than 1.3 sec.

(15) Song duration: time from the beginning to the end of a song. Nonvocal sounds (e.g., audible wing flaps) were not included in the song duration. 0: less than 0.6 sec, 1: 0.6 sec to 1.4 sec, 2: greater than 1.4 sec.

(16) Note percentage: summed duration of all notes in a song divided by the song duration. 0: less than 70%, 1: 70% to 98%, 2: greater than 98%.

(17) Tone percentage: summed duration of tones (i.e., not broadband notes) in a song divided by the song duration. 0: less than 45%, 1: 45% to 96%, 2: greater than 96%.

(18) Note overlap: summed duration of overlapping notes (indicating the production of two different sounds, or ''two voices'', 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 8%, 1: 8% to 24%, 2: greater than 24%.

(19) Longest note: longest continuous sound measured in a song. 0: less than 0.5 sec, 1: 0.5 sec to 1.35 sec, 2: greater than 1.35 sec.

(20) Longest pause: longest pause between notes in a song. 0: less than 0.01 sec, 1: 0.01 sec to 0.09 sec, 2: greater than 0.09 sec.

TABLE 1. Continued.

(21) Average pause duration: summed pause duration divided by the number of pauses in a song. 0: less than 0.01 sec, 1: 0.01 sec to 0.055 sec, 2: greater than 0.055 sec.

(22) Pause rate: number of pauses in a song divided by the song duration. 0: less than 0.5/sec, 1: 0.5/sec to 18/sec, 2: greater than 18/sec.

(23) Rattle rate: number of notes per second during an introductory rattle (see 1). 0: less than 2/sec, 1: 2/sec to 11/sec, 2: 11/sec to 17/sec, 3: greater than 17/sec.

(24) Trill rate: number of notes per second during a trill (see 6). 0: less than 10/sec, 1: greater than 10/sec.

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

(26) Highest peak frequency: highest instantaneous peak frequency occurring at any point in a song. Instantaneous peak frequencies were determined by measuring the frequency with the highest amplitude at 15 to 20 msec intervals throughout each song. 0: less than 7.4 kHz, 1: greater than 7.4 kHz.

(27) Lowest peak frequency: lowest instantaneous peak frequency occurring at any point in a song. 0: could not be parsed into more than one character state.

(28) Range in peak frequencies: difference between the highest and lowest peak frequencies (see 26 and 27) in a song. 0: less than 6.8 kHz, 1: greater than 6.8 kHz.

(29) Frequency shift rate: number of frequency shifts in a song divided by the song duration. A frequency shift was defined as a change in instantaneous peak frequency greater than 1 kHz in less than 20 msec. 0: less than 3.5/sec, 1: 3.5/sec to 6.5/sec, 2: greater than 6.5/sec.

(30) Maximum frequency shift: the largest frequency shift measured in a song. 0: less than 4 kHz, 1: greater than 4 kHz.

(31) Frequency slope: reflects the overall frequency pattern of a song. Scored by first measuring the temporal positions (1st, 2nd, 3rd, or 4th quarter of the song) of the highest and lowest peak frequencies (see 26 and 27), and then subtracting the position of the lowest peak frequency from the position of the highest peak frequency. 0: less than $-1$, 1: $-1$ to 0.5, 2: greater than 0.5.

(32) Amplitude peak: reflects the overall amplitude pattern of a song, based on the temporal positions of the instantaneous peak amplitude (1st, 2nd, 3rd, or 4th quarter of the song). 0: could not be parsed into more than one character state.

molecular phylogenetic analysis. These included two species, *P. viridis* and *G. guatimozinus*, and one subspecies, *P. angustifrons oleagineus*. We estimated phylogenetic affinities of these taxa based on characteristics of their songs by performing a maximum parsimony analysis of the entire song dataset in PAUP*, with the molecular phylogeny (Fig. 1) used as a topological constraint. To assess the effectiveness of the song characters in estimating phylogeny, we compared these song-based relationships to previous classifications of these three taxa (e.g., Blake 1968; Sibley and Monroe 1990), and in relation to other potentially informative characters (e.g., morphological similarities).

## RESULTS

### *Character Scores for Taxa*

A total of 32 characters reflecting intrataxonomically invariant aspects of the structure and organization of oropendola song were identified (Table 1). Ten characters (1–10, Table 1) describe complex acoustic or behavioral patterns that were either present or absent in a taxon's song. Typically,

TABLE 2. Matrices of song character scores for oropendolas in (a) the *Psarocolius* group and (b) the *Ocyalus* group. Character states are described in Table 1. *N,* number of individuals sampled. ?, insufficient data available to score.

| | | | Character | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 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 | 27 | 28 | 29 | 30 | 31 | 32 |
| (a) | *P. dec. decumanus* | 6 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | *P. d. insularis* | 2 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | *P. d. melanterus* | 3 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | ? | ? | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | *P. d. maculosus* (P) | 6 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | *P. d. maculosus* (B) | 10 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | *P. viridis* | 11 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 3 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 |
| | *P. atrovirens* | 27 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| | *P. ang. angustifrons* | 7 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| | *P. a. alfredi* | 23 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| | *P. a. atrocastaneus* | 3 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| | *P. a. oleagineus* | 6 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| | *P. wagleri* | 11 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| | *G. montezuma* | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 2 | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 |
| | *G. bifasciatus* | 15 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| | *G. guatimozinus* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | ? | ? | 0 | 0 | 2 | 2 | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 |
| (b) | *P. oseryi* | 16 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | | | | | | | | | | | | | |
| | *O. latirostris* | 11 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | | | | | | | | | | | | | | | | | | |

a ‘‘present’’ character was found in nearly all of a taxon’s songs in the *Psarocolius* group, but in only a portion of the more variable songs of each species in the *Ocyalus* group. The remaining 22 characters (11–32, Table 1) describe character states derived from measurements of continuous variables. Of the latter, three characters (25, 27, and 32) could not be parsed into more than one character state and thus were constant among taxa. Altogether, the songs of oropendolas provided 29 song characters (16 binary and 13 multistate) that varied across taxa, and thus were potentially informative about evolutionary history.

The 15 taxa in the *Psarocolius* group were assigned scores for all of the 32 song characters (Table 2a). Two taxa, *G. guatimozinus* and *P. decumanus melanterus*, were not scored for characters 11 (song versatility) and 12 (intersong interval) because we could not obtain tape recordings of these taxa long enough to make accurate measurements of these features. Several other continuous characters were represented as zero because they were based on features that were absent in certain taxa. For example, the rate and duration of wing flaps (characters 13 and 14), the rattle rate (character 23), and the trill rate (character 24) were not measured in oropendola taxa that did not have a wing flap (character 10), introductory rattle (character 1), or trill (character 6), respectively, present in their songs.

The two species in the *Ocyalus* group were given scores only for characters 1–14 (Table 2b). Unlike members of the *Psarocolius* clade, these species produce a wide variety of song patterns. Consequently, we could not apply characters 15–32 because we were unable to find or measure any invariant features in the acoustic structure of their songs.

### *Reconstructed Evolutionary Changes in Songs*

Tracing unambiguous changes in the song characters on the molecular tree revealed that most of these features evolved in a highly conservative manner (Fig. 2). For example, our reconstructions suggest that the trill (character 6) evolved only once, and now defines a subclade comprising *P. atrovirens* and the three *P. angustifrons* subspecies included in this analysis. Similarly, the click (character 5) was lost on the branch leading to *P. decumanus* and the two *Gymnostinops* species and now does not appear in any of the songs of these descendant taxa. The mean interval between songs during a singing bout (character 12) also changed on this branch, so that descendant taxa have longer intersong intervals than other oropendola species. The bow display (character 9) evolved in the ancestors of the *Psarocolius* group and is now present only in these taxa. Also on this branch, song versatility (character 11) appears to have decreased; all species in the *Psarocolius* clade sing relatively few song types per minute in comparison to members of the *Ocyalus* group and in comparison to most cacique species (J. Price and S. Lanyon, unpubl. data), the oropendolas’ closest taxonomic relatives (Freeman and Zink 1995; Lanyon and Omland 1999; Price and Lanyon 2002).

Of the 29 song characters that varied across taxa, only 10 (characters 1–4, 7, 10, 13, 20, 21, 23) showed any evidence of evolutionary reversal or convergence on the molecular phylogeny. The crash sound (character 7) evolved once and was later lost, and the introductory rattle (character 1) was lost on two separate occasions (Fig. 2). The presence or absence of a wing flap (character 10) also exhibited homoplasy on the tree; however, our reconstructions could not resolve whether this display evolved once on the branch leading to the *P. decumanus–Gymnostinops* subclade and was then lost in *G. montezuma* (a reversal) or evolved twice independently on the branches leading to *P. decumanus* and *G. bifasciatus* (a convergence). Our reconstructions were also ambiguous about whether the relatively high pause durations (characters 20 and 21) found in *P. a. atrocastaneus* and *P. atrovirens* are the result of an evolutionary reversal on the tree or independent increases in this feature in each of these taxa.

Branches with multiple evolutionary changes in songs occur in several parts of the phylogeny. By far the largest concentration appears on the branch leading to *G. montezuma*, the Montezuma oropendola (Fig. 2). Fully 40% of the un-

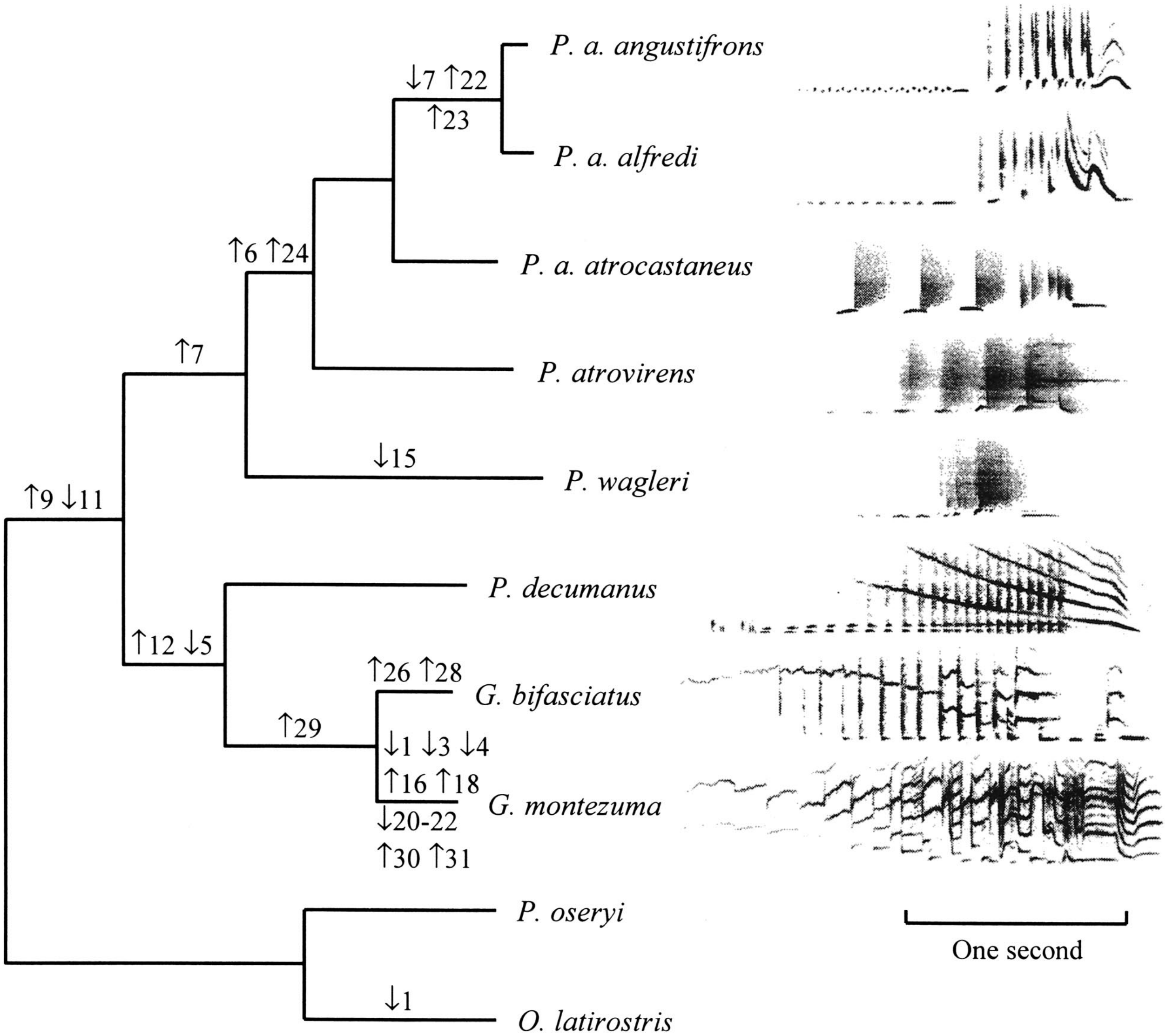

FIG. 2. Unambiguous evolutionary changes in oropendola songs reconstructed on the molecular tree. Arrows and character numbers on branches show the gain/increase (up arrows) or loss/decrease (down arrows) in particular song characters. Spectrograms show typical song patterns for taxa; those of *P. oseryi* and *O. latirostris* are not shown because these species have multiple species-typical songs. Subspecies of *P. decumanus* are collapsed into a single branch because their songs did not differ in any consistent way. Changes at the base of the *Psarocolius* group are supported by additional comparisons to cacique (*Cacicus*) taxa. Branch lengths on the tree reflect molecular changes.

ambiguous changes reconstructed on the molecular tree have occurred on this relatively short branch. In particular, the note percentage (character 16), proportion of note overlap (character 18), and range of the maximum frequency shift (character 30) all increased markedly. Pauses in songs (characters 20–22) were lost on this branch as well; accordingly, extant members of this species produce longer continuous sounds than any other taxon in the group (mean note duration = 1.8 sec, SE = 0.1 sec, *n* = 8). Other notable changes have occurred at nearby points on the tree (Fig. 2), such as increases in the highest peak frequency (character 26), the range in peak frequencies (character 28), and the frequency shift rate (character 29). Multiple song changes were also found among the *P. angustifrons* subspecies. The songs of *P. a. angustifrons* and *P. a. alfredi* are nearly indistinguishable from each other, yet they differ in several ways from those of the third subspecies, *P. a. atrocastaneus*.

A plot of pairwise song differences as a function of molecular sequence divergence (Fig. 3) shows that songs have evolved at a relatively constant rate during much of the history of the *Psarocolius* group. Changes in the songs of most lineages have accumulated almost linearly with increasing genetic distance, so that, among most taxa, degree of song similarity is a reasonably accurate indicator of phylogenetic affinity. (Statistical analyses were not performed on this plot because some comparisons are not phylogenetically independent.) In contrast, comparisons between the songs of *G. montezuma* and other taxa show a very different pattern of change. *G. montezuma* songs are markedly different from those of all other oropendolas, even relatively closely related

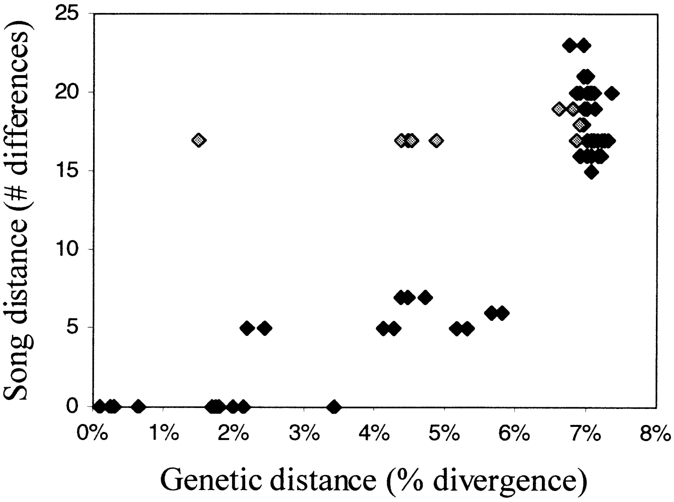

FIG. 3. Pairwise song distance (measured as the total number of character state differences) versus genetic distance (percent sequence divergence in cytochrome *b* and ND2) in comparisons between oropendola taxa in the *Psarocolius* group. Comparisons between all taxa except *Gymnostinops montezuma* (black diamonds) show that song differences have accumulated nearly linearly with molecular divergence. Comparisons between *G. montezuma* and other oropendolas (gray diamonds), however, suggest that songs have changed relatively rapidly in this species.

taxa. (The gray diamond on the far left of Fig. 3 represents a comparison between *G. montezuma* and its closest relative, *G. bifasciatus*.) Thus, song features appear to have changed relatively rapidly in the recent ancestors of this species.

TABLE 3. Measures of homoplasy for oropendola song characters that varied among taxa. Consistency index (CI) and retention index (RI) values are for individual characters mapped onto the molecular tree.

| | Character (Overall index) | CI (0.78) | RI (0.88) |
|---|---|---|---|
| 1 | Introductory rattle | 0.50 | 0.00 |
| 2 | Tonal rattle | 0.50 | 0.80 |
| 3 | Broadband rattle | 0.50 | 0.80 |
| 4 | Rattle-whistle | 0.50 | 0.80 |
| 5 | Click | 1.00 | 1.00 |
| 6 | Trill | 1.00 | 1.00 |
| 7 | Crash | 0.50 | 0.50 |
| 8 | Squawk | 1.00 | 1.00 |
| 9 | Bow | 1.00 | 1.00 |
| 10 | Wing flap | 0.50 | 0.80 |
| 11 | Song versatility | 1.00 | 0.00 |
| 12 | Intersong interval | 1.00 | 1.00 |
| 13 | Wing flap rate | 0.50 | 0.80 |
| 14 | Wing flap duration | 1.00 | 1.00 |
| 15 | Song duration | 1.00 | 1.00 |
| 16 | Note percentage | 1.00 | 1.00 |
| 17 | tone percentage | 1.00 | 1.00 |
| 18 | Note overlap | 1.00 | 1.00 |
| 19 | Longest note | 1.00 | 1.00 |
| 20 | Longest pause | 0.67 | 0.00 |
| 21 | Average pause duration | 0.67 | 0.00 |
| 22 | Pause rate | 1.00 | 1.00 |
| 23 | Rattle rate | 0.75 | 0.50 |
| 24 | Trill rate | 1.00 | 1.00 |
| 26 | Highest peak frequency | 1.00 | 0.00 |
| 28 | Range in peak frequencies | 1.00 | 0.00 |
| 29 | Frequency shift rate | 1.00 | 0.00 |
| 30 | Maximum frequency shift | 1.00 | 0.00 |
| 31 | Frequency slope | 1.00 | 1.00 |

### *Congruence between Song and Molecular Data*

The song characters exhibited a remarkable lack of homoplasy when mapped onto the molecular phylogeny (Table 3). The overall CI was 0.78 and the overall RI was 0.88, with phylogenetically uninformative characters excluded from the analysis. For comparison, the unweighted molecular data used to derive this topology had a CI of 0.68 and a RI of 0.81, with uninformative characters excluded. Of the 29 variable song characters, about two thirds had CIs of 1.0 and the same proportion had RIs of 0.80 or more (Table 3). Fourteen characters were perfectly congruent with phylogeny (CI = RI = 1.0), nine of which were based on temporal characteristics of songs (characters 12, 13–19, 22, 24). Seven characters were phylogenetically uninformative because they could not be parsed into discrete states (characters 25, 27, 32) or were autapomorphic for terminal taxa (characters 26, 28–30). All except one of these seven (character 32) were based on frequency measures. A total evidence tree, in which the song and molecular data sets were combined in a parsimony analysis in PAUP*, was identical in topology to the tree based on molecular data alone (Fig. 1), further evidence for the compatibility between the song characters and the molecular phylogeny.

Despite the high CI and RI values exhibited by the song characters, the partition homogeneity test indicated a significant degree of conflict between the song and molecular data sets ($P < 0.05$). The relatively large number of changes observed on the branch leading to *G. montezuma* (Figs. 2, 3) suggests that much of this conflict can be attributed to this species, and an analysis with this taxon removed from the dataset supports this idea. After removing *G. montezuma* from the analysis, the overall CI and RI both increased (CI: from 0.78 to 0.85; RI: from 0.88 to 0.93) and the conflict between the song and molecular data largely disappeared (partition homogeneity test: $P = 0.29$).

### *Relationships Estimated Using Song*

Phylogenetic relationships based on song characters for the three taxa for which we lack molecular data are shown in Figure 4. This analysis resolved *G. guatimozinus* as sister to *G. montezuma*, which was not unexpected given that none of the 32 characters distinguished between the songs of these two taxa (Table 2a). Our analysis also resolved *P. viridis* as sister to *G. bifasciatus*, which places this species within the genus *Gymnostinops*. Characters supporting the close relationship between *P. viridis* and *G. bifasciatus* include similarities in these species' wing flap durations (character 14), highest peak frequencies (character 26), ranges in peak frequency (character 28), and frequency shift rates (character 29). All of these characters had CIs and RIs of 1.0 when *P. viridis* was included on the tree at this position.

The subspecies *P. angustifrons oleagineus* was found to be sister to a subclade consisting of the other three *P. angustifrons* subspecies and the species *P. atrovirens* (Fig. 4). Thus, our phylogenetic analysis of song characters suggests that the *P. angustifrons* species complex is paraphyletic as cur-

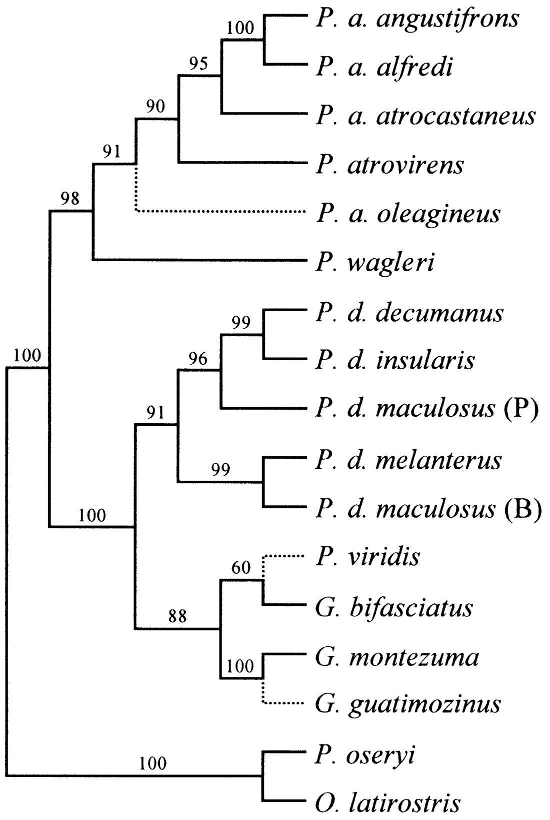

FIG. 4. Predicted phylogenetic affinities for three oropendola taxa (dotted branches) based solely on comparisons of song characters (length = 56, CI = 0.77, RI = 0.89). Relationships among other taxa (solid branches) were constrained to the molecular phylogeny. Numbers above branches are bootstrap proportions calculated using the song data.

rently recognized. Further investigation revealed that this relationship was supported by only one synapomorphic character, the trill (character 6), which is present in the songs of *P. a. angustifrons, P. a. alfredi, P. a. atrocastaneus,* and *P. atrovirens* (see Fig. 2), but not present in the songs of *P. a. oleagineus.*

## DISCUSSION

The elaborate songs of male oropendolas include many features that are surprisingly conservative in their evolution. Of the 32 song characters that were invariant within taxa, 29 varied across taxa; however, only about a third of these variable characters showed evidence of evolutionary convergence or reversal when mapped onto the molecular tree. This lack of homoplasy was reflected in overall consistency and retention indices that were relatively high (CI = 0.78, RI = 0.88). In many respects, the highly stereotyped and complex sound patterns of most oropendola songs are analogous to the ritualized courtship movements of other avian displays, which are known to evolve in a similarly conservative manner (Lorenz 1941; Tinbergen 1959; Van Tets 1965; McKinney 1965; Wood 1984; Prum 1990; Paterson et al. 1995; Foster et al. 1996; Irwin 1996; Kennedy et al. 1996; Slikas 1998; Johnson et al. 2000).

Aspects of oropendola displays have changed little over long periods of evolutionary history. For example, reconstructions of a variety of temporal components on the tree, such as the mean intersong interval (character 12), song duration (character 15), note percentage (character 16), and tone percentage (character 17) suggest that each has changed only occasionally during oropendola evolution. Even more striking, the bow display (character 9) has remained largely unchanged, other than the addition of a wing flap in some species, at least since the common ancestor of the *Psarocolius* clade (Fig. 2).

The patterning of song types during display, measured in this study as song versatility (character 11), has also changed little over time. All members of the *Psarocolius* group repeat their songs for several minutes or more, often with high precision, before introducing another song type, thus versatility appears to have remained low throughout the evolution of the clade. This aspect of song organization has been included in several previous comparative studies of songbirds (Kroodsma 1977; Read and Weary 1992; Spector 1992; Irwin 1988, 1990), and our results underscore the usefulness of this feature in such analyses by showing that it is a relatively conservative character. We were not able to measure the song repertoire sizes of individual males in our study, but previous evidence suggests that it is also evolutionarily conserved (Kroodsma and Canady 1985; Irwin 1988; Spector 1992; Baptista 1996; but see Irwin 1990).

In contrast to these conservative characters, patterns of change in several other song components indicate levels of evolutionary lability that are comparatively high. For instance, among the variable characters based on frequency properties of songs (characters 26, 28–31), all had character states that were autapomorphic (i.e., uniquely derived) for terminal taxa, which indicates rapid changes in these features in recent lineages. Likewise, characters based on the durations of pauses between notes (characters 20 and 21) exhibited relatively high degrees of homoplasy on the molecular tree (see Table 3), which also suggests rapid evolutionary changes. These patterns are consistent with previous proposals that sound frequencies and note repetition rates tend to evolve more rapidly than other aspects of bird song because these features are particularly vulnerable to the effects of attenuation and degradation during transmission in different habitats (Morton 1975; Wiley and Richards 1978; Hunter and Krebs 1979; Ryan and Brenowitz 1985; Wiley 1991; McCracken and Sheldon 1997).

### *Evidence for Selection on Songs*

Oropendola songs appear to have fundamental roles in courtship and in aggressive interactions between males (Jaramillo and Burke 1999), strong evidence that these displays are subject to sexual selection (Catchpole and Slater 1995, Searcy and Yasukawa 1996). Members of the *Psarocolius* group are among the most extreme examples of sexual size dimorphism known in birds (Webster 1992) and studies suggest that some, if not all, of these species are highly polygynous (Robinson 1986; Webster 1994). Consequently, we might expect selection in this group to be especially intense.

The extent to which *G. montezuma* has diverged from closely related taxa in song characteristics (Figs. 2, 3) is especially suggestive that strong selection has influenced these signals. Such extensive changes might indicate that sexual selection has been more intense in this species than in other oropendolas, an idea that is not clearly supported by corresponding differences in known mating behaviors or in levels of sexual dimorphism (Robinson 1986, Jaramillo and Burke 1999). Another possibility is that dramatic evolutionary events such as we observed in *G. montezuma* have occurred throughout the phylogeny, perhaps due to shifts in constraints on selection (Irwin 2000, Podos 2001), and changes in the *G. montezuma* lineage are more detectable in our analysis simply because they are more recent. Characters with high evolutionary lability tend to exhibit homoplasy in phylogenetic reconstructions (e.g., Omland and Lanyon 2000) and, therefore, might be less likely to leave evidence of these changes when they occur in the more distant past.

While vocalizations are an undoubtedly important component of male advertising displays, the importance of particular acoustic features of song in mate attraction and male-male competition, and hence the likelihood of those features being influenced by sexual selection, is unknown in oropendolas. Characteristics that influence a song's potency have been identified in other oscine species, however, which might provide insight into the evolutionary patterns revealed here. For example, King and West (1983) demonstrated that songs by male brown-headed cowbirds (*Molothrus ater*) that include the production of two different sounds at once are more attractive to females than songs without such note overlap. Likewise, a song's attractiveness appears to be influenced by the relationship of high and low frequency notes and by the fact that males switch rapidly between these frequencies while singing (King and West 1983; Allan and Suthers 1994). Similar female preferences for dramatic frequency shifts in male song have been demonstrated in canaries (Vallet et al. 1998) and have been suggested for other species (e.g., Podos 1997).

Interestingly, several of the acoustic features that have become relatively extreme in members of the *Psarocolius* clade, particularly in *G. montezuma*, correspond well to components that enhance song potency in other oscine species (King and West 1983; Vallet et al. 1998). These features include the proportion of note overlap in songs (character 18), the range in peak frequencies (character 28), and the rate and magnitude of rapid frequency shifts (characters 29 and 30). Whether or not these evolutionary changes have indeed been driven by female mating preferences can only be confirmed through rigorous behavioral investigations of individual species.

Selection on song structure is also suspected in the vocalizations of *P. a. atrocastaneus*, *P. a. oleagineus*, and *P. atrovirens*. All three taxa have much longer pauses in their songs than other oropendolas (characters 20 and 21; see Table 2a) and are also the only birds in this study found regularly at high elevations (Blake 1968; Jaramillo and Burke 1999). Molecular evidence from two of these taxa, *P. a. atrocastaneus* and *P. atrovirens*, indicates that these birds are not a monophyletic group (Fig. 1; also see Fig. 4), therefore this pattern cannot be explained entirely by phylogeny. Rather, our evidence suggests an association between long pause durations in songs and montane habitats.

### *The Phylogenetic Content of Song*

Previous phylogenetic analyses using relatively few vocal characters have suggested that aspects of bird song reflect phylogeny. Payne (1986), for example, derived a hypothesis of relationship for five wood-warblers of the genus *Dendroica* based on four synapomorphous acoustic patterns in their songs. This song-based phylogeny is largely consistent with topologies derived from biogeographic patterns (Payne 1986) and from mitochondrial sequence data (Lovette and Bermingham 1999). Likewise, in a study of song evolution in sparrows, Irwin (1988) found that a repertoire of only a single song type is a derived character state defining the genus *Zonotrichia*, which agrees with molecular relationships (Zink 1982). Observations in other taxa have also suggested that parts of oscine song contain historical information (e.g., Spector 1992; Irwin 1988, 1996; Martens 1996; but see Rice et al. 1999).

Our study confirms these previous suggestions by showing that a variety of features in oropendola song reflect phylogenetic relationships. With few exceptions, complex patterns of sound (characters 1–8) are present only in the songs of a few closely related taxa, and close relatives are more similar than distant taxa in measurements of continuous song features (characters 11–32).

Oropendola song characters even supported several molecular relationships that disagree with previous classifications. Among the three subspecies of *P. angustifrons* for which molecular data are available, our study found no differences between the songs of *P. a. angustifrons* and *P. a. alfredi*, but both were found to differ substantially from the songs of *P. a. atrocastaneus*. This corresponds well to relationships based on DNA sequence data (Fig. 1; Price and Lanyon 2002), but disagrees with previous proposals suggesting a deep split between *P. a. angustifrons* and other subspecies in this complex (e.g., Ridgely and Tudor 1989; Sibley and Monroe 1990; Jaramillo and Burke 1999). Our song data also support a close relationship between *P. oseryi* and *O. latirostris*, which is in agreement with molecular data (Freeman and Zink 1995; Price and Lanyon 2002) but which had not been proposed previously. Song patterns thus provide further support for the exclusion of *P. oseryi* from the genus *Psarocolius*. However, we have yet to determine this species' closest allies within the oropendola–cacique clade, so we await a more detailed analysis of cacique phylogeny before suggesting a revised classification.

Comparing levels of homoplasy in different characters suggests some broad conclusions about the relative phylogenetic informativeness of various aspects of song. Temporal components, for example, were generally more congruent with phylogeny than frequency components (Table 3). Of the 13 characters based on temporal measures (characters 12–24), all were phylogenetically informative and nine had RIs of 1.0. In contrast, of the seven characters based on frequency measures (characters 25–31), only one (character 31: frequency slope) had an RI of 1.0. The other six were uninformative about phylogenetic relationships, either because they could not be parsed into discrete states (characters 25 and 27) or because they included one or more autapomorphic character states (characters 26, 28–30). The presence or absence of complex acoustic or behavioral patterns (characters 1–10) exhibited a medium level of phylogenetic signal (four of 10 had RIs of 1.0). Thus, at least in oropendolas, frequency characteristics appear to be less reliable than other components of song for predicting phylogeny (also see McCracken and Sheldon 1997).

The overall retention index of 0.88 for this study is difficult to evaluate in relation to other phylogenetic investigations because few have calculated RIs. The overall consistency index (CI = 0.78) is also difficult to compare because, although many previous studies have calculated CIs, these values are known to be negatively correlated with the number of taxa included in a sample (Sanderson and Donoghue 1989). Nevertheless, accounting for this trend, the CI for our study is higher than that found in any of the four studies with the same number of taxa (14) reported in Sanderson and Donoghue's (1989) survey of morphological and molecular studies (mean = 0.57, range = 0.47–0.72). The overall CI for oropendola songs is also higher than values calculated for the courtship displays of ducks (Anseriformes: CI = 0.69, 14 taxa) and storks (Ciconiidae: CI = 0.65, 17 taxa), but lower than the value calculated for manakins (Pipridae: CI = 0.85, 19 taxa), when these displays were mapped onto morphology-based trees (Irwin 1996: reanalyzed from data of Lorenz 1941; Wood 1984; and Prum 1990, respectively).

### *Using Song to Estimate Phylogeny*

Given the strong phylogenetic signal in oropendola song characters, we are optimistic about our estimates of relationship for the three taxa for which we lack DNA samples (*G. guatimozinus*, *P. a. oleagineus*, and *P. viridis*). The phylogenetic position of *G. guatimozinus* as sister to *G. montezuma* (Fig. 4) is corroborated by the fact that these species are nearly identical in morphology and are geographically closer to each other than either is to any other member of the genus (Ridgely and Tudor 1989; Sibley and Monroe 1990; Jaramillo and Burke 1999; Howell and Webb 2000). No consistent differences were found in this study between these birds' songs; however, our results were based on only a single representative of *G. guatimozinus*, and a comparison between these taxa including more individuals might well reveal subtle acoustic differences not detected in this study.

The placement of the subspecies *P. a. oleagineus* on the tree is somewhat more surprising, as it results in the paraphyly of the *P. angustifrons* species complex (Fig. 4). This paraphyly was supported by only one song character, the trill (character 6), which is absent in the songs of *P. a. oleagineus* but present in the songs of the other three *P. angustifrons* subspecies and in *P. atrovirens*. A likely, though slightly less parsimonious, explanation for this pattern is that *P. angustifrons* is actually monophyletic and the trill has been lost in songs of the *oleagineus* subspecies. Monophyly of *P. angustifrons* is supported by a variety of subtle morphological similarities between *P. a. oleagineus* and the other *P. angustifrons* subspecies (Jaramillo and Burke 1999), but paraphyly is also likely based on the geographic locations of these taxa. *Psarocolius atrovirens* is even suspected to hybridize with members of *P. a. alfredi* (Ridgely and Tudor 1989), although it is important to note that the ability to hybridize is often uninformative about phylogenetic relatedness (McKitrick and Zink 1988). Molecular analysis including sequence data from *P. a. oleagineus* is needed to confirm which of these alternative topologies is more likely to be true.

The positioning of *P. viridis* within the *Gymnostinops* genus by our analysis is also surprising. This species has the most controversial relationships of the three (Jaramillo and Burke 1999); yet to our knowledge, no previous author has proposed inclusion of *P. viridis* as a member of this genus (e.g., see Blake 1968; Ridgely and Tudor 1989; Sibley and Monroe 1990; Jaramillo and Burke 1999). On the contrary, Jaramillo and Burke (1999) have suggested that *P. viridis* has closest affinities to *P. decumanus*, based on certain similar behaviors. As shown in this study, a variety of shared song characters indicate that *P. viridis* is most closely related to *G. bifasciatus* (Fig. 4). Furthermore, consistent with our results, *P. viridis* shares several morphological characteristics with *Gymnostinops* oropendolas that are not present in other taxa, such as a bare patch of skin on the face and an orange-tipped bill (Ridgely and Tudor 1989; Jaramillo and Burke 1999). A molecular analysis to determine the phylogenetic affinities of *P. viridis* is underway, and analyses of the other two taxa which will provide a more conclusive test of the reliability of song for reconstructing phylogeny are planned.

### *Conclusions*

The fact that song characters chosen strictly because of their relative invariance within taxa mapped consistently onto a molecular phylogeny suggests that such an approach can be applied in reconstructing vocal evolution in other songbird groups. Like the displays of *Psarocolius*-group oropendolas, the songs of many oscine species are highly stereotyped and contain acoustic elements that are present across all conspecifics (e.g., Marler and Pickert 1984; Spector 1992; Kroodsma 1999). Analysis of these elements using phylogenetic comparative methods might well reveal patterns of conservative evolution similar to those found here (e.g., see Payne 1986). Our methods might also be applicable for species with more variable modes of singing, although, as demonstrated in our analysis of *Ocyalus*-group oropendolas, identifying homologous acoustic structures in songs can be more problematic.

Many of the historical patterns revealed in this study might be universal in the evolution of bird song. For example, as found in McCracken and Sheldon's (1997) study of vocal evolution in herons, vocal elements unlikely to be influenced by selection from the habitat are particularly conservative aspects of song, whereas elements thought to be more susceptible to environmental degradation and attenuation tend to evolve relatively rapidly (also see Morton 1975; Wiley and Richards 1978; Ryan and Brenowitz 1985; Wiley 1991). Components of song targeted by sexual selection can also exhibit rapid evolutionary change (e.g., Fig. 3), although the particular elements affected might be more difficult to predict (R. Irwin 1990, 1996; D. Irwin 2000). A particularly interesting finding was the evolution of high vocal stereotypy (i.e., low song versatility) in members of the *Psarocolius* group. These species exhibit higher levels of polygyny (measured as harem size) and sexual size dimorphism than other members of the oropendola–cacique clade (Robinson 1986; Leak and Robinson 1989; Webster 1992; Jaramillo and Burke 1999), which suggests that versatility in song production has decreased with increased intensity of sexual selection. This pattern is the opposite to what is commonly presumed in discussions of songbird evolution (e.g., Read and Weary 1992; Catchpole and Slater 1995; Searcy and Yasukawa 1996) and needs to be investigated in comparative studies of other oscine groups (also see Catchpole 1980; Catchpole and McGregor 1985).

The influence of learning on vocal development in oropendolas is unknown; however, variability in certain acoustic features among the songs of conspecifics and among different songs within each male's repertoire (not measured in this study) suggest that vocal learning plays a role. The song components focused on in this study are relatively invariant within taxa and highly evolutionarily conserved. These components are therefore likely to be largely, if not entirely, innate. Nevertheless, learned aspects of song might also be consistent with phylogeny to some degree, as these features are normally culturally transmitted only along taxon-specific lines (Payne 1986) and the selective acquisition of these elements during learning is often under strict genetic control (Marler and Pickert 1984, Mundinger 1995, Baptista 1996).

The high levels of congruence found between the song and molecular data indicates that most character states shared among taxa in this study are homologous rather than convergent. This refutes previous proposals that behavior, and specifically bird song, is too evolutionarily labile and homoplasious to provide useful characters for phylogenetic investigations. Atz (1970), for instance, argued that similar behaviors should appear repeatedly by chance because these traits evolve rapidly and have a limited number of ways in which they can be performed. Although components of oropendola song do indeed have the capacity for rapid change, few have evolved convergently. Such evolutionary mutability combined with low homoplasy suggests that, within certain constraints on signal design (e.g., Podos 1997, 2001), oropendola songs are relatively unlimited in the forms they can take. This pattern is similar to that found in phylogenetic studies of other avian courtship displays (reviewed in Irwin 1996), but differs from the relatively high levels of convergence found in evolutionary reconstructions of other sexually selected characters (e.g., plumage patterns in other icterids: Omland and Lanyon 2000, Johnson and Lanyon 2000).

Agreement between the song and molecular data also confirms that aspects of bird song, even songs that are extremely acoustically complex, can be used in assessing phylogenetic relationships among avian taxa. Such noninvasive methods might be particularly useful in species that are rare and poorly known (e.g., the baudo oropendola, *Gymnostinops cassini*). Rather than impeding such analyses, high vocal complexity can actually provide an advantage in systematic studies. Complex traits with multiple components, such as the stereotyped songs of many oscine taxa, should be more useful than simpler traits for reconstructing phylogenetic history because they contain a larger and more diverse pool of potentially homologous characters for comparison. The difficulty is in identifying which of these characters are informative.

## ACKNOWLEDGMENTS

We thank A. Priori at the Macaulay Library of Natural Sounds for invaluable assistance in obtaining oropendola recordings. A. Jaramillo and M. Webster were also helpful in sharing their expertise on oropendola behavior in the field. M. Eaton, A. Jones, A. Kesson, J. Podos, and two anonymous reviewers provided useful comments on the manuscript. Financial support for this work was provided by the Bell Museum of Natural History at the University of Minnesota.

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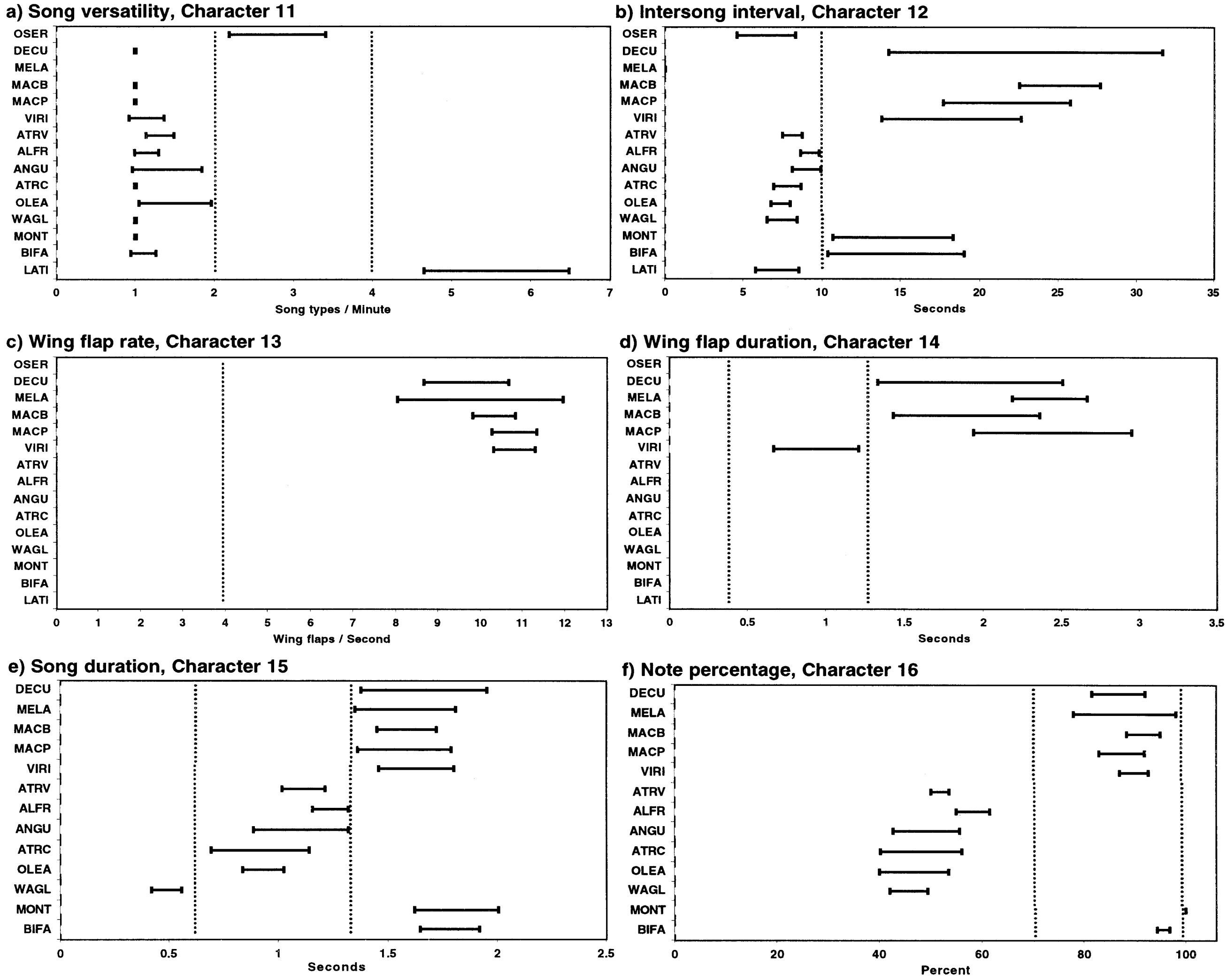
Corresponding Editor: P. Dunn

## APPENDIX

Graphs used in parsing measurements of continuous variables into discrete character states (characters 11–32 in Table 1). For each character, 95% confidence intervals for measurements of song features (horizontal solid bars) were divided into categories based on where they did not overlap (vertical dotted lines). Taxon identification codes: OSER, *P. oseryi*; DECU, *P. d. decumanus*; MELA, *P. d. melanterus*; MACB, *P. d. maculosus* (B); MACP, *P. d. maculosus* (P); VIRI, *P. viridis*; ATRV, *P. atrovirens*; ALFR, *P. a. alfredi*; ANGU, *P. a. angustrifrons*; ATRC, *P. a. atrocastaneus*; OLEA, *P. a. oleagineus*; WAGL, *P. wagleri*; MONT, *G. montezuma*; BIFA, *G. bifasciatus*; LATI, *O. latirostris*.

APPENDIX.



a) Song versatility, Character 11

b) Intersong interval, Character 12

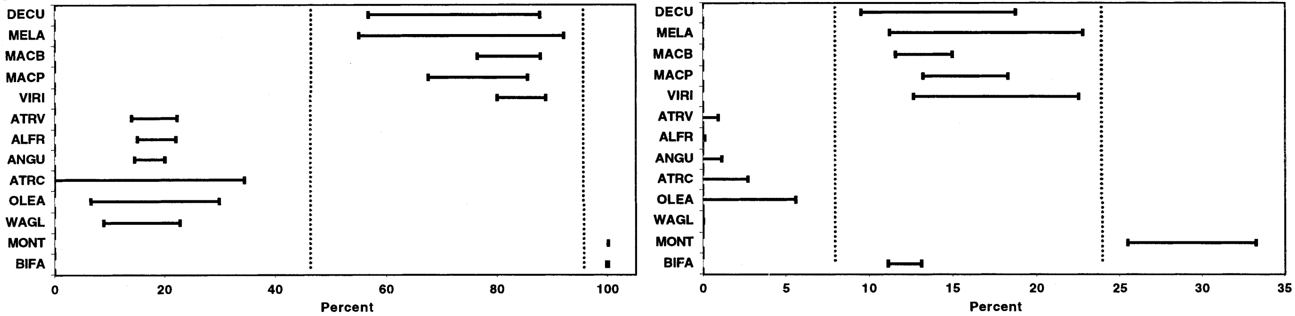
c) Wing flap rate, Character 13

d) Wing flap duration, Character 14

e) Song duration, Character 15

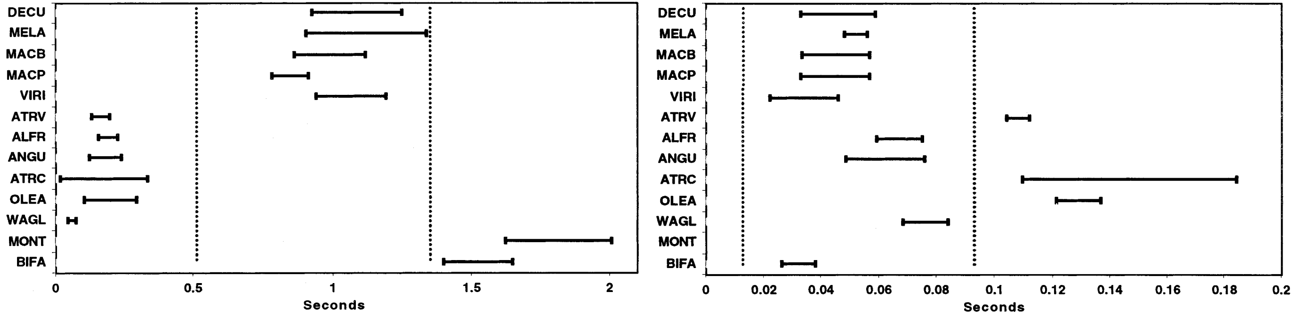
f) Note percentage, Character 16

Appendix. Continued.



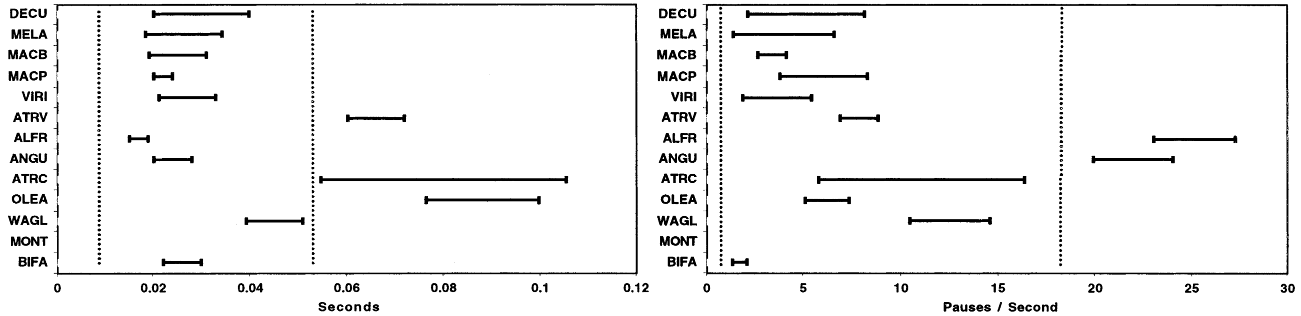
g) Tone percentage, Character 17

h) Note overlap, Character 18



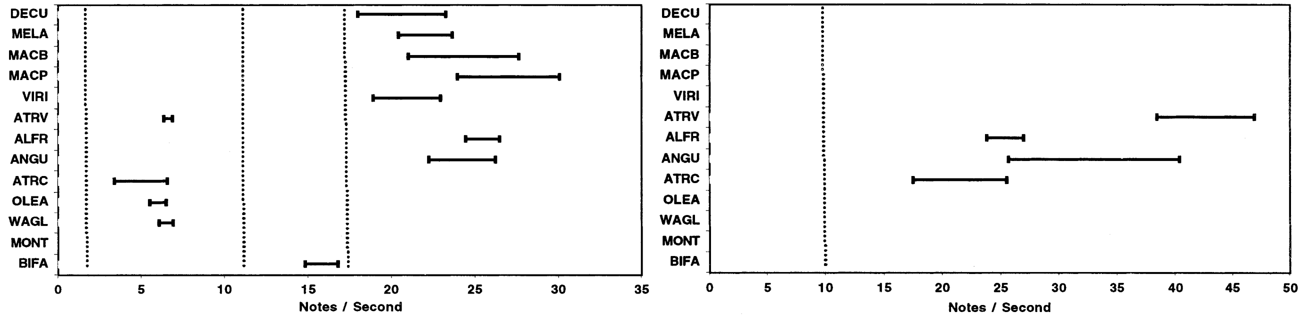
i) Longest note, Character 19

j) Longest pause, Character 20



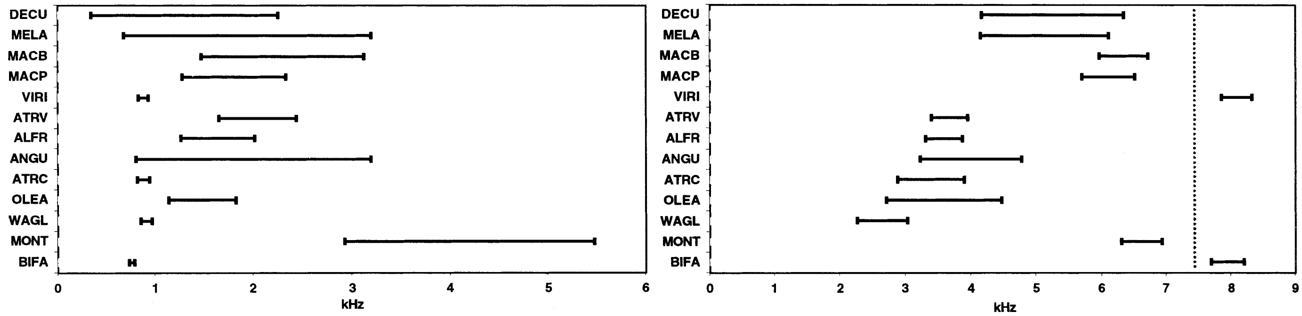
k) Average pause duration, Character 21

l) Pause rate, Character 22



m) Rattle rate, Character 23

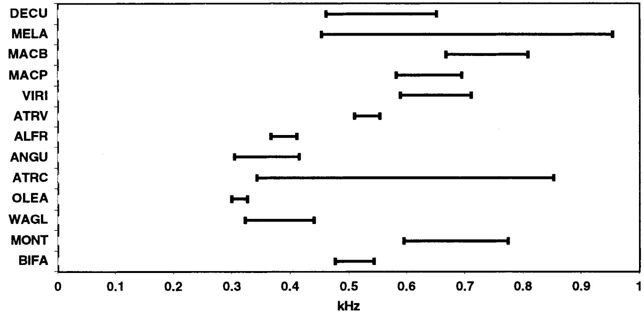
n) Trill rate, Character 24

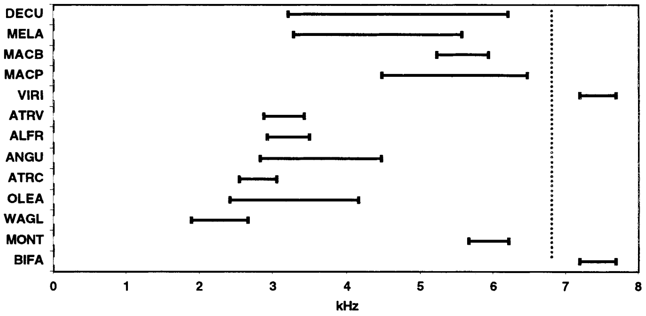


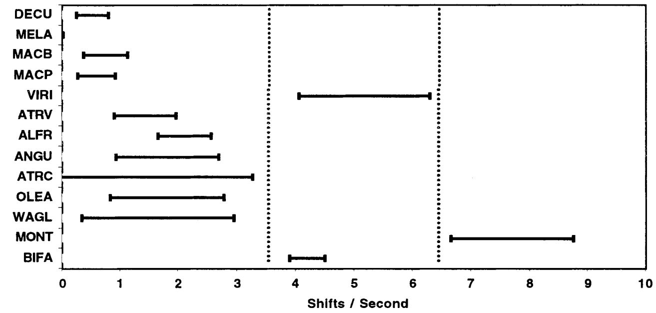
o) Overall peak frequency, Character 25

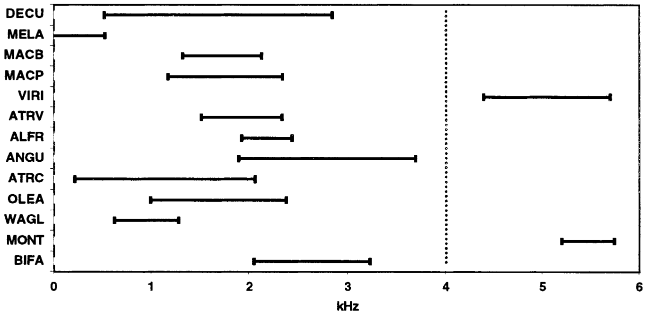
p) Highest peak frequency, Character 26

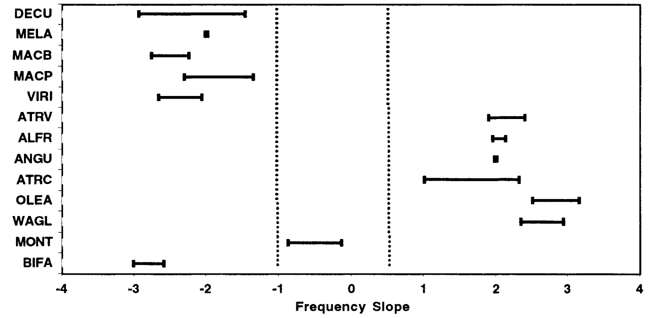
APPENDIX. Continued.

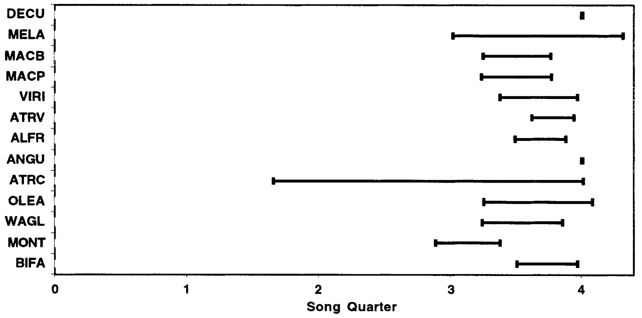

q) Lowest peak frequency, Character 27


r) Range in peak frequencies, Character 28


s) Frequency shift rate, Character 29


t) Maximum frequency shift, Character 30


u) Frequency slope, Character 31


v) Amplitude peak, Character 32