Behavioral Ecology Vol. 15 No. 3: 485–497
DOI: 10.1093/beheco/arh040

Patterns of song evolution and sexual selection in the oropendolas and caciques

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Although oscine bird song is widely thought to have evolved under the influence of sexual selection, few studies have used phylogenetic comparative methods to investigate how these vocalizations have changed historically. In the present study, we use a molecular phylogeny based on mitochondrial sequence data to reconstruct vocal evolution in the oropendolas and caciques, an oscine group with diverse taxon-specific song patterns and a wide range in levels of sexual size dimorphism. Our reconstructions show that large changes in song organization and structure have occurred on branches of the phylogeny with relatively high levels of size dimorphism. The particular vocal components that changed, however, often differed in different phylogenetic lineages. These patterns indicate that sexual selection has had important influences on song evolution in these birds, but has targeted different components of song in different taxa. Our results provide insight into how sexual selection influences bird song and suggest directions for future research to uncover the behavioral mechanisms driving vocal evolution. *Key words:* behavioral evolution, independent contrasts, mating display, mtDNA, New World blackbirds, spectrogram. *[Behav Ecol 15:485–497 (2004)]*

The complex songs of male songbirds rival other well-known sexually selected traits in both their degree of elaboration and their diversity among taxa (Catchpole and Slater, 1995; Wiley, 2000). Such diversity is presumably the result of interspecific differences in the strength of sexual selection and in factors that constrain these influences on signal design (Andersson, 1994; Harvey and Bradbury, 1991; Searcy and Yasukawa, 1996). Yet, comparative studies of bird song have provided little clear support for this idea, as trends found among taxa have often disagreed with mechanisms of selection found in individual avian species (see Catchpole, 1980; Catchpole and McGregor, 1985; Irwin, 1990; Read and Weary, 1992). A problem in these comparative studies is that few have controlled for phylogenetic associations using well-supported estimates of phylogeny, which make any resultant trends difficult to interpret (Felsenstein, 1985b; Harvey and Pagel, 1991).

Comparative studies of sexual selection have typically examined an individual characteristic (e.g., the size of a male feature) across species to see if it varies in predictable ways under different selective regimes (Andersson, 1994; Harvey and Bradbury, 1991). In complex mating signals such as oscine song, however, evidence suggests that sexual selection can influence different aspects of display in different species (Gil and Gahr, 2002; Irwin, 1990; Irwin, 2000; Kroodsma, 1977). Traits such as song repertoire size, vocal output, and aspects of the acoustic structure of song might evolve independently in different lineages, which could preclude finding a general trend in any particular song feature even after controlling for phylogeny. Thus, reconstructing changes in multiple rather than individual traits on a phylogenetic tree might be a more effective method for investigating how songs have historically responded to selection.

Characteristics of song that are costly to develop or perform are likely targets of sexual selection, as these features can provide reliable information to listeners about male condition or quality (Grafen, 1990; Kodric-Brown and Brown, 1984; Zahavi, 1975). Repertoire size, or the number of different elements or songs that a male bird can produce, is a well-known candidate for such selection and has been studied extensively (Catchpole and Slater, 1995; Hasselquist et al., 1996; Searcy, 1992; Searcy and Yasukawa, 1996). Increasing evidence, however, suggests that the manner in which songs are performed, rather than just the number that can be produced, can also influence male mating success and thus might be subject to sexual selection as well (Gil and Gahr, 2002). For example, males with higher song outputs (i.e., ones that produce more sounds in a given time period) often acquire mates earlier (pied flycatchers, *Ficedula hypoleuca*: Alatalo et al., 1990; blackcaps, *Sylvia atricapilla*: Hoi-Leitner et al., 1995) and have fewer extrapair offspring in their nests (barn swallows, *Hirundo rustica*: Møller et al., 1998) than do other males. Mating success might also be affected by how males organize their songs during display (i.e., whether they sing in a repetitive or versatile manner), although this possibility has rarely been studied directly. In general, versatile modes of singing are thought to be more attractive to females than repetitive song patterns (Searcy and Yasukawa, 1996).

Even less well investigated is the idea that the component parts of songs themselves might be subject to sexual selection. Certain types of sounds are likely to be particularly difficult for males to develop and produce because, for instance, they require fine motor control or special respiratory mechanisms (Suthers et al., 1999). In line with this idea, Podos (1996, 1997) demonstrated that the frequency range and note repetition rate of songs are subject to constraints and that birds face consequent trade-offs in performance between these two measures. Other song features such as long continuous sounds, very high frequencies, or the production of two different sounds at once are also likely to be physiologically demanding for singers (Suthers et al., 1999; Allan and Suthers, 1994). Little is known about how these features affect male mating success in the field, but laboratory experiments on a range of species indicate that such physically challenging sounds can be especially attractive to

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Received 7 January 2003; revised 5 August 2003; accepted 17 August 2003.

females (e.g., brown-headed cowbirds, *Molothrus ater*: King and West, 1983; canaries, *Serinus canaria*: Vallet et al., 1998; swamp sparrows, *Melospiza georgiana*: Ballentine et al., 2004). If any such song features have an influence on mating success, selection is expected to favor birds that perform them near the upper limits of what is physically possible (Gil and Gahr, 2002).

In the present study, we investigated the consequences of sexual selection on bird song by reconstructing vocal evolution in the caciques (genus *Cacicus*) and oropendolas (*Psarocolius*, *Gymnostinops*, *Ocyalus*), a monophyletic group of New World blackbirds (family Icteridae) found from Mexico to Argentina (Sibley and Monroe, 1990). Species in this clade can differ dramatically in mating system and in degree of sexual size dimorphism (Jaramillo and Burke, 1999; Robinson, 1986; Webster, 1992), from species that are monogamous and sexually monomorphic (e.g., *Cacicus solitarius*) to some of the most extreme examples of polygyny and sexual size dimorphism known in birds (e.g., *Gymnostinops montezuma*; Webster, 1994; 1997). Taxa also exhibit a diversity of song patterns and species-typical singing styles, which range from highly repetitive (repeating a single song type many times in succession) to highly versatile (producing a variety of different song types during a singing bout). Thus, this is an ideal group for exploring the effects of sexual selection on oscine song.

We used mitochondrial DNA (mtDNA) sequence data to construct a nearly complete phylogeny for the caciques and oropendolas, which we used to address three main objectives. First, we determined the monophyly of currently recognized taxa. Phylogenetic relationships among many members of this clade are poorly known, and previous studies have suggested that some currently recognized taxonomic groups are not monophyletic (Freeman and Zink, 1995; Price and Lanyon, 2002b). Second, we used comparative methods in combination with this molecular phylogeny to reconstruct historical changes in various aspects of song, including song output (SO), versatility, and several measures of the acoustic structure of songs. Finally, we compared these patterns of vocal evolution to measures of sexual size dimorphism to investigate how songs have changed under different levels of sexual selection.

METHODS

Molecular analysis

We obtained tissue samples from 49 individuals representing nearly all described subspecies and geographic variants within 17 of the 20 recognized species of cacique and oropendola (Blake, 1968; Sibley and Monroe, 1990). We also obtained samples from four representatives of the monotypic cup-nesting cacique, *Amblycercus holocericeus*, which were used as outgroups in this study based on evidence of distant relationships between this species and other icterids (Lanyon and Omland, 1999). Three additional outgroup taxa were chosen to represent the other three major New World blackbird clades: *Agelaius phoeniceus* for the grackles and allies, *Sturnella neglecta* for the meadowlarks and allies, and *Icterus galbula* for the orioles. We included multiple samples from different locations for 15 taxa, including *A. holocericeus*, to test for potential within-population diversity and for errors in sequencing. Voucher information and collecting localities for the 56 specimens used in this study are listed in Appendix A.

We obtained DNA sequence data for constructing a molecular phylogeny from two protein-coding mitochondrial genes: cytochrome *b* (cyt *b*) and NADH dehydrogenase subunit 2 (ND2). Methods used in mtDNA extraction, amplification, and sequencing and the list of primers used in this analysis are detailed in Price and Lanyon (2002b). In total, we sequenced 2011 base pairs (bp) of mtDNA from each sample, representing a large portion of the cyt-*b* gene (920 bp) and the entire ND2 gene (1091 bp). These sequences have been deposited in GenBank under the accession numbers AF472362–AF472411 and AY117697–AY117752. Sequence data for the three noncacique outgroup taxa were obtained from GenBank from the study of Klicka et al. (2000; accession numbers AF290127, AF290130, AF290134, AF290164, AF290167, AF290173).

Phylogenetic analyses of the molecular data were performed in PAUP* (Swofford, 2002). A partition homogeneity test using the two gene regions as partitions under equal weighting found no significant difference in their phylogenetic signal ($p = .97$), so we combined these sequences in all subsequent analyses. We constructed a maximum-likelihood (ML) tree for the oropendolas and caciques by using the general time reversible model of sequence evolution, with invariant sites and with rates at variable sites following a gamma distribution (GTR + I + G; proportion of invariant sites = 0.5653; gamma shape parameter = 1.6548; $R_{\mathrm{ac}} = 1.1$, $R_{\mathrm{ag}} = 25.7$, $R_{\mathrm{at}} = 0.8$, $R_{\mathrm{cg}} = 0.2$, $R_{\mathrm{ct}} = 20.0$, $R_{\mathrm{gt}} = 1.0$; molecular clock not enforced). This model was selected using likelihood-ratio tests in Modeltest (Posada and Crandall, 1998).

To test whether the ML tree was robust to alternative tree-building methods, we constructed additional phylogenies using maximum parsimony (MP). We used six-parameter weighting (Williams and Fitch, 1989) as our primary weighting scheme in this analysis, as it accounts for base composition biases as well as differences in the frequencies of transitions and transversions. We obtained weighting values by finding the shortest combined-data tree using equally weighted parsimony and then reconstructing transformations onto this topology in MacClade (Maddison and Maddison, 2000). Weights were then derived by computing the negative natural log (–ln) of the frequency of each of the six types of base substitution, without regard to polarity. We further explored the sensitivity of this topology to weighting scheme by performing parsimony searches with transversion to transition weightings of 1 : 1 (equal weighting), 3 : 1, 6 : 1, and 9 : 1. For each of these analyses, we estimated the degree to which our results were dependent on character composition by performing full heuristic bootstrap analyses (Felsenstein, 1985a) with 1000 replicates.

Song measures

We obtained tape recordings of cacique and oropendola songs from the Macaulay Library of Natural Sounds, Cornell University, and from a variety of commercially available cassette tapes (Coffey and Coffey, 1984, 1989; Hardy et al., 1998; Parker, 1985; Moore, 1993, 1994, 1997; see Appendix B). These recordings included representatives of all 17 species, and all but one recognized subspecies (*Gymnostinops bifasciatus neivae*), included as ingroup taxa in the molecular analysis. For each taxon, we obtained multiple recordings from geographically distant recording locations whenever possible to sample the widest possible diversity of song patterns. We also maximized the number of recordists who contributed to our data set for each taxon so as to minimize potential bias. Three subspecies (*Psarocolius wagleri wagleri*, *Cacicus chrysonotus peruvianus*, and *Cacicus uropygialis pacificus*) were excluded from the analysis because we could not obtain more than one recording of each. Recordings made at different locations and/or on different dates were assumed to be of different individual birds, and songs were assumed to be from males for most taxa. For species in which female song has been reported (*Cacicus solitarius*, *C. chrysonotus*, *C. uropygialis*, and *C. chrysopterus*). we used published descriptions of vocalizations (Jaramillo and Burke, 1999) and recordists' notes in an attempt to measure only the songs of males. We avoided using sections of recordings in which multiple birds were vocalizing at the same time. In all, we included songs from 206 individual males in this study, with two to 27 individuals (mean = 7.9, SE = 1.2) representing each of 26 genetically distinct taxa.

We generated spectrograms of songs using Canary sound analysis software (version 1.2.4, Cornell Laboratory of Ornithology; sampling frequency = 22.05 kHz, frequency resolution = 349.7 Hz, temporal resolution = 11.6 ms, 93.75% overlap of frames in successive transforms). All of our measurements were made during continuous singing bouts by males, when songs were produced at relatively regular intervals. Some taxa in this group produce a variety of sound patterns in relatively rapid succession during a singing bout (e.g., *Cacicus cela cela*; Feekes, 1982), which makes classifying what sounds constitute a "song" in these birds less clearcut than in most other oscines. In our study, we defined a song as any pattern of sound longer than 0.4 s in duration that was preceded and followed by pauses greater than 0.5 s. These thresholds, based on preliminary analyses, allowed us to exclude from most analyses a variety of short (less than 0.4 s), low-amplitude calls that seemed unlikely to function as advertising displays.

To analyze patterns of song organization, we classified the songs of each individual male into song types using SoundEdit 16 (version 2; Macromedia). Songs that were indistinguishable by visual inspection of spectrograms and by ear were classified as the same song type, and those that differed were classified as different song types (also see Price, 1998). To confirm our classifications, we analyzed seven undistorted recordings of different taxa by using the Correlator function in Canary to calculate a matrix of similarity scores between each of the spectrograms from each singing bout. These scores were then imported into the program Neighbor in PHYLIP (Felsenstein, 1993) to construct a neighbor-joining network for each taxon which grouped spectrograms that had similar acoustic structure (also see Irwin, 2000). In all cases, our classifications of songs into types corresponded to these groupings.

We measured the SO of singers by calculating the summed duration of all sounds produced during the period from the beginning of one song to the beginning of the next, excluding any pauses between sounds and including short calls (less than 0.4 s), as a proportion of this time interval. We made three separate measurements of SO to give a mean for each singer and then used these values to calculate a mean for each taxon. SO could potentially vary among birds owing to differences in singing rate or in the duration of each song produced (Wasserman and Cigliano, 1991), or both, so we also measured the mean song duration and mean intersong interval in each taxon to explore these possibilities.

We measured song versatility (SV) as the mean number of distinct song types occurring during the production of eight consecutive songs. Individuals characterized by high SV values are those that sing with immediate variety (i.e., switch frequently between song types during a singing bout). Individuals with lower SV values are typically those that sing with eventual variety (i.e., repeat a song type several to many times before switching to another) or those that produce only a single song type. Eight songs were used as a standard in these measurements because different species sing at different rates, and for several taxa, we were unable to obtain recordings with more than eight consecutive songs.

We measured aspects of the acoustic structure of songs using Canary. The frequency range (FR) of each taxon was measured as the mean difference between the highest and lowest peak frequencies occurring in each song. We calculated the pause rate (PR), by dividing the number of pauses (intervals with no measurable amplitude and with durations from 5–500 ms) in each song by the song duration. This measure was intended to reflect the rate of sound production by a singer in much the same manner as note rates measured in some previous studies (see Podos, 1996, 1997, 2001). We measured PRs rather than note rates in the present study in part because the production of multiple sounds at the same time made defining a "note" problematic for some taxa. Moreover, because pauses indicate parts of a song in which a bird might breath or otherwise recover between periods of sound production (Suthers et al., 1999), we felt that the rate of pauses in spectrograms was a more physiologically meaningful measure than the rate of note production. The maximum note length (NL) was the duration of the longest continuous sound (i.e., interval between pauses) that occurred in each song. Note overlap (NO) was measured as the summed duration of all portions of notes in a song that appeared to overlap each other temporally, which indicates the production of two sounds, or "two voices," at the same time. Notes were counted as overlapping only if their frequencies were not integer multiples of each other (i.e., they were not related harmonics) and/or they had different slopes in spectrograms.

For measurements of acoustic structure, we attempted to maximize the independence of our samples by analyzing only one to three representative songs from each tape recording. We selected only one song from a recording if it included a single repeated song type. For recordings that contained more than one song type, we analyzed up to three songs, each of a different type. Because no song type appeared in more than one individual in each species, no song type was measured more than once in our analysis, and we obtained measurements from a range of song patterns in each taxon.

Phylogenetic comparative analysis

To search for consistent vocal differences between taxa that might indicate historical changes in song design, we converted our song measurements into discrete characters and then mapped them onto the molecular tree using simple parsimony in MacClade (Maddison and Maddison, 2000). We parsed each continuous character into discrete ordered character states by plotting means and standard errors for taxa and then dividing these measures into states where error bars did not overlap (Figure 1) (also see Price and Lanyon, 2002a). This method allowed us to detect statistically discontinuous evolutionary changes while controlling for within-taxon variability in song organization and structure.

Reconstructions of character evolution are only as good as the phylogenies upon which they are based (Harvey and Pagel, 1991). Thus, if parts of the molecular tree were not clearly resolved in our phylogenetic analyses, we performed multiple reconstructions by using each of the possible alternative topologies to test the robustness of our results. One oropendola species, *Psarocolius decumanus*, was analyzed as a single sample, rather than as its component subspecies, based on previous evidence that named subspecies are not monophyletic (Price and Lanyon, 2002b) and that songs do not differ among conspecifics with respect to the song characteristics included in this study (Price and Lanyon, 2002a).

We tested for clade-wide correlations between song measures by using independent contrasts (Felsenstein, 1985b).

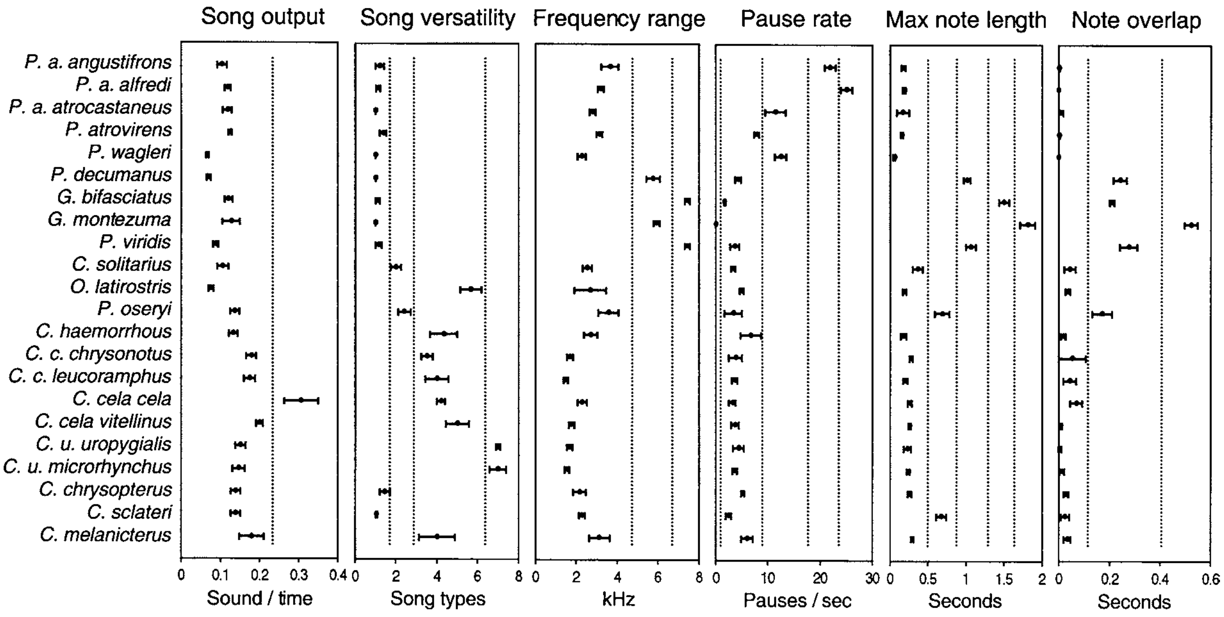

Figure 1

Mean (±SE) measurements of six components of song in the oropendolas and caciques. Vertical dotted lines indicate where measurements were divided into discrete character states for reconstructing historical changes.

This method incorporates phylogeny into comparisons of continuous variables among taxa to correct for statistical nonindependence caused by shared history (Harvey and Pagel, 1991). We used the Contrast program in PHYLIP (Felsenstein, 1993) to calculate values for each character on each node, with phylogenetic relationships and branch lengths taken from the ML tree, and then used these contrast values to test for potential associations. All regressions were forced through the origin.

Sexual selection

We used the relative degree of sexual size dimorphism in taxa as an approximate indicator of relative strength of sexual selection in this study. Size dimorphism is closely associated with mating system in the New World blackbird family; species with larger average harem sizes generally have greater differences in body size between the sexes (Webster, 1992). We did not use mating system itself as an indicator of the relative strength of sexual selection because this aspect of life history is not well known for many of the study taxa (Jaramillo and Burke, 1999). We used the ratio of male tarsus length to female tarsus length as a measure of dimorphism in body size. Mean measurements of tarsus length for taxa were obtained from Jaramillo and Burke (1999), except for measurements of *Psarocolius wagleri* and *Cacicus haemorrhous*, which were not available in that text and so were obtained from Webster (1992). Measurements of the same species in these two sources were similar. In general, species reported to have polygynous mating systems (Irwin, 1990; Jaramillo and Burke, 1999; Leak and Robinson, 1989; Robinson, 1986; Webster, 1992) were ones in which males were 15% or more larger than were females. Putative monogamous species, in contrast, generally exhibit much lower levels of dimorphism.

Sexual size dimorphism can arise through multiple evolutionary pathways (i.e., increases or decreases in the size of either sex) and so is not necessarily homologous across taxa (Hormiga et al., 2000). Therefore, to estimate size dimorphism in ancestors, we reconstructed changes in tarsus length in each sex independently on the tree using squared-change parsimony (Maddison, 1991) as implemented in MacClade (Maddison and Maddison, 2000), and then used these ancestral values to calculate size ratios for each internal branch.

We tested whether evolutionary changes in songs are consistently associated with high levels of sexual size dimorphism (males 15% larger than females) on the molecular tree using the concentrated-changes test (Maddison, 1990) in MacClade. We also tested for associations between each of our song characters and dimorphism by using independent contrasts, after natural log-transforming all size measurements.

RESULTS

Molecular relationships

ML (Figure 2) and MP trees were nearly identical in topology. Both methods indicate that the oropendolas and caciques are not reciprocally monophyletic. Rather, as shown in a previous molecular systematic study of oropendola relationships (Price and Lanyon, 2000b), oropendolas are divided into two separate groups: a clade including the genus *Gymnostinops* and all but one member of the genus *Psarocolius* (hereafter, called the "true oropendolas") and a clade consisting of *Psarocolius oseryi* and *Ocyalus latirostris*. Each of these oropendola groups is more closely related to cacique species than they are to each other.

Twenty eight of the 30 ingroup nodes in the ML tree were resolved in a 50% bootstrap analysis of the six-parameter weighted MP tree, and 20 nodes were supported in at least 95% of bootstrap pseudoreplicates (Figure 2). The monophyly of every recognized species received at least 98% bootstrap support. Furthermore, of the subspecies with multiple representatives in our study, the monophyly of all but one received at least 94% bootstrap support. The exception was *Psarocolius decumanus maculosus*, the three representatives of which were not found to be each others' closest relatives. Parsimony analyses using additional transversion/transition weightings of 1 : 1, 3 : 1, 6 : 1, and 9 : 1 differed from the ML topology only in resolution and in levels of bootstrap support.

Only two nodes on the ML phylogeny were not clearly supported in MP analyses. The position of *Cacicus chrysonotus* and *C. sclateri* on the ML tree were resolved in the six-parameter weighted analysis and in additional MP analyses with transversion biases of 3 : 1 or more, but this position did not receive more than 50% bootstrap support under any weighting scheme. Likewise, ML analysis resolved *Psarocolius oseryi* as sister taxon to *Ocyalus latirostris*, whereas six-parameter weighted MP analysis resolved it as sister to *C. haemorrhous*. This latter relationship received no bootstrap support, however, and neither topology was resolved in MP analyses using other weighting schemes. For both of these weakly supported nodes, we consider the ML phylogeny to provide our best estimates of relationship (Figure 2). Nevertheless, we used all nine possible trees resulting from alternative relationships at these nodes (i.e., with three possible topologies at each) in our reconstructions of character evolution.

Patterns of song evolution

Mapping our song characters onto the molecular phylogeny (Figure 3, arrows and character abbreviations above branches) indicated that evolutionary changes are not distributed uniformly across the tree. At least three aspects of song changed on each of the branches leading to *G. montezuma*, *P. oseryi*, and the clade comprising *P. decumanus*, *P. viridis*, and the two *Gymnostinops* species. Changes on other branches involved individual song components, most of which changed multiple times in different regions of the tree. Only one of the reconstructed changes was altered when song characters were mapped onto the nine alternative trees: the decrease in SV at the base of the true oropendolas was found to occur on an earlier branch if *C. chrysopterus* and *C. sclateri* were placed as sister to *C. solitarius* and the true oropendolas.

G. bifasciatus and *P. viridis* exhibited the highest FRs in the clade (Figure 1); however, our reconstructions were ambiguous about whether this property increased independently in these two lineages, as shown in Figure 3, or increased on an earlier branch and then decreased in *G. montezuma*. Likewise, PRs in the songs of *P. wagleri* and *P. a. atrocastaneus*, although not as extreme as in *P. a. angustifrons* and *P. a. alfredi*, were high in comparison to the rest of the clade, but we could not resolve whether these rates increased independently (Figure 3) or increased in a common ancestor and then decreased in *P. atrovirens*.

Reconstructing male/female size ratios on the tree (Figure 3, values below branches) showed that changes in song characters were concentrated on portions of the phylogeny with relatively high levels of sexual size dimorphism. For example, the high degree of size dimorphism in *P. oseryi* corresponded with changes in at least three aspects of song on this branch. Likewise, increased dimorphism in both *C. cela* and *C. sclateri* corresponded with increases in SO and maximum NL, respectively, in these two species. The highest levels of size dimorphism, found in the true oropendolas, were associated with increased PRs in one region of this clade and increases in FR, maximum NL, and NO in the other.

Overall, eight of the ten branches of the tree that showed unambiguous changes in one or more song characters also exhibited size ratios in which males were at least 15% larger than females (concentrated changes test: $p = .033$). Furthermore, of the seven branches on which male-female size difference increased by 3% or more, only the branch leading to *C. haemorrhous* was not associated with any notable change in one of our song characters. Similar patterns were found when dimorphism was reconstructed onto all of the nine potential phylogenies.

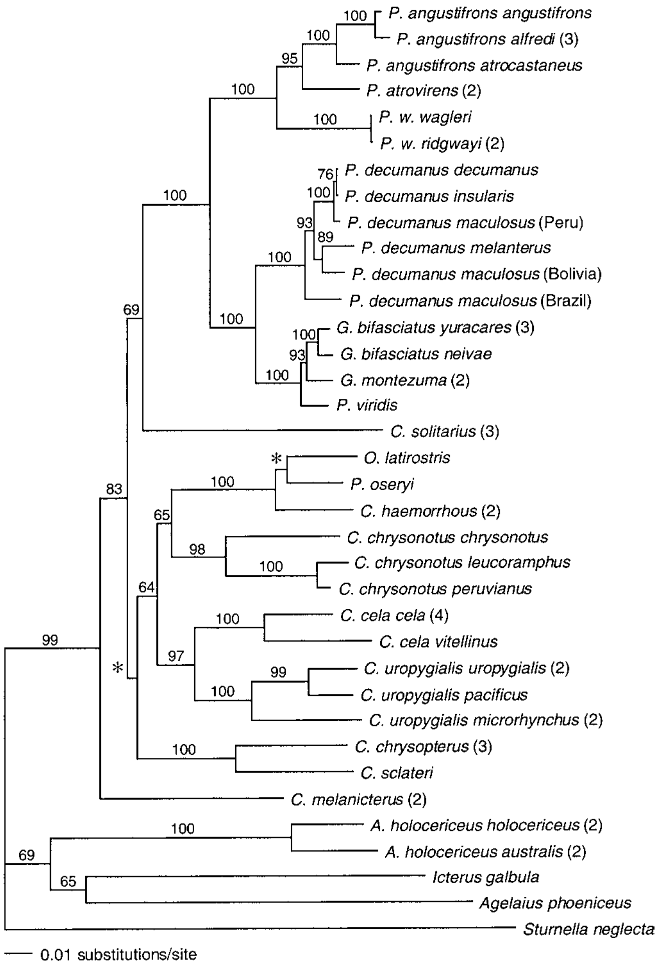

Figure 2
Maximum likelihood (ML) estimate of phylogeny for the oropendolas and caciques based on cytochrome *b* and ND2 sequence data (–lnL = 13316.52). Maximum parsimony (MP) analysis using a range of weighting schemes resolved nearly identical relationships. Numbers above branches are bootstrap proportions on the six-parameter weighted tree. Asterisks indicate two nodes not consistently supported in all analyses. Branches are collapsed where appropriate to show only recognized species and subspecies (all collapsed clades received 100% bootstrap support). Numbers in parentheses indicate the number of representatives from each taxon included in the original analysis. Country names in parentheses indicate that representatives of one subspecies, *P. decumanus maculosus*, from three locations are not each other's closest relatives. Branch lengths are proportional to the number of nucleotide substitutions. *C* indicates *Cacicus*; *G*, *Gymnostinops*; *O*, *Ocyalus*; and *P*, *Psarocolius*.

SO increased notably only on the branch leading to *C. cela cela* (Figure 3). SOs in all other taxa were relatively uniform and differed little from the overall mean of the clade (mean = 13.6%, SE = 0.1) (Figure 1). Consistent with this uniformity, the two main components of SO—song duration and intersong interval—differed markedly between taxa (range in mean song durations = 0.5–3.3 s, intersong intervals = 2.9–22.1 s), yet were strongly positively correlated in independent contrasts so that birds with longer songs nearly always had longer intervals between songs as well ($F_{1,20} = 13.46$; $r^2 = .42$;

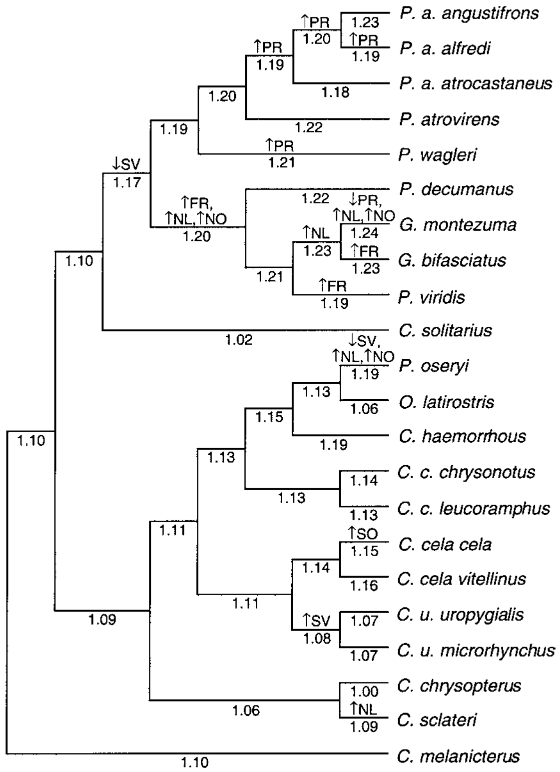

Figure 3

Evolutionary changes in song (above branches) and levels of sexual size dimorphism (below branches) reconstructed on the molecular phylogeny. Arrows and character abbreviations above branches indicate increases (up arrows) or decreases (down arrows) in song output (SO), song versatility (SV), frequency range (FR), pause rate (PR), maximum note length (NL), and note overlap (NO). Numbers below branches show male/female size ratios (male tarsus length/ female tarsus length) estimated by reconstructing size measurements of each sex independently on the tree using squared-change parsimony.

$p = .0015$). Maximum NL and NO were also positively associated with each other ($F_{1,20} = 22.61$; $r^2 = .53$; $p = .0001$).

Independent contrasts of individual song characters against sexual dimorphism (Table 1) showed that the maximum NL of songs increased with increased male-female size ratios ($F_{1,20} = 5.31$; $r^2 = .22$; $p = .033$) (Figure 4). Contrasts of FR, NO, PR, and SO also showed evidence of a positive relationship with sexual size dimorphism, although none of these was significant ($p > .05$). Rather, different combinations of song components have often increased with dimorphism in different phylogenetic lineages (Figure 3).

Table 1

Independent contrasts of sexual size dimorphism (SSD) versus six measures of song on the maximum likelihood tree

SSD versus	Regression coefficient	F value	r^2
Frequency range	7.744	2.268	.102
Maximum note length	3.204	5.312	.218
Note overlap	0.803	1.780	.082
Pause rate	9.762	0.210	.010
Song output	0.183	1.018	.071
Song versatility	−9.381	3.759	.158

Regressions of the residuals of phylogenetically independent contrasts were forced through the origin.

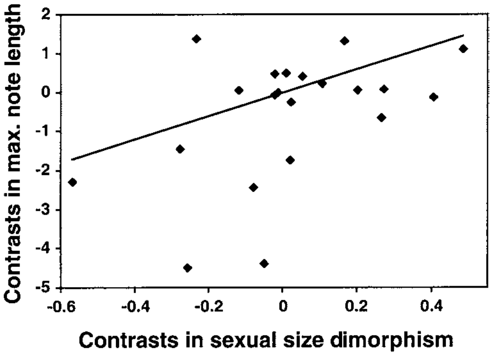

Figure 4

Independent contrasts of maximum note length in comparison to sexual size dimorphism.

SV showed an association with dimorphism ($F_{1,20} = 3.76$; $r^2 = .16$; $p = .067$); however, in contrast to other song characters, this relationship was negative (Figure 5). Versatility decreased along with large increases in dimorphism in *P. oseryi* and at the base of the true oropendolas (Figure 3). Furthermore, the one increase in SV on the tree, that found in *C. uropygialis*, was associated with a decrease in sexual size dimorphism.

DISCUSSION

Evolutionary reconstructions based on a molecular phylogeny with strong bootstrap support show that increases in the intensity of sexual selection, measured in the present study as sexual size dimorphism, have frequently been accompanied by notable changes in song. The aspects of song that changed in each case, however, were not necessarily the same, so that few individual vocal features are strongly associated with dimorphism across the clade. Song appears to provide multiple potential targets for selection in these birds, and as a consequence, different evolutionary patterns have emerged in different lineages.

Our findings confirm previous suggestions that oscine song can evolve along a variety of possible trajectories in response to sexual selection. In a previous comparative study of the New World blackbirds, R. Irwin (1990) found that interspecific differences in one aspect of song, song repertoire size, is not explained by directional sexual selection on this feature across the entire family. Rather, selection appears to have influenced vocalizations in different ways in different icterine groups. Likewise, D. Irwin (2000) examined song variation in

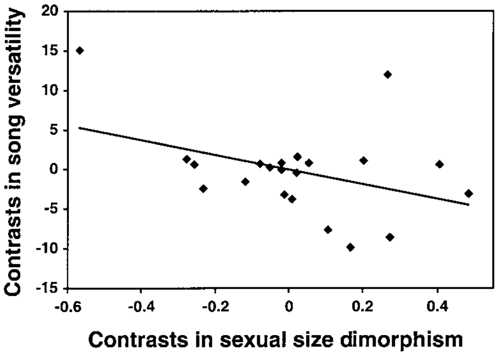

Figure 5

Independent contrasts of song versatility in comparison to sexual size dimorphism.

the greenish warbler (*Phylloscopus trochiloides*) along two latitudinal gradients on either side of the Tibetan plateau of central Asia. Within both populations, songs have become more complex in northern areas, where sexual selection is presumably more intense (Irwin, 2000). These increases in complexity, however, have involved changes in different vocal components in each north—south cline, and the songs of the two northern populations are now strikingly different as a result.

The positive relationship in our study between the maximum NL of songs and male/female size ratios (Figure 4) can be explained in part by the fact that males of more dimorphic species are generally larger than are males of less dimorphic taxa. Larger males presumably have greater lung capacities than do smaller males, and thus are able to expel more air and produce longer continuous sounds. Maximum NL was strongly associated with male size, measured as tarsus length (independent contrasts: $F_{1,20} = 22.57$; $r^2 = .543$; $p = .0001$), which supports the idea that smaller males are limited in their abilities to produce long sounds. Furthermore, the fact that some larger species (e.g., *P. decumanus*, *P. viridis*, and the two *Gymnostinops* species) (Figure 1) produce songs that include both very long notes and high levels of NO (which requires the expiration of air through both sides of the syrinx simultaneously; Suthers et al., 1999) suggests that these males are performing near the upper limits of their abilities.

Although some song features have occasionally changed in parallel during vocal evolution (e.g., maximum NL and NO), increases in the PR and FR of songs have never occurred together (Figure 3). This agrees with Podos (1996, 1997, 2001), who has demonstrated in experimental and comparative studies that a trade-off exists in the performance of these two components of song. Birds that produce relatively rapid note repetition rates, reflected in our study as PRs, are constrained in their abilities to produce a wide range of frequencies, and vice versa. In the oropendolas, this trade-off appears to have resulted in taxa with extremes of either one or the other of these features, but never both. Constraints on song production, in addition to stochastic patterns of selection, have probably played an important role in vocal divergence among these species.

The strong correlation between song durations and intersong intervals, and the consequent uniformity of overall SOs across most taxa, suggests another constraint on vocal production. Birds that produce longer, and presumably more energetically expensive, songs also tend to take longer breaks between them. Thus, the high mean SO measured in the South American subspecies of the yellow-rumped cacique, *Cacicus cela cela* (Figures 1 and 3), indicates a dramatic increase in overall sound production above that of other taxa. This difference could be a product of the short time-windows we used in our measurements, which would have skewed our results if birds take relatively long pauses between each singing bout rather than between each song. However, it is interesting to note that this subspecies is also known to have larger vocal repertoires than other closely related taxa (Irwin, 1990), including its sister subspecies *C. cela vitellinus* (Feekes, 1982), which corroborates our evidence that selection has had a strong influence on the displays of this taxon.

Our study found no evidence that SV has increased under sexual selection in the oropendolas and caciques. On the contrary, singing patterns have tended to become more repetitive with increased levels of sexual selection, which is the opposite of what is generally presumed in discussions of song evolution (see Catchpole, 1980; Catchpole and Slater, 1995; Kroodsma, 1977; Read and Weary, 1992; Searcy and Yasukawa, 1996). In many dimorphic species in this clade (e.g., *C. sclateri*, *P. oseryi*, and the true oropendolas) (Figure 3), increases in size dimorphism have been accompanied not by increases in species-typical song versatilities, but by increases in the relative extravagance of other attributes of song. Examples include large FRs, rapid PRs, and long continuous notes. Decreases in SV thus appear to have been compensated in some cases by increases in the complexity of other vocal characters.

Another surprising result was the convergence in several acoustic features between the casqued oropendola (*Psarocolius oseryi*) and the true oropendolas. The songs of both contain extremely long notes and high levels of NO in comparison to other members of the oropendola-cacique clade (Figure 1). Casqued oropendola songs also often begin with a rapid series of notes that resemble the introductory rattles of many true oropendola displays (Price and Lanyon, 2002a). These vocal similarities, as well as similarly high levels of sexual size dimorphism, might partly explain why this species had previously been placed in the genus *Psarocolius* (Blake, 1968; Jaramillo and Burke, 1999; Sibley and Monroe, 1990). However, the results of our molecular analysis confirm that these birds are in fact distantly related and that these attributes are almost certainly independently derived.

The present study demonstrates the importance of obtaining well-supported estimates of phylogeny in studies of behavioral evolution. Historical changes in the songs of oropendolas and caciques have resulted in the divergence, and in some cases convergence, of a variety of vocal features across taxa. Without a detailed understanding of phylogeny, these patterns would not have been apparent. Our findings also suggest directions for future research into the behavioral mechanisms driving these evolutionary trends. For example, song features that show large, recent changes on our tree (e.g., increases in maximum NL and NO in *Gymnostinops montezuma* and *Psarocolius oseryi*) (Figure 3) should be investigated in studies of individual species to see if these features influence male mating success in present populations. Studies using the phylogenetic comparative approach in other oscine groups are also needed to see if any of the trends revealed here, such as the apparent decrease in SV under strong sexual selection, are more widespread in the evolution of bird song.

APPENDIX A

Tissue samples used in the study

Species	Catalogue no.	Locality	Subspecies	Museum*
Psarocolius oseryi	(Monotypic)	LSU	120394	Peru, Loreto
Psarocolius decumanus	*decumanus*	LSU	LAA1011	Peru, Loreto
Psarocolius decumanus	*insularis*	STRI	TR-PDE1	Trinidad
Psarocolius decumanus	*melanterus*	LSU	164425	Panama, Colón
Psarocolius decumanus	*maculosus*	FMNH	334605	Bolivia, Santa Cruz
Psarocolius decumanus	*maculosus*	FMNH	324065	Peru, Madre de Dios
Psarocolius decumanus	*maculosus*	USNM	GRG1812	Brazil, Para
Psarocolius viridis	(Monotypic)	USNM	609202	Guyana
Psarocolius atrovirens	(Monotypic)	FMNH	324106	Peru, Cuzco
Psarocolius atrovirens	(Monotypic)	LSU	129462	Peru, Pasco, Cushi
Psarocolius angustifrons	*alfredi*	FMNH	324068	Peru, Madre de Dios
Psarocolius angustifrons	*alfredi*	FMNH	SML1047	Peru, Madre de Dios
Psarocolius angustifrons	*alfredi*	LSU	JPO7958	Peru, Cajamarca
Psarocolius angustifrons	*angustifrons*	LSU	120397	Peru, Loreto
Psarocolius angustifrons	*atrocastaneus*	LSU	JCM8604	Ecuador, Pichincha
Psarocolius wagleri	*wagleri*	STRI	HAPWA-HA29	Honduras, La Ceiba
Psarocolius wagleri	*ridgwayi*	LSU	MJB126	Costa Rica, Cartago
Psarocolius wagleri	*ridgwayi*	LSU	B26395	Panama, Panamá
Gymnostinops montezuma	(Monotypic)	LSU	ATP91-36	Mexico
Gymnostinops montezuma	(Monotypic)	LSU	164424	Panama, Colón
Gymnostinops bifasciatus	*yuracares*	FMNH	324076	Peru, Madre de Dios
Gymnostinops bifasciatus	*yuracares*	FMNH	SML1059	Peru, Madre de Dios
Gymnostinops bifasciatus	*yuracares*	LSU	153616	Bolivia, Santa Cruz
Gymnostinops bifasciatus	*neivae*	USNM	GRG1888	Brazil, Para
Ocyalus latirostris	(Monotypic)	ANSP	177928	Peru, Loreto
Cacicus cela	*cela*	FNMH	390070	Brazil, Rondonia
Cacicus cela	*cela*	FMNH	339733	Venezuela, Sucre
Cacicus cela	*cela*	FMNH	324080	Peru, Madre de Dios
Cacicus cela	*cela*	KU	88289	Guyana
Cacicus cela	*vitellinus*	LSU	163850	Panama, Colon
Cacicus haemorrhous	*haemorrhous*	USNM	621068	Guyana
Cacicus haemorrhous	*haemorrhous*	UGA	173	Guyana
Cacicus uropygialis	*uropygialis*	LSU	B6093	Ecuador, Morona Santiago
Cacicus uropygialis	*uropygialis*	LSU	98015	Peru, Cajamarca
Cacicus uropygialis	*pacificus*	ANSP	182884	Ecuador, Esmeradas
Cacicus uropygialis	*microrhynchus*	STRI	PACUR-PC103	Panama
Cacicus uropygialis	*microrhynchus*	STRI	PACUR-PC99	Panama
Cacicus chrysopterus	(Monotypic)	USNM	620761	Argentina
Cacicus chrysopterus	(Monotypic)	KU	88493	Paraguay
Cacicus chrysopterus	(Monotypic)	KU	B131	Paraguay
Cacicus chrysonotus	*chrysonotus*	LSU	103278	Bolivia, La Paz
Cacicus chrysonotus	*leucoramphus*	ANSP	182883	Ecuador, Imbabura
Cacicus chrysonotus	*peruvianus*	LSU	98016	Peru, Cajamarca
Cacicus sclateri	(Monotypic)	ANSP	177931	Peru, Loreto
Cacicus solitarius	(Monotypic)	FMNH	324089	Peru, Madre de Dios
Cacicus solitarius	(Monotypic)	FMNH	324091	Peru, Madre de Dios
Cacicus solitarius	(Monotypic)	USNM	609510	Argentina
Cacicus melanicterusm	(Monotypic)	UWBM	52204	Mexico, Oaxaca
Cacicus melanicterusm	(Monotypic)	UWBM	52185	Mexico, Oaxaca
Amblycercus holocericeus	*holocericeus*	KU	1928	Mexico, Yucatan
Amblycercus holocericeus	*holocericeus*	KU	2075	Mexico, Yucatan
Amblycercus holocericeus	*australis*	LSU	98900	Peru, Puno
Amblycercus holocericeus	*australis*	LSU	106927	Peru, Pasco
Icterus galbula	*bullockii*	FMNH	342938	USA, California
Agelaius phoeniceus	*phoeniceus*	FMNH	341893	USA, Louisiana
Sturnella neglecta	(Monotypic)	FMNH	330039	USA, California

ANSP indicates Academy of Natural Sciences Philadelphia; FMNH, Field Museum of Natural History; KU, University of Kansas Museum of Natural History; LSU, Louisiana State University Museum of Natural Science; USNM, National Museum of Natural History; STRI, Smithsonian Tropical Research Institute; UGA, University of Georgia; and UWBM, University of Washington Burke Museum.

APPENDIX B

Song recordings used in the study

Taxon	Recording source	#Birds	Recording location	Recordist	Date
Psarocolius oseryi					
	LNS 11446*	2	Peru	T.A. Parker	6/20/77
	LNS 12824	1	Peru	T.A. Parker	6/30/77
	LNS 17894	3	Peru	V. Emanuel	7/1978
	LNS 29545	1	Peru	T.A. Parker	8/18/82
	LNS 29938	1	Peru	T.A. Parker	9/14/82
	LNS 31294	1	Peru, Madre de Dios	B. Spencer	7/21/82
	LNS 31938	1	Peru, Madre de Dios	T.A. Parker	7/24/83
	LNS 35182	1	Peru, Madre de Dios	L. Kibler	8/12/85
	LNS 35487	1	Peru, Madre de Dios	T.A. Parker	8/14/85
	LNS 60400	2	Ecuador, Napo	P. Coopmans	12/6/92
	Moore 1994	1	Ecuador, Napo	J.V. Moore	unknown
	Moore 1993	1	Ecuador, Napo	J.V. Moore	3/1989
Psarocolius decumanus decumanus					
	LNS 11513	1	Surinam	T.H. Davis	11/4/79
	LNS 12603	1	British Guiana	D.W. Snow	4/1961
	LNS 28633	1	Ecuador, Napo	A.B. van den Berg	2/16/81
	LNS 37405	1	Peru, Loreto	M.B. Robbins	8/29/85
	LNS 51310	1	Ecuador, Napo	G. Budney	1/27/91
	Moore 1997	1	Ecuador, Napo	J.V. Moore	11/1993
Psarocolius decumanus insularis					
	LNS 12605	2	Trinidad	D.A. Ward	1/20/65
Psarocolius decumanus melanterus					
	LNS 12617	1	Panama	L I. Davis	4/6/62
	LNS 12618	1	Panama	L.I. Davis	4/7/62
	Hardy et al. 1998	1	Colombia, Choco	F.G. Stiles	12/18/90
Psarocolius decumanus maculosus (Peru)					
	LNS 12830	1	Peru, Madre de Dios	T.A. Parker	6/30/77
	LNS 12863	1	Peru, Madre de Dios	T.A. Parker	7/22/77
	LNS 18114	1	Peru	M. Palmer	11/10/79
	LNS 29764	1	Peru, Madre de Dios	T.A. Parker	8/30/82
	LNS 30114	2	Peru, Cuzco	T.A. Parker	9/27/82
Psarocolius decumanus maculosus (Bolivia)					
	LNS 17123	1	Bolivia, La Paz	T.A. Parker	1/30/79
	LNS 51809	1	Bolivia, Beni	T.A. Parker	6/20/89
	LNS 51810	1	Bolivia, Beni	T.A. Parker	6/20/89
	LNS 87848	3	Bolivia, Beni	B.A. Hennessey	10/8/96
	LNS 87850	1	Bolivia, Beni	B.A. Hennessey	10/8/96
	LNS 87860	1	Bolivia, Beni	B.A. Hennessey	10/9/96
	LNS 87861	1	Bolivia, Beni	B.A. Hennessey	10/9/96
	Hardy et al. 1998	1	Argentina, Jujuy	J.M. Barnett	9/30/97
Psarocolius viridis					
	LNS 29177	1	Peru, Loreto	T.A. Parker	5/26/82
	LNS 29279	1	Peru	T.A. Parker	unknown
	LNS 31498	1	Brazil, Amazonas	R. Bierregaard	12/4/83
	LNS 32478	1	Brazil, Amazonas	R. Bierregaard	1/18/84
	LNS 42882	1	Brazil, Amazonas	R. Bierregaard	9/4/88
	LNS 49377	2	Venezuela, Bolivar	C.D. Duncan	8/23/89
	LNS 50912	1	Venezuela, Bolivar	L.R. Macaulay	1/31/92
	LNS 50914	1	Venezuela, Bolivar	L.R. Macaulay	1/31/92
	Hardy et al. 1998	1	Venezuela, Bolivar	D.J. Delanay	1/26/89
	Hardy et al. 1998	1	Venezuela, Bolivar	A. Jaramillo	3/6/97
Psarocolius atrovirens					
	LNS 10489	1	Peru	T.A. Parker	1975
	LNS 11010	2	Peru	T.A. Parker	7/1975
	LNS 13803	2	Bolivia	T.A. Parker	6/10/79
	LNS 17148	1	Bolivia	T.A. Parker	6/30/79
	LNS 17168	1	Bolivia	T.A. Parker	7/2/79
	LNS 17820	1	Peru	V. Emanuel	7/6/79
	LNS 33706	2	Bolivia, Cochabamba	T.A. Parker	10/13/83
	LNS 33709	3	Bolivia, Cochabamba	T.A. Parker	10/14/83
	LNS 33712	1	Bolivia, Cochabamba	T.A. Parker	10/14/83
	LNS 87618	1	Bolivia, La Paz	B.A. Hennessey	9/12/97
	LNS 87628	1	Bolivia, La Paz	B.A. Hennessey	9/13/97
	LNS 87631	1	Bolivia, La Paz	B.A. Hennessey	9/13/97

APPENDIX B, continued

Taxon	Recording source	#Birds	Recording location	Recordist	Date
	LNS 87661	1	Bolivia, La Paz	B.A. Hennessey	10/4/97
	LNS 87663	3	Bolivia, La Paz	B. A. Hennessey	10/4/97
	LNS 87670	2	Bolivia, La Paz	B.A. Hennessey	10/11/97
	LNS 87680	1	Bolivia, La Paz	B.A. Hennessey	10/12/97
	LNS 87682	1	Bolivia, La Paz	B.A. Hennessey	10/12/97
	Hardy et al. 1998	1	Peru, Cuzco	A.J. Begazo	11/1994
	Hardy et al. 1998	1	Peru, Cuzco	A.J. Begazo	11/1994
Psarocolius angustifrons angustifrons					
	LNS 29234	1	Peru, Loreto	T.A. Parker	6/2/82
	LNS 31725	1	Peru, Loreto	T.A. Parker	6/23/83
	LNS 34167	1	Peru, Loreto	T.A. Parker	1/13/85
	LNS 34208	1	Peru, Loreto	T.A. Parker	1/15/85
	LNS 60427	2	Napo, Ecuador	P. Coopmans	1/12/93
	Moore 1997	1	Napo, Ecuador	J.V. Moore	3/1994
Psarocolius angustifrons alfredi					
	LNS 17847	1	Peru, Huanuco	V. Emanuel	7/16/79
	LNS 23823	1	Peru, Madre de Dios	T.A. Parker	5/31/81
	LNS 23959	2	Peru, Madre de Dios	T.A. Parker	5/31/81
	LNS 29032	1	Peru, Madre de Dios	A.B. van den Berg	9/1/80
	LNS 29702	1	Peru, Madre de Dios	T.A. Parker	8/24/82
	LNS 29984	1	Peru, Madre de Dios	T.A. Parker	9/20/82
	LNS 30123	1	Peru, Cuzco	T.A. Parker	9/27/82
	LNS 41257	1	Ecuador, Morona-Sant.	M.B. Robbins	6/24/84
	LNS 44425	2	Bolivia, La Paz	T.A. Parker	8/17/88
	LNS 44426	1	Bolivia, La Paz	T.A. Parker	8/17/88
	LNS 51809	2	Bolivia, Beni	T.A. Parker	6/20/89
	LNS 51810	1	Bolivia, Beni	T.A. Parker	6/20/89
	LNS 87838	2	Bolivia, Beni	B.A. Hennessey	9/30/96
	LNS 87839	2	Bolivia, Beni	B.A. Hennessey	9/30/96
	LNS 87842	2	Bolivia, Beni	B.A. Hennessey	9/30/96
	Hardy et al. 1998	1	Peru, Cuzco	A.J. Begazo	11/1994
	Coffey & Coffey 1984	1	Peru, Madre de Dios	B. B. Coffey	unknown
Psarocolius angustifrons atrocastaneus					
	LNS 43502	1	Ecuador, Pinchincha	M.B. Robbins	8/18/86
	LNS 48980	2	Ecuador, Esmeraldas	M.B. Robbins	8/20/87
Psarocolius wagleri ridgwayi					
	LNS 12613	1	Costa Rica	L.I. Davis	3/25/58
	LNS 12614	1	Costa Rica	L.I. Davis	3/13/60
	LNS 12619	2	Costa Rica	L.I. Davis	4/9/62
	LNS 12620	1	Costa Rica	L.I. Davis	4/22/62
	LNS 12622	2	Panama	E.S.M.	11/22/65
	LNS 28996	1	Panama	A.B. van den Berg	4/10/81
	LNS 55264	1	Panama	D. Ross	2/3/91
	LNS 56598	1	Costa Rica	L. R. Macaulay	12/10/91
	Hardy et al. 1998	1	Colombia, Choco	F. G. Stiles	12/18/90
Gymnostinops montezuma					
	LNS 12606	1	Mexico, Veracruz	L.I. Davis	2/24/55
	LNS 12607	1	Mexico, Veracruz	L.I. Davis	2/27/55
	LNS 12608	1	Mexico, Campeche	L.I. Davis	5/12/56
	LNS 12609	1	Mexico, Veracruz	L.I. Davis	4/15/53
	LNS 12610	1	Mexico, Veracruz	L.I. Davis	3/13/54
	LNS 12611	1	Mexico, Campeche	L.I. Davis	5/3/59
	LNS 12612	1	Guatemala, Peten	R.L. Shaw	3/23/68
	Hardy et al. 1998	1	Guatemala, Peten	R.A. Bradley	12/12/74
Gymnostinops bifasciatus yuracares					
	LNS 12804	1	Peru	T.A. Parker	6/26/77
	LNS 17604	1	Peru	T.A. Parker	10/1974
	LNS 29023	1	Peru	A.B. van den Berg	8/30/80
	LNS 29673	1	Peru	T.A. Parker	8/28/82
	LNS 31960	1	Peru, Madre de Dios	T.A. Parker	7/28/83
	LNS 31985	1	Peru, Madre de Dios	T.A. Parker	7/23/83
	LNS 32024	1	Peru, Madre de Dios	T.A. Parker	8/12/83
	LNS 35525	1	Peru, Madre de Dios	T. A. Parker	8/15/85
	LNS 51810	1	Bolivia, Beni	T.A. Parker	6/20/89
	LNS 51886	1	Bolivia, Santa Cruz	T. A. Parker	8/31/89
	LNS 52412	1	Bolivia, La Paz	T.A. Parker	5/23/90
	LNS 87889	2	Bolivia, Beni	B.A. Hennessey	11/18/96

APPENDIX B, continued

Taxon	Recording source	#Birds	Recording location	Recordist	Date
	Hardy et al. 1998	1	Ecuador, Napo	R.A. Behrstock	7/17/94
	Hardy et al. 1998	1	Venezuela, Amazonas	D.J. Delanay	2/4/93
Ocyalus latirostris					
	LNS 31712	1	Peru	T.A. Parker	6/23/83
	LNS 31717	1	Peru	T.A. Parker	6/23/83
	LNS 31719	1	Peru	T.A. Parker	6/23/83
	LNS 31721	1	Peru	T.A. Parker	6/23/83
	LNS 31743	1	Peru	T.A. Parker	6/25/83
	LNS 31764	1	Peru	T.A. Parker	6/25/83
	LNS 34417	1	Peru, Loreto	G. Budney	1/21/85
	LNS 35419	1	Peru, Loreto	T.A. Parker	6/29/85
	LNS 35427	1	Peru, Loreto	T.A. Parker	7/10/85
	LNS 37421	1	Peru, Loreto	M.B. Robbins	9/1/85
	LNS 81559	1	Peru, Loreto	P. Donahue	12/29/88
Cacicus cela cela					
	LNS 45954	1	Peru, Madre de Dios	T.A. Parker	7/30/87
	Hardy et al. 1998	1	Ecuador, Napo	A. Jaramillo	12/2/74
	Hardy et al. 1998	1	Ecuador, Napo	A. Jaramillo	11/10/97
	Parker 1985	1	Peru, Madre de Dios	T.A. Parker	unknown
	Coffey & Coffey 1984	1	Peru, Madre de Dios	B.B. Coffey	1984
Cacicus cela vitellinus					
	LNS 25678	1	Panama	T.A. Parker	2/4/82
	LNS 25693	1	Panama	T.A. Parker	2/4/82
Cacicus haemorrhous					
	LNS 22106	1	Brazil	T.A. Parker	10/29/80
	LNS 87849	1	Bolivia, Beni	B. Hennessey	10/8/96
	Hardy et al. 1998	1	Argentina	J. Arvin	10/31/90
	Hardy et al. 1998	2	Brazil, Sao Paulo	E.O. Willis	3/28/84
	Hardy et al. 1998	1	Paraguay	R.A. Behrstock	8/26/89
Cacicus uropygialis uropygialis					
	Hardy et al. 1998	2	Napo, Ecuador	R.A. Behrstock	12/29/93
Cacicus uropygialis microrhynchus					
	LNS 28237	1	Costa Rica	A. Van den Berg	5/16/81
	LNS 56597	3	Costa Rica	L. Macaulay	12/10/91
	Hardy et al. 1998	1	Costa Rica	J.W. Hardy	7/14/81
Cacicus chrysopterus					
	LNS 20164	3	Brazil	P. Schwartz	11/27/71
	LNS 23783	1	Brazil	T.A. Parker	11/16/80
	Hardy et al. 1998	2	Brazil	G.W. Clayton	10/23/89
Cacicus chrysonotus chrysonotus					
	LNS 85605	1	Bolivia	R.A. Rowlett	10/26/79
	Hardy et al. 1998	2	Peru, Cuzco	A. J. Begazo	1/1993
Cacicus chrysonotus leucoramphus					
	LNS 58860	2	Ecuador	L. Macaulay	12/2/93
	Hardy et al. 1998	1	Colombia, Cundinam.	F.G. Stiles	6/14/92
Cacicus sclateri					
	LNS 17509	1	Peru	T.A. Parker	8/6/78
	Moore 1997	2	Ecuador, Kapawi Lodge	J.V. Moore	1/1996
Cacicus solitarius					
	LNS 30766	1	Peru	T.A. Parker	1/14/83
	LNS 51820	1	Bolivia, Beni	T.A. Parker	6/20/89
	Hardy et al. 1998	2	Peru, Ucayali	B.B. Coffey	10/30/75
	Hardy et al. 1998	2	Brazil	D.J. Delaney	10/13/90
	Coffey & Coffey 1984	1	Peru, Madre de Dios	B.B. Coffey	1984
Cacicus melanicterusm					
	LNS 12398	1	Mexico, Nayanit	L.I. Davis	7/8/59
	LNS 12401	1	Mexico, Sinaloa	R. Bradley	6/24/74
	Hardy et al. 1998	1	Mexico, Sinaloa	R. Bradley	6/9/74
	Hardy et al. 1998	1	Mexico, Sinaloa	D.J. Delaney	7/13/86
	Coffey & Coffey 1989	1	Mexico, Acapulco	B.B. Coffey	1989

We thank Andrea Priori at the Macaulay Library of Natural Sounds for assistance in obtaining song recordings, and the curators and staff at the following institutions for acquiring and loaning tissue samples: Academy of Natural Sciences Philadelphia, Field Museum of Natural History, Louisiana State University Museum of Natural Science, Smithsonian National Museum of Natural History, Smithsonian Tropical Research Institute, University of Kansas Museum of Natural History, and University of Washington Burke Museum. Jeff Podos, Elizabeth Price, Robert Zink, and three anonymous reviewers provided valuable comments on the manuscript. Financial support for this work was provided by the Bell Museum of Natural History.

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