



Relationship between song characters and morphology in New World pigeons

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We studied the pattern of variation in song characters among 16 New World pigeon species belonging to different taxonomic groups defined by morphological characters. Structural, temporal and frequency characters of the song were analysed. Principal components analyses showed that species belonging to the same taxonomic group were also grouped together by their song characters. In addition, individuals were correctly assigned into taxonomic groups by discriminant function analyses in more than 87.8% of cases. These analyses also showed that more than 87.5% of the individuals could be correctly classified by species when all song characters were included. Correct classification of individuals by species and taxonomic groups dropped when character types were analysed separately, thus showing that structural, as well as temporal and frequency characters are fundamental to define species- and group-specific identities of New World pigeon's songs. Correspondence between patterns of vocal and morphological variation found in this study can be a consequence of evolutionary changes in morphology affecting song production, as for example body size changes that constrain the syrinx to produce certain acoustic frequencies.

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ADDITIONAL KEY WORDS: Columbidae – pigeons – song – song similarity – song evolution.

INTRODUCTION

Perch coo vocalizations of pigeons and doves (hereafter referred to as songs) are considered as functionally similar to the territorial song of passerines (Goodwin, 1983). These songs are innate, that is they do not need to go through a learning process to develop normally (Lade & Thorpe, 1964; Nottebohm & Nottebohm, 1971; Baptista, 1996). Therefore, dove coos are not affected by auditory experience, and several studies have shown that interspecific variation exceeds intraspecific variation, making dove songs clearly species-specific, and useful for species identification (Slabbekoorn, de Kort & ten Cate, 1999). Field experiments have shown that individuals respond selectively to their own species songs and are sensitive to changes in their acoustic variables, suggesting that song is important for recognition of conspecifics and assessment of their quality (Slabbekoorn & ten Cate, 1998; de Kort & ten Cate, 2001).

Interspecific song differences result from apomorphic

changes affecting song structure. However, as closely related species share most of their characters as a legacy from their last common ancestor, it is likely that they tend to have both more similar songs and morphology. We will test this hypothesis by comparing the songs of New World pigeons (genus *Columba*), a group that comprises 17 species.

Although no phylogeny is known for New World pigeons, monophyly of this group is supported by several kinds of evidence: surface antigens (Irwin & Miller, 1961), electrophoretic analysis of ovalbumin tryptic peptides (Corbin, 1968), behavioral and morphological characters (Goodwin, 1983; Baptista, Trail & Horblit, 1997), and DNA sequencing analysis (Johnson & Clayton, 2000). No thorough phylogenetic analyses have been conducted on New World pigeons, either on molecular or morphological data, but different authors have suggested the existence of certain morphologically based groups of closely related species, that will serve as a basis for our analysis.

As stated above and because of the innate nature of pigeon song, the songs of closely related species (similarity inherited from the last common ancestor) should resemble each other more than those of species

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Table 1. Number of individuals studied for each species of New World pigeons. Taxonomic groups as defined by Johnston (1962). In parenthesis, distinctive morphological features of each group are mentioned

Group/subgroup	Species	Number of individuals
<i>Oenoenas</i> (small size, plain plumage, rounded tails, small bills)	<i>C. goodsoni</i>	2
	<i>C. nigrirostris</i>	3
	<i>C. plumbea</i>	20
	<i>C. subvinacea</i>	11
'Band-tailed' (tails with terminal bands, iridescent neck)	<i>C. araucana</i>	1
	<i>C. caribaea</i>	1
	<i>C. fasciata</i>	9
<i>Patagioenas</i> – cayennensis (no display plumage, except <i>C. cayennensis</i> , which has an iridescent head)	<i>C. cayennensis</i>	20
	<i>C. inornata</i>	1
	<i>C. flavirostris</i>	4
	<i>C. oenops</i>	0
<i>Patagioenas</i> – leucocephala (iridescent neck, dark plumage)	<i>C. leucocephala</i>	3
	<i>C. squamosa</i>	5
<i>Patagioenas</i> – picazuro (white edged outer wing coverts)	<i>C. corensis</i>	2
	<i>C. maculosa</i>	2
	<i>C. picazuro</i>	4
<i>Patagioenas</i> – speciosa (scaly appearance)	<i>C. speciosa</i>	14

belonging to different taxonomic groups. If true, song characters will group together species belonging to the same taxonomic group and separate them from others belonging to different taxonomic groups. We will test the congruence between song- and morphologically based taxonomic groups in New World pigeons.

MATERIAL AND METHODS

NEW WORLD PIGEON TAXONOMIC GROUPS

Johnston (1962) defined three main groups of New World pigeons based on morphology: the *Oenoenas* group (*C. goodsoni*, *C. nigrirostris*, *C. plumbea* and *C. subvinacea*), the 'Band-tailed' group (*Columba araucana*, *C. caribaea* and *C. fasciata*), and the *Patagioenas* group (*C. cayennensis*, *C. inornata*, *C. flavirostris*, *C. oenops*, *C. leucocephala*, *C. squamosa*, *C. corensis*, *C. maculosa*, *C. picazuro* and *C. speciosa*).

Within the *Patagioenas* group, he distinguished four subgroups: (1) *cayennensis*, including *C. cayennensis*, *C. inornata*, *C. flavirostris* and *C. oenops*; (2) *leucocephala*, including *C. leucocephala* and *C. squamosa*; (3) *picazuro*, including *C. corensis*, *C. maculosa* and *C. picazuro*; and (4) *C. speciosa* – a single species not attributable to any of the former subgroups (Table 1).

Goodwin (1983) also recognized the *Oenoenas* group, but preferred to merge 'Band-tailed' and *Patagioenas* into one major group. Within this latter group, he also discussed possible relationships between species, but without a clear indication of taxonomic subgroups. Therefore, we chose the species subdivision of Johnston (1962) as the basis for our analysis.

SONG ANALYSIS

Analyses of songs were based on recordings published by Hardy, Reynard & Coffey (1989) which were obtained from Hardy *et al.*, the National Sound Archive Wildlife Section (U.K.) and the Library of Natural Sounds, Cornell University (U.S.A.). The entire data set included songs of all New World pigeons, except *C. oenops*. The number of recordings available for each species was variable, ranging from one to 21, and belonging to a maximum of 20 different individuals per species (Table 1).

Song recordings were analysed with Canary v. 1.2 software (Charif, Mitchell & Clark, 1995). Songs are always composed of a stereotyped sequence of similar or different notes (we define *note* as a continuous sound in time). Notes can be arranged into stereotyped units called coos or presented alone as an introductory note (an element emitted before the sequence of coos), as a closing note (an element emitted after the sequence of coos), or simply as a unique element that is not repeated in the song, like in the *Oenoenas* species (Fig. 1).

Song structure was described by a number of qualitative and quantitative variables, which presented low intra- and interindividual variation. The former included the presence of an introductory note (INT) and a closing note (CLO). The latter included number of notes in the coo (NOCOO), total duration of the song (TODUR), duration of the coo (COODUR), maximum frequency (MAX), minimum frequency (MIN), bandwidth (BAND = MAX – MIN) and emphasized frequency (ENF, the frequency with higher amplitude in the song).

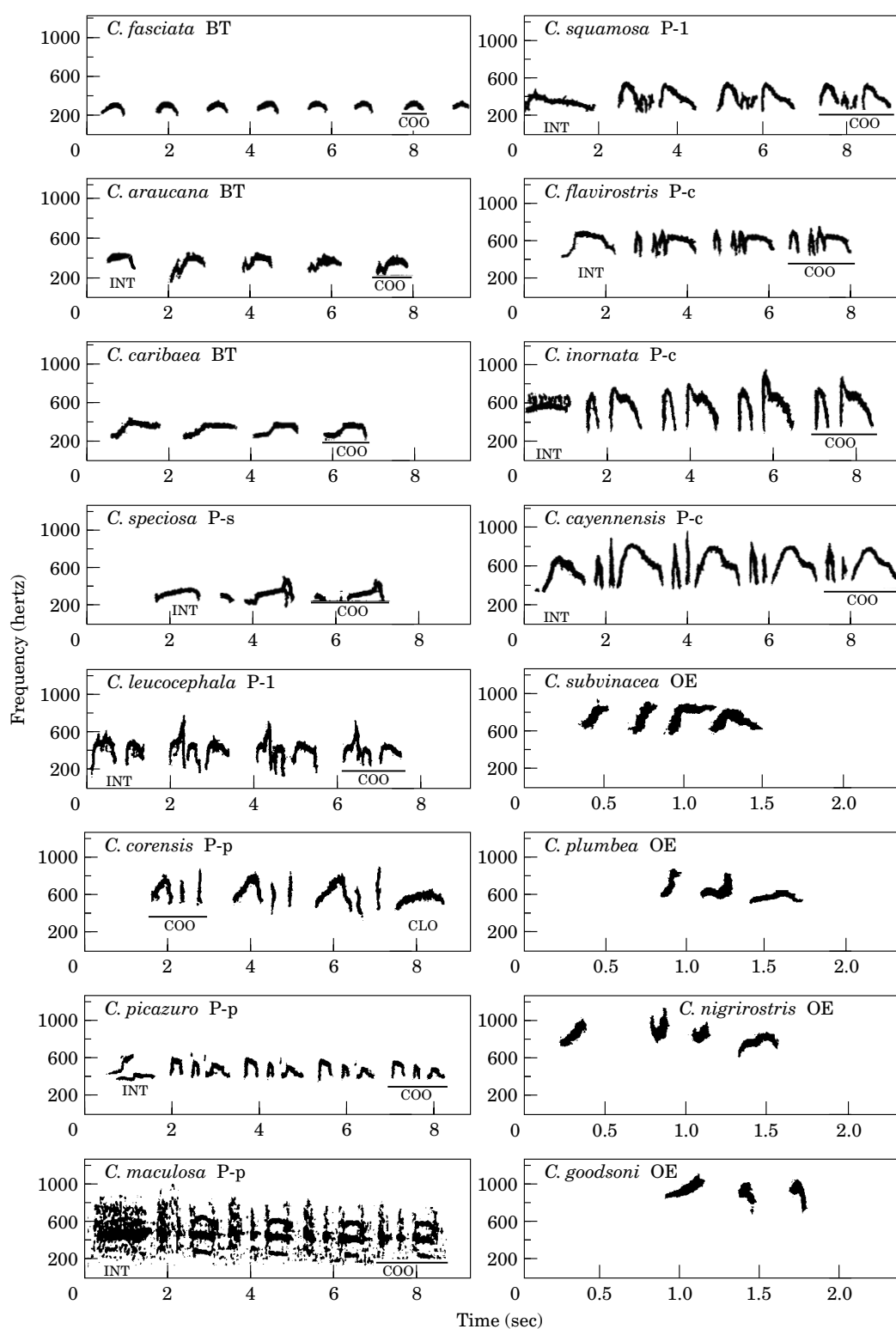


Figure 1. Representative songs of the New World pigeons included in the analysis. Some of the constitutive elements of the songs are indicated: INT: introductory note; CLO: closing note; COO: OE: *Oenoenae* group; BT: 'Band-tailed' group; P-c: *Patagioenas* – cayennensis; P-l: *Patagioenas* – leucocephala; P-p: *Patagioenas* – picazuro; P-s: *Patagioenas* – speciosa.

For each individual, we measured one to six songs, depending on the number of song recordings available. Average values were calculated for each variable.

The analysis was divided in two parts: the first included all species, in order to analyse the song structure in the three main groups defined by Johnston (1962), and the second included the species belonging to the *Patagioenas* group, in which the song structure of its four subgroups was analysed.

STATISTICAL ANALYSIS

Variables were log-transformed and standardized; when some individual had zero as value, one unit was added to all individuals before applying the log-transformation. All statistical analyses were performed with Statistica v. 4.2 software.

To make the data set more balanced, a maximum of ten individuals per species were included in the analysis. For species with a high number of recordings, we randomly selected ten individuals.

The set of song variables was subjected to a principal components analysis (PCA). PCA transforms a large number of correlated variables into a few orthogonal variables (the principal components, PCs). Only PCs with eigenvalues >1 were included in the analysis. The scores of the individuals for the different PCs were plotted in two dimensions and the separation of the different groups was analysed. We also applied discriminant function analysis (DFA) to the PCs, to test whether individuals could be correctly classified by species and by groups. Temporal (TODUR, COODUR), acoustic frequency (MAX, MIN, ENF, BAND) and structural variables (INT, CLO, NOCOO) were also analysed separately by DFA. *C. araucana*, *C. caribaea* and *C. inornata* were excluded from the DFA analyses, because only one recording was available for each species.

RESULTS

ALL NEW WORLD PIGEON SPECIES

In the PCA including 16 New World pigeon species, three PCs were extracted from the original data set and taken together, they accounted for 90.5% of the total variance (Table 2). PC1 was determined by acoustic frequencies (MAX, MIN, ENF), temporal variables (TODUR, COODUR), and one variable related to song complexity (NOCOO); PC2 was not particularly related to any variable, although bandwidth (BAND) and two structural variables (NOCOO, INT) were the variables that contributed most to this component; and PC3 was determined by the presence of the closing note (CLO). Figure 2 shows

Table 2. Factor loadings of the nine song variables on the three PCs with eigenvalues >1, for the analysis including all New World pigeon species, except *C. oenops*. The eigenvalues and its explained variance are given at the bottom of the table

Song variable	PC1	PC2	PC3
MAX	-0.871	0.476	0.068
MIN	-0.881	0.198	-0.151
ENF	-0.864	0.447	0.060
BAND	-0.636	0.593	0.241
TODUR	0.896	0.265	-0.057
INT	0.594	0.607	0.275
CLO	-0.001	0.372	-0.917
NOCOO	0.763	0.603	0.034
COODUR	0.926	0.318	-0.008
Eigenvalues	5.282	1.858	1.009
% Variance explained	58.7	20.6	11.2

that the individuals of *Oenoenas* species got well separated from the other species by PC1, indicating that their songs have higher acoustic frequencies, shorter duration and a more simple structure (Fig. 1). The 'Band-tailed' and the *Patagioenas* species were clearly separated by PC2, indicating a difference in song structure between both groups, and a narrower bandwidth in 'Band-tailed' species (Fig. 1). When DFA was applied to the three PCs, individuals were classified correctly into their respective groups in 100% of cases. This procedure was also employed to test how well individuals were classified by species, and this resulted in 93.2% correct classifications. When variables were analysed separately, correct classification of individuals by groups and species dropped significantly (Table 3). Structural variables were more informative for classifying individuals by groups, whereas acoustic frequency variables were more informative for classifying them by species.

PATAGIOENAS SPECIES

In the second part of the analysis, which only included the *Patagioenas* species, three PCs were extracted from the original data set and accounted for 77.5% of the total variance (Table 4). PC1 was mainly determined by the acoustic frequencies and the number of notes of the coo (NOCOO), PC2 by COODUR, and PC3 was not particularly related to any variable. In the scatterplot of individuals for PC1 and PC2 (Fig. 3), *C. speciosa* became clearly separated from the remaining

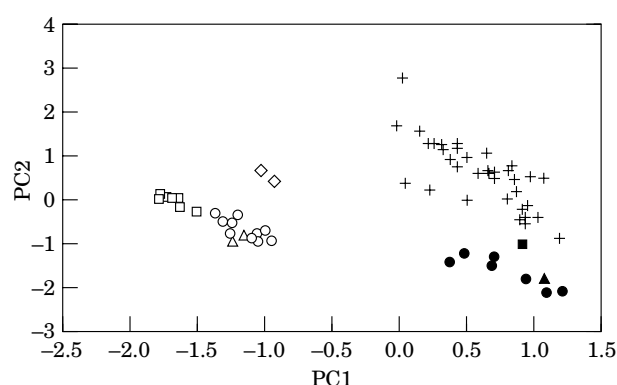


Figure 2. Scatterplots of individuals for PC1 and PC2. Open symbols correspond to *Oenoenass* species, filled symbols to 'Band-tailed' species and crosses to *Patagioenas* species. (\diamond) *C. goodsoni*; (\triangle) *C. nigrirostris*; (\circ) *C. plumbea*; (\square) *C. subvinacea*. (\blacksquare) *C. araucana*; (\blacktriangle) *C. caribaea*; (\bullet) *C. fasciata*.

Patagioenas subgroups by PC1. This indicates that this species has lower acoustic frequencies, a narrower bandwidth and fewer notes in the coo of its song (Fig. 1). The separation of the other three subgroups (*cayennensis*, *leucocephala* and *picazuro*) was not as clear as for *C. speciosa*, although a tendency could be observed (Fig. 3). Individuals belonging to the *cayennensis* subgroup tended to have lower PC1 values. This means that species of this subgroup do have higher acoustic frequencies, a broader bandwidth and a more complex coo structure (Fig. 1). Of the *leucocephala* subgroup only individuals of *C. squamosa* showed lower PC2 values (Fig. 3), indicating a longer duration of the coo. Within the *picazuro* subgroup, *C. corensis* showed a very different song from the other two members of the group, *C. picazuro* and *C. maculosa*, both in PC1 and PC2. These differences are due to higher acoustic frequencies in *C. corensis* and the presence of a closing note in its song (Fig. 1). The DFA, based on the three PCs, showed 87.8% of correct assignment of individuals into the four subgroups and 87.5% of correct assignment into species (Table 5). Again, correct assignments dropped when variable types were analysed separately. Structural variables

Table 4. Factor loadings of the nine song variables on the three PCs with eigenvalues >1, for the analysis including *Patagioenas* species. The eigenvalues and explained variance are given at the bottom of the table

Song variable	PC1	PC2	PC3
MAX	-0.951	0.094	-0.237
MIN	-0.730	0.427	0.344
ENF	-0.919	0.133	-0.226
BAND	-0.759	-0.187	-0.555
TODUR	-0.522	-0.453	0.520
INT	0.225	-0.483	0.119
CLO	-0.371	0.672	0.354
NOCOO	-0.844	-0.269	0.226
COODUR	-0.353	-0.783	0.105
Eigenvalues	4.156	1.819	1.006
% Variance explained	46.2	20.2	11.2

showed no variability within some species and groups (at least in our song sample), making the DFA analysis not possible for this data set. Acoustic frequency variables were more informative than temporal variables for classifying individuals by species and groups (Table 5).

DISCUSSION

SONG CHARACTERS DIFFER AMONG BOTH SPECIES AND SPECIES GROUPS

Multivariate analyses based on frequency, structural and temporal variables of the song showed that morphologically based taxonomic groups defined by Johnston (1962) could also be recognized by song characters. In addition, DFAs suggest that these song variables are quite informative to differentiate a species and that intraspecific variation is mostly within the parameters that define a particular species' song.

Our study showed similarities and differences when compared to the one of Slabbekoorn *et al.* (1999) on the genus *Streptopelia*. In particular, they found that most of the *Streptopelia* species could be correctly differentiated by song, but they could not find clear

Table 3. DFA results for 74 individuals of New World pigeons belonging to 13 species and three taxonomic groups. Percentages of correctly classified individuals by species and groups for temporal, acoustic frequency and structural variables analysed together and separately. (—) Some species lacked variability for the structural variables included in the analysis, making DFA not possible

Individuals classified by	All variables	Temporal variables	Acoustic frequency variables	Structural variables
Groups	100.0%	87.0%	90.9%	96.1%
Species	93.2%	45.9%	74.3%	(—)

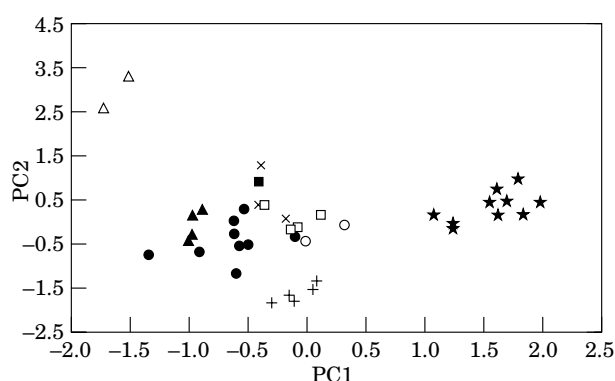


Figure 3. Scatterplots of individuals of the *Patagioenas* subgroups for PC1 and PC2. Filled symbols: cayennensis subgroup; crosses: leucocephala subgroup; open symbols: picazuro subgroup; stars: speciosa subgroup. (●) *C. cayennensis*; (■) *C. inornata*; (▲) *C. flavirostris*. (X) *C. leucocephala*; (+) *C. squamosa*. (△) *C. corensis*; (○) *C. maculosa*; (□) *C. picazuro*. (★) *C. speciosa*.

Table 5. DFA results for 40 individuals belonging to eight species and four *Patagioenas* groups. Percentages of correctly classified individuals by species and groups for all variables and for temporal and acoustic frequency variables analysed separately

Individuals classified by	All variables	Temporal variables	Acoustic frequency variables
Groups	87.8%	63.4%	75.6%
Species	87.5%	52.5%	77.5%

correspondence between groups defined by song structure and by morphology. They also found that species and groups were better differentiated by temporal features of the song rather than by frequency ones. Congruently, our study showed that species could be correctly classified by song variables, although with some error. In contrast, we found that song characters are useful to differentiate groups. This is particularly true for the *Oenoenas* species, which diverged from the other New World pigeons, due to their simple, short and higher frequency songs. Additionally, we found that frequency variables can be equally or more useful than temporal variables to differentiate species and groups. We also analysed structural variables, which describe the number of notes of the song and how they are arranged. These variables were less accurate for differentiating species and taxonomic groups when analysed separately from the other variables, but gave additional information when analysed together. Correct classification of individuals by species and taxonomic groups was always maximal when all variables

were included in the analysis, thus showing that structural, as well as temporal and frequency characters are fundamental to define species- and group-specific identities of New World pigeon's songs.

SONG CHARACTERS ARE RESTRICTED BY MORPHOLOGY

Previous studies have shown the existence of a negative relationship between body size and acoustic frequencies of the song (Wallschläger, 1980; Tubaro & Mahler, 1998). Although the cause of this body size-frequency allometry is not clearly understood, it is probably mediated by anatomical and morphological characters of the vocal tract (Ballintijn & ten Cate, 1997). We interpret our finding of higher frequency songs in *Oenoenas* species as an acoustical consequence of their small body size (Dunning, 1993), indicating the existence of a constraint to song structure caused by morphology.

Slabbekoorn *et al.* (1999) also suggested that frequency variables are restricted by morphology, causing a bad performance of such parameters to differentiate morphologically similar species and species' groups in the genus *Streptopelia*. In contrast, he found that temporal features of the song were more accurate indicators of species identity, as they are less dependent on morphology, and thus more prone to change. In New World pigeons, results of DFAs indicate that both frequency and temporal variables of the song are equally useful for differentiating species and groups. This diversity of results suggests that additional studies are necessary to assess the applicability of the idea that vocal characters linked to morphology might be more conservative than those essentially determined by the neural circuitry of the brain (Ryan, 1988; Cocroft & Ryan, 1995).

SONG- AND MORPHOLOGICALLY BASED SPECIES GROUPS ARE SIMILAR

Behavioral characters have been considered labile in comparison to other morphological and molecular characters and thus of limited utility beyond the diagnosis of species (Payne, 1986). Labile characters can be more homoplastic and therefore of little use for phylogenetic reconstruction, or can change so fast as to delete any historical cue of affinity. Although it has been shown that behavioral characters are not more homoplastic than morphological ones (de Queiroz & Wimberger, 1993; Wimberger & de Queiroz, 1996), it is not clear that avian vocal characters contain significant amount of phylogenetic information except in a few cases (Payne, 1986). However, if vocal characters change in a very different way from morphology, traditional morphologically based taxonomic groups would not be differentiated using vocal variation, as is shown in

this study. Correspondence between patterns of morphological and vocal variation can be a consequence of evolutionary changes in morphology affecting song production, for example, body size changes that constrain the syrinx to produce certain acoustic frequencies. But this study shows that not only morphologically related song variables are useful to differentiate taxonomic groups, as temporal features of the song can also differentiate them. This indicates that, although independent of changes in morphology, temporal variables of the song are not sufficiently labile to lose any indication of species relatedness. The correspondence between patterns of morphological and vocal variation found in this study supports the view that, at least for certain groups, innate vocal characters change congruently with morphological characters, and may contain information of species relatedness.

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