

ACOUSTIC FREQUENCIES AND BODY MASS IN NEW WORLD DOVES¹

PABLO LUIS TUBARO AND BETTINA MAHLER

Laboratorio de Biología del Comportamiento, Instituto de Biología y Medicina Experimental, Obligado 2490,
1428 - Buenos Aires, Argentina,
e-mail: ptubaro@proteus.dna.uba.ar

Abstract. We studied the acoustic frequencies contained in the songs of 44 species of New World doves of eight genera in relation to body mass and habitat structure. On each sonogram, maximum (MAX), minimum (MIN), emphasized frequency (ENF), and frequency bandwidth (BAND = MAX – MIN) were measured. Log-transformed frequencies and body mass data were subjected to a comparative analysis of independent contrast, using Goodwin's (1983) phylogeny. We show the existence of a negative relationship among frequencies and body mass, irrespective of the model of character evolution chosen. Similar results were obtained in raw contrast comparisons among 13 pairs of closely related species. Residuals of variation in song frequencies, after control for the effect of body mass and phylogeny, differed among habitats. In particular, closed habitat species use significantly higher MAX than their more open habitat relatives. This pattern contrasts with the one reported in studies based on community-wide comparisons, which in general do not correct song data for phylogeny and body mass, or include oscine species.

Key words: body mass, comparative analysis, song, habitat, New World doves.

INTRODUCTION

Since the work of Wallschläger (1980), ornithologists have accepted the existence of a negative relationship between body mass and the frequencies used by birds in their songs. In addition, a more recent study showed that the shape of this relationship depends upon the particular group of birds considered (Ryan and Brenowitz 1985).

The cause of this body size–frequency allometry is not clearly understood, but it has been related to both anatomical and physiological factors, such as tracheal length and vocal track resonances, that covary with body size and mass (Wallschläger 1980, Baptista 1996, Lambrechts 1996). For example, in the Ring Dove (*Streptopelia decaocto*), vocalizations with higher fundamental frequencies and more overtones are produced by females, which also have a similar, but smaller version of the male's syrinx (Ballintijn and Ten Cate 1997).

Although the relationship between song frequencies and body size seems to be well established in comparisons across a large number of species, in general these studies have not accounted for the lack of independence among species generated by their phylogeny. This sit-

uation biases these analyses in the direction of rejecting the null hypothesis that there is no relationship between body mass and song frequencies, because of the inflated degrees of freedom of the statistical tests (Felsenstein 1985).

In contrast, other studies have failed to find a negative relationship between body mass and song frequencies when comparisons are restricted to couples of closely related species, or to the intraspecific pattern of song variation. For example, in *Geospiza difficilis* (Bowman 1979, 1983) and *Piranga rubra* (Shy 1983), larger individuals have songs of higher frequencies. In addition, in the Rufous-collared Sparrow (*Zonotrichia capensis*), Handford and Lougheed (1991) found that larger birds tend to have lower-frequency songs and that syrinx size was not related to body size. They suggested that the size of the sound-producing organ does not constrain the frequencies used in song, and that individual differences in song frequencies probably are related to a learning phenomenon associated with the structure of the habitat. According to this view, song learning may be not only adapting song structure to the habitat (Hansen 1979, Nottebohm 1985), but also freeing the song from constraints imposed by body size. In fact, it has been shown that song frequencies also are related to habitat structure (Morton 1975, Wiley 1991), even when the effect of the body size-

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frequency allometry is controlled (Ryan and Brenowitz 1985).

Doves' songs seem to be rigidly programmed and do not need auditory feedback for their normal development (Lade and Thorpe 1964, Nottebohm and Nottebohm 1971, Baptista 1996). Thus, members of the family *Columbidae* are suitable models for a comparative study because any relationship between body mass and the acoustic frequencies of their songs would not be confounded by other phenomena like song learning. In this study, we present the results of several comparative tests about the existence of a negative relationship between body mass and song frequencies, based upon the species belonging to the genus *Columbina*, *Scardafella*, *Claravis*, *Metriopelia*, *Geotrygon*, *Starnoenas*, *Zenaida*, and *Leptotila*. In addition, we analyze the residuals of song variation after removing the effect of body mass and phylogeny, looking for any significant relationship between the habitat used by the species and the acoustic frequencies of their songs.

METHODS

The analysis of songs was based upon recordings published by Hardy et al. (1989), and on the following specimens obtained from the National Sound Archive Wildlife Section (London, United Kingdom): *Geotrygon costarricensis* (cut 18738, by R. Ranft); *G. linearis* (cut 32018, by M. Pearman); *G. veraguensis* (cut 15906, by R. Ranft); and *Metriopelia melanoptera* (cut 23435, by N. Krabbe). The whole sample included songs of 44 out of 51 New World doves. We based our analysis on the advertising call (hereafter referred to as "song"), which is considered homologous to the song of Passerines (Nottebohm and Nottebohm 1971). Because the song of pigeons and doves is basically innate and thus highly stereotyped (Lade and Thorpe 1964, Nottebohm and Nottebohm 1971), we made sonograms of several songs of each species and selected the best signal-to-noise ratio song for frequency measurements. In addition, we compared our sonograms with the published figures from Baptista et al. (1983), Fraga (1983), Robbins et al. (1983), and Blockstein and Hardy (1989), corroborating the highly stereotyped structure of the song in some of the species under study.

On each sonogram (made with a Proaudio Spectrum 16 Sound Blaster [Media Vision] and the ADDA 16 software [Gurlekian et al. 1992])

we measured the following variables: maximum and minimum frequencies (MAX and MIN, respectively), bandwidth (BAND = MAX-MIN), and emphasized frequency (ENF, the frequency with the higher amplitude in the song). The frequency resolution of the analysis was 20 Hz, and ENF values were obtained using a peak finding routine of the ADDA 16 software. All these measurements were done by a person who knew neither the phylogenetic relationship nor the body mass of the species under study. Body mass data were obtained from Dunning (1993), and completed (in a few cases) with unpublished information submitted by different ornithologists. We could not find information about the body masses of *Uropelia campestris* and *L. pallida*, therefore these species were deleted from the comparative tests but still considered in different ways in the construction of the phylogenies as well as in the estimation of ancestral states of the characters. Because of the uncertainties regarding the phylogenetic position of *Zenaida galapagoensis*, we decided to exclude this species from the comparative analysis, but we will comment on its song structure below.

We based our phylogenetic analysis on the phylogenetic hypotheses of Goodwin (1983). These hypotheses are not based on the acoustic structure of the song, but on the morphological (mainly plumage) characters. Unfortunately, they were not built with a cladistic methodology, so their use may potentially cause comparative problems. In order to reduce this source of error, we also made a comparative test using a selected sample of 14 closely related species, accepting the structure of the phylogenetic hypothesis only at the lowest level (Felsenstein 1988, Harvey and Pagel 1991, Harvey and Purvis 1991). In this test, the comparison between *Geotrygon versicolor* and *G. caniceps* was excluded because the two song types included in the sample of *G. caniceps* were very different (one of them has a strong harmonic structure, Table 1). Thus, we worked with 13 pairs of species that represent the closest relationship for which there were body mass and song data. Additional sources of information considered in selecting the species pairs included: Whitman (1919a, 1919b), Goodwin (1958, 1959), Johnston (1961), Baptista et al. (1983), Blockstein and Hardy (1989).

Based upon the phylogenies available, we estimated the ancestral states of the characters using two different models of evolution: the ran-

TABLE 1. Database used in the comparative analysis of the relationship between body mass and song frequencies. For acronyms see Methods.

Species	MAX (Hz)	MIN (Hz)	ENF (Hz)	BAND (Hz)	Body mass (g)	Habitat ^a	Phylogenetic position ^b
<i>Columbina talpacoti</i>	527	429	527	98	46.5	open	AAAAAAA
<i>Columbina buckleyi</i>	606	503	566	103	57.5	mixed	AAAAAAB
<i>Columbina cruziana</i>	2,291	548	1,427	1,743	41.2	open	AAAAABA
<i>Columbina picui</i>	527	420	527	107	50	open	AAAAABB
<i>Columbina minuta</i>	589	459	586	130	33.2	open	AAAAAB
<i>Columbina passerina</i>	702	589	664	113	30.1	open	AAAAABB
<i>Columbina cyanopis</i>	ND	ND	ND	ND	ND	open	AAAB
<i>Claravis mondetoura</i>	427	332	410	95	89.7	closed	AABAA
<i>Claravis godefrida</i>	ND	ND	ND	ND	ND	closed	AABAB
<i>Claravis pretiosa</i>	467	409	449	58	67.3	mixed	AABB
<i>Scardafella inca</i>	1,057	762	1,054	295	47.5	open	AACA
<i>Scardafella squammata</i>	1,031	694	976	337	54.2	open	AACB
<i>Uropelia campestris</i>	1,273	885	1,269	388	ND	open	AAD
<i>Metriopelia ceciliae</i>	ND	ND	ND	ND	ND	open	AAEAA
<i>Metriopelia morenoi</i>	ND	ND	ND	ND	ND	open	AAEAB
<i>Metriopelia ayмара</i>	ND	ND	ND	ND	ND	open	AAEB
<i>Metriopelia melanoptera</i>	2,254	1,521	2,049	733	113	mixed	AAEC
<i>Zenaida aurita</i>	645	484	508	161	159	mixed	ABAA
<i>Zenaida galapagoensis</i>	239	180	215	59	100 ^c	mixed	
<i>Zenaida graysoni</i>	565	400	449	165	192	open	ABABAA
<i>Zenaida macroura</i>	737	466	527	271	123	mixed	ABABAB
<i>Zenaida auriculata</i>	570	313	566	257	114	open	ABAB
<i>Zenaida asiatica</i>	786	530	684	256	153	mixed	ABBA
<i>Zenaida meloda</i>	566	377	488	189	216	open	ABBB
<i>Ectopistes migratorius</i>	ND	ND	ND	ND	ND	mixed	ABC
<i>Geotrygon chrysia</i>	408	340	352	68	171	mixed	BAAAAAA
<i>Geotrygon mystacea</i>	387	358	371	29	230	mixed	BAAAAAB
<i>Geotrygon violacea</i>	567	508	508	59	97.8	closed	BAAAAB
<i>Geotrygon montana</i>	367	313	332	54	115	closed	BAAB
<i>Geotrygon linearis</i>	508	469	508	39	245	closed	BAABAA
<i>Geotrygon albifacies</i>	373	271	332	102	316	closed	BAABAB
<i>Geotrygon chiriquensis</i>	365	296	352	69	308	closed	BAABAC
<i>Geotrygon frenata</i>	333	309	313	24	311	closed	BAABB
<i>Geotrygon versicolor</i>	430	290	430	140	225	closed	BABAAA
<i>Geotrygon caniceps</i>							
(song type 1)	299	256	273	43	210	closed	BABAAB
(song type 2)	375	303	371	72	210		
(song type 2 ^d)	780	303	703	477	210		
<i>Geotrygon veragua</i>	433	355	433	78	155	closed	BABAB
<i>Geotrygon saphirina</i>	1,230	940	1,172	290	203	closed	BABBA
<i>Geotrygon goldmani</i>	586	334	391	252	258	closed	BABBB
<i>Geotrygon lawrencii</i>	858	602	743	256	220	closed	BABBBB
<i>Geotrygon costaricensis</i>	332	271	313	61	320	closed	BABBB
<i>Starnoenas cyanocephalus</i>	596	452	488	144	242	closed	BAC
<i>Leptotila verreauxi</i>	527	389	469	138	153	mixed	BBAA
<i>Leptotila megalura</i>	430	390	430	40	218	closed	BBAB
<i>Leptotila ochraceiventris</i>	546	361	469	185	146	closed	BBBA
<i>Leptotila conoveri</i>	ND	ND	ND	ND	ND	mixed	BBBB
<i>Leptotila cassini</i>	496	441	488	55	159	mixed	BBBC
<i>Leptotila rufaxilla</i>	758	547	566	211	157	closed	BBCAAA
<i>Leptotila wellsi</i>	488	411	461	77	200	mixed	BBCAAB
<i>Leptotila plumbeiceps</i>	338	257	312	81	170	mixed	BBCAB
<i>Leptotila pallida</i>	511	467	488	44	ND	mixed	BBCB
<i>Leptotila jamaicensis</i>	505	392	449	113	160	mixed	BCC

^a Based on Parker et al. 1996.^b After Goodwin 1983, and according to the convention of Purvis and Rumbaut 1995.^c Approximate value, after Grant 1986.^d Includes the first harmonic.

ND: no data.

dom walk model and the punctuated model (Harvey and Purvis 1991). The random walk model assumes that changes occurred at each time interval along the branches of the phylogeny and that the direction of that change is random. The ancestral values of the characters may be reconstructed according to the values of the derived species adjusted by their branch length. The punctuated model assumes that changes occurred only at the nodes of a tree. Details of the general procedure for estimating the character values in the ancestors are in Felsenstein (1985). Finally, we made nondirectional comparative tests using the independent contrasts method (Felsenstein 1985) and the CAIC software v. 2.0 (Purvis and Rumbaut 1995). In short, this method is based upon comparison between pairs of sister species. Each comparison produces a new variable termed "contrast" which results from the difference between the values of the variable measured on the species within the pair. Contrasts may be standardized if divided by the square root of the length of the branches under comparison, or raw if they are left uncorrected. These contrasts are independent among pairs of sister species because they result from the evolutionary divergence that occurred after the origin of each pair. Thus, any association between contrasts belonging to different variables may be statistically detected using a standard linear regression model adjusted to pass through zero or a binomial test. In computing comparative analyses, polytomies were solved by the method of Pagel (1992), or the test was repeated on all alternative phylogenies.

Because the body mass and song data did not belong to the same individual, and even the number of individuals weighed varied among species (range = 1–284 subjects), we assessed the robustness of our analyses by increasing or decreasing by 10% the body mass and acoustic frequencies assigned to each species. Body mass and acoustic frequencies were varied independently. Because we have a complete set of song, body mass, and phylogenetic data for 41 species, the theoretical number of possible matrices is about 4.8×10^{24} . Therefore, we only made a random subset of 10 additional data matrices, like the one depicted in Table 1, and repeated the comparative analyses.

Finally, data on habitat use were obtained from Parker et al. (1996). Based upon this information, New World doves' habitats were

pooled into three categories: closed, including tropical lowland, montane evergreen and river edge forest; mixed, including forest edge and tropical deciduous forest; and open, including all nonforest habitats sensu Stotz et al. (1996). For the comparative analysis, these three categories were coded as 2, 1 and 0, respectively. Although admittedly imperfect, we assume that this gross sketch of the main habitat of each species reduced subjectivity to a minimum and retained enough ecological information to show any potential trend in the design of the songs. At the same time, the use of three categories instead of only two gave us a number of independent contrasts amenable to be treated statistically using binomial tests. All statistical tests were two tailed and performed on the log-transformed values of the original variables.

RESULTS

BODY MASS AND SONG VARIABLES

We found a significant negative relationship between acoustic frequencies of the song and body mass, even when comparisons are framed in a phylogenetic context. Because the results of the analyses were similar regardless of the model of character evolution employed, we only present the ones obtained under the random walk model. In particular, the slope of the regression between contrasts for MAX, MIN, ENF, BAND, and body mass was negative and significant ($\beta \leq -0.39$, $F_{1,33} > 6.03$, $P < 0.02$, see Fig. 1). This means that the heavier species in the pairs being compared also have the lower MAX, MIN, ENF, and BAND in their songs. We assessed the robustness of these results by running the independent contrast tests using ten replicates of the data matrix. All 40 regressions (four variables by ten replicates) were negative, and in 25 out of 40 tests the slope was significant.

Finally, the comparisons between closely related species yielded 13 independent contrasts. The analysis revealed that there is an excess of negative MAX contrasts associated with positive body mass contrasts (binomial tests $P[x \leq 2] < 0.05$, see Fig. 2), indicating a negative relationship between body mass and maximum frequency. This result is independent of the pairs of species chosen for comparison when polytomies composed by *Geotrygon goldmani*, *G. lawrencii* and *G. costaricensis*, or *G. albifacies*, *G. linearis*, and *G. chiriquensis*, were solved.

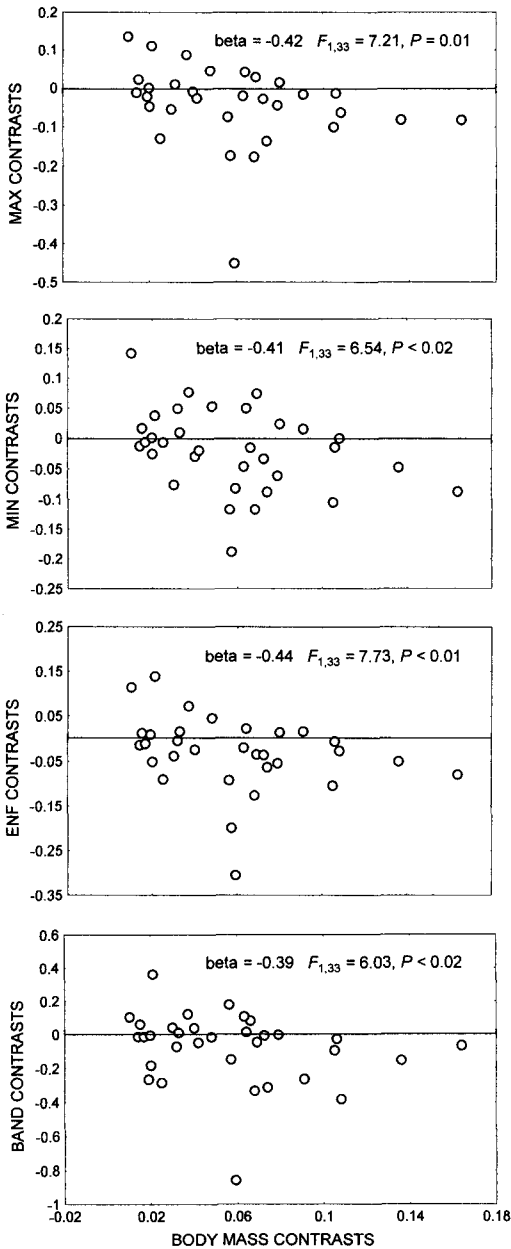


FIGURE 1. Scatterplots of standardized contrasts of acoustic frequencies on body mass of New World doves belonging to the genus *Zenaida*, *Claravis*, *Columbina*, *Scardafella*, *Metriopelia*, *Geotrygon*, *Starnoenas*, and *Leptotila*. Contrasts were calculated using the log-transformed variables and the random walk model of character evolution. Horizontal lines separate positive vs. negative contrasts. The slope (beta) of the regression (forced to pass through zero) and its significance are inside each graph. For acronyms see Methods.

However, the results of this analysis are more sensitive to changes in the data matrix because only four out of ten replicates of the analysis showed a significant excess of negative MAX contrasts associated to positive body mass contrasts.

HABITAT STRUCTURE AND ACOUSTIC FREQUENCIES

We removed the effect of body mass on song variables using the slope of the regression among their respective contrasts (Harvey and Pagel 1991, Purvis and Rumbaut 1995). Thus, residuals of song variation under the two models of character evolution were compared to the habitat used by the species, but controlling again for the phylogenetic effects. This procedure gave us 11 independent contrasts among species differing in habitat use. Ten out of 11 positive MAX contrasts were associated with positive habitat contrasts (binomial tests $P[x \leq 1] = 0.01$), indicating that the species living in more closed habitats have the higher MAX. We also found 9 out of 11 positive ENF and BAND contrasts associated with positive habitat contrast. Although these relationships suggest that closed habitat species also may have higher ENF and wider-band songs than their more open habitat

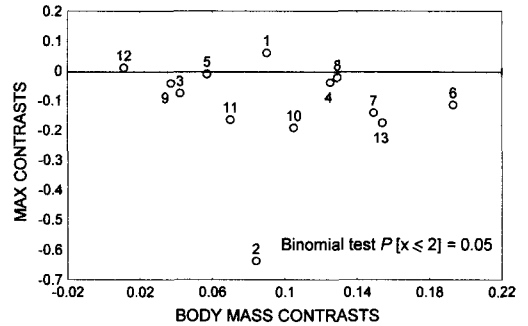


FIGURE 2. Scatterplot of raw contrasts of MAX and body mass among closely related species. Raw contrasts (calculated using log-transformed variables) are as follows: 1: *Columbina buckleyi*—*C. talpacoti*; 2: *Columbina picui*—*C. cruziana*; 3: *Columbina minuta*—*C. passerina*; 4: *Claravis mondetura*—*C. pretiosa*; 5: *Scardafella squammata*—*S. inca*; 6: *Zenaida graysoni*—*Z. macroura*; 7: *Zenaida meloda*—*Z. asiatica*; 8: *Geotrygon mystacea*—*G. chrysis*; 9: *Geotrygon goldmani*—*G. lawrencii*; 10: *Geotrygon albifacies*—*G. chiquensis*; 11: *Leptotila wellsi*—*L. rufaxilla*; 12: *Leptotila cassini*—*L. ochraceiventris*; 13: *Leptotila megalura*—*L. verreauxi*. Horizontal lines separate positive vs. negative contrasts. For acronyms see Methods.

relatives, binomial tests were not significant. No pattern was evident in MIN.

DISCUSSION

This study shows the existence of a negative relationship between body mass and song frequencies, even when interspecific comparisons between New World doves are framed in a phylogenetic context. This result is robust with changes in the hypothesis about character evolution, phylogeny, and values of both body mass and acoustic frequencies. Ideally, this study should be carried out using body mass and song data from the same bird. Unfortunately, due to the fact that tape-recorded birds almost never are captured and measured, this goal is beyond the limit of the actual databases. In addition, information about individual, interindividual, and geographic variation of songs also would be needed. Although dove song is highly stereotyped in relation to those of songbirds, this does not mean that it is devoid of variation. For example, subtle variants in the "coo" call of the Collared Dove (*Streptopelia decaocto*) have been described by Ten Cate (1992). Among New World doves, some interindividual variation was reported in *Leptotila verreauxi* (Fraga 1983) and *Zenaida macroura* (Hitchcock et al. 1988), among others. In addition, the song of *Columbina passerina* (Howell and Webb 1995), *Columba subvinacea* (Ridgely 1996), *Leptotila jamaicensis* (Hardy et al. 1989), and *L. rufaxilla* (D. Blockstein, pers. comm.) was found to vary geographically. We made an effort to include this mostly unknown intraspecific variability in our analyses, varying by $\pm 10\%$ acoustic and body mass values. This procedure did not lead to changes in the results when Goodwin's (1983) phylogeny was used to generate 34 independent contrasts. Results of the analysis including only 13 pairs of closely related species were found to be more sensitive to intraspecific variation, probably as a consequence of the small degrees of freedom involved and the use of a less powerful statistical test (binomial test). However, if "intraspecific" song variation implies that some cryptic species are lumped into current recognized taxa, then the phylogeny of the group should be changed. In turn, the inclusion of new branches may change the pairs of species compared and the inferences about the ancestral values of the characters. *Zenaida galapagoensis* is clearly one of the additional branches that must

be connected to the phylogeny. According to Goodwin (1983) it is the sister species of *Z. aurita*, which is bigger and has higher frequencies than *Z. galapagoensis*. Another possibility is that *Z. galapagoensis* should not be considered inside *Zenaida*, because its calls and displays are unlike all other congeners, which are similar to each other (L. Baptista, pers. comm.). This is the reason why we excluded *Z. galapagoensis* from the formal comparative tests.

Based upon hybridization studies and interspecific comparisons, Baptista (1996) concluded that there is no evidence for direct genetic control on the acoustic frequencies of the song. An interesting possibility is that in birds with innate vocal behavior, such as doves, acoustic frequencies may be determined by body size and morphology, presumably through their influence on syrinx physics and physiology. Our finding of a negative relationship between acoustic frequencies and body mass supports this contention. However, during vocal ontogeny, doves exhibit a phenomenon known as "breaking of the voice" (Abs 1983) which consists in the relatively sudden drop of call frequencies without appreciable change in body mass. This fact may be explained in terms of a rigid developmental program, but it questions the existence of a fixed relationship between body mass and song frequencies.

In species with song learning, a less rigid developmental program may eliminate (or at least reduce) morphological constraints, freeing the song to adapt to ecological factors such as habitat structure (Hansen 1979, Nottebohm 1985). Several studies have shown the existence of a relationship between song frequencies and habitat structure (Morton 1975, Ryan and Brenowitz 1985). In particular, these studies found that birds use lower frequencies in closed habitats such as forest than in more open ones such as grasslands or savannas. In contrast, we report here that in New World doves, closed habitat species tend to have higher MAX, and possibly higher ENF and wider BAND, when differences in body mass and phylogenetic relationships are controlled. *Zenaida galapagoensis* fits well in this pattern of song variation, because is an open or mixed habitat species of small mass, and also has a low frequency call.

A potential problem regarding the finding of a habitat-related pattern of variation in maximum frequencies is that these frequencies are

rapidly attenuated with distance. Thus, MAX may be affected by differences in the mean recording distance of the song samples taken in different habitats (Wiley 1991). Another possible source of uncontrolled variation is the microhabitat used by the species. For a grassland bird that lives and sings from within the grass, the habitat is more closed than the one experienced for a species on the floor of a mature tropical rain forest. Moreover, even ground-dwelling species use song perches at different heights, complicating the interpretation of the data.

Assuming long range communication, selective pressures for adapting song structure to differences in habitat acoustics may be stronger in small Passeriformes because of their limited energy storage capacity relative to their daily energy needs (Morton 1986). In contrast, the relatively bigger doves may be more free to respond to other factors, causing a different pattern of song-habitat structure. Perhaps the lack of vocal learning also may be involved. We suggest that additional studies in other non-Passeriformes (characterized by the lack of vocal learning) should be carried out to assess the generality of the pattern of song-habitat structure found in New World doves. For example, it might be possible to replicate this study on other diverse clades of doves such as Emerald Doves, Bronzewings and Geopelias (genus *Chalcophaps*, *Henicophaps*, *Phaps*, *Petrophassa*, *Geophaps*, *Ocyphaps*, and *Geopelia*), Green Doves (genus *Treron*), and pigeons (genus *Columba*), which include closed and open habitat species. Cuculiforms also are amenable for research because, like doves, their songs seem to be innate, and phylogenetic hypotheses are now available (Hughes 1996).

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