

GEOGRAPHIC, ECOLOGICAL AND SUBSPECIFIC VARIATION IN THE SONG OF THE RUFIOUS-BROWED PEPPERSHRIKE (*CYCLARHIS GUJANENSIS*)¹

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Abstract. We describe the patterns of song variation in the Rufous-browed Peppershrike (*Cyclarhis gujanensis*). Individual variation was estimated using a sample of 659 songs belonging to 21 individuals. This analysis showed that this species uses a repertoire of up to seven song types. Geographic, ecological, and subspecific patterns of variation were estimated using four songs from each of 93 birds recorded from Mexico to Argentina. On each sonogram we measured 10 temporal, frequency, and structural features of the song. Principal component analysis based on the correlation matrix of these data showed that subspecies sing similar songs. However, there were significant relationships between principal component values and latitude, indicating that songs from equatorial areas are shorter in duration, have higher maximum frequency and number of syllables, broader bandwidth and are less repetitive than those from more temperate areas. In addition, we classified the recording sites into three categories according to the actual vegetation: open, mixed, and closed. A multivariate analysis of variance after removing the effect of latitude and altitude, showed that habitat types differ in song structure. Songs from open and mixed areas have a narrow bandwidth, and a lower maximum, minimum and emphasized frequencies than those from closed sites. We analyzed these patterns according to the current ideas about sound propagation in natural environments and the geographical pattern of body size variation in the Rufous-browed Peppershrike.

Key words: *Rufous-browed Peppershrike; Cyclarhis gujanensis; song; subspecies; latitude; altitude; habitat; reverberation hypothesis; Bergmann's rule.*

INTRODUCTION

The analysis of bird-song features and their relationship to habitat structure has been a subject of research since the pioneering studies of Chapuis (1971) and Morton (1975). Those studies showed the existence of song differences between bird communities living in tropical forests and open fields. In particular, Morton (1975) found that the frequencies used by tropical forest species are lower than those from open tropical areas. This relationship remained valid even when differences in body size and phylogenetic effects were accounted for (Ryan and Brenowitz 1985). More recently, Wiley (1991) found that, on average, the maximum frequency of temperate forest songs is lower than those of marsh and grassland. However, the causes of this relationship are not clear.

Early attempts to explain the relationship between frequency of songs and habitat focused on

the attenuation of different frequencies (Morton 1975, Marten and Marler 1977, Marten et al. 1977). These studies reported the existence of an "acoustic window" near the forest ground which favors the use of low frequencies for long-range communication in closed habitats. However, this observation does not explain why species living one or two meters above the ground or in open areas do not use still lower frequencies, since they presumably would propagate even better. Ryan and Brenowitz (1985) suggested that differences in spectral distribution of ambient noise could explain such a difference. In addition, Wiley and Richards (1982) stressed the effects of reverberation rather than differences in frequency attenuation among habitats as the main selective factor in song design. According to this view (henceforth referred to as the "reverberation hypothesis"), in addition to frequency, the temporal structure of the song is important for long-range communication. Slowly modulated signals are favored in forests, because they avoid the acoustic degradation generated by the accumulation of echos. In open fields, the main source of acous-

¹ Received 3 January 1995. Accepted 1 May 1995.

tic degradation is random amplitude fluctuation produced by moving cells of air with different temperature and humidity. This favors signals with high rates of repetition (Wiley and Richards 1978, Richards and Wiley 1980).

The predominance of rapidly modulated sounds in songs from grass and edge habitats, and the presence of pure tone, slowly modulated songs in forest, was described by Morton (1975). A recent study of the vocalizations from bird communities of eastern North America also showed that temporal properties of song were strongly associated to habitat (Wiley 1991). Specifically, birds of forest avoided the use of notes with short repetition periods, as predicted by the reverberation hypothesis.

Another line of research on song design concerns the study of single species living in a diversity of habitats. In spite of the limited generality of this approach, it has the advantage of reducing the confounding effects of phylogeny and morphology in song comparisons. Studies of the White-throated Sparrow (*Zonotrichia albicollis*, Wasserman 1979, Waas 1988), the Summer Tanager (*Piranga rubra*, Shy 1983), the Northern Cardinal (*Cardinalis cardinalis*, Anderson and Conner 1985), and the Great Tit (*Parus major*, Hunter and Krebs 1979) indicate the use of lower frequencies and narrower bandwidth in forested than in more open habitats. However, the Rufous-collared Sparrow (*Zonotrichia capensis*) appears to show the opposite pattern, with higher frequency and broader bandwidth associated with more closed and mesic environments (Nottebohm 1975, Handford and Loughheed 1991). This species also avoids the use of rapid trills in forested areas, thus conforming to the predictions of the reverberation hypothesis (Nottebohm 1975, Handford 1988, Handford and Loughheed 1991, Tubaro et al. 1993).

This diversity of phenomena indicates the need for other comparative studies. In this paper we present an analysis of the pattern of song variation in the Rufous-browed Peppershrike (*Cyclarhis gujanensis*). This species lives in a variety of habitats ranging from mesic forest to xeromorphic woodlands and arid savannas, and from the sea level to 3,500 m in the Andes Mountains. It also shows a high degree of polytypism, with 21 subspecies described in its range from eastern Mexico to central Argentina (Howard and Moore 1991). This provides the possibility for clarifying the extent to which phylogenetic, geographical,

and ecological factors may influence song structure.

The song of the Rufous-browed Peppershrike has not been described using representative samples of sonograms and quantitative measurements of frequency and temporal variables. This species has a repertoire of two song types: a very infrequent, slow series of four to eight descending notes (which is attributed to the female), and a musical whistled song, with multiple ascending and descending modulated notes (Skutch 1967). We considered the later as the primary song of the species and we will refer exclusively to it hereafter.

METHODS

Recordings used in this study were derived from a variety of sources; recording localities and other details are provided in Appendix 1. The sample includes songs of 93 individuals from within the ranges of seven subspecies (sample sizes indicated in parentheses): *C. g. flaviventris* (5), *nicaraguae* (16), *subflavescens* (10), *ochrocephala* (32), *gujanensis* (12), *parvus* (8), and *saturatus* (10). These samples cover almost the entire range of latitudes and altitudes over which this species is found (Fig. 1). Subspecific identity was assigned according to the geographic location of the song recording and the following bibliographic sources: Chapman (1917, 1926), Griscom (1932), Hellmayr (1935), Dickey and Van Rossem (1938), Pinto (1944), Phelps and Phelps (1963), Olrog (1979), and Howard and Moore (1991). Environmental information (altitude and habitat type) was derived from the data sheets accompanying the recordings. Latitude was inferred in missing cases, using the geographic coordinates of the recording site. Habitat types were classified into three categories: closed (including tropical humid forest and montane forest), mixed (including coniferous forest, mixed forest and deciduous forest), and open (arid scrub, gardens, and savannas).

On each sonogram (made with a Proaudio Spectrum 16 Sound Blaster [Media Vision] and the ADDA 16 software [LIS 1992]) we measured the following variables (see Fig. 2): song length (SOLEN), note length (NOLEN), internote interval (INI), maximum and minimum frequencies (MAX and MIN, respectively), bandwidth (BAND = MAX-MIN), emphasized frequency (frequency with the higher amplitude in the song, ENF), number of notes (NN), number of syllable

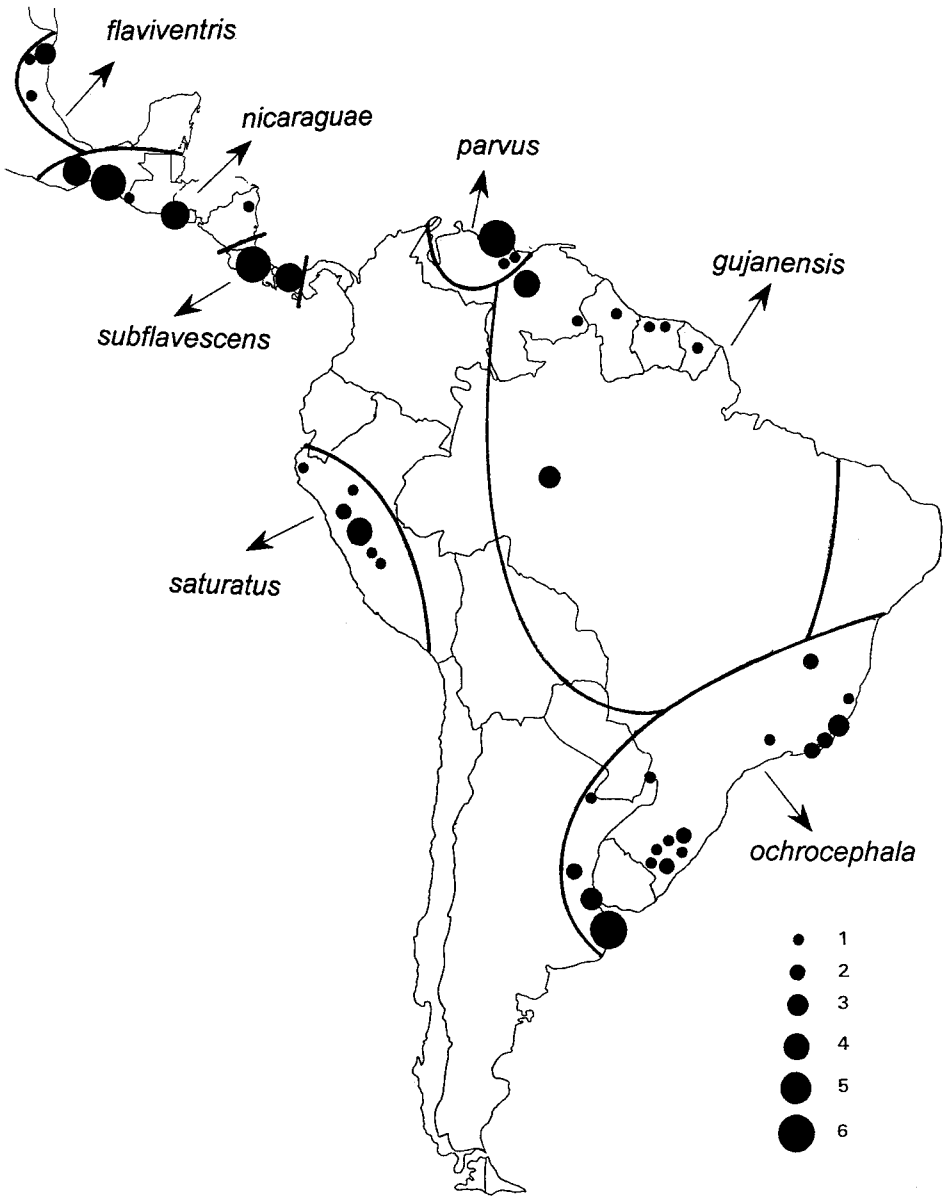


FIGURE 1. Location of song samples, as well as the approximate distribution of the subspecies considered. The size of the filled circles indicates the number of birds recorded in each site.

bles (NS), and a “repetition index” (RI). The RI is the mean number of times a syllable type is consecutively repeated in a single song. We define notes and syllables according to Tubaro (1992).

Individual variation was studied using 659 sonograms belonging to 21 subjects with recorded samples greater than 15 songs each (range =

15–100). Details of the provenance of these recordings are shown in Appendix 2. Song types were defined according to the shape and order of syllables. Since we found that the Rufous-browed Peppershrike has a repertoire of several song types (mean = 1.95, range = 1–7), we used a “bootstrap” approach in the study of geographical variation in song. We randomly chose one

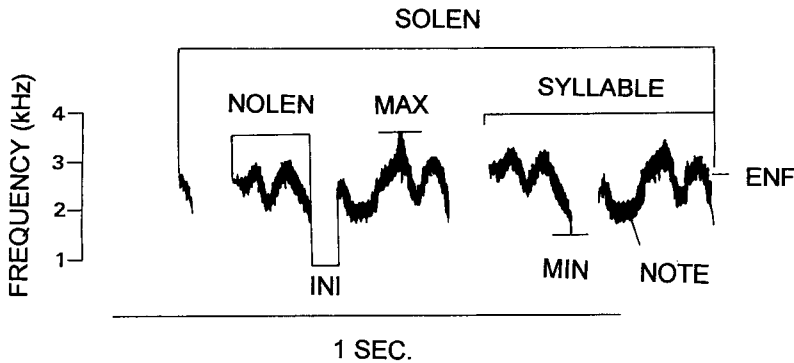


FIGURE 2. Sonogram of a song of *Cyclarhis gujanensis* showing some of the variables measured. For acronyms see Methods.

song from each individual in the original sample ($n = 93$ individuals) and ran the multivariate analyses described in the subsequent paragraph. To assess the robustness of our results we repeated this procedure four times, including different song types or different renditions of the same type depending on the repertoire size of each individual.

For each bootstrap replicate, we performed a Principal Component Analysis (PCA). This procedure summarizes major trends of a data set and reduces the ten variables measured on songs to a small number of independent variables. Then, we regressed the principal component scores of all individuals on \log_e -transformed values of both latitude and altitude. We also compared the residuals of variation (i.e., partitioning out the effect of altitude and latitude) among habitats using a multivariate analysis of variance (MANOVA).

Although there are no morphological measurements of the recorded birds included in this study, geographic variation in body size was estimated using the wing chord and tail length of 90 skins deposited in the Museo Argentino de Ciencias Naturales Bernardino Rivadavia. In addition, we found some measures published in: Chapman (1917), Gyldenstolpe (1945), and Wetmore et al. (1984). Unfortunately, most of these authors reported only means and their data therefore were deleted from the statistical analysis.

RESULTS

Since the results of the analysis of the four sets of data were similar, we only present details of one set (Tables 1, 2, and 3). Principal component

analysis showed that PC1 varies positively with BAND, MAX, NS, and negatively with SOLEN. PC2 corresponds to an axis of increasing SOLEN, NN, and RI. Finally, PC3 corresponds to an axis of decreasing ENF, MAX, MIN and INI. Taken together, these three axis account for 69.5% of the total variance in the original set of data.

Subspecific variation. Six of seven subspecies included in the study sing very similar songs, as suggested by the high degree of overlap in the 95% confidence ellipses depicted in Figure 3. Only *C. g. ochrocephala* (the race living along the Atlantic coast of South America) tended to score lower in PC1 and higher in PC2, indicating songs with relatively narrow bandwidth, lower maximum frequency and highly repetitive structure. Since these differences are not absolute (i.e., there are still wide overlaps in both PC1 and PC2, as well as in PC3 values among all subspecies) we proceeded with geographic and ecological analyses of song variation, pooling all subspecific samples.

Latitude and altitude. Multiple regression of the 65 birds in which information about the environmental variables was complete shows that a significant amount of variation in PC1 ($R^2 = 0.23, P < 0.003$) and PC2 ($R^2 = 0.25, P < 0.0001$), but not in PC3 ($R^2 = 0.035, P > 0.3$), was explained by both altitude and latitude. In both cases, latitude was the only variable which contributed significantly to variation in PC1 (partial correlation = $-0.28, t_{63} = -2.32, P = 0.0238$) and PC2 (partial correlation = $0.49, t_{63} = 4.44, P < 0.0001$). These analyses indicated that, at higher latitudes, songs are longer, more repetitive, have narrow bandwidth, lower maximum frequency, and a higher number of notes than

TABLE 1. Descriptive statistics of the variables measured on songs of each subspecies. For acronyms see Methods.

	<i>flaviventris</i> n = 5	<i>nicaraguae</i> n = 16	<i>subflavescens</i> n = 10	<i>ochrocephala</i> n = 32	<i>guyanensis</i> n = 12	<i>parvus</i> n = 8	<i>saturatus</i> n = 10
SOLEN ^a	1,040 ± 334 ^b (32.12) ^c	1,154 ± 400 (34.66)	1,029 ± 159 (15.45)	1,251 ± 193 (15.43)	920 ± 175 (19.02)	1,024 ± 133 (12.99)	1,121 ± 244 (21.77)
NOLEN ^a	187 ± 52 (27.81)	131 ± 70 (53.44)	160 ± 33 (20.63)	189 ± 46 (24.34)	152 ± 32 (21.05)	136 ± 16 (11.76)	161 ± 35 (21.74)
INI ^a	73 ± 14 (19.18)	45 ± 12 (26.67)	59 ± 10 (16.95)	58 ± 15 (25.86)	48 ± 13 (27.08)	44 ± 5 (11.36)	57 ± 18 (31.58)
MAX ^d	3,012 ± 146 (4.85)	3,209 ± 296 (9.22)	3,405 ± 424 (12.45)	2,941 ± 240 (8.16)	3,364 ± 295 (8.77)	3,350 ± 121 (3.61)	3,720 ± 508 (13.66)
MIN ^d	1,361 ± 102 (7.49)	1,446 ± 109 (7.54)	1,535 ± 151 (9.84)	1,671 ± 191 (11.43)	1,694 ± 260 (15.35)	1,612 ± 113 (7.01)	1,756 ± 266 (15.14)
BAND ^d	1,650 ± 126 (7.64)	1,763 ± 317 (17.98)	1,967 ± 342 (17.39)	1,270 ± 240 (18.90)	1,671 ± 248 (14.84)	1,738 ± 155 (8.92)	1,964 ± 516 (26.27)
ENF ^d	2,606 ± 290 (11.13)	2,865 ± 409 (14.28)	2,790 ± 386 (13.84)	2,685 ± 239 (8.90)	2,717 ± 250 (9.20)	2,821 ± 201 (7.13)	2,977 ± 508 (17.06)
NN	4.40 ± 1.52 (34.55)	7.44 ± 2.78 (37.37)	5.10 ± 0.99 (19.41)	5.59 ± 1.56 (27.91)	5.00 ± 1.13 (22.60)	6.00 ± 0.93 (15.50)	5.50 ± 1.27 (23.09)
NS	4.40 ± 1.52 (34.55)	6.88 ± 2.39 (34.74)	5.10 ± 0.99 (19.41)	3.91 ± 0.89 (22.76)	4.83 ± 1.27 (26.29)	6.00 ± 0.93 (15.50)	5.30 ± 1.49 (28.11)
RI	1.00 ± 0.00 (0.00)	1.21 ± 0.49 (40.50)	1.03 ± 0.08 (7.77)	1.95 ± 0.99 (50.77)	1.04 ± 0.14 (13.46)	1.03 ± 0.07 (6.80)	1.20 ± 0.25 (20.83)

^a In milliseconds.^b $\bar{x} \pm$ SD.^c Coefficient of variation (\bar{x}/SD) \times 100.^d In hertz.

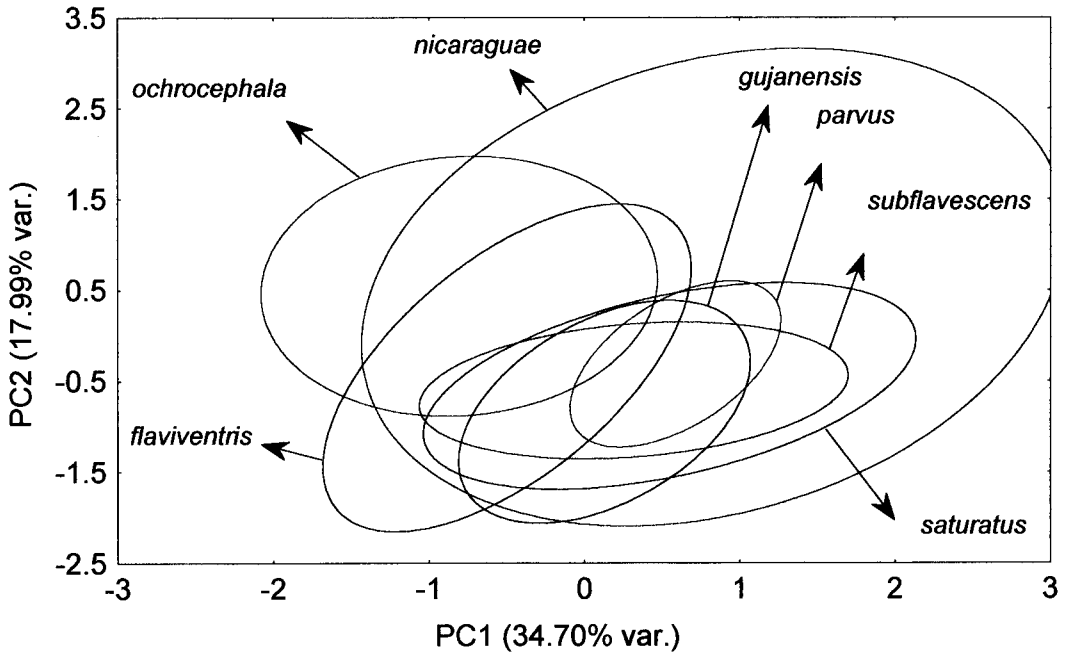


FIGURE 3. 95% confidence ellipses around subspecies means of song characters PC1 and PC2. PC1 correspond to an axis of increasing BAND, MAX, NS and decreasing SOLEN. PC2 correspond to an axis of increasing SOLEN, NN and RI. For acronyms see Methods.

those recorded near the equator (Fig. 4). In only one of four sets of data was there a significant relationship between principal components and altitude, with the songs of the highlands having wider bandwidth, shorter notes and longer internote interval.

Habitat. The MANOVAs on the residuals of variation in principal components values (after removing the effects of altitude and latitude) showed a significant or marginally significant influence of habitat on song structure (in three of four “bootstraps”). These analyses indicated that the songs from open and mixed sites have shorter

internote intervals, narrow bandwidth, and lower maximum, minimum and emphasized frequencies than those from closed sites.

Bergmann’s Rule. Body size, as estimated by wing chord and tail length, showed a positive trend with latitude ($R^2 = 0.289, P < 0.0001$, and $R^2 = 0.537, P < 0.0001$, respectively). Thus, *Cyclarhis gujanensis* seems to conform to Bergmann’s Rule (Fig. 5). Although most of the empirical evidence supporting Bergmann’s Rule comes from temperate regions, at least two other neotropical species have shown such a pattern of variation: the Carbonated Flower-Piercer (*Di-*

TABLE 2. Correlation (Pearson) matrix among song variables. For acronyms see Methods.

	SOLEN	NOLEN	INI	MAX	MIN	BAND	ENF	NN	NS	RI
SOLEN	1.00									
NOLEN	0.22	1.00								
INI	0.27	0.38	1.00							
MAX	-0.09	-0.38	-0.03	1.00						
MIN	-0.04	0.08	0.11	0.27	1.00					
BAND	-0.08	-0.43	-0.07	0.81	-0.30	1.00				
ENF	0.16	-0.24	0.07	0.55	0.25	0.40	1.00			
NN	0.52	-0.64	-0.25	0.17	-0.15	0.24	0.31	1.00		
NS	0.17	-0.57	-0.39	0.31	-0.27	0.46	0.29	0.69	1.00	
RI	0.35	0.41	0.17	-0.34	0.10	-0.40	-0.09	-0.04	-0.25	1.00

TABLE 3. Factor loadings from the principal component analysis carried out on the song variables. These results are derived from only a single bootstrap. For acronyms see Methods.

Component loadings	PC1	PC2	PC3
SOLEN	0.002	0.848	-0.358
NOLEN	-0.794	0.043	-0.255
INI	-0.369	0.060	-0.589
MAX	0.693	-0.370	-0.516
MIN	-0.156	-0.226	-0.591
BAND	0.773	-0.253	-0.173
ENF	0.525	0.032	-0.635
NN	0.671	0.665	0.060
NS	0.792	0.334	0.212
RI	-0.497	0.516	-0.211
% variance	34.699	17.985	16.818

glossa carbonaria, Graves 1991), and the Yellow-billed Cacique (*Amblycercus holosericeus*, Kratter 1993).

DISCUSSION

This study shows the existence of a relationship between song structure and geographic and environmental variables such as latitude, and habitat. In particular, songs from equatorial areas have broader bandwidth, with higher maximum frequencies, and are shorter and less repetitive than those from more temperate latitudes.

The presence of higher frequencies in the Rufous-browed Peppershrike songs from closed areas contrasts with most previous work on other species. For instance, the occurrence of wider band sounds with higher maximum frequencies is characteristic of open habitats from tropical and temperate areas (Chappuis 1971, Morton 1975, Wiley 1991). These studies also showed that, in general, closed habitats have narrow bandwidth sounds, with lower frequencies, thus conforming to the findings for the northern Cardinal (Anderson and Conner 1985), the Summer Tanager (Shy 1983), the White-throated Sparrow (Wasserman 1979, Waas 1988), and the Great Tit (*Parus major*, Hunter and Krebs 1979). In contrast, but similar to the Rufous-browed Peppershrike, the songs of the Rufous-collared Sparrow are up to 3 kHz higher near the equator (Nottebohm 1975) and the use of higher maximum frequencies is associated with mesic, densely vegetated habitats (Handford and Loughheed 1991). Acoustical reasons for the use of different frequencies in different habitats are

not clear yet, because the lower the frequency the less it attenuates with distance when broadcast at a height greater than one meter above the ground (Morton 1975, Marten and Marler 1977, Marten et al. 1977).

In our study, the presence of higher frequencies in the songs from tropical areas might have been expected since: (a) body size in the Rufous-browed Peppershrike increases with latitude, thus conforming to the Bergmann's rule, and (b) there is a negative relationship between body size and frequencies used in the song (Bowman 1979, 1983; Wallschläger 1980; Ryan and Brenowitz 1985). We therefore expect birds from tropical areas to use higher frequencies in their songs. However, this explanation must be taken with caution because the allometric relationship between frequency of the song and body size may not apply for some species or frequency features. For example, Handford and Loughheed (1991) found that syrinx size is not related to body size, suggesting the absence of a physical constraint on frequencies used in the song. In addition, in *Geospiza difficilis* (Bowman 1979, 1983), and *Piranga rubra* (Shy 1983), larger individuals have song with higher frequencies. Unfortunately, we lack data to test this possibility in the Rufous-browed Peppershrike.

Superficially, latitudinal differences in body size may seem to explain why in closed habitats, usually occurring near the equator where birds are smaller, songs have both higher maximum and emphasized frequencies than in open habitats, usually occurring at higher latitudes where birds are bigger. We have attempted to remove the effect of latitude and altitude from our analyses and, thus, the presence of higher frequencies in closed habitats would appear to be due to some other factor. However, we do not know if there are body size differences among habitats that are unrelated to latitude. For example, natural selection might favor smaller birds in densely vegetated areas compared to more open habitats. This association would not have been removed by the regression analysis of song features on latitude, and thus the effect of body size may still be confounding our attempts to examine the relationship between habitat and song structure.

More recent studies about the effect of ecological factors on song design have focused on temporal aspects of the signal (Wiley and Richards 1978, Richards and Wiley 1980, Wiley 1991). According to the reverberation hypothesis, we

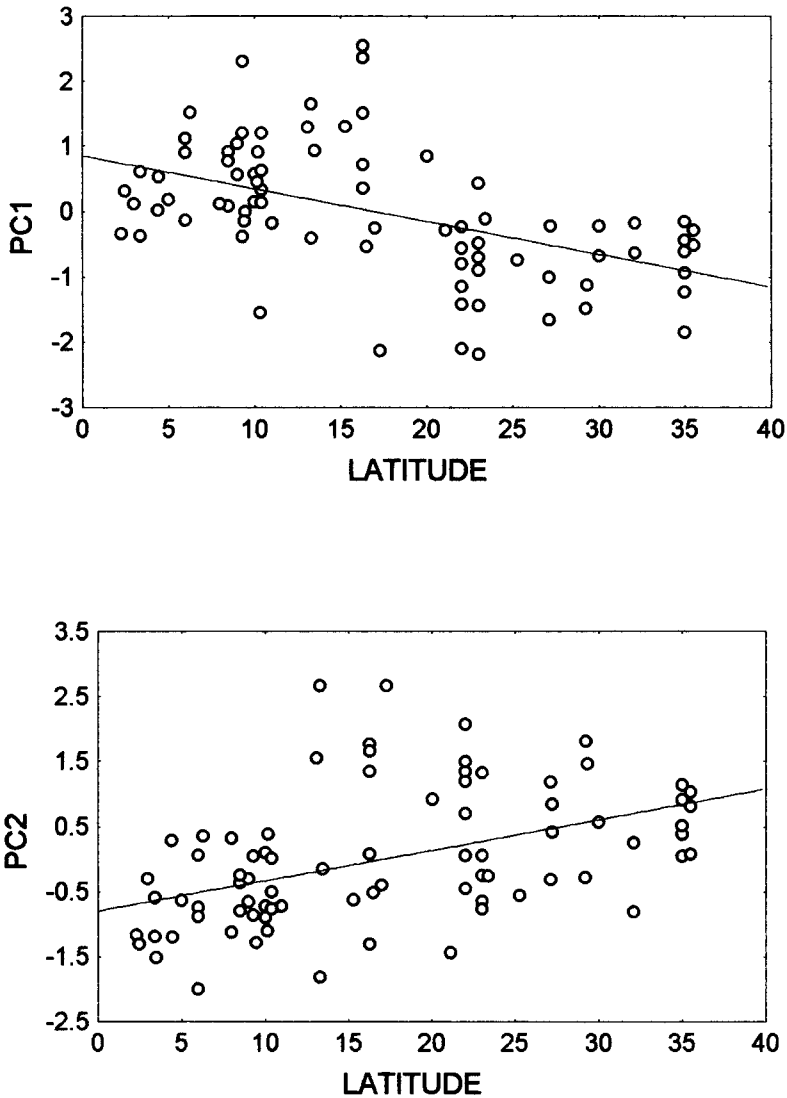


FIGURE 4. Regression of PC1 scores (top), and PC2 scores (bottom) on latitude. For acronyms see Methods.

could expect longer silence gaps among song notes in densely vegetated habitats, as a way to avoid degradation caused by echos. In fact, we found slightly longer internote intervals in closed areas than in more open ones.

Regarding the relationship between variability of song syntax and complexity of the acoustic environment, Marler (1952) suggested that the song of a local population of a species should differ significantly from that of other species sharing the same local habitat. Thus, birds living in regions with impoverished avifaunas, such as

islands, tend to have simpler and more variable songs (see also Lack and Southern [1949]). Thielcke (1973) developed essentially the same idea using the term "loss of contrast" for referring to the loss of species-specific differences in song in the absence of coexisting related species. The importance of the "sound environment" in shaping the species' song has been further developed and partly tested in recent years. Nelson (1988, 1989) demonstrated that both variability and a feature's central tendency relative to other species in the local acoustic environment are im-

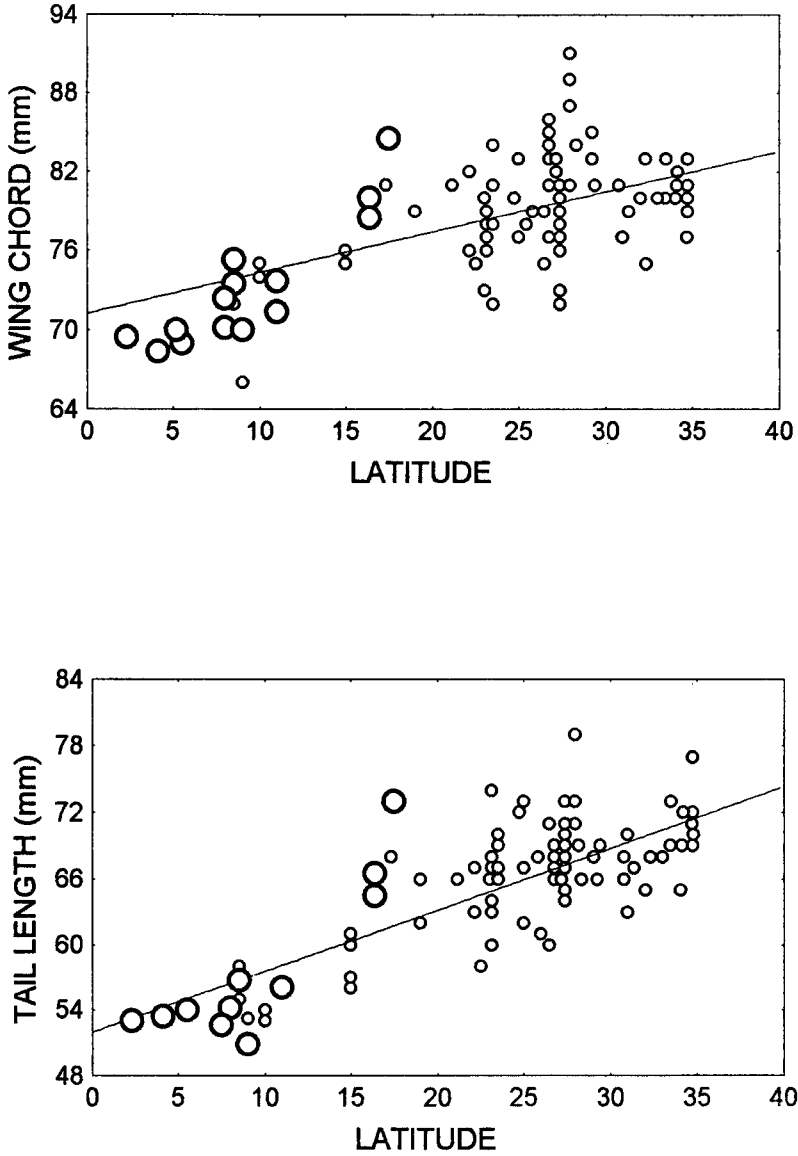


FIGURE 5. Regression of wing chord and tail length (both in millimeters) on latitude. Small circles indicate individual values. Large circles correspond to data published elsewhere, and they were not included in statistical analysis.

portant in species-song recognition. According to these hypotheses and considering the existence of a higher diversity of birds in the tropical forest than in more temperate or open areas, we predict the occurrence of simpler (i.e., with less number of notes and syllables) and more variable songs (i.e., with less repetitive structure and/or higher coefficient of variation in their features) in the latter than in the former habitat. Contrary to our

prediction, there is no trend in song variability among subspecies, (table 1), in spite of differences in latitude (see Fig. 1). In addition, the songs *C. g. ochrocephala* are clearly more repetitive than those of the other subspecies living in more tropical or forested environments (like *C. g. gujanensis* or *C. g. parvus*). Songs of *ochrocephala*, and to a less extent in *nicaraguae* and *saturatus*, are composed of notes grouped into

syllables. These, in turn, are repeated consecutively. It is improbable that variation in body size among subspecies could explain these differences in song syntax. Rather subspecific variation in syntax is probably the result of phylogenetic, historical, learning, and ecological phenomena.

ACKNOWLEDGMENTS

We thank A. Lemoine, G. Lichtenstein, S. Lougheed, J. C. Reboreda, R. Fraga, and P. Handford for their comments on several versions of the manuscript, and J. Navas for making available the collection of the Museo Argentino de Ciencias Naturales. We also thank the recordist mentioned in Appendix 1 and 2, the National Sound Archive Wildlife Section, the Bioacoustic Archives and Library, the Florida Museum of Natural History, and the Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, New York, for providing the material for this study. This work was supported by the Consejo Nacional de Investigaciones Científicas y Técnicas, and the University of Buenos Aires, Argentina.

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- ## APPENDIX 1
- Source of songs, grouped by subspecies. Abbreviations are as follows: LNS: Library of Natural Sounds, Cornell Laboratory; NSA: National Sound Archive Wildlife Section; BAL: Bioacoustic Archives and Library, Florida Museum of Natural History; ARA 7: Songs of the vireos and their allies. Cassette compiled and edited by J. C. Barlow and J. W. Hardy; PLT: Pablo Luis Tubaro personal collection; AR: Argentina; BR: Brazil; CO: Colombia; VE: Venezuela; PE: Peru; SU: Suriname; GU: Guyana; PA: Panama; NI: Nicaragua; SA: El Salvador; CR: Costa Rica; ME: Mexico. The number following recording's source identify the specimen studied according to the respective catalog. Recordist's name in parenthesis.
- C. g. ochrocephala*: PLT 158, 159, 160, 161 (P. L. Tubaro), Estancia El Destino, Partido of Magdalena, Buenos Aires Province, AR; PLT 156, 157 (P. L. Tubaro), Atalaya, Partido of Magdalena, Buenos Aires Province, AR; PLT 170, 171, 172 (P. L. Tubaro), Delta of Parana River, Buenos Aires Province, AR; PLT 162, 163 (P. L. Tubaro), Campo Rico Island, Santa Fe Province, AR. PLT 165 (P. L. Tubaro), El Cerrito Island, Chaco Province, AR; LNS 34060 (T. Parker), Iguazu Falls, Misiones Province, AR; LNS 34040, 23754 (T. Parker), Itambezhino, Rio Grande do Sul, BR; LNS 20136, 20138 (W. Belton), Tenente Portela, Rio Grande do Sul, BR; LNS 19852 (W. Belton), Canela, Rio Grande do Sul, BR; LNS 20137 (W. Belton), Sao Francisco de Assis, Rio Grande do Sul, BR; LNS 22108, 22123, 22127, 32203, 32223 (T. Parker), Itatiaia National Park, Rio de Janeiro, BR; LNS 20140 (W. Belton) Itatiaia do Sul, Rio Grande do Sul, BR; LNS 20139 (W. Belton), Lagoa do Jacare, Rio Grande do Sul, BR; LNS 32183, 32185 (T. Parker), Tijuca Forest, Rio de Janeiro, BR; NSA 4083 (D. W. Snow), Boraceia Forest, San Pablo, BR; LNS 39090, 39092 (T. Parker), Itatiaia National Park, Minas Gerais, BR; LNS 10962 (R. Ward), Santa Teresa, Espirito Santo, BR.
- C. g. gujanensis*: LNS 48713 (M. Cohn-Haft), Manaus, Amazonas, BR; LNS 32419, 32441 (R. Bierregaard), Manaus, Amazonas, BR; ARA 7 (W. B. McGillivray), Saul, GU; NSA 8983 (V. J. Mees-Balchin), Rappel Savanne, SU; NSA 29370 (V. J. Mees-Balchin), Dadanawa Ranch, Rupumuni, SU; LNS 45518, 45528, 45531, 45537 (T. Parker), El Dorado, Bolivar, VE; LNS 30478 (T. Parker), Santa Elena, Bolivar, VE; LNS 38970 (T. Parker), Pando, BO.
- G. g. parvus*: ARA 7 (J. C. Hardy), Caracas, VE; LNS 47830 (M. Isler), Miranda, VE; LNS 40360 (P. Coopmans), Aragua, VE; LNS 10948, 10950, 10956 (P. Schwartz), Petare, Caracas, VE; LNS 10952, 10953 (P. Schwartz), Los Palos Grandes, Caracas, VE.
- C. g. saturatus*: LNS 28761 (A. B. van den Berg), Huanuco, PE; LNS 17389, 17392 (T. Parker), Cumpang, La Libertad, PE; NSA 25528 (N. Krabbe), Pachachupar, Huanuco, PE; LNS 18023 (J. P. O'Neill), Bagua, Amazonas, PE; LNS 21620 (T. Parker), Huanabamba, Piura, PE; LNS 29412 (T. Parker), Huanuco, PE; LNS 26918 (M. Isler & P. Isler), Huanuco, PE; NSA 25525 (N. Krabbe), Carpish mountains, Huanuco, PE. BAL 2 (T. Parker), Huanuco, Cordillera Divisoria, PE.
- C. g. subflavescens*: LNS 10966, 10967 (E. S. Morton & L. B. Morton), Volcan de Chiriqui, PA; LNS 10959 (L. I. Davis & D. Davis), Cerro Punta, PA; LNS 10968 (E. S. Morton), Volcan de Chiriqui, PA; LNS 28245 (A. B. van den Berg), Monteverde, Puntarenas, CR; BAL 6, 7 (G. Stiles), Valle Central, CR; BAL 22 (J. Arvin), Tupuntec National Wildlife Refuge, Heredia Province, CR; LNS 37750 (D. Minia), Tapanti Wildlife Reserve, Cartago, CR; NSA 18734 (R. Ranft), Volcan Barra, CR.
- C. g. nicaraguae*: LNS 10971, 20376 (W. A. Thurber), Parque Deneinger, La Libertad, SA; LNS 10969 (W. A. Thurber), Chanmico, La Libertad, SA; LNS 20346 (W. A. Thurber), Cerro Verde, Santa Ana, SA; LNS 10960 (L. I. Davis & D. Davis), Esteli, NI; BAL 10, 11, 12, 13, 14, 15 (T. Webber), Parque Nacional Lagunas de Montebello, Chiapas, ME; BAL 1 (J. W. Hardy), Pueblo Nuevo, Chiapas, ME; BAL 20 (G. Lasley), Paval, Chiapas, ME; LNS 10942 (L. I. Davis), Puente Central, Chiapas, ME; LNS 10943 (L. I. Davis), Tuxtla Gutierrez, Chiapas, ME; LNS 10944 (L. I. Davis), Comitán, Chiapas, ME.
- C. g. flaviventris*: BAL 4 (J. W. Hardy), Gomez Farias, Tamaulipas, ME; LNS 45648, 45649, 45671 (C. D. Duncan), Tamaulipas, ME; LNS 10961 (L. I. Davis & D. Davis), Jacala, Hidalgo, ME.

APPENDIX 2

Source of songs used in the analysis of the individual variation. Abbreviations are as in Appendix 1.

LNS 10942 (L. I. Davis), Chiapas, ME; LNS 10948, 10956 (P. Schwartz), Petare, Caracas, VE; LNS 10961 (L. I. Davis and D. Davis), Hidalgo, ME; LNS 10962 (R. Ward), Espirito Santo, BR; LNS 10966 (E. S. Morton and L. B. Morton), Volcan de Chiriqui, PA; LNS 10968 (E. S. Morton), Volcan de Chiriqui, PA; LNS 10971 (W. A. Thurber), Parque Deneinger, La Libertad, SA; LNS 17392 (T. Parker), Cumpang, La Libertad, PE; LNS 19852 (W. Belton), Moro Pelado, Rio

Grande do Sul, BR; LNS 20137 (W. Belton), Sao Francisco de Assis, Rio Grande do Sul, BR; LNS 20138 (W. Belton), Turvo Forest Reserve, Rio Grande do Sul, BR; LNS 20346 (W. Thurber), Cerro Verde, Santa Ana, SA; LNS 20376 (W. Thurber), Parque Deneinger, La Libertad, SA; LNS 23092 (R. Waide), Cozumel Island, Quintana Roo, ME; LNS 22127 (T. Parker), Itatiaia National Park, Rio de Janeiro, BR; LNS 21620 (T. Parker), Huancabamba, Piura, PE; LNS 26918 (M. Isler and P. Isler), Huanuco, PE; LNS 48713 (M. Cohn-Haft), Manaus Reserve, Amazonas, BR; LNS 45518, 45537 (T. Parker), El Dorado, Bolivar, VE.