

VARIATION IN DURATION AND FREQUENCY CHARACTERS IN THE SONG OF THE RUFIOUS-COLLARED SPARROW, *ZONOTRICHIA CAPENSIS*, WITH RESPECT TO HABITAT, TRILL DIALECTS AND BODY SIZE¹

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Abstract. We present data on variation in frequency and duration characters of the advertising song of *Zonotrichia capensis*, the Rufous-collared sparrow, and information on the qualitative structure of the introductory "theme." These data are analyzed with respect to their relationships with altitude, habitat type, body size, syrinx size and the dialect variation shown by the terminal trill.

Principal components analysis shows that the major axis of variation (PC1) in the frequency and duration variables is one primarily of increasing frequency and bandwidth of the trill (mainly due to increasing maximum trill frequency), increasing frequency of the theme, and of increasing song length, mainly contributed by theme length; increasing values on PC2 correspond to an increasing theme bandwidth and maximum theme frequency, with decreasing theme length and increasing trill length.

PC1 scores from this analysis are negatively correlated with altitude over the whole sample. Higher-altitude habitats are usually structurally open, lower-altitude habitats usually mixed or closed. Songs from the nine categories of original, natural vegetation differ significantly in their PC1 scores, while contemporary vegetation structure has no significant effect: songs from the open-country habitats, desert, puna and grassland are shorter, have lower frequency and narrower bandwidth than all woodland, thornscrub and forest songs.

With the exception of the very slow-trilled songs from the Monte desert dialect, there is a positive relationship between trill interval and PC1 score: slower-trilled songs (longer trill interval; lower trill rate) are longer, of higher frequency and broader bandwidth. The slow-trill Monte dialect songs are anomalous in having PC1 characteristics like the fastest-trilled dialect songs (puna and grassland).

There is a significant negative relationship between body size and PC1, though it is non-linear: birds from all habitats but puna are very similar in having smaller body size. Syrinx size is not correlated either with measures of body size or with habitat. It is concluded that most variation in song modal frequency and bandwidth is due to learning processes, rather than to size constraints of the body or organs.

Key words: *Zonotrichia capensis*; Rufous-collared sparrow; dialects; song variation; ecological correlates; body size; morphological constraints.

INTRODUCTION

It is now some twenty years since Nottebohm (1969) made the first description of vocal variation in *Zonotrichia capensis*, the Rufous-collared sparrow. He considered variation in the number and form of the notes in the first part of the song, the theme, and in the rate of delivery of the stereotyped elements of the second part, the terminal trill. Geographical patterns in the form of the trill, as measured by the interval between adjacent trill elements, were evident, and song dialects in this species have been defined (Nottebohm 1969) on the basis of this vari-

ation. Virtually all subsequent work on song variation in this species has concentrated on the trill (King 1972; Nottebohm and Selander 1972; Nottebohm 1975; Handford and Nottebohm 1976; Handford 1981, 1988; Lougheed et al. 1989). These studies have emphasized the clarity and long-term temporal stability of trill-dialect zones, and Handford (1988) recently demonstrated a close large-scale association between the distribution of trill-rate dialects and the original vegetation types across northwest and west-central Argentina. By contrast, King (1972) reported local geographical variation in the form and number of theme notes, although the pattern of this variation seemed to be more complex than that shown by the trill. In addition, Nottebohm (1975) discussed variation in song frequency characters.

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Given the unique association of trill dialect with natural ecological features in this species (Handford 1988) and the theory regarding the relationship of modal frequency and phrasing in bird song with habitat features (e.g., Morton 1975; Bowman 1979, 1983; Wiley and Richards 1982), it is of interest to analyze covariation among these characteristics of the song of *Zonotrichia capensis* with respect to habitat and trill dialects. Here we report on character variation in frequency and duration of the theme, the trill, and the song as a whole, and also consider variation in the qualitative structure of the theme. We consider the covariation of these song variables, their relationships with some environmental variables, and with trill dialect type. We also compare the patterns of variation in song frequency characteristics with both body size and mass, and with syrinx size.

STUDY AREA, MATERIALS AND METHODS

The data on song characteristics are derived from a recent study of trill-rate dialects (Handford 1988). They derive from a diversity of vegetation types spread over a large area (approximately 1,200 by 350 km) in northwestern and west-central Argentina between the Bolivian border at the 22nd parallel and central Mendoza province at the 34th parallel (see Fig. 1 in Handford 1988). The topography of the region is extremely diverse, ranging from open plains in the east, through a central complex of high mountains and basins, to the main Andean ranges and high plateaux in the west: altitudes range from less than 400 m in the eastern plain to peaks of over 5,000 m.

The natural vegetation is correspondingly complex (see Handford 1988, for a description and for distribution maps). The categories of natural vegetation used here are: (1) lowland chaco, a hot, seasonal, thornscrub and xeric woodland system of the Argentine plain; (2) montane chaco, a higher elevation, more closed and mesic, thorn woodland; (3) transition forest, a drought-seasonal open forest of large-statured trees, mostly lying between the chaco to the east and the moist montane forests further west; (4) moist, partly evergreen, montane forest on the eastern flanks of the first high mountain ranges; (5) montane alder woodland, above the montane forest; (6) grasslands (virtually all high montane in this region); (7) arid montane prepuna scrub; (8) hot

Monte desert scrub, largely restricted to western inter-montane basins and valleys; and (9) puna, a very high altitude open scrub and grassland system. Three hundred seventy sites (see definition below) were assigned to these categories, while a further 195 sites were from ecotones between categories. These categories relate to the *potential natural* vegetation; in many sites, the original vegetation has been replaced by agriculture or degraded by pasturage. The Rufous-collared sparrow is primarily an open-country, scrub and edge species; recordings from forest habitats were made within 30 m of an edge, provided by a roadway, a river or by clearances. However, in many "woodland/forest" localities the straight line between singers was essentially closed canopy vegetation.

All recordings were made between 30 September 1984 and 20 January 1985, when birds were breeding residents. Recording sites were concentrated in the central part of the study area, with over half of the sites in the provinces of Tucuman and Salta. Sites were almost entirely restricted to regions accessible by truck, and most recordings were made within 500 m of a road or track. At each site, the altitude was noted and the *existing* vegetation classified as (1) open: scrub, pasture, grassland or crop fields; (2) mixed: parklands, partly cleared woodlands, forest edge; (3) closed: uncleared woodlands and forest. Finally, the original natural vegetation was noted: since sites were located in areas ranging from pristine or only lightly affected (41.1% of sites) to totally modified (25.4% of sites), in some cases it was necessary to assign the original vegetation by inference from relict vegetation fragments and from vegetation maps. Latitude and longitude were inferred from 1:500,000 maps (Instituto Geografico Militar, Buenos Aires).

Recordings were made with a Sennheiser MKH 816 "shotgun" microphone and a Uher CR260 AV tape recorder. Recordings were analyzed on a Uniscan II spectrum analyzer (Multigon Industries) set at 10 kHz with a timebase of 1.6 sec. Analyses are based on sound spectrograms prepared from recordings of 1,764 individuals (1,336 from the nine vegetation types listed above and 428 from ecotones; these latter were included only in analyses which ignore vegetation type).

The measurements made on the songs were (see Fig. 1): maximum and minimum frequencies and duration of both theme and trill (THMAX, THMIN, THLEN, TRMAX,

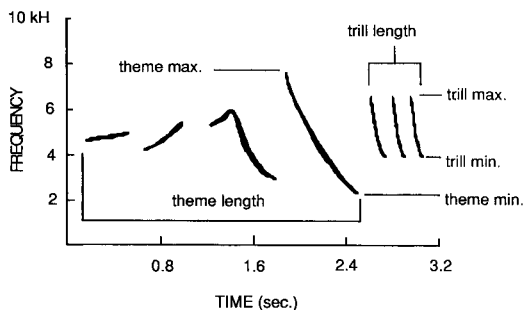


FIGURE 1. A stylized sound spectrogram of a song of *Zonotrichia capensis* showing the pitch and duration measures. The theme notes are, in left to right sequence, 1, 2, 4, 3.

TRMIN, TRLEN); theme and trill bandwidth (THBAN and TRBAN), the differences between the respective maxima and minima; and song length (SOLEN), the total length of the song, including the space between the theme and trill. Mean trill interval (TRINT) of each recording site was taken from an earlier study (Handford, 1988). A recording site is a locality where from 5 to 10 different singing birds were recorded, separated by at least 5 km (and often much more) from other such localities. Finally, the qualitative form and sequence of notes in the theme were designated as: Type 1—level inflection, or nearly so; Type 2—rising inflection; Type 3—falling inflection; Type 4—rising then falling. There were other forms of note, but at such low incidence that they have been ignored here. The theme type shown in Figure 1 is "1243."

The data on body form and size derive from 474 further male specimens collected from 24 localities (approximately 20 per locality) of known song-type by S.C.L. between September 1987 and March 1989 in the same study area. These samples form part of a study of the covariation of morphological, allozymic and mtDNA characters, with respect to song variation and habitat type (Lougheed MS). Samples were equally dis-

tributed among six of the above vegetation types: lacking are montane chaco, prepuna and montane forest. Morphological measurements follow Handford (1983) and Zink (1986) and include wing chord (WC), tarsus length (TA), hind toe plus claw (HT), outer rectrix (OR), bill depth (BD), bill width (BW), culmen length (CUL), and bill length from the gape (GAPE).

Syrinx data derive from an additional sample of 46 males taken from nine sites (approximately five per site) along an altitudinal transect (approx. 1,800 m to 3,000 m), which includes four vegetation types (alder woodland, grassland, moist puna and prepuna), along Provincial Route 307 in the Aconquija mountains, due east of Tucuman city (Lougheed MS; see Handford and Nottebohm 1976; Handford 1981, 1988 for maps and descriptions of this locality). Eight external measures (as above, to 0.01 mm) and fresh weight (WT, to 0.1 mg) were taken. Syringes were removed according to the method of Ames (1971), and the width of the A-7 cartilaginous element of the syringeal drum (SYR) was measured to 0.01 mm on the fresh material.

Statistical analysis was carried out using the SAS (SAS Institute 1985), and SYSTAT (Wilkinson 1987) packages; some data displays were prepared in MacSpin (Donoho et al. 1985).

RESULTS

FREQUENCY AND DURATION VARIABLES

Table 1 shows simple summary descriptive statistics for all frequency and duration variables, calculated from the 370 non-ecotonal site means (total of 1,336 individuals) to permit comparison with other results. The means are not significantly altered when these statistics are calculated from all individual cases, including ecotonal sites. The same descriptive statistics, analyzed by natural vegetation groups, are given in Appendix 1.

The correlation structure of the various song measures is shown in Table 2. Correlations have

TABLE 1. Descriptive statistics of the frequency (kHz) and duration (sec) characters from 370 non-ecotonal sites. For acronyms see Materials and Methods.

	THMAX	THMIN	THBAND	TRMAX	TRMIN	TRBAND	THLEN	TRLEN	SOLEN
	kiloHertz						seconds		
Min.	4.050	2.267	1.050	3.800	2.375	1.067	0.160	0.280	0.830
Max.	8.767	4.050	5.667	8.760	4.950	5.700	1.170	1.530	2.070
Mean	6.022	3.180	2.840	6.240	3.286	2.961	0.509	0.913	1.495
SD	0.749	0.289	0.766	0.542	0.388	0.628	0.163	0.193	0.190

TABLE 2. Pearson correlation coefficients among trill rate, theme and trill pitch and duration variables, calculated using listwise deletion of cases with missing data.

	TRINT	THMAX	THMIN	THBAN	TRMAX	TRMIN	TRBAN	THLEN	TRLEN
THMAX	-0.304	1.0							
THMIN	0.168	0.109	1.0						
THBAN	-0.356	0.926	-0.264	1.0					
TRMAX	0.023	0.272	0.331	0.138	1.0				
TRMIN	-0.514	0.056	0.022	0.045	0.087	1.0			
TRBAN	0.344	0.196	0.271	0.086	0.784	-0.540	1.0		
THLEN	0.367	-0.107	0.362	-0.239	0.342	-0.253	0.447	1.0	
TRLEN	-0.294	0.376	-0.169	0.429	0.002	0.208	-0.126	-0.438	1.0
SOLEN	0.060	0.266	0.171	0.194	0.306	-0.020	0.274	0.432	0.610

been calculated from site mean values of the non-ecotonal sites, to permit comparison with the trill dialect character (TRINT; see below). Similar analyses (excluding TRINT, which varies markedly with vegetation type) performed on these data by vegetation type show similar correlation structures. The relationships among the variables are rather complex and so this correlation matrix (excluding TRINT) was subjected to a principal components analysis. All principal component axes are orthogonal to each other by definition; that is, the effects which they measure are independent of one another.

Table 3 shows the four components having Eigenvalues in excess of one. PC1 corresponds to an axis primarily of increasing bandwidth of the trill (mainly due to rising maximum trill frequency), increasing frequency of the theme, and of increasing song length (mainly theme length, i.e., relative trill length declines). Increasing values on PC2 correspond to an increasing theme bandwidth and maximum theme frequency, with decreasing theme length and increasing trill

length. PC3 shows increasing minimum frequencies and corresponding narrowing bandwidths. PC4 is not readily interpretable. Together, these four components account for 84.33% of the total variance in these data. These results are virtually unchanged if the analysis is carried out on individual cases, or includes ecotonal data.

Altitude. A regression of PC1 scores on altitude shows a significant negative relationship, with much variation around the predicted slope ($P \ll 0.001$; $R^2 = 0.16$; Fig. 2). The result is virtually identical if ecotonal sites are included and if calculated on individual cases. These results indicate that, across the whole data set, songs from higher altitudes are somewhat shorter and lower-pitched, especially in the trill, and have a narrower trill bandwidth. No other principal component shows any significant relationship with altitude. The overall negative relationship between PC1 score and altitude is not reproduced within *all* vegetation subgroups: in some cases, e.g., lowland chaco and transition forest, the relationship is significantly positive.

TABLE 3. Results of a principal components analysis carried out on mean song length and frequency variables from 370 non-ecotonal sites.

Component loadings	PC1	PC2	PC3	PC4
THMAX	0.522	0.675	-0.226	0.292
THMIN	0.416	-0.382	0.408	0.365
THBAND	0.379	0.795	-0.371	0.146
TRMAX	0.786	-0.136	0.095	0.352
TRMIN	-0.251	0.360	0.663	0.514
TRBAND	0.820	-0.338	-0.325	-0.022
THLEN	0.529	-0.613	0.154	0.160
TRLEN	0.181	0.774	0.333	-0.387
SOLEN	0.646	0.219	0.483	-0.531
Eigenvalues	2.703	2.524	1.277	1.086
% Variance	30.04	28.04	14.19	12.06

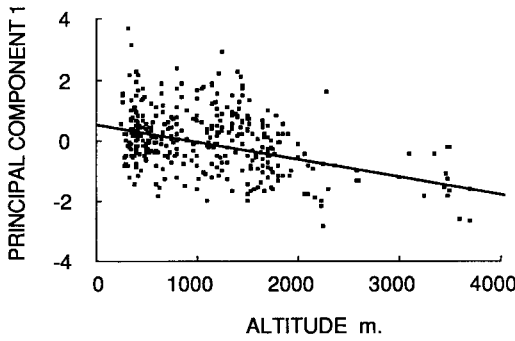


FIGURE 2. Regression of PC1 scores, from the analysis shown in Table 2, on altitude.

Trill interval. The relationship of trill interval with PC1 is clearly non-linear (Fig. 3a), and the fitted quadratic equation is significant ($P \ll 0.001$; $R^2 = 0.239$). The major non-linearity is contributed by the very-slow-trilled songs from the Monte desert sites (Fig. 3b). It is clear that, with respect to PC1, there are two kinds of very-slow-trilled (trill interval > 250 msec) songs: those from the Monte, which in terms of PC1 most resemble the fastest-trilled songs, and those from other vegetation types (virtually all transition forest and montane chaco). The great majority of these latter follow the same pattern as the other faster-trilled songs. That is, the slower the trill, the higher the PC1 score, and the higher the frequency, the broader the bandwidth of the trill and the longer the song (theme). The songs of slow-trilled birds from the Monte desert are therefore anomalous: they have short, low pitched songs and narrow band-width trills more typical of fast-trilled songs such as are found in grasslands and the puna. The relationship of trill interval with PC2 (Fig. 4) is also significant ($P \ll 0.001$; $R^2 = 0.262$) and negative. Thus, more rapid trills are longer, and are found in songs which have higher-pitched, broader-band and shorter themes. In this case, the Monte desert songs do not appear to be aberrant.

Vegetation type. A two-way analysis of variance of PC scores by original vegetation type and by contemporary vegetation structure was significant ($F_{(3,366)} = 39.42$; $P \cong 0.000$; $R^2 = 0.244$). The interaction between the two factors was non-significant ($P = 0.096$) and the effect of original, natural vegetation dwarfed that of contemporary vegetation structure ($P \cong 0.000$ and $= 0.753$, respectively). Songs from the open-country habitats (Monte desert, puna and grassland) have

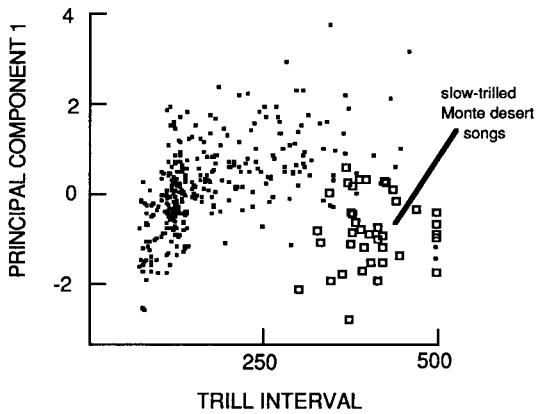
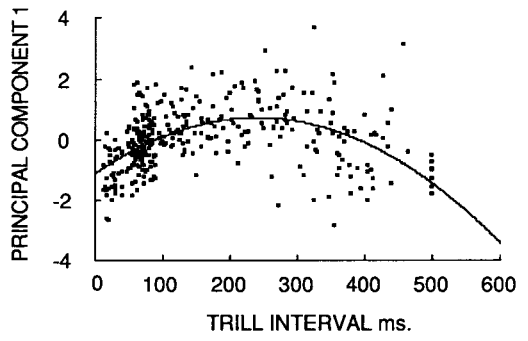


FIGURE 3. Top (a) regression of PC1 scores, from the analysis shown in Table 2, on trill interval. Bottom (b) as Fig. 3a, with slow-trilled Monte desert songs identified with squares.

low PC1 scores (Fig. 5). For clarity, the prepuna ellipse has been omitted although, as will be seen below, it coincides closely with the puna, grassland and desert samples. There is almost total overlap in PC1 scores among the thornscrub, woodland and forest habitats. Only alder woodland is distinctive, scoring lower on PC2 (having narrower-band, lower-pitched, longer themes, and shorter trill than other woodland habitat songs). This separation into two groups of habitats is clarified when the principal components analysis considers frequency variables alone (Table 4; Fig. 6).

Songs from open scrub and grassland habitats are lower-pitched (Fig. 6), narrower-band, and shorter (Fig. 5) than woodland, thornscrub and forest songs. The alder woodland group is markedly different from the other closed habitat samples with respect to PC2, having narrower-banded, longer themes and broader-band, shorter trills. The relationships among the vegetation types with respect to all frequency and duration variables

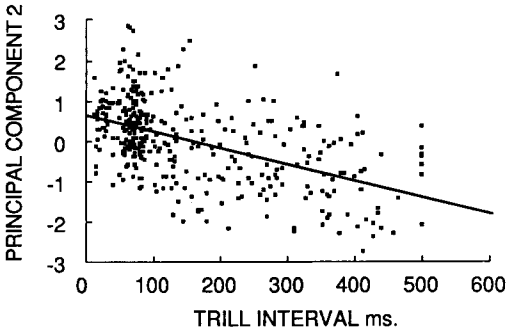


FIGURE 4. Regression of PC2 scores, from the analysis shown in Table 2, on trill interval.

are summarized in Figure 7. The clusters have been produced using a Euclidean distance measure and the complete linkage method, but the topology of the patterns is very robust with respect to clustering method. The upper tree uses the formation in PC 1-4, and the dichotomy between open and closed habitats is clear. Note the association of prepuna with puna and the aberrance of the alder sample within the woodland and forest cluster. The distinctiveness of these two clusters is even clearer in the middle diagram, where PC1 alone has been used. The lower diagram shows the clustering based on PC2 only. Here, the aberrance of the alder habitat songs is dramatically shown.

BODY SIZE AND SYRINX DIMENSIONS

Song data were from free-flying birds, so direct comparison of song characters and body morphology is not possible. However, since this geographic variation appears to be stable (Handford 1988), it is legitimate to compare these song data with data on body form from other samples taken in the same area (in some cases the same sites) three and four years later. In all cases, recordings were made (Lougheed, unpubl. ms.) at the capture sites to confirm their location with respect

TABLE 4. Results of a principal components analysis carried out on song frequency variables only.

Component loadings	PC1	PC2
THMAX	0.602	-0.070
THMIN	0.666	0.304
TRMAX	0.802	0.075
TRMIN	0.234	-0.942
Eigenvalues	1.504	0.990
% Variance	37.6	24.8

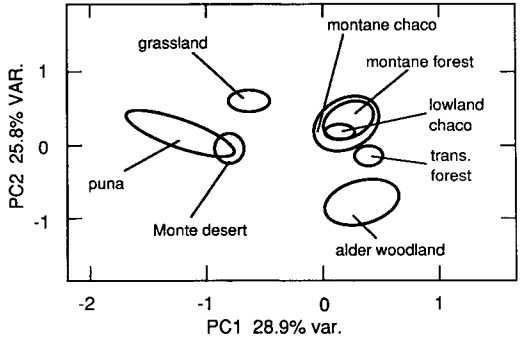


FIGURE 5. 95% confidence ellipses around vegetation group means of song characters PC1 and PC2 (see Table 2 for meaning of axes).

to the song-dialect zones described previously (Handford and Nottebohm 1976; Handford 1981, 1988).

Body size. The correlation matrix of the eight external variables measured on the 474 specimens was subjected to principal components analysis (Table 5). The first component represents overall body size, while the second relates to the heaviness of the bill. Regression of the mean PC1 (morphology) scores of each of the six vegetation groups against the respective PC1 (song) scores from the analysis shown in Table 3 yields a significant negative relationship ($P = 0.029$; $R^2 = 0.670$). By vegetation group, the songs of larger birds are shorter and lower-pitched and have a narrower bandwidth, especially in the trill. This simple statement is misleading, however. Although the samples are arranged along the size

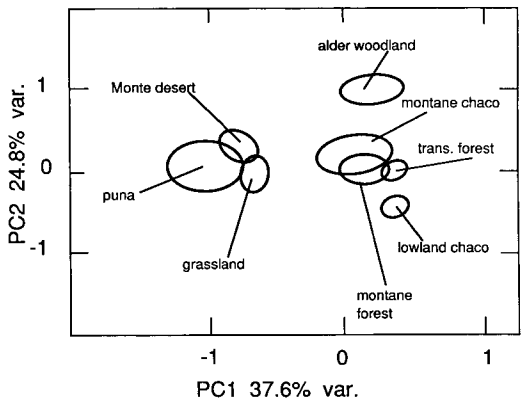


FIGURE 6. 95% confidence ellipses around vegetation group means on principal components 1 and 2 calculated from song frequency characters only (see Table 3 for meaning of axes).

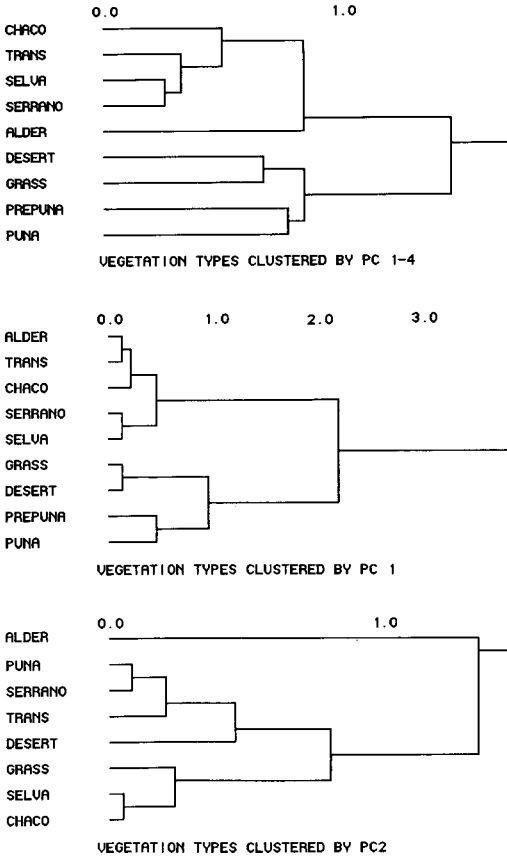


FIGURE 7. Vegetation groups clustered according to principal component scores. Chaco = lowland chaco, Trans = transition forest, selva = montane forest, serrano = montane chaco; the remainder are self-explanatory.

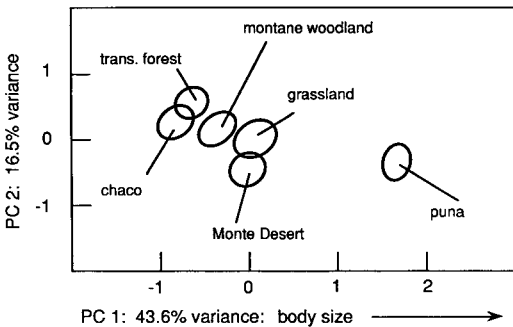


FIGURE 8. 95% confidence ellipses around vegetation group means on principal components 1 and 2 calculated from external body characters.

TABLE 5. Results of a principal components analysis carried out on eight external morphological variables measured on 474 males from six vegetation types.

Component loadings	PC1	PC2
Outer rectrix	0.830	-0.262
Wing chord	0.823	-0.239
Hind toe + claw	0.666	0.015
Tarsus	0.746	-0.095
Bill depth	0.201	0.781
Bill width	0.228	0.745
Culmen	0.762	0.136
Gape	0.670	0.066
Eigenvalues	3.489	1.323
% Variance	43.61	16.54

dimension PC1 roughly in order of increasing altitude (lowland chaco, transition forest, montane (alder) woodland, desert scrub, grassland and puna), it is clear that puna birds are strongly divergent from all the others in their larger structural size (Fig. 8). A similar analysis on skeletal characters (Lougheed, unpubl. ms.) produces a virtually identical result. These results confirm the findings of Chapman (1940), Handford and Nottebohm (1976) and Handford (1983, 1985). Thus, although there is a significant inverse relationship between body size and the frequency and bandwidth characteristics of the song, it is not a linear one. In particular, there is no reflection of the two clusters of habitat groups seen in song characteristics (Figs. 5-7).

Syrinx dimensions. The syrinx data derive from nine samples ($n = 46$) taken along a 50 km transect ranging from 1,800 m to over 3,000 m through alder woodland, grassland, moist puna and prepuna (Table 6). An analysis of measurement error was conducted, following Bailey and Byrnes (1990), on a subsample of birds. The analysis shows that 88.4% of the variance in measurements was attributable to individual differences, with the remainder attributable to measurement error.

We used four measures of body size: wing chord, tarsus, cube root of the body mass, and the score on the first principal component calculated from the correlation matrix from the raw variables reported in Table 6. All have been used as body size indices in other studies and several have been subjected to adverse criticism (see Rising and Somers 1990). Correlations were carried out among the four indices of body size and the syrinx dimension using both the individual data

TABLE 6. Character means of nine samples of males from a transect in the Aconquija mountains. Samples are identified by their kilometer distance along Provincial Route 307. Lengths in mm; mass in g; for acronyms, see Materials and Methods.

Locality	OR	WC	HT	TA	BW	BD	GAPE	CUL	WT	SYR
Sample 1. km. 46 alder woodland	62.39	68.51	12.85	23.24	6.00	6.58	14.10	12.26	21.51	1.54
Sample 2. km. 52 grass/scrub	61.92	67.80	13.16	23.90	5.79	6.57	13.68	11.63	22.68	1.52
Sample 3. km. 58 grass/orchards	62.34	70.67	12.98	22.94	6.09	6.69	14.45	12.03	21.75	1.47
Sample 4. km. 78 grassland	62.48	68.28	12.79	22.77	6.26	6.11	14.03	12.10	21.77	1.50
Sample 5. km. 81 grass/moist puna	62.07	69.72	12.86	22.49	5.75	6.48	14.27	12.21	21.7	1.59
Sample 6. km. 85 moist puna	62.91	70.86	12.92	23.18	5.93	6.48	14.08	12.05	22.46	1.65
Sample 7. km. 88 moist puna/prepuna	66.13	73.11	12.54	23.47	5.68	6.56	14.00	12.34	20.33	1.53
Sample 8. km. 91 arid prepuna	65.48	74.66	12.83	23.01	5.74	6.45	14.11	12.23	21.68	1.54
Sample 9. km. 95 arid prepuna	67.24	75.86	12.87	23.42	5.77	6.51	13.58	11.80	22.70	1.59

and the site means. In addition, a general linear model was developed to predict variation in the syrinx dimension using PC1 (size) score and collection site. In no case was the variation in the diameter of the A-7 syrinx cartilage related to any measure of body size, and there was no linear trend along the transect.

QUALITATIVE FEATURES OF THE THEME

Note number. Overall, the mean number of notes per song is 2.87 (SD = 0.67), and the class frequencies are: 1-note themes: 0.5%; 2-note: 27.6%; 3-note: 58.0%; 4-note: 13.0%; 5-note: 0.8%; 7-note: 0.1%. These values vary little with natural vegetation. Three-note themes comprise 50% or more in all but alder woodland, where 2-note themes account for 63% of songs, and puna, where 2- and 3-note themes are equally common at 42%. Similarly, there is little variation in note-number with altitude. Three-note themes predominate at most altitudes, although above 1,500 m, 2-note themes approach, and occasionally overtake, them in abundance.

Note type. All theme notes are essentially pure-tone whistles, either level, rising, falling, or rising then falling in frequency (Fig. 1). Overall, the absolute abundance of note-types in the sample is: Type 1: 15.93%; Type 2: 32.01%; Type 3: 39.76%; Type 4: 11.39%; other: <1.0%. On a notes-per-song basis, their incidence is: Type 1: 0.46; Type 2: 0.92; Type 3: 1.14; Type 4: 0.32. Analysis of per-song note-type incidence by vegetation type shows that in the mixed and closed habitats (lowland chaco, montane chaco, transition forest and montane forest) rising notes (Type 2) predominate, whereas in the open habitats (grassland, desert scrub and puna) falling notes (Type 3) are most common ($\chi^2 = 291.7$; $df = 28$). Given the altitudinal distribution of habitat types, there is also a non-random distribution of note-type incidence with altitude ($\chi^2 = 739.7$; $df = 72$). Below 1,000 m, rising notes (Type 2) are commonest (0.8–1.50 notes per song); between 1,000 and 1,400 m, Types 2 and 3 are about equally common (around one note per song); above 1,400 m, Type 3 (falling) notes are commonest (1.6–1.78 notes per song).

Note sequence. Overall, most themes (>80%) begin equally commonly with either Type 1 or 2 notes. This is true in all habitats except desert scrub and puna, where themes begin with Type 3 notes in 35–58% of songs. The terminal note in all habitat types is usually (60–90% of songs) the Type 3 note. Otherwise, themes end with a Type 4 note. Thus, virtually all songs end with a falling whistle.

However, vegetation types do differ in the final two-note phrase: in mixed and closed habitats, 53 to 72% of themes end in either the Type 2–3 or Type 2–4 sequence, while in open habitats 50 to 75% of themes end in either the Type 3–3, Type 4–3 or Type 3–4 sequence. Contingency table analysis shows this pattern to be highly significant. This open/closed pattern is also a high/low altitude pattern. Up to 1,500 m, the Type 2–3 ending predominates (40–50%); between 1,500 and 1,700 m, Type 2–3 and 3–3 endings are equally abundant at 30–40%; above 1,700 m, 60–70% of themes end in the Type 3–3 sequence.

DISCUSSION

In summary, 30.04% of the variance in the frequency and duration variables relates to increasing bandwidth and frequency of the trill, increasing frequency of the theme, and increasing song length, mainly due to theme length (relatively shorter trill); 28.04% of the variance concerns increasing theme frequency and bandwidth, shorter theme, and a compensatingly longer trill. Songs from higher altitudes and from sites actually or potentially with open natural vegetation types (grassland, prepuna, desert scrub and puna) are lower in frequency, narrower in trill bandwidth and shorter in total length (mainly due to a shorter theme, giving a relatively longer trill) than are songs from lower altitudes and sites with more closed natural habitat types (lowland and montane chaco, transition and montane forest, alder woodland). Among these closed habitats, the alder woodland samples stand out with narrower-band, lower-pitched, longer themes, and shorter trill. Variation in these frequency and duration characters is far more closely related to the original vegetation than to its contemporary structure. This result parallels that in Handford (1988) where variation in trill interval (trill dialect) mapped closely onto the original vegetation types, while contemporary vegetation structure was of little explanatory virtue.

In a comparison of continentally-distributed

samples, Nottebohm (1975) noted a markedly (up to 3 kHz) higher maximum song frequency in songs from mesic tropical environments than in those from open-scrub habitats in temperate latitudes. Minimum song frequencies are also somewhat higher in the tropics. Thus, mean overall song frequency is significantly higher and song bandwidth broader in the mesic tropics than it is in dryer temperate latitudes. He also noted a similar pattern in a series of samples from a single transect in the Aconquija mountains (the same area as that from which our syrinx samples derive). Maximum frequencies drop about 0.7 kHz in moving from 400 m with closed mesic vegetation, to the scrub, open grasslands and moist puna between 2,000 and >3,000 m (Nottebohm 1975). Our larger and more extensive samples substantiate and clarify these trends. Higher frequency and broader bandwidth (and longer songs) are associated with lower altitudes and with more closed, mesic, natural environments.

Nottebohm (1975) observed, following Evans and Bass (1972), that sites with higher relative humidity (RH), while not *requiring* higher frequencies, might nevertheless permit their use in vocalizations, since the absorption of sound (to which higher frequencies are particularly susceptible) is significantly reduced at higher RH. However, empirical studies on sound transmission in different habitats have shown *greater* attenuation of high frequencies in forests than in open habitats (Morton 1970, 1975; Chappuis 1971) and Marten and Marler (1977) have shown that near the ground in forests, there is a “sound window,” such that frequencies between 1–2 kHz showed the least attenuation. Morton (1970) argued that open-country birds *should* use lower emphasized frequencies than they do, and attributed this discrepancy to the generally smaller size of these species. He suggested that they were too small to produce the lower frequencies needed to overcome “shadow zones” and wind fluctuations, without an unacceptable reduction in source amplitude. He also concluded that, because of this problem, open country species commonly opt for the use of temporal structure (e.g., trill and buzzes) in their songs rather than frequency characteristics and that this, too, will lead to broader-band vocalizations with higher maxima.

The applicability of such simple rules has been strongly questioned by Wiley and Richards (1982). They conclude that no clear predictions

can be made about differences among natural habitats in the optimal frequency for long-range communication. On the contrary, they maintain that for maximum efficiency such communication should always employ the lowest frequencies possible, regardless of habitat. However, there are studies showing differences in average song frequency and bandwidth among habitats. All of the species concerned are primarily woodland/forest species. None has truly open-country populations, but *Zonotrichia capensis* is primarily a species of open country and scrub. It only enters the margins of truly closed habitats, even though in many cases, road or stream margins are often deeply embedded in largely undisturbed closed habitat. With this in mind, Hunter and Krebs (1979) report higher maximum frequencies and wider bandwidth in songs of the Great Tit, *Parus major*, in open woodlands than in denser forests. Wasserman (1979) found in the White-throated Sparrow, *Zonotrichia albicollis*, that the frequency of the first two notes of songs from field habitats was higher than those from forest samples. Shy (1983) found that in Summer Tanagers, *Piranga rubra*, from eastern North America, where forest habitats have a higher tree density, songs have lower maximum frequencies and narrower bandwidth than in the west, where tree densities are lower. In the Northern cardinal, *Cardinalis cardinalis*, song maximum frequency and bandwidth were highest in a pine sapling stand with no canopy; maximum song frequency and bandwidth were lowest in a 60-year-old stand with a sparse understory and closed canopy (Anderson and Conner 1985). Sorjonen (1986a, 1986b) reports higher average frequencies and wider bandwidths in the vocalizations of open habitat species of European passerines, and concludes that body size, singing behavior and the acoustic nature of the song-community are often more important variables than habitat. Waas (1988) corroborates that the frequency of White-throated Sparrow songs is inversely correlated with the foliage density of the habitat. These studies are consistent with the expectations of Morton (1970) that open habitats should favor trills, giving a broader bandwidth through higher song maxima. Our results concerning frequency, corroborating the findings of Nottebohm (1975), are largely in contradiction to these studies, although they do accord in some respects with the model advanced by Bowman (1983, Fig. 144, p. 296). However, with respect to frequency and

duration characters, our results accord with Morton's predictions (1970, pers. comm.) that closed-habitat birds should show longer themes and shorter trills than open-habitat birds. This is so here for all closed habitats, especially alder woodland. He also argues that open-habitat birds should have the *lowest*-pitched trills and this is also the case (Tables 3, 4; Figs. 5, 6; Appendix 1).

Nottebohm (1975) suggested that body size may influence song frequency in *Zonotrichia capensis*, noting that Chapman (1940), King (1972) and Handford and Nottebohm (1976) indicate that *Z. capensis* from higher altitudes and latitudes are generally larger. Studies of variation in body size in this species (Handford 1983, 1985) confirm that birds from higher altitudes and latitudes are structurally larger. Handford (1988), noting the results of Snape and Wrobel (unpubl. MSS) on variation in song frequency in this species, provisionally interpreted the trends in frequency in this species as simply reflecting trends in body size.

Although Greenwalt (1968) concluded that there is little correlation between body size and maximum song frequency, there is good evidence that modal song frequency, or emphasized frequency, is related inversely to body size among species (Darwin's Finches, Bowman 1979, 1983; European oscine passerines, Wallschläger 1980; Neotropical oscines, suboscines and non-passerines, Ryan and Brenowitz 1985). These authors find a negative relationship among species between emphasized song frequency and body size. They conclude that the residual variation in frequency remaining after the effect of body size has been removed relates to ecological variables and Wallschläger (1980) and Ryan and Brenowitz (1985) claim that higher frequencies tend to be emphasized in birds from more open habitats. However, although Bowman worked with a closely-related subfamily, the latter two studies compare very diverse species, and may therefore be misleading when considering variation at the intraspecific level.

Our results show that in *Zonotrichia capensis* there is the expected overall negative relationship between body size and song frequency, but the relationship is not a simple linear one (Figs. 5, 6, 8). Frequency is clearly influenced by other factors associated with the specific habitat type. Further, it seems that *lower* frequencies are generally emphasized in birds from more open hab-

itats. Recall that regressions of PC1 (song) on altitude *within* vegetation types sometimes indicate a positive relationship, rather than duplicating the overall clear negative relationship. This suggests that there is no simple *determination* of song frequency characters by body size alone, which is supported by the results of the analysis of syrinx dimensions (see below).

Only two other studies consider *intraspecific* variation in song frequency and body size: Bowman (1979, 1983) on *Geospiza conirostris* and *G. difficilis*, and Shy (1983) on the Summer Tanager. Bowman (1979, 1983) shows that in *Geospiza conirostris*, larger individuals produce songs which are broader-banded and slightly lower in modal frequency. In *Geospiza difficilis*, larger birds, while showing a broader-band song, have an additional, strong, high-frequency mode, giving a higher mean frequency. Thus, the picture presented by these two closely-related species is contradictory. Bowman (1979, 1983) points out that although there is a good correlation between both average body size and syrinx size and the mean emphasized frequency of songs within the Geospizinae as a whole, there is considerable variation in frequency characteristics about the regression lines. This indicates to him their "... capacity to adapt their vocalizations to ecological factors ...". In the Summer Tanager (Shy 1983), western individuals are larger in size than eastern ones, yet they have higher-pitched, broader-band songs (higher maximum frequency, see above).

Thus, Bowman's results contradict the "body-size rule"; Shy's findings in *Piranga rubra* are consistent with the general finding that more open habitat songs are higher-pitched, but also contradict the "body-size rule." Our results are to the contrary. They are partly consistent with the "body-size rule," and they contradict most empirical findings about habitat-frequency relations, yet are consistent with Morton's expectations (1970, pers. comm.).

Our results indicate that syrinx size in Rufous-collared sparrows is not related to body size. This suggests that the size of the sound-producing organ does not constrain the songs' emphasized frequencies. The range of body size shown in our samples (see Table 6) is approximately 40% of that found in the species as a whole, making it unlikely that the insignificance of our analyses is attributable to a small range of variation in the sample. In addition, over this same transect, there is significant change in both body size and the

frequency characteristics of the song (this study; Nottebohm 1975; Handford and Nottebohm 1976; Handford 1983). We provisionally infer that, in *Zonotrichia capensis*, frequency characteristics of the song primarily reflect learning processes rather than being the passive consequence of constraints produced by body- or organ-size differences.

In the absence of data on the acoustic transmission and degradation characteristics of these specific habitat types, we suggest that our results may be associated with habitat-specific ambient noise profiles (Ryan and Brenowitz 1985). We have yet to address this matter in a systematic way, but in a χ^2 comparison among 141 recordings made in open (puna, grassland, Monte desert) and in mixed and closed (lowland chaco transition forest, montane woodland) habitats, and qualitatively assessed for low, moderate and high levels of background noise in the 0–2 kHz and 6–10 kHz bands, we found no trends in noise levels by habitat in the high frequency band and only a borderline-significant trend towards higher noise levels in the low-frequency band in open environments. This is a familiar trend, and larger samples would probably have shown the effect to be significant because open habitats have higher levels of wind-induced, low-frequency noise. If ambient noise were influencing vocalizations in *Zonotrichia capensis*, we should expect this species, like others, to show higher-frequency songs in open habitats. The converse is true.

Our findings may also be related to the habitats' avifauna (Handford and Nottebohm 1976; Handford 1981, 1988; Nottebohm 1985; Sorjonen 1986a, 1986b; see also Bowman 1979, 1983, on song convergence). Given that variation in both the trill rate (Handford 1988) and frequency and duration characters (this study) are more closely related to the *original* vegetation type than to its present physical structure, and for other reasons (Handford 1988), avifaunal effects seem to us to be likely. There are distinctive species profiles in most of the habitat types (Short 1975, Olrog 1979, Olrog and Capllonch 1986), but it is not clear that there are obvious "open-habitat" and "closed-habitat" faunas corresponding to the two clusters in Figures 5, 6 and 7.

We now consider the relationship between frequency and duration characters and the dialect-defining variation in trill interval. Here, we make some new inferences regarding the qualitative structure, and the ontogeny, of the song in Monte

desert populations of *Zonotrichia capensis*, and describe what may be termed a "behavioral phenocopy" phenomenon.

Fast-trilled songs are short, low-pitched and of narrow bandwidth, especially in the trill (Fig. 3a). This harmonizes both with the finding that high altitude, open country, songs have these frequency and duration characteristics, and with the finding (Handford 1981, 1988) that the fastest-trilled songs (trill interval < 50 msec) are typical of high grasslands and puna. Closed (mesic) habitat populations show slow to very slow trills and these are longer, higher-pitched and broader-band. Intermediate are the samples from mixed to semi-open habitats. Only the very-slow-trilled songs from the Monte desert depart from this overall pattern. These have extremely slow trills (300–500 msec), yet the habitat is arid and almost uniformly open and low-statured. In addition, these songs have the frequency and duration characteristics typical of songs with the fastest trills (Fig. 3b). Such fast trills are the rule in open and low-statured vegetation. Thus, both from the point of view of their frequency characteristics and of their habitat type, slow-trilled Monte desert songs "should have" much faster-trilled songs. The anomalous nature of songs from the Monte desert has been noted before (Nottebohm 1975; Handford 1981, 1988), particularly in regard to the empirical finding (Morton 1970, 1975) and theoretical prediction (Wiley and Richards 1982) that open-country birds should use temporal modulation to avoid signal degradation through amplitude fluctuation. Except for the slow-trill Monte songs, trill rate in *Zonotrichia capensis* accords well with this general expectation (Handford 1988, Fig. 5).

Until the songs of this species had been examined in the provinces of San Juan and Mendoza, all recordings from the Monte desert showed a remarkable uniformity in this very slow trill. But in the Monte desert of central Mendoza and parts of southwestern San Juan, songs like the typical Monte song, but including a very rapid trill of falling frequency, were observed (Handford 1988, Fig. 5b). These songs have the "expected" trill type for open country, together with low frequency and narrow bandwidth. These Monte desert songs fall in the main sequence of songs in Figure 3b. That is, they are virtually indistinguishable from the puna songs, both in terms of trill rate and in terms of frequency and duration characteristics. In the relationship between trill rate and PC2 (Fig. 4) the slow-trilled

Monte songs are not anomalous, and fall in the same statistical population as the rest. Inspection of Table 3 reveals that PC1 relates most strongly to the trill characters TRMAX and TRBAND, while PC2 relates mainly to theme characters THMAX and THBAND. This suggests that the slow-trilled Monte songs are anomalous only with regard to the trill itself.

These results raise the possibility that "slow-trill" Monte desert songs have lost the trill (and often elaborated the theme), rather than having a "true" trill of large interval. However, this is probably not true for all desert singers. In some cases, detailed transects across some ecotones between other vegetation types and the Monte desert show a steady reduction of trill rate over several tens of kilometers (Handford 1988, Fig. 8a). On the other hand, some transitions are abrupt and the trill seems to disappear in less than a kilometer. An example is the transition from the 20 msec trill zone in the moist puna on the eastern-facing crest of the Aconquija mountains to the >300 msec trill zone in the arid prepuna on the western-facing crest (Nottebohm 1975, Figs. 4, 5 and 6). Our impression is that where the desert adjoins vegetation with trills that are already slow (e.g., montane chaco—mean trill interval 163 msec), the languid quality of the desert song is achieved by a progressive slowing of the true trill. At other transitions, from rapid-trill zones (e.g., puna or grassland—mean trill intervals 18 and 53 msec, respectively), the effect apparently is achieved by the loss of the "true" trill. This suggests what may be termed a "behavioral phenocopy" phenomenon: the acquisition during ontogeny of a given behavioral phenotype (a languid, whistled song) by two structurally distinct means. All this, of course, still leaves the question of what is the apparently compelling reason for birds in the more northerly reaches of the Monte desert to slow down, or lose, their trill? Conversely, why do southern Monte birds show a trill which is appropriate both to the theoretical expectations for open environments and to the frequency characteristics of the rest of the song (Handford 1988)?

Except for the "whistle vs. trill" dichotomy there is little consideration in the literature of the "adaptive qualitative morphology" of the individual syllables or elements of bird songs. King (1972) employed a more finely-discriminating note classification than is used here, but the commonest themes he encountered in the western lowland chaco, approximately 50 km east of Tu-

cuman city, were, in our terms, 1-4, 1-2-3 and 1-2-4. In the grassy scrub around Tafi village in the Aconquija mountains west of Tucuman, the principal themes were 2-3, 1-3-3 and 1-4. This finding is consistent with those reported here.

In virtually all *Zonotrichia capensis* songs known, regardless of massive variation in the nature of the trill (from insect-like buzz to slow whistle), the song is always preceded by a whistle-note theme. This suggests that the theme and trill serve distinct functions (Handford 1981, 1988). Richards (1981), developing an idea of Shiovitz (1975), argues that song introductions serve an alerting function. Richards hypothesized (1981) that this function is non-specific and that the alerting notes carry little or no species-specific information; they merely alert to the arrival of a message which may be from a conspecific. However, Shiovitz (1975) saw the introductory notes as a "species-signature," alerting conspecifics to the imminent arrival of a more complex signal. This coincides better with our impressions gained in the field that, without these theme notes, the trill of *Zonotrichia capensis* alone provides a poor indication of the species-identity of the singer because the trill in this species shows much geographical variation and since there are several other species which have similar trills (Handford and Nottebohm 1976). The theme notes appear truly characteristic of the species, at least to the human observer.

In summary, the habitat, body-size and syrinx analyses all suggest a major learning component to variation in the frequency characteristics of the song of *Zonotrichia capensis*, rather than it being due simply to body or organ size constraints. This is contrary to the previous view of Handford (1988). It seems reasonable that this is true for the other characteristics considered here. The inferences made regarding the origin of the slow-trilled desert songs serve to support this conclusion.

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APPENDIX 1. Descriptive statistics of the frequency (kHz) and duration (sec) characters from all non-ecotonal specimens by habitat type (see Materials and Methods for acronyms).

	THMAX	THMIN	THBAND	TRMAX	TRMIN	TRBAND	THLEN	TRLEN	SOLEN
Lowland chaco <i>n</i> = 293									
Min.	4.60	2.10	1.30	5.20	2.60	1.50	0.15	0.31	0.95
Max.	8.40	4.10	5.20	7.70	4.30	4.70	0.96	1.61	2.04
Mean	6.24	3.28	2.96	6.41	3.49	2.92	0.54	0.92	1.53
SD	0.76	0.26	0.73	0.48	0.30	0.55	0.16	0.20	0.22
Montane chaco <i>n</i> = 62									
Min.	4.10	2.70	1.40	5.00	2.50	1.20	0.21	0.54	1.18
Max.	8.00	4.10	4.90	7.30	3.80	4.50	0.81	1.37	2.15
Mean	6.21	3.19	3.01	6.29	3.22	3.07	0.49	0.94	1.50
SD	0.89	0.29	0.88	0.47	0.29	0.58	0.16	0.20	0.21
Transition forest <i>n</i> = 424									
Min.	4.70	2.40	1.20	4.80	2.30	1.30	0.18	0.28	0.86
Max.	8.90	4.00	6.00	9.00	4.50	5.90	1.21	1.52	2.08
Mean	6.23	3.26	2.95	6.58	3.30	3.28	0.55	0.88	1.52
SD	0.81	0.28	0.88	0.60	0.33	0.75	0.17	0.19	0.21
Montane forest <i>n</i> = 100									
Min.	4.50	2.10	0.90	5.40	2.30	1.90	0.18	0.30	1.05
Max.	8.10	3.80	5.50	8.60	3.90	5.60	1.02	1.54	2.12
Mean	6.25	3.18	3.07	6.35	3.27	3.08	0.49	0.92	1.48
SD	0.72	0.32	0.85	0.47	0.35	0.59	0.18	0.21	0.19
Alder woodland <i>n</i> = 65									
Min.	4.90	2.80	1.20	4.80	2.20	2.00	0.35	0.49	0.96
Max.	7.40	3.90	3.90	8.00	3.40	5.30	0.87	1.14	1.93
Mean	6.02	3.46	2.55	6.36	2.84	3.51	0.58	0.77	1.44
SD	0.68	0.26	0.70	0.56	0.25	0.62	0.14	0.18	0.19
Grassland <i>n</i> = 156									
Min.	4.30	2.00	1.20	5.00	2.50	0.90	0.13	0.60	0.98
Max.	7.60	3.50	5.10	7.20	5.20	4.50	0.88	1.42	2.08
Mean	5.85	2.95	2.91	5.98	3.38	2.60	0.42	0.96	1.45
SD	0.62	0.29	0.78	0.42	0.55	0.72	0.16	0.18	0.21
Prepuna <i>n</i> = 12									
Min.	4.70	2.30	2.30	5.00	3.00	1.70	0.15	0.84	1.13
Max.	7.10	3.20	4.40	6.00	3.70	2.90	0.45	1.30	1.70
Mean	5.93	2.80	3.13	5.62	3.24	2.38	0.29	1.07	1.42
SD	0.74	0.34	0.66	0.26	0.20	0.39	0.08	0.16	0.18
Monte desert <i>n</i> = 174									
Min.	3.90	2.30	0.80	2.90	2.10	1.50	0.12	0.22	0.92
Max.	7.00	3.80	4.20	7.10	4.10	4.60	1.25	1.45	2.09
Mean	5.46	3.02	2.43	5.65	2.99	2.66	0.48	0.89	1.46
SD	0.67	0.32	0.74	0.58	0.36	0.54	0.24	0.25	0.22
Puna <i>n</i> = 33									
Min.	4.20	2.50	1.50	4.20	2.60	1.10	0.12	0.45	0.83
Max.	5.80	3.30	3.10	7.00	3.80	4.00	0.95	1.02	1.51
Mean	5.25	2.80	2.45	5.95	3.18	2.77	0.37	0.86	1.28
SD	0.39	0.18	0.42	0.67	0.24	0.75	0.16	0.11	0.14