Adaptive Morphology of Song Dialects in Darwin's Finches *)

By Robert I. Bowman

Field ornithologists have long been aware of regional variations in the songs of many species of birds (MAYR 1942), but only within the past two decades have detailed spectrographic analyses been used to document this widespread "dialect phenomenon" (MARLER & TAMURA 1962, 1964; THIELCKE 1965, 1969; LEMEON 1971; HARRIS & LEMON 1972; KING 1972; NOTTEBOHM 1972, 1975; GRIMES 1974; OREJUELA & MORTON 1975; BAPTISTA 1976; LANYON 1978). Apparently, vocal learning establishes a "filial tradition" so that individuals of one species in a particular region sing more nearly like each other than like conspecifics from another region (MARLER 1970; NOTTEBOHM 1972; LEMON, 1975).

Reports of vocal variation on islands have been concerned mainly with disjunct populations of continental species of birds or their close relatives (CHAPMAN 1940; LACK & SOUTHERN 1949; MARLER & BOATMAN 1951; MARLER 1960; LANYON 1967; MIRKSY 1976), and in the case of earlier studies, were not based on tape recordings or sound spectrograms. CHAPIN (in MAYR 1942) gives his impressions of the often marked inter-populational differences in the song of *Acrocephalus* warblers on south Pacific islands, and for the Galápagos Islands, ROTHSCHILD & HARTERT (1899, 1902), SNODGRASS & HELLER (1904), GIFFORD (1919), BEEBE (1924, 1926), and LACK (1945) present onomatopoetic descriptions of many species' songs and island dialects. Recently, BILLEB (1968) and GULLEDGE (1970) have presented spectrographic descriptions of the song dialects of Galápagos warbler-finches *(Certhidea)* and mockingbirds *(Nesomimus)*, respectively. WARD (1964) has also made an objective description of inter-island variation in vocalizations of the endemic Hawaiian honeycreeper, *Himatione sanguinea*.

Within the past few years studies on habitat acoustics have indicated that sound transmission peculiarities of environments might significantly affect the form of long-distance communication signals (KONISHI 1970a, CHAPPUIS 1971; JILKA & LEISLER 1974; MORTON 1975; MARTEN & MARLER 1977; MARTEN, QUINE & MARLER 1977).

---

*) Contribution No. 231 of the Charles Darwin Research Station, Galapagos.

In this summarial report I attempt to correlate vocal dialects in Darwin's finches with sound attenuation characteristics of the natural environments in the Galápagos Archipelago. An ecological explanation is proposed for specific song dialects on specific islands, for parallel shifts in the songs of sympatric species, and for the intra-island variation in the song of one species in different vegetations.

Materials and Methods

Field and laboratory procedures are summarized below. Numerous details are presented elsewhere (BOWMAN 1980).

a. Field recordings

Tape recordings of songs of Darwin's finches were made with Nagra III-B and IV recorders at a tape speed of 15 i. p. s., using American D-33 microphones mounted in 25-inch aluminum parabolic reflectors, and reflectorless Sennheiser "ultra-directional" microphones (models MKH 805 and 815 U) equipped with windscreens (models MZW 815 or 804). A variety of "3 M" brand polyester base magnetic tapes (nos. 200, 202, and 207) was used. Only those songs recorded from birds in fully adult plumages (BOWMAN 1961) were employed in the spectrographic analyses.

b. Laboratory analyses

Three types of spectrographic display were prepared for each song using the Kay Elemetrics Spectrum Analyzer ("Sona-graph" model 6061 B, range 85—16,000 Hz) equipped with an Amplitude Display (model 6070 A) tuned to the "flat" response setting (Fig. 1).

The amplitude contour accessory to the "Sona-graph" converts the sound signal into a display in which amplitude distribution is defined by six contour lines, each with a 6 dB interval. Only the four highest contour areas, namely 6, 5, 4, and 3 (Fig. 1) were used in this study because the perimeter of amplitude area 3 approximates that of wide and narrow band displays of the same song, and probably delimits most if not all of the critical sound energy used in long-distance transmission.

Since there is an approximate doubling of sound amplitude with each 6 dB pressure increment (PETERSON & GROSS 1972), numerical values of 1, 2, 4, and 8 were assigned to the contour levels 3, 4, 5, and 6, respectively, in order that the logarithmic values (decibels) of the amplitude contour display could be converted proportionately to linear values of the amplitude grid score. This allows us to add the linear values when calculating relative amplitude distribution for entire songs (Fig. 1).

Within the confines of any given square of the grid, the amplitude shading with the highest numerical value determines the value assigned to the entire square, even though shades of lesser value may also be present. Thus, the machine-generated amplitude contour display of a song is translated into a mosaic composed of four numbers, viz. 1, 2, 4, and 8. The total energy contained within a 250 Hz bandwidth across the song was obtained by adding together all linear values of the grid squares in the band. Using the band totals of all songs, histograms were constructed showing the amplitude distribution according to frequency for songs of individuals (Fig. 1) and populations (Figs. 7, 8, 11, 12 and 13).

c. Measurement of decibel level of song

There have been few successful attempts at measuring the absolute sound levels of the vocalizations of non-captive song-birds. Recent studies by WITKIN (1977) and HEUWINKEL (1978) are noteworthy for their use of modern instrumentation and for the behavioral significance of their findings.
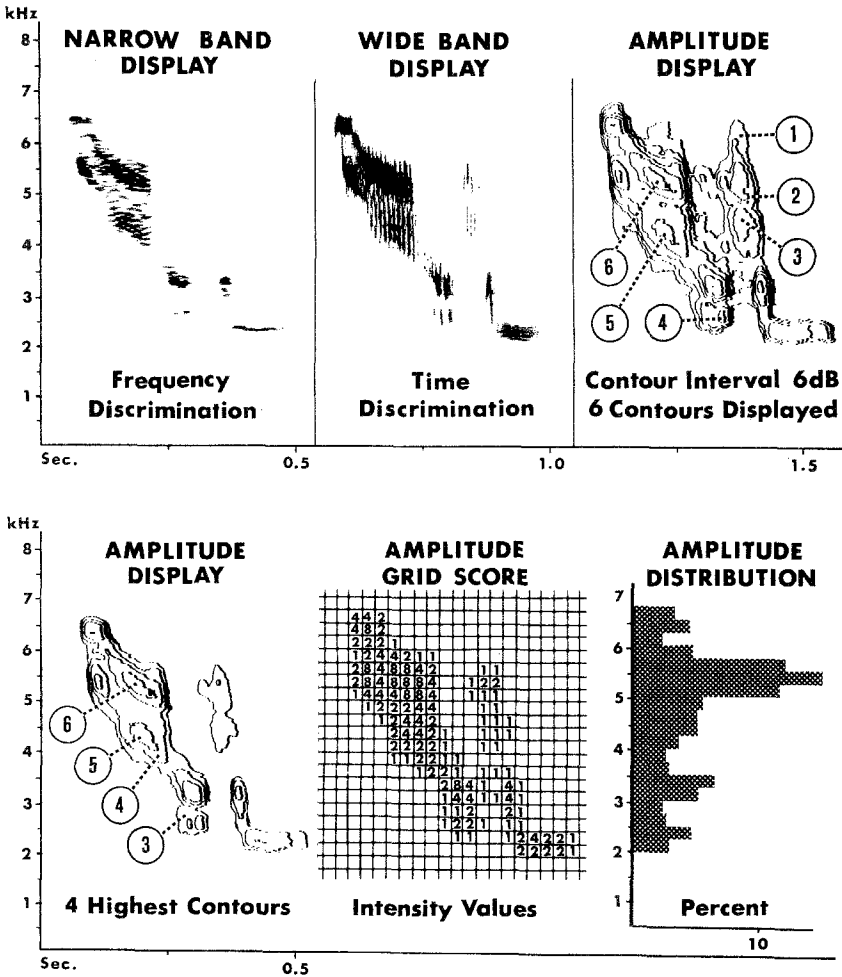
Fig. 1. Comparison of three types of graphic display of bird song (above) and method of analysis of relative amplitude of song (below), according to a scheme developed by HOPE (1976). See text for details.

In the Galápagos, sound pressure levels of territorial songs were measured on four species of Darwin's finches on islas Genovesa and Wolf (Fig. 2). Playback of a tape recording of an individual's song was used to attract the bird to within three feet or less of a handheld microphone (Brüel & Kjaer type 4131) equipped with a random incidence corrector (B & K type UA 0055) and windscreen (B & K type UA 0082). The entire. transducer system was mounted on a Sennheiser microphone boom (model MZS 805) and connected to a sound level meter (B & K type 2203) with octave filter set (B & K type 1613) by means of a ten-foot extension cable (B & K type AO 003). The microphone output was calibrated with a piston-phone (B & K type 4220). The non-weighted signal from the sound level meter was fed into a Kudelski Nagra III-B tape recorder (operating speed, 15 ips), the two instruments being "matched" by using the dB level of the sound level meter calibration tone as a standard of reference (see BOWMAN 1980 and WILSON 1968).

In the field an estimate was made of the distance between the bill of a singing bird and the end of the microphone. This information along with that pertaining to the nature of the alignment between bird and microphone, the readings of the attenuator setting on the sound level meter, the date, time, temperature and relative humidity, were recorded on the sound tapes. In the laboratory, recordings were analyzed using essentially the same equipment and arrangement thereof as employed in the analyses of sound transmission (see below, and Fig. 6).

The "all pass" dB level readings from the output of the graphic level recorder (B & K type 2305) were "adjusted" for each song recording because of differences in subject-to-microphone distance. Since sound pressure level diminishes with increasing distance at the rate of about 6 dB with each doubling of distance from the sound source (i. e. "inverse square law"; WOOD 1947), the recording distance of a singing bird was "halved" a sufficient number of times in order to bring the effective distance between bird and microphone to about one inch (actual range, 0.9—1.5 inches). With each halving of distance, a factor of 6 dB was added to the dB value shown on the output of the level recorder. For example, if the latter was 75 dB, and the estimated recording distance was 36 inches, then, as a result of dividing 36 inches by 2, and each successive quotient by 2, then as a result of a series of 5 such divisions we arrive at an effective working distance of 1.125 inches between bird bill and front end of microphone. To the level recorder output of 75 dB was added 30 dB (i. e. 5 times 6 dB) thereby making a total song pressure level of 105 dB at a point very close to the source of the sound. In order to minimize the effect on the calculations of potential errors in estimating bill-to-microphone distance and in judging goodness of alignment between microphone and bird, most of the dB values of song were arrived at by averaging comparable data points from two or more song recordings from the same individual (see Table 4).

d. Measurement of sound transmission

Sound transmission in the song environments of the finches was studied on several main islands of the Galápagos Archipelago (Figs. 2 and 3). Measurements of sound penetration were made shortly after sunrise (6:00 a. m.) when the air was calm and relatively free of heat stratification. An amplified "pink noise" spectrum, originating from a battery powered
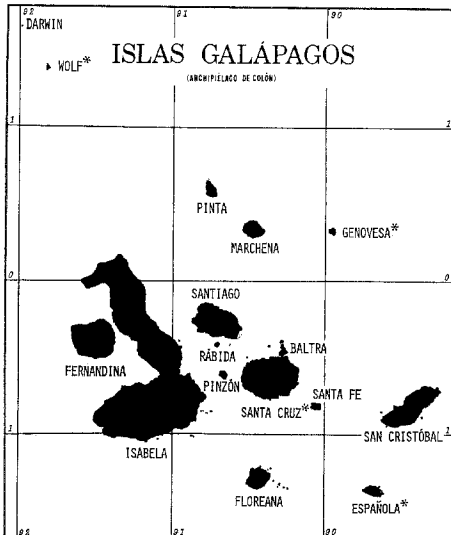

Fig. 2. Map of the Galápagos Archipelago with principal islands mentioned in the text flagged with an asterisk (*).

noise generator (custom built for this study by the acoustical consulting firm of Wilson, Ihrig, and Associates of Oakland, California; see WILSON 1968) was broadcast through a speaker system (Altec Lansing driver model 802 D and horn 811 B) mounted on a Tiltall metal tripod one meter above ground level (Figs. 4 and 5). The transmitted noise was recorded through a

Fig. 3. Galápagos vegetation. a, Isla Santa Cruz; coastal zone around Academy Bay showing tree-like *Opuntia echios*. b, Isla Santa Cruz; *elevation* 500 m, north-central region showing forest of tree composite *Scalesia pedunculata*. c, Isla Española; coastal zone of Punta Suarez. d, Isla Genovesa; dwarf *Bursera graveolens* forest around Darwin Bay. Note human figure in lower right corner of picture. e, Isla Wolf; patch of *Opuntia helleri* in foreground and shrubs of *Croton scouleri* in background on north-central mesa.
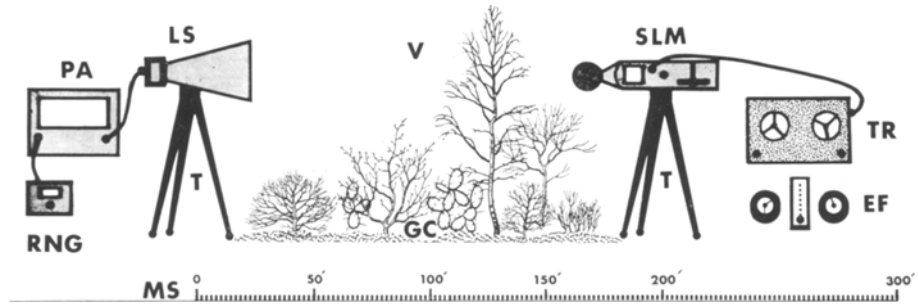
Fig. 4. Arrangement of equipment used for measuring sound transmission in Galápagos environments. Key to symbols: EF, environmental factors; GC, ground conditions; LS, loud speaker; MS, monitoring stations; PA, power amplifier; RNG, random noise generator; SLM, sound level meter; T, tripod; TR, tape recorder; and V, vegetation.

sound level meter, equipped as described above for measurement of dB level of song, using the nonweighted network, and also positioned one meter above ground level on a tripod at six stations along a straight line transect 25, 50, 100, 150, 200, and 300 feet from the front of the speaker. (See BOWMAN 1980 and WILSON 1968 for additional details).

Transmission efficiencies of pink noise and vocal spectra of the finches are assumed to be the same for individual frequencies.

e. Display of sound transmission data

Recordings of transmitted pink noise were analyzed by means of a sound filter (General Radio Sound and Vibration Analyzer model 1564) at one-third octave intervals from 500 Hz to approximately 10,000 Hz. Sound pressure levels (dB values) were obtained from the strip chart of the graphic level recorder (Fig. 6) and plotted on graph paper having frequency (kHz) on the vertical axis and distance in feet from the sound source on the horizontal axis (e. g. Fig. 13). Points of equal absolute sound pressure were connected to produce an "iso-decibel" contour line. Contour lines were plotted at 3 dB intervals, with their dB values shown near the top or bottom of each line. In this way a "sound transmission isopleth" was
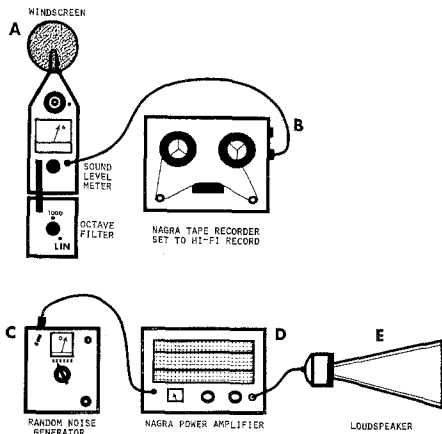

Fig. 5. Details of equipment arrangement for recording (A and B) and generating (C, D and E) "pink" noise in the field.
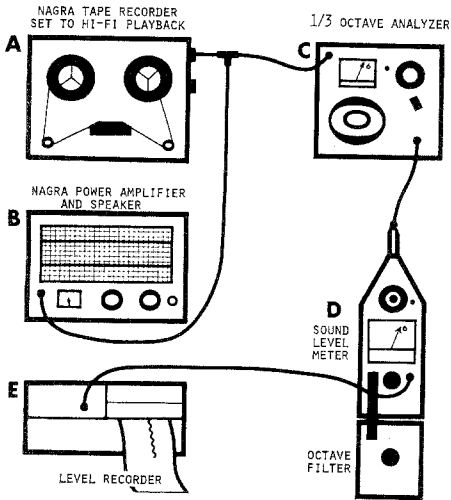
Fig. 6. Details of laboratory arrangement of equipment for analyzing sound pressure levels of recorded "pink" noise and bird vocalizations.

generated, showing the pattern of sound transmission in a given environment. In practice, the results obtained from the analyses of at least two or more sample sound lines were averaged before the data were plotted as an isopleth. Also, average dB levels of filtered background noise were plotted for selected one-third octave center frequencies, and these are shown at the right-hand slide of the isopleth.

The histograms (frequency/amplitude distributions) may be "projected" onto the corresponding "song fields" (sound transmission isopleths) to allow for visual detection of possible correlations between the most intensively used frequencies in songs and the most energy conserving transmission channels in the environments.

As indicated in fig. 20, only a very small percentage of the geospizine song frequencies occurs below one kHz (cf. KONISHI 1970 a). Consequently, we need have little concern here for the marked diminution of low frequency amplitudes and the loss of transmission efficiency that characterize all the isopleths below 1.0 kHz. Presumably, this phenomenon is due to ground attenuation (INGÅRD 1953) and varies according to the height of instrumentation above ground level (MARTEN & MARLER 1977). In those Galápagos environments tested up to now, the most energy efficient channels for sound transmission occur in the frequency range of 1.5 to 2.0 kHz (cf. MORTON 1975). This is below the modal amplitudes, but within the low frequency ranges, of most songs of Darwin' finches.

Results and Discussion

1. Song frequencies

Data presented in fig. 20 support the conclusion of GREENEWALT (1968) that there is little if any direct correlation between the size of a song-bird and the highest frequency in its song. For example, Isla Wolf *Geospiza magnirostris* (the second largest species of Darwin's finches) and Isla Genovesa *Geospiza difficilis* (the second smallest species) sing some of the highest frequencies in their advertising songs, whereas Isla Española *Geospiza conirostris* (the third largest species) and Isla

Table 1. Comparison of attenuation rates of song frequencies of *Geospiza conirostris* on islas Española and Genovesa, and of *Geospiza scandens* on Isla Santa Cruz, Galápagos.

Column	A	B	C	D	E			F	G
Line	Song Environment	Song Frequency Class	Song Frequency Range Hz	Total Bandwidth of song (kHz)	Cumulative Loss in Amplitude (dB) Between Monitoring Stations			Mean Rate of dB Loss per 100 ft. Between 25' and 300' Stations	Difference Between Mean HI-LO Rates of dB Loss
					25/100'	100/200'	200/300'		
1.	Española song in Española environment	HI	6 500	6.00	14	11	8	11*	1
		LO	500		17	13	6	12	
2.	Genovesa song in Española environment	HI	5 750	4.25	14	11	8	11	1
		LO	1 500		10	14	7	10	
3.	Genovesa song in Genovesa environment	HI	5 750	4.25	17	17	11	15	3
		LO	1 500		10	13	12	12	
4.	Española song in Genovesa environment	HI	6 500	6.00	27	17	11	18	6
		LO	500		18	10	7	12	
5.	Santa Cruz song in Santa Cruz environment	HI	6 500	5.25	20	16	9	15	3
		LO	1 250		14	13	9	12	

$$* \text{ Mean Rate} = \frac{14 + 11 + 8}{3} = \frac{33}{3} = 11$$

Santa Cruz *Certhidea olivacea* (the smallest species) sing some of the lowest frequencies. Furthermore, the so-called "whistle" song of most of Darwin's finches, including largest and smallest species, begins in the frequency range of 13—14.5 kHz (see Fig. 17 A and Bowman 1980).

Konishi (1970 a) has suggested the possibility that the lowest frequencies of song may be correlated with the size of the internal tympaniform membrane of the syrinx. A comparison of data in figures 20 and 21 shows that such a correlation is none too good for Darwin's finches. Rather, the correlation seems to be much better when modal amplitudes of song frequency spectra are compared with average membrane dimensions. Although *Certhidea olivacea* (the smallest finch) is capable of membrane vibrations at a fundamental frequency as low as in *Geospiza conirostris* (the third largest finch according to body weight), the smallest absolute size of the membrane in *Certhidea olivacea* presumably causes it to vibrate at a modal frequency that is considerably higher.

2. Island song dialects of *Geospiza conirostris*

The song populations of *Geospiza conirostris* on islas Genovesa and Española differ most obviously in frequency spread. Genovesa song has a bandwidth that is significantly narrower than that of Española song, i. e. 4.25 kHz versus 6.0 kHz, respectively (see Table 1 and Figs. 7 and 20). The greater spread of Española song may be correlated with the broadening of the most energy efficient transmission channel on Isla Española, as evidenced by the more vertical orientation of the isodecibel contour lines between approximately 2.0 and 4.25 kHz (cf. sound transmission isopleths for islas Genovesa and Española in Fig. 7).

Since we know (a) the frequency/amplitude distributions of the songs and (b) the manner in which the natural environments transmit the song frequencies contained in our pink noise spectrum, it is possible to calculate the rate of decay of the signal as it traverses the environment, and to determine if any significant disparity in absolute sound intensities develops between any two frequencies at a specified distance from the sound source.

With reference to the pink noise signal, the difference in d e c a y r a t e s between highest and lowest frequencies of Española *G. conirostris* song over a distance of 300 feet from the sound source, is only one decibel (i. e. 12 minus 11 dB, Table 1, Line 1, Column F), and the difference in a b s o l u t e i n t e n s i t y at 300 feet between highest and lowest frequencies in the central band which carries 80—85 percent of the sound energy, is only two decibels (i. e. 54 minus 52 dB; see Table 2, Line 1, Column D).

Comparable calculations for Genovesa *G. conirostris* yield a d e c a y r a t e differential of only three decibels over 300 feet (Table 1, Line 3, Column G) and an a b s o l u t e i n t e n s i t y difference between highest and lowest frequencies of four decibels at the 300-foot distance (Table 2, Line 3, Column D).
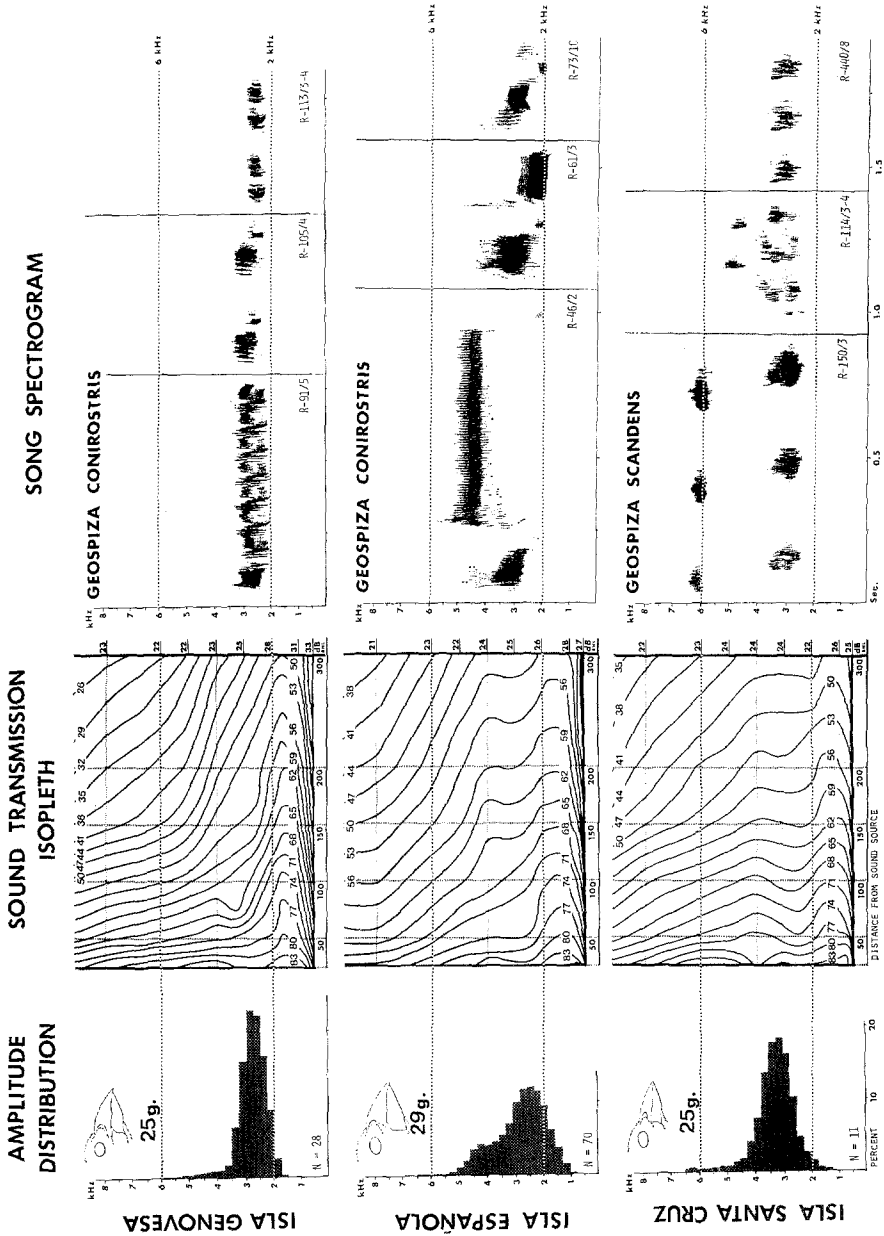
Fig. 7. Comparison of song amplitude distributions, body weights, sound transmission isopleths and sample song spectrograms for *Geospiza conirostris* populations on Isla Genovesa (top), Isla Española (middle), and *Geospiza scandens* on Isla Santa Cruz (bottom). Decibel values for contour lines are shown near their upper and lower ends. Background noise levels according to selected frequencies are shown at the right-hand edge of each isopleth. Body weight datum for Isla Genovesa, courtesy of P. R. GRANT.

Table 2. Comparison of "intensity" differences between high and low song frequencies of *Geospiza conirostris* (islas Española and Genovesa) and *Geospiza scandens* (Isla Santa Cruz), after compensation for relative differences in auditory sentitivities.

Column	A	B	C	D				E	F				G			
Line	Song Environment	Song Frequency Class	Frequency (Hz) Range Containing 80—85 % of Song Energy (dB) Around Mode	Absolute Intensity (dB) of HI and LO Frequencies at Distances from the Sound Source of				Auditory Sensitivity Factor (Rel. dB)*	Absolute intensity. Less Auditory Sensitivity Factor (Columns D minus E) at Distances of				Difference in dB Between Corrected HI and LO Frequencies at Distances from the Sound Source of			
				50'	100'	200'	300'		50'	100'	200'	300'***	50'	100'	200'	300'
1.	Española song in Española environment	HI	3 750	74	67	59	52	6.0	68	61	53	46	1	1	5	5
		LO	1 500	80	75	61	54	13.2	67	62	48	41				
2.	Genovesa song in Española environment	HI	3 000	74	69	59	51	1.0	73	68	58	50	4	9	3	3
		LO	2 250	74	64	60	52	5.0	69	59	55	47				
3.	Genovesa song in Genovesa environment	HI	3 000	74	64	53	43	1.0	73	63	52	43	1	0	2	1
		LO	2 250	77	68	55	47	5.0	72	63	50	42				
4.	Española song in Genovesa environment	HI	3 750	74	61	48	40	6.0	68	55	42	34	0	7	7	7
		LO	1 500	81	75	62	50	13.2	68	62	49	37				
5.	Santa Cruz song in Santa Cruz environment	HI	3 750	78	69	54	45	6.0	72	63	48	39	0	1	3	4
		LO	2 500	75	67	54	46	3.2	72	64	51	43				

* Auditory sensitivity factors for *Serinus canarius* are from DOOLING, MULLIGAN & MILLER, 1971: 703, Fig. 3. On the average this species has its greatest sensitivity between 2.0 and 4.0 kHz. Sensitivity declines about 15 dB/octave as frequency is decreased below 2.0 kHz, declines about 25 dB between 4.0 and 8.0 kHz, and declines 13 dB between 8.0 and 9.0 kHz.

** All values are 10 dB or more above background noise levels.

These data suggest that long-distance sound transmission on Isla Genovesa is less efficient than on Isla Española, irrespective of frequency. A comparison of the isopleths for the two islands (Fig. 7) reveals a closer spacing of the isodecibel contour lines on Isla Genovesa, a condition indicating a relatively higher rate of sound attenuation. Whereas on Isla Genovesa the 3 kHz sound, for example, is reduced to an intensity level of 43 dB at 300 feet from the sound source, on Isla Española the same frequency is reduced to only 52 dB, thereby affecting an energy "saving" of 9 dB by the Española environment.

Perhaps a more revealing demonstration of the adaptiveness of the two *conirostris* song populations to their respective (concordant) environments can be made by "projecting" song dialects into discordant song environments, as is done in Tables 1 and 2, Lines 2 and 4. When the "narrow bandwidth" song of Genovesa *conirostris* is transmitted through the "wideband" efficient discordant environment of Isla Española, there develops only a very small disparity in d e c a y r a t e s (i. e. 1 dB; Table 1, Line 2, Column G) and absolute s o u n d i n t e n s i t i e s (i. e. 1 dB; Table 2, Line 2, Column D) between high and low frequencies over the 200-foot transect. However, when the "wide bandwidth" song of Española *conirostris* is transmitted through the "narrowband" efficient discordant environment of Isla Genovesa, there develops a much larger disparity in d e c a y r a t e s (i. e. 6 dB; Table 1, Line 4, Column G) and absolute s o u n d i n t e n s i t i e s (i. e. 10 dB; Table 2, Line 4, Column D) between high and low frequencies over a 300-foot transect.

Although nothing specific is known about the sensitivity of the geospizine ear, some information is available (cf. Dooling, Mulligan & Miller 1971; Konishi 1970 a) for song birds and particulary for a distantly related finch, the canary *(Serinus canarius)*, which data we may apply, perhaps simplistically, to the condition in Darwin's finches (Table 2). I am assuming, for want of information to the contrary, that a source adjustment has not already been made in the songs of the birds to compensate for the differential frequency sensitivity of their ears. Consequently, it is necessary to subtract relative dB values (as derived from a graph given by Dooling, Mulligan & Miller 1971) from our absolute sound intensity values (Table 2, Column F). Presumably now the dB levels of the high and low frequency components of the songs at stations 50, 100, 200, and 300 feet better reflect the relative intensities as the birds might hear them in nature.

What emerges from an analysis of these data is a better understanding of the adaptiveness of song to specific environments. Dialects in concordant song environments (Table 2, Lines 1, 3, and 5, Column G) are efficient in the sense that most of the song energy is concentrated in a transmission bandwidth that travels with the least distortion of all frequency components over great distance. Dialects in discordant environments (Table 2, Lines 2 and 5, Column G) develop notable intensity disparities (7—9 dB) between frequency components during short-range transmission (e. g. 100 ft.), which, I assume results in an early (i. e. short-range) loss of intelligibility.

Differences in the song ecology of the two island populations of *Geospiza conirostris* suggest that certain vagrant males might experience formidable difficulties in establishing themselves on another island because of possible mis-matching of song structure and transmission pattern, with all the attendant problems (e. g. mate finding and territorial defense) normally mediated by song.

In a vocally polymorphic population such as Española *G. conirostris,* certain song types ("morphs") would fare better than others if transplanted to a "foreign" environment such as that of Isla Genovesa. For example, an Española song of narrow bandwidth (such as R-73/10, Fig. 7) would be less maladapted than a song of wide bandwidth (such as R-46/2) when transmitted in the narrow bandwidth, energy efficient channel of the Genovesa environment.

Field observations and laboratory experimentation indicate that geospizine song is culturally transmitted from "father to son" during the male parent-dependent fledgling stage (BOWMAN 1980). Such filial tradition in song acquisition does, however, allow for structural alteration of the signal such as occasionally takes place when a young orphan becomes imprinted on the song of the foster male parent (BOWMAN 1980).

A further demonstration of the adaptive relationship between the bandwidth (frequency spread) of song and attenuation characteristics of the environment can be made by comparing song transmission data for *Geospiza scandens* (Isla Santa Cruz) with those for *Geospiza conirostris* (Isla Española). Refer to Tables 1 and 2, and Fig. 7. These allopatric species are very similar ecologically.

The upper frequency limit of song (6.5 kHz) is the same for both species (Table 1, Lines 1 and 5, Column C), and the sound transmission isopleths for islas Santa Cruz and Española are quite similar, except for the fact that the isodecibel contours of the Santa Cruz isopleth are more vertically oriented above 4 kHz (Fig. 7). Whatever transmission advantage this latter situation might confer to the high frequency components of *Geospiza scandens* song, is probably offset by the slightly greater average decay rate for the highest song frequency in the Santa Cruz environment than in the Isla Española environment (see Table 1, Lines 1 and 5, Columns F and G). This difference is exemplified by the fact that at 300 feet from the sound source, the 5 kHz frequency band is attenuated 42 dB on Isla Santa Cruz whereas on Isla Española it is only down to 48 dB. Nevertheless, in its environmental adaptiveness Santa Cruz *G. scandens* song parallels closely Española *G. conirostris* song, and this fact is corroborated by data on intensity differences between high and low song frequencies abjusted to the presumed auditory sensitivities of the birds (Table 2, Lines 1 and 5, Column G).

Parallel structural variation in the songs of two groups of sympatric species of finch in the coastal zone of Isla Santa Cruz are shown in figs. 9 and 10. In each group I attribute this phenomenon to similar acoustical "constraints" of the sound transmission environment and to similar behavior (i. e. all species whose songs are pictured in fig. 9 are "tree-finches," ecologically; those pictured in fig. 10 are

TOTAL AMPLITUDE
DISTRIBUTION
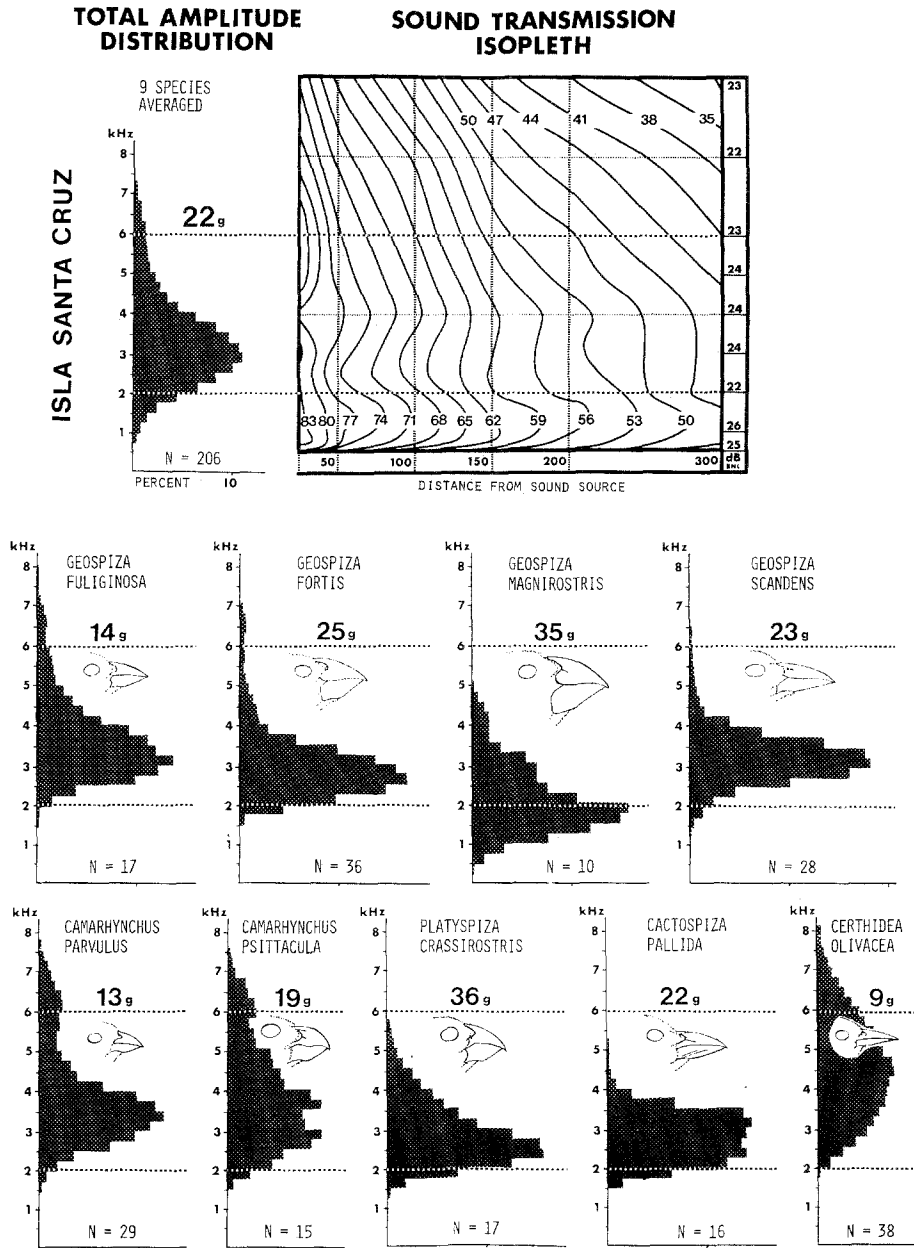
SOUND TRANSMISSION
ISOPLETH

Fig. 8. Song amplitude distributions of nine sympatric species of Darwin's finches on Isla Santa Cruz.
Top row: Average of all species distributions (left) and sound transmission isopleth for coastal zone
(right). Middle and bottom rows: Amplitude distribution of songs of nine sympatric species.
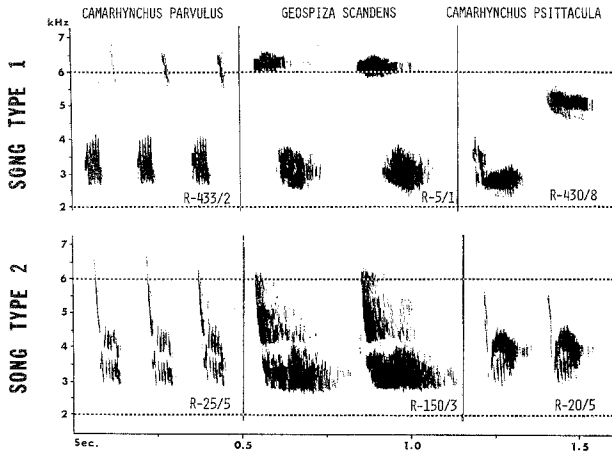
Fig. 9. Parallelism in two song types of three species of Darwin's finches recorded at Academy Bay, Isla Santa Cruz. *Camarhynchus parvulus*, *Camarhynchus psittacula* and *Geospiza scandens* are "tree-finches".

"ground-finches," ecologically). Of course, since all available evidence indicates that the sub-family Geospizinae constitutes a monophyletic group (Bowman 1961; Jo 1980; Lack 1945; Polans 1980), it is reasonable to assume that close genetic affinity accounts for some sharing of song parameters, such as temporal subdivisions of their "basic" songs (see Bowman 1980), but it probably does not account for much of the parallel structural patterns and energy distributions among species of Darwin's finches living in ecologically similar "sound environments."

Song bandwidth seems to be correlated neither with high nor low incidence of sympatry. Evidence for this is as follows: Songs of *Geospiza scandens* on Isla Santa
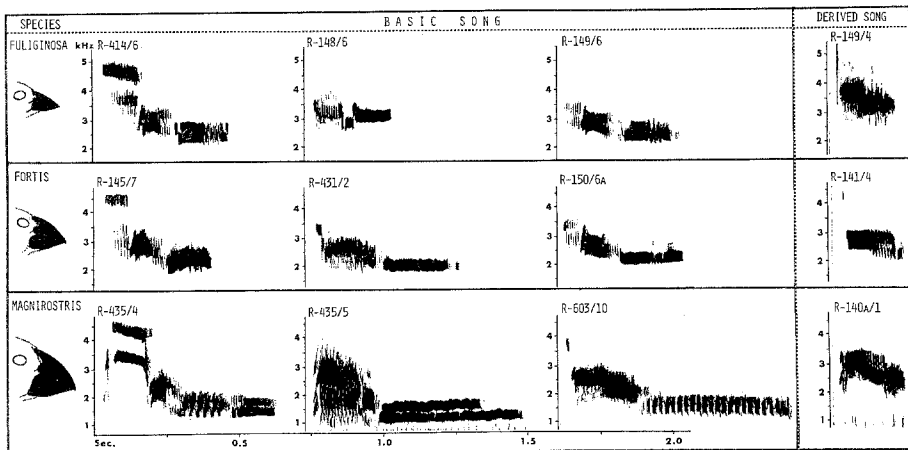
Fig. 10. Parallelism in songs of three sympatric species of *Geospiza recorded* at Academy Bay, Isla Santa Cruz. Ecologically, *Geospiza magnirostris, G. fortis,* and *G. fuliginosa* are "ground-finches". Basic and derived song type designations refer to a developmental scheme described by Bowman (1979).

Cruz (where nine species reside sympatrically; see Fig. 8) and *Geospiza conirostris* on Isla Española (where three species reside sympatrically; see Fig. 7) are equally variable, and considerably more variable than the song of *G. conirostris* on Isla Genovesa (where four species reside sympatrically; see Fig. 11). In other words, the bandwidth of long-distance song signals appears to be functionally related more to environmental qualities affecting sound transmission than to the number and kind of coinhabitants present.

To summarize, the preceeding examples demonstrate the following principles:

1. Island dialects in the songs of Darwin's finches are local behavioral adaptations (cf. KING 1972; NOTTEBOHM 1972) characterized by a frequency/amplitude distribution that least disturbs the integrity of the sound signal over the greatest possible distance.

2. Transmission rates for high and low sound frequencies are peculiar to each island environment.

3. Character convergence in various structural details of songs, in both sympatric and allopatric species, is a response to similar physical characteristics of the environment affecting sound transmission (cf. BROWN & WILSON 1956; CODY 1969, 1973 & 1974; CODY & BROWN 1970; GRANT 1966).

4. Frequency breadth (bandwidth) of song is greatest on islands where environments show the least disparity between high and low frequency transmission rates.

3. Comparison of songs on islas Genovesa and Wolf

The geospizine faunae on islas Genovesa and Wolf are very similar. Both islands support resident populations of *Geospiza difficilis*, *Geospiza magnirostris*, and *Certhidea olivacea* (cf. Figs. 11 and 12). In addition to these species, Isla Genovesa has *Geospiza conirostris*. (The breeding of *G. conirostris* on Isla Wolf has been reported only by CURIO & KRAMER 1965. Neither this writer, who has visited Isla Wolf during the breeding season of the finches in 1964, 1968, and 1979, nor PETER R. GRANT, who visited the island in 1978 — personal communication — have observed this species on Isla Wolf.)

Conspecifics on the two islands display marked song dialects (cf. Fig. 11 and 12). A comparison of amplitude distributions of the songs shows that the largest species, *G. magnirostris*, possesses a monomodal distribution of energy at 2.5 kHz on Genovesa, but a trimodal distribution on Wolf at 2.5, 5.0, and 8.0 kHz. A rather similar type of upward shift in frequency emphasis prevails in the case of *Geospiza difficilis,* with a bimodal distribution of energy on Genovesa at 4.0 and 9.5, and 14.0 kHz! The songs of the smallest species, *Certhidea olivacea*, although quite alike in their frequency distribution ranges on the two islands, differ in their amplitude distributions, with the Wolf population strongly skewed toward the higher frequencies (Fig. 12). Although small sample sizes for *G. magnirostris* and *C. olivacea*
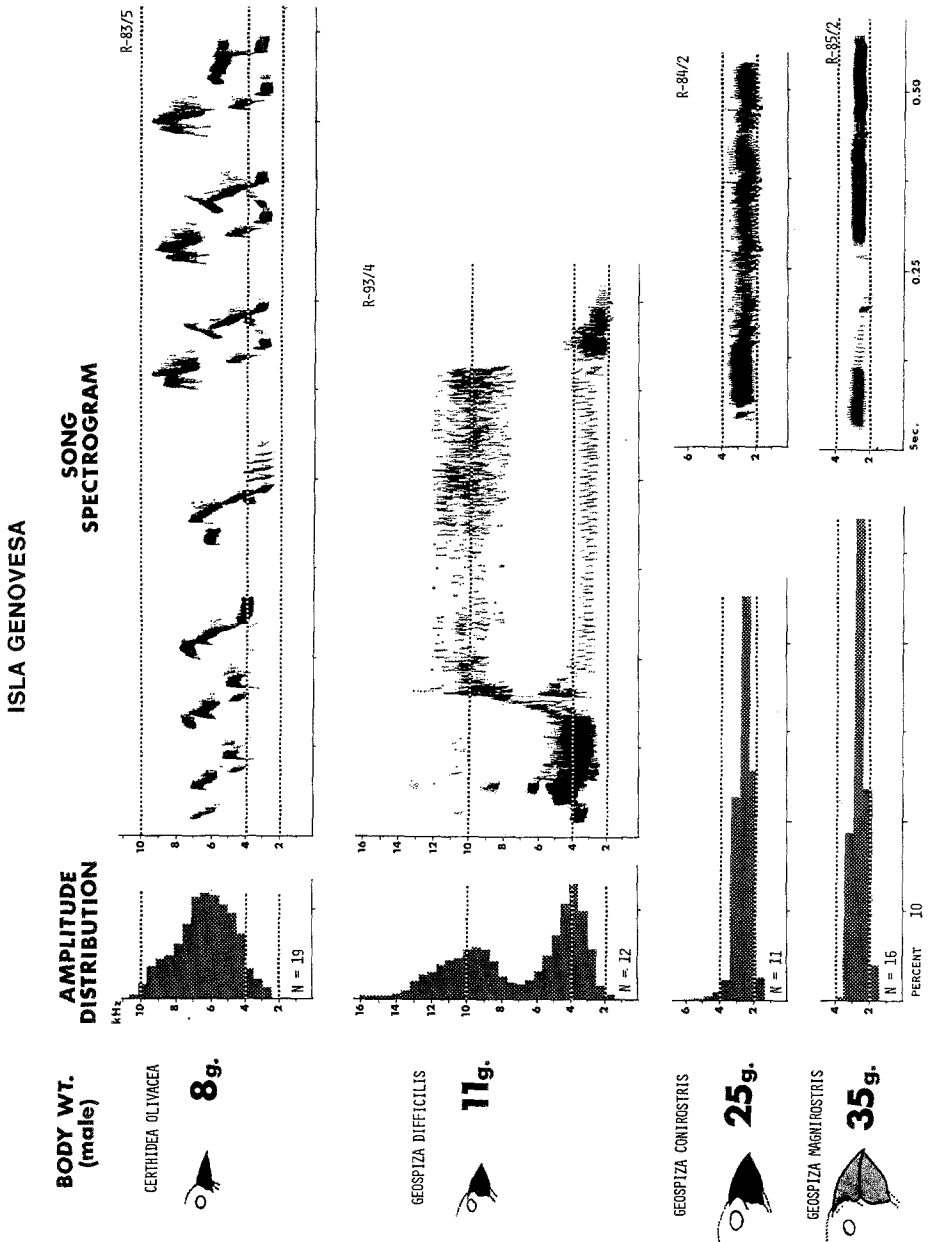
Fig. 11. Comparison of song spectrograms, song amplitude distributions, and body sizes of four species of Darwin's finches from Isla Genovesa, Galápagos. Body weight data courtesy of P. R. GRANT.
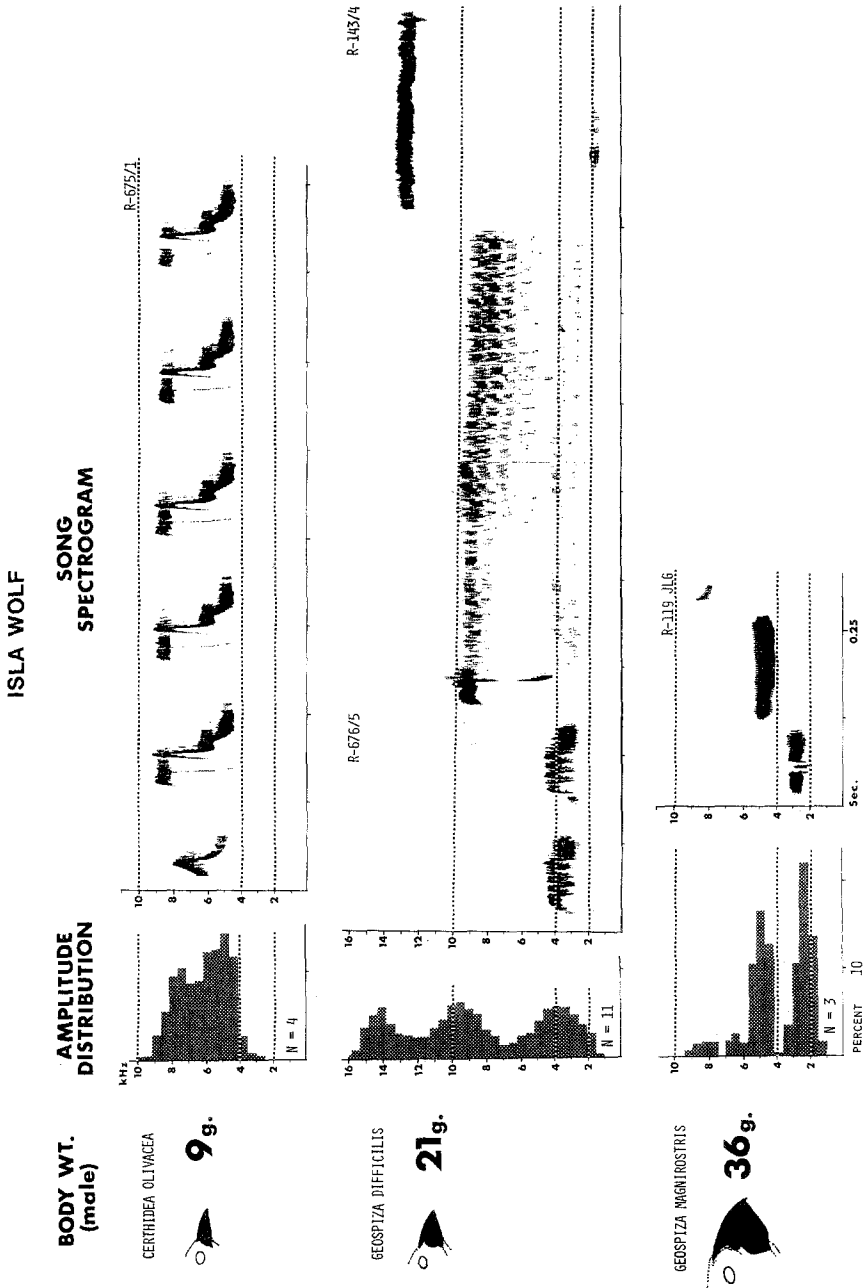
R. I. BOWMAN

Fig. 12. Comparison of song spectrograms, song amplitude distributions, and body sizes of three species of Darwin's finches from Isla Wolf. Body weight data courtesy of P. R. GRANT.

on Wolf make it necessary to draw conclusions cautiously, it does appear that there is a significant amplitude shift into higher frequencies in the songs of all Wolf species of Darwin's finches.

If we average song amplitude distributions of all finch species for an island, we obtain histograms as shown in fig. 13. With reference to these we can better see how the average energy spectra of the songs differ on islas Genovesa and Wolf, and how this difference is related to the patterns of sound transmission. On Genovesa the total song energy distribution, though broad, is rather narrowly concentrated in the 2.5 kHz mode, whereas on Wolf the equally broad energy distribution has an emphasis in the 2.0—2.5 kHz, the 5.0 kHz, and slightly in the 8.0 kHz regions.

In relating song amplitude distributions to sound transmission isopleths, it should be noted that the contour lines closest to the sound source on Wolf are almost vertically oriented for the first 50 feet of the transect, in the 2.5—10.0 kHz bandwidth, and are positioned very close together. (Each contour line on the isopleth borders a 3 dB change in sound pressure level). In other words, a n y f r e q u e n c y w i t h i n t h i s s o u n d s p e c t r u m (2.5—10. kHz) s h o u l d e x p e r i e n c e l i t t l e d i f f e r e n t i a l f r e q u e n c y - d e p e n d e n t l o s s o f s o u n d p r e s s u r e i n t r a v e l l i n g 50 f e e t f r o m t h e s o u n d s o u r c e. For frequencies between 2.5 and 10.0 kHz the average cumulative attenuation over this remarkably short distance is 15 dB (range is 12—17 dB). For frequencies between 1.0 and 2.0 kHz the average dB loss for the first 50 feet is 6 dB (range is 5—7 dB). So rapidly is sound attenuated by the Isla Wolf environment that at 4 kHz there is a 36 dB loss between the sound source and a point 100 feet distant! Compared with all other islands studied, the Isla Wolf environment attenuates sound most rapidly, and this is true of all frequencies between 2 and 10 kHz. An "optimum" efficiency in transmission is achieved at a narrow frequency bandwidth centered at 2.0—2.5 kHz where an 18 dB loss is experienced at 100 feet from the sound source. Despite a slightly improved transmission efficiency at this frequency and a small modal peak on the amplitude histogram of combined songs, the bulk of the song energies is concentrated in higher frequencies (Fig. 13).

The comparatively poor sound transmission that characterizes the Isla Wolf environment has shaped the vocalizations of its song-bird inhabitants so as to "free" them from the environmental constraints which, as on Isla Genovesa, have kept them from singing high frequencies. Indeed, even the large sized *G. magnirostris,* whose conspecifics on other islands of the Galápagos have songs with unimodal amplitudes at 2—3 kHz (Figs. 8 and 11), find remarkable "release" on Wolf.

Field observations indicate that Isla Wolf has a rather dense and often patchy vegetation dominated by *Opuntia* and *Cordia* shrubs (Fig. 3 e) which supports a high density population of finches, mainly of *G. difficilis.* The abundance of finches and their foods, I speculate, has encouraged relatively small territory sizes, the consequence of which is as follows.

   Territorial song, which is generally perceived as a l o n g - d i s t a n c e signal,
is operating at close range on Isla Wolf, and within an acoustical environment where
there is no selective energetic d i s a d v a n t a g e in singing songs punctuated with
high frequencies. By "invading" a higher frequency spectrum the birds may be
taking better advantage of increased information that can be used for binaural
localization, i. e. directional hearing (MARLER 1955; KONISHI 1970 b, 1973). The fact
that *G. magnirostris* sings very high-pitched sounds on Isla Wolf, despite the species'
structural disposition to sing lower modal frequencies — because of its relatively
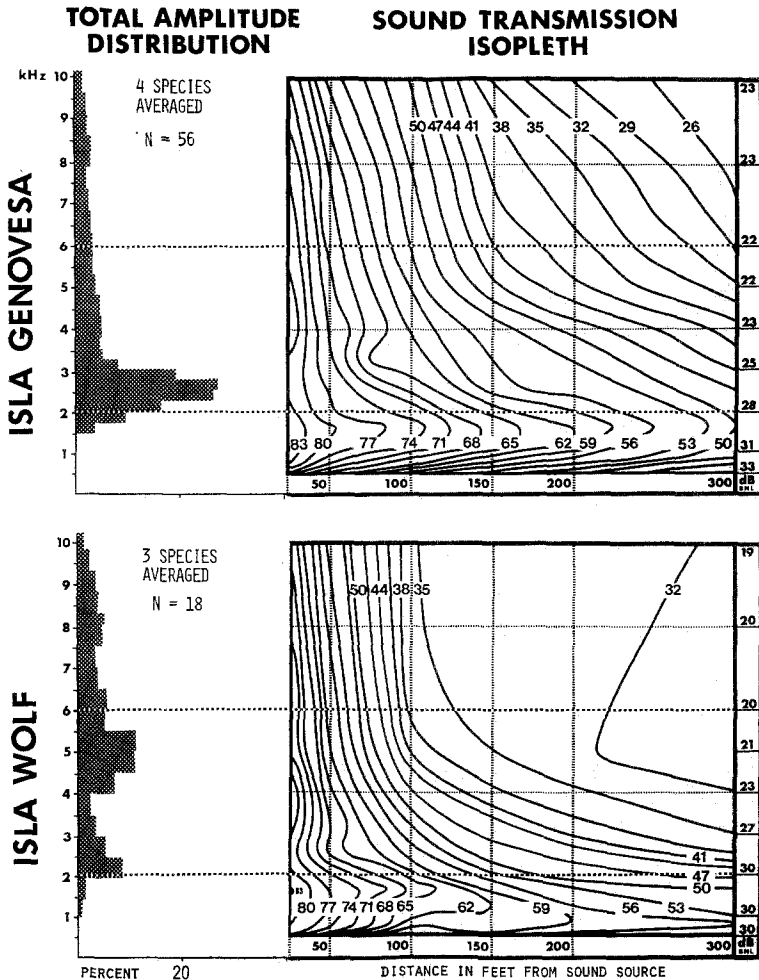
Fig. 13. Average of amplitude distributions of songs of all species of Darwin's finches on islas Genovesa
and Wolf (left), and sound transmission isopleths for the same islands (right). Background noise levels
are shown at the right-hand side of each isopleth.

large body size (Fig. 20) and internal tympaniform membrane (Fig. 21) — it may be presumed that a strong selective pressure exists favoring high frequency vocalizations. We can probably rule out any effect attributable to sound "masking" by the coastal surf or sea-bird colonies, because the background noise level is about average for Galápagos environments (see dB levels at right side of isopleths). DOOLING, MULLIGAN & MILLER (1971) have suggested that song energies are focused in frequency regions at which a bird has maximum auditory sensitivity. If we compare the average song amplitude distribution of all finch species on Isla Genovesa (Fig. 13, top) with the auditory sensitivity curves presented by DOOLING, MULLIGAN & MILLER (1971) we find unimodal coincidence near 3 kHz. The same is not true for the averaged finch songs on Isla Wolf. Because of an amplitude shift to higher frequencies (Fig. 13, bottom), one might conclude, possibly erroneously, that the Wolf birds have different hearing sensitivities than their conspecifics on nearby Isla Genovesa. Whatever advantage might be conferred on the finches through intensive use of high frequencies in their songs must surely be founded in the unusual ecological (acoustical) conditions prevailing on Wolf island.

The sound transmission isopleth for Isla Genovesa shows a general resemblance to that of Wolf (Fig. 13), primarily in the near parabolic shape of the dB contours. There are important differences, however, in such details as the less vertical orientation and more open spacing of the contour lines.

It should be noted that the graded lowering of modal amplitudes that is associated with an increase in body size in the Genovesa species (Fig. 11 and 20) may be due to the effect of "scaling" (cf. SIMKIN 1973 and BERGMANN 1976).

Although we presently lack data on territory size for the geospizines, it is here asumed that larger bodied species such as G. magnirostris and G. conirostris hold larger territories on Isla Genovesa than do the smaller bodied species such as G. difficilis and Certhidea olivacea. This notion is in agreement with the general findings of territorial studies made on continents (WELTY 1975), notwithstanding the many complicating circumstances that might alter such a relationship. In addition, if we assume that a more or less direct relationship exists between population density and territory size, then we may infer from the relative abundance data on species of Geospiza obtained by ABBOTT, ABBOTT & GRANT (1977) on Isla Genovesa, that difficilis (the smallest species of the genus) has a smaller territory size than magnirostris (the largest species), with conirostris (the medium-sized species) having a territory somewhat intermediate in size between the two former species, but probably closer to that of G. magnirostris.

Defense of a l a r g e area is facilitated by the use of a long-distance vocal signal. The development of a low-frequency modal amplitude (3 kHz) and a narrow bandwith in the songs of the two larger species of Genovesa finches, has promoted a highly adapted advertising signal that is capable of exploiting the most energy efficient transmission channel in the environment (cf. Fig. 11 and 13). The second smallest species on Genovesa, G. difficilis, shows a bimodal amplitude distribution in its song

and a significantly wider bandwith that is broadly spread in the higher frequencies,
insignificantly "occupied" by the songs of the larger species. The greater relative
abundance and presumed smaller territory sizes in G. *difficilis* and *Certhidea oliva-
cea,* have lessened the "need" for a far-flung vocal signal, and may have encouraged
the use of higher frequencies whose energies, when compared with those of lower
frequencies, are not disproportionately squandered by the environment or made
functionally ineffective within the shorter communication distances that are likely
to be involved. It may be in error to always equate operationally "territorial song"
to "long-distance signal". In general, smaller sized and more abundant spleies of song
birds in possession of smaller territories probably produce lower amplitude songs,
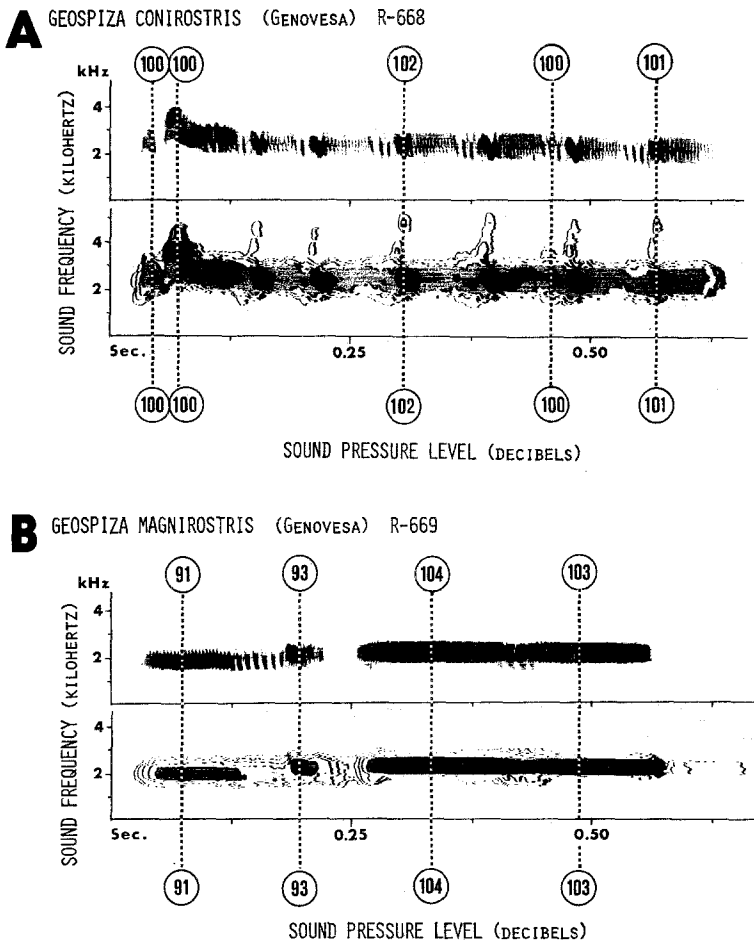
Fig. 14. Advertising songs of *Geospiza conirostris* (A) and *Geospiza magnirostris* (B) from Isla Genovesa,
showing average decibel levels at several points in time. Wide-band display above and amplitude
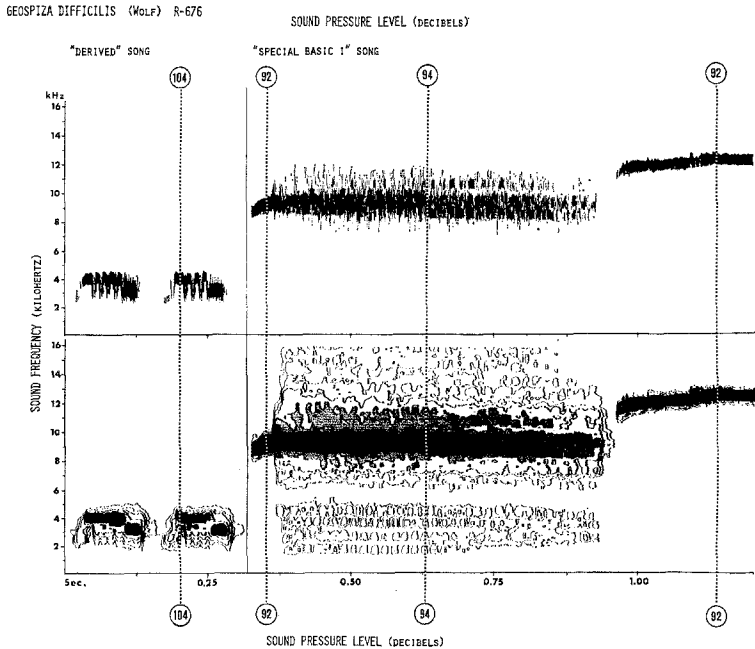contour display below.

GEOSPIZA DIFFICILIS (Genovesa) R-668
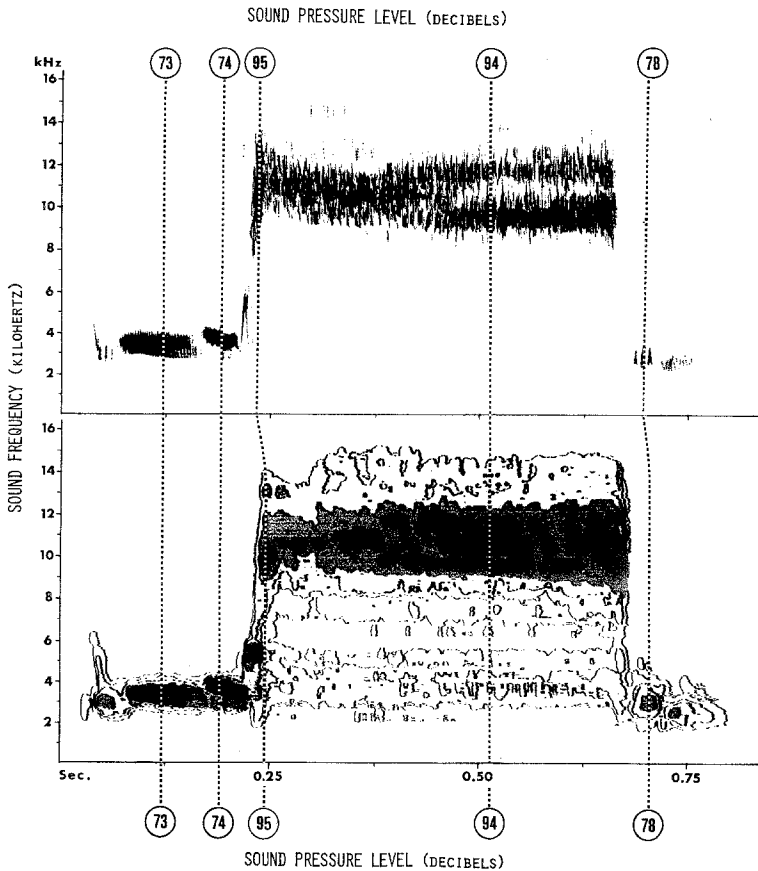
Fig. 15. Advertising song of *Geospiza difficilis* from Isla Genovesa, showing average decibel levels at several points in time. Wide-band display above and amplitude contour display below.

spread over a wider frequency spectrum, than is the case with larger sized and less abundant species of song birds. This results in a reduction of effective transmission distance of the songs, which, nevertheless, meets the requirements necessary, among other things, for territory maintenance and mate attraction (cf. HEUWINKEL 1978).

Data on sound pressure levels of territorial songs of free-living Darwin's finches are available for islas Genovesa and Wolf (Table 3 and Figs. 14—17), which indicate that larger sized species have somewhat more powerful songs than do smaller sized species. For example, on Isla Genovesa the two larger species, *G. magnirostris* and *conirostris*, have song intensities ranging from 91 to 104 dB and from 100 to 102 dB, respectively, whereas the two smaller species, *G. difficilis* and *Certhidea olivacea* have ranges from 73 to 95 dB and from 84 to 99 dB, respectively. If we examine

R. I. Bowman

Table 3. Sound pressure levels of advertising songs of four species of Darwin's finches.

Species	Island	Mean body weight g	No. of songs	Mean dB level by song region*					Song Spectrogram
				1	2	3	4	5	
Geospiza magnirostris	Genovesa	35	4	91	93	104	103	—	Fig. 14
Geospiza conirostris	Genovesa	25	4	100	100	102	100	101	Fig. 14
Geospiza difficilis	Genovesa	11	6	73	74	95	94	78	Fig. 15
Geospiza difficilis	Wolf	21	1	104	92	94	92	—	Fig. 16
Certhidea olivacea	Genovesa	8	2	82	93	91	97	—	Fig. 17 c

* Regions refer to points in time along the song, as shown in Figs. 14—17 c. Decibel values are adjusted so as to represent sound pressure levels at approximately one inch from the bill of the bird. See text for details.

Fig. 16. Advertising song of *Geospiza difficilis* from Isla Wolf, showing average decibel levels at several points in time, "Derived" song, left; "special basic" song, right (see BOWMAN, 1980 for and explanation of song-type designations). Wide-band display above and amplitude contour display below.

only the song regions with the highest dB values. (Fig. 18) it is fairly obvious that the larger-sized species inject more energy into their songs than do the smaller-sized species.

A picture emerges of the relationship between decibel level and modal frequency of song, on the one hand, and relative body size and abundance on the other (see Fig. 19; cf. JILKA & LEISLER 1974).

4. Intra-populational variation in song of *Camarhynchus parvulus*

On the south-facing slope of Isla Santa Cruz, the parid-like tree-finch, *Camarhynchus parvulus,* breeds from the coastal cactus plains up through the fog-drip *Scalesia* forest at an elevation of about 200 m (see Fig. 3 a, b and BOWMAN 1963). Although the birds exhibit no obvious morphological differentiation throughout this range, their galaxy of songs shows a "clinal" shift along a lowland-highland vegetation transect. Songs heard in the arid coastal zone are structurally somewhat more diverse than those heard in the highland zone (Fig. 22). Whereas the *Scalesia* forest highlands are "home" for basically one form of song, namely type "B," the lowlands play host to many song forms whose extreme is type
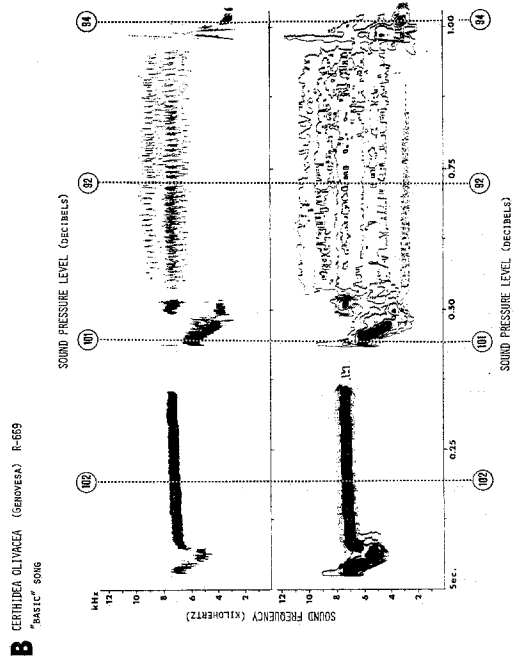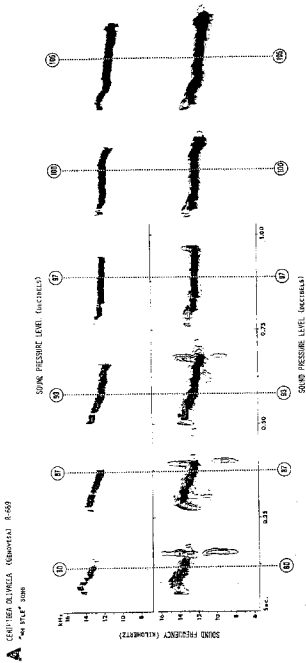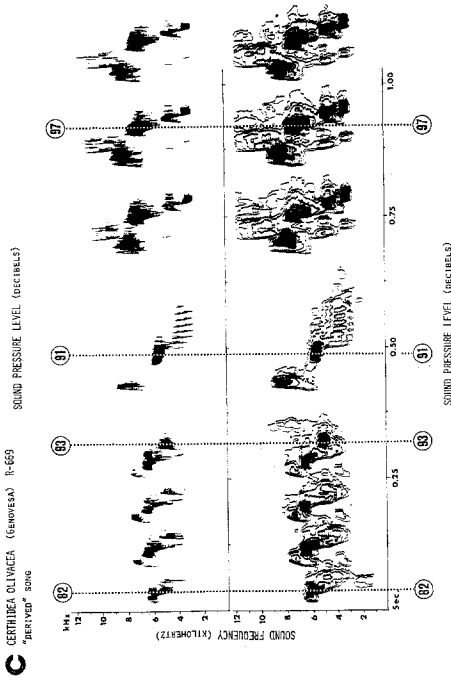
Fig. 17. Three songs of *Certhidea olivacea* from Island Genovesa, showing average decibel levels at several points in time. A, "whistle" song; B, "basic" song; and C, "derived" song (see BOWMAN 1980 for explanation of song type designations). Wide-band display above and amplitude contour display below.
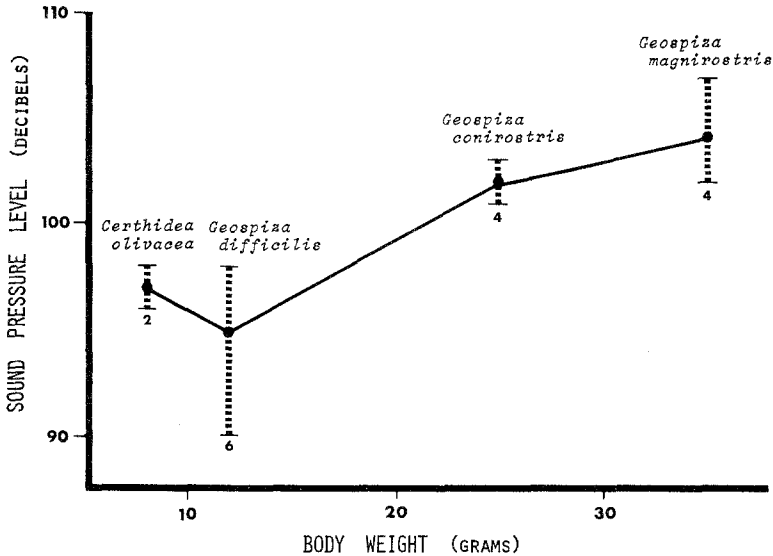
Fig. 18. Decibel values for the "loudest" region of the songs of four species of Darwin's finches on Isla Genovesa arranged according to body weight. Solid line connects mean values and the broken vertical lines indicate ranges of variation in dB levels, with the number of songs analyzed shown at the lower end of each line. Compare with Table 3 and Figs. 14—17.

"A." The difference is striking. Coastal song types are reminiscent of certain vocalizations of *Parus inornatus* (see BOWMAN 1980), *Junco oreganus* and *Spizella passerina* of western North America, whereas the highlands song shows some acoustical resemblance to the territorial "chick-a-dee" utterances of *Parus atricapillus*
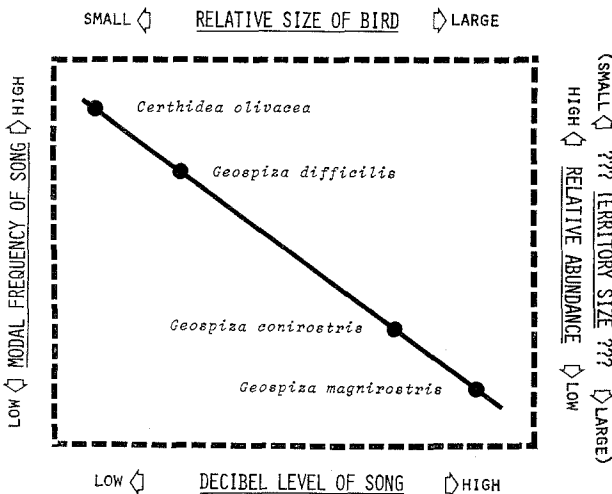
Fig. 19. Scheme showing the relationship between frequency and decibel level of song, and relative size of bird and abundance, as it pertains to the four sympatric species of Darwin's finches on Isla Genovesa.
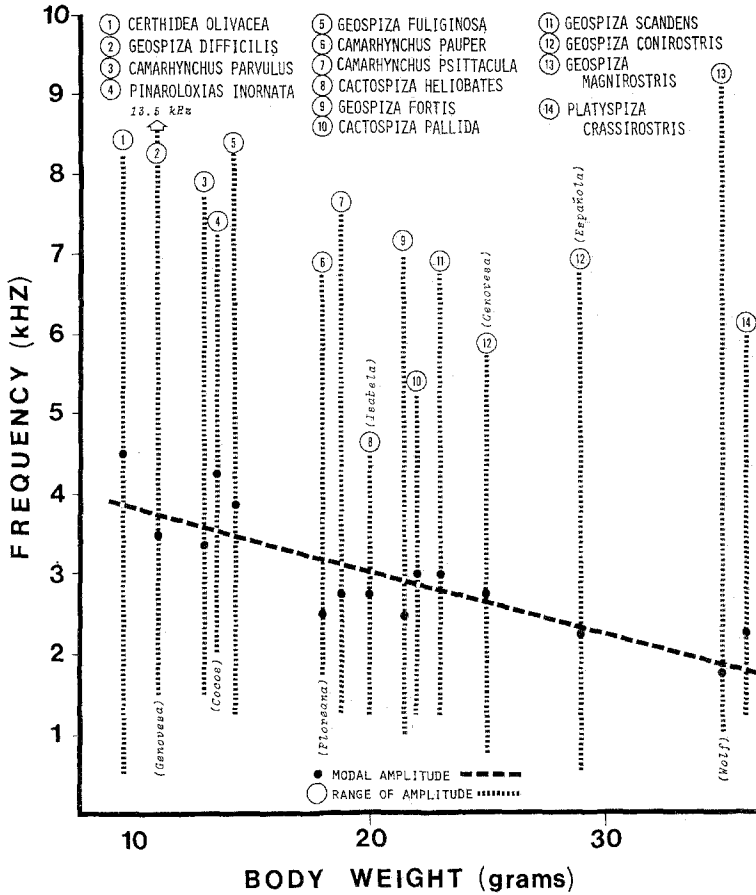
Fig. 20: Relationship between modal amplitude of song to frequency spread and mean body weight for 14 species of Darwin's finches. Data on males only are from Isla Santa Cruz, except as indicated.

and *P. inornatus*, also of North America. This writer has never heard an "A" type song in the *Scalesia* forest, but the "B" type song is sometimes heard in the lowlands.

In order to explain this rather unusual song distribution (one which could change with continued destruction of the *Scalesia* forest for purposes of agriculture), let us compare amplitude distributions for highland and lowland songs with their respective sound transmission isopleths. To facilitate the analysis, and to better appreciate the adaptive significance of the song type distributions, I have superimposed two black vertical bar, labelled "A" and "B," of different length and cross-hatching, on the lowland and highland isopleths at points 100 ft. and 125 ft., respectively, distant from the sound source. The bar height corresponds approximately to the frequency spread

of the song type. The coastal type "A" song is high-pitched to the human ear and has a very broad frequency spread (2.5—7.0 kHz) and a total bandwith of 4.5 kHz. The highland type song "B" has a comparatively narrow frequency spread (2.5— 4.0 kHz) and a total bandwith of 1.5 kHz, and consequently sounds lower-pitched. In Panamá, MORTON (1970) noted a similar difference in pitch between the songs of birds living in "tropical" forests and those living in more open habitats (e. g. grass-lands).

Song type "B" travels with minimal distortion for hundreds of feet in the coastal zone, largely because of the narrow bandwidth, which allows this signal to "fit" into the 2.5—4.0 kHz transmission channel where the contour lines of the coastal zone isopleth (Fig. 22) proceed like square-ended wave-fronts through the thorn-scrub cactus forest (Fig. 3 a). Sound pressure levels of high and low frequencies decrease uniformly over the entire bandwidth and the transmission field illustrated (see Table 4, Line 3, Column F). Clearly, this vocal signal is well adapted for long-range communication in the coastal zone of Isla Santa Cruz. The same can be said about song type "B" in the *Scalesia* forest zone, except that here the overall rate of attenuation is somewhat greater in the first 150 feet from the sound source, as
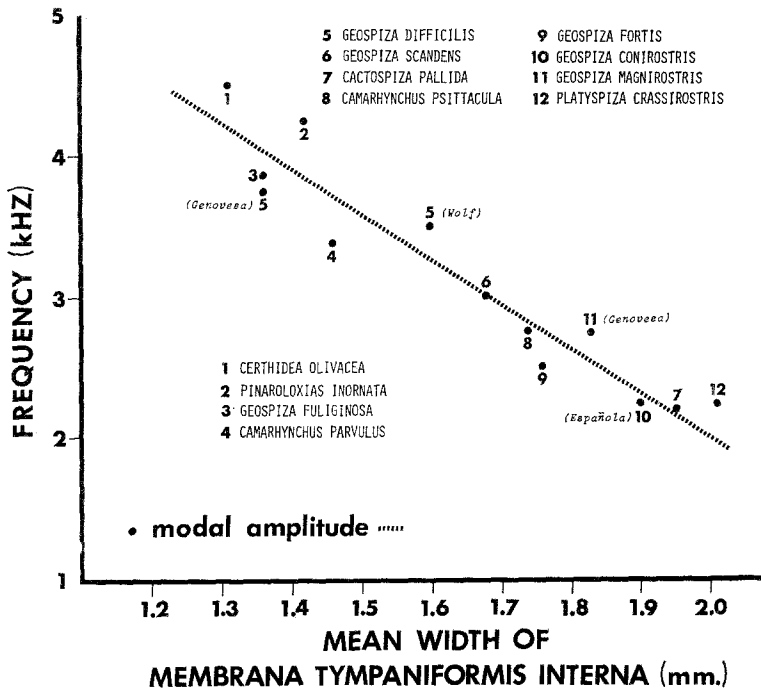
Fig. 21. Relationship of modal amplitude of song to frequency and man width of the Membrana tympaniformis interna in 12 species of Darwin's finches. Data on males only are from Isla Santa Cruz, except as indicated. Membrane data are from males in singing condition (CUTLER 1970).

Table 4. Comparison of "intensity" differences between high and low frequencies in song types "A" and "B" of *Camarhynchus parvulus* in the coastal and *Scalesia* forest zones of Isla Santa Cruz.

Column	A	B	C	D				E				F			
Line	Song Environment	Song Frequency Class	Maximum Frequency Range (Hz)	Absolute Intensity (dB) of HI and LO Frequencies at Distances from the Sound Source of				Cumulative dB loss at HI and LO Frequencies at Distances from the Sound Source of				Difference in Absolute Intensity (dB) between HI and LO Frequencies (Column D) at Distances from Sound Source of			
				50'	100'	200'	300'	50'	100'	200'	300'	50'	100'	200'	300'
1.	Song "A" in coastal zone environment*	HI LO	7 000 2 500	74 75	65 67	49 54	40 46	11 8	20 16	36 29	44 27	1	2	5	6
2.	Song "A" in *Scalesia* forest environment	HI LO	7 000 2 500	74 74	50 63	40 46	[31]** 38	8 9	32 20	42 37	51 45	0	13	6	7
3.	Song "B" in coastal zone environment	HI LO	4 000 2 500	78 75	69 67	54 54	45 46	1 8	10 16	25 29	34 37	3	2	0	1
4.	Song "B" in *Scalesia* forest environment	HI LO	4 000 2 500	73 74	59 63	43 46	[34] 38	10 9	24 20	40 37	49 45	1	4	3	4

* See Fig. 22 for sound spectrograms of song types and sound transmission isopleths for coastal and *Scalesia* forest zones.

** Brackets around an intensity value indicate a level of 10 dB or less above background noise level and, presuably, close to the auditory threshold.

evidenced by the more closely positioned and vertically oriented contour lines (Fig. 22). With increasing distance, the type "B" sound channel in the highlands becomes ever so slightly less efficient than in the coastal zone. Because the dB loss rate for the type "B" song frequencies is higher in the *Scalesia* forest zone than in the coastal zone (compare cumulative dB loss figure in Table 3, Lines 3 and 4, Column E), the intensity of the song, at least in the higher frequencies, is reduced to a level that is only slightly above that of the background noise at a distance between 200 and 300 feet from the sound source (Table 4, Line 4, Column D), even though the highest frequencies of song type "B" are comparatively low when compared to those of song type "A." At this distance we must assume that the signal loses intelligibility and is soon lost totally in the environment. These findings suggest the possibility that *Camarhynchus parvulus* may have slightly smaller territory size in the moister resource-richer *Scalesia* forest zone than in the drier coastal zone.
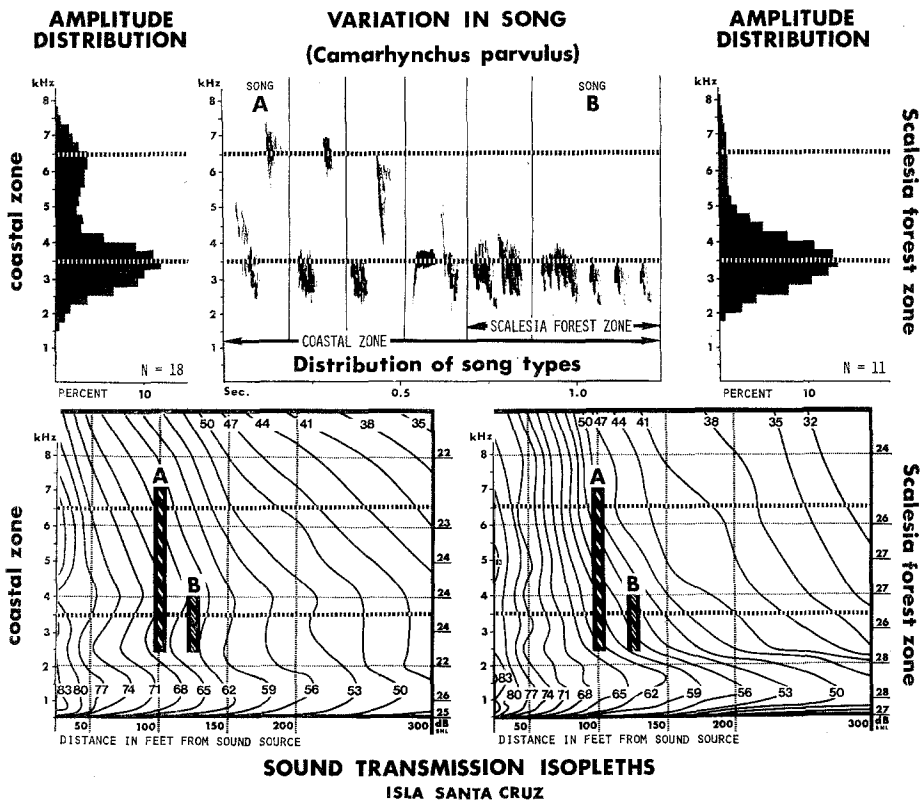
Fig. 22. Examples of song types of *Camarhynchus parvulus* recorded on the south-facing slope of Isla Santa Cruz (above), showing histograms of amplitude distribution of populations in the coastal zone (left) and *Scalesia* forest zone (right). Vertical bars on isopleths (below) represent song types "A" and "B". See text for explanation.

Song type "A" has a strong emphasis on the higher frequencies (see Fig. 22), which decay at a slightly higher rate than the lower frequencies, resulting in an ever increasing disparity between the two from 1 dB to 6 dB at 50 and 300 feet, respectively, from the sound source (see Table 4, Line 1, Column F).

Thus the wideband "A" type song seems to be almost as well adapted as the narrowband "B" type song to the first 100 feet of the coastal transmission environment of Isla Santa Cruz, but with the "B" type song, and its predominantly lower frequencies, slightly more efficient at greater distances (up to 300 feet). See Table 4, Lines 1 and 3, Column F.

The fact that the "A" type song of *Camarhynchus parvulus* is one of the most common forms to be heard in the outer coast zone of Isla Santa Cruz suggests that whatever slight disadvantage this broadband signal might have at 200—300 ft. distances is probably offset by whatever benefits accrue through the use of high frequencies in long-distance vocal communication.

If type "A" song were sung in the highlands of Isla Santa Cruz it would surely be non-adaptive beyond the 50—100 ft. range because of a serious frequency dependent amplitude disparity in transmission rates (i. e. 13 dB) that sets in and causes early disruption of the information content of the song (see Table 4, Line 2, Column F).

Conclusions

In view of the numerous inter- and intra-island differences (and similarities) in the patterns of sound transmission in Galápagos environments, it was probably inevitable that highly variable patterns of song should have developed in the finches through the process of natural selection. Song patterns permit the birds to adapt to and exploit the many different and often overlapping sound niches that accompany the overlapping feeding niches. In Darwin's finches the occurrence of song dialects may reasonably be interpreted as local adaptions to specific acoustical conditions of the environment (cf. Thielcke 1969). Mutual occupancy and exploitation of Galápagos environments for species maintenance and reproduction has fostered parallel ecological adjustments in the advertising songs of the finches. These adjustments take the form of modifications of the communication signal that tend to minimize transmisson loss by matching song structures with specific sound propagation characteristics of the environment. Genetic differentiation of populations has probably been facilitated by energy economizing adaptions of song to specific environments, thereby tending to promote and maintain philopatry.

Summary

1. This study describes the structure and functional significance of numerous song dialects in island populations of Darwin's finches from the Galápagos Archipelago.

2. The following acoustical information was obtained from tape recordings made in the islands:

a. For songs: Frequency bandwidth, relative amplitude distribution according to frequency, and absolute sound pressure levels (dB).

b. For the environment: Attenuation characteristics of a broadband frequency spectrum ("pink" noise) broadcast into various vegetations.

Song data are displayed graphically as frequency/amplitude histograms, and pink noise attenuation as sound transmission isopleths.

3. A comparison of modal amplitudes of song frequency spectra with mean dimensions of the vibratory (internal tympaniform) membrane of the syrinx and mean body weights, indicates that larger bodied species of Darwin's finches sing songs with peak energy at a lower frequency than do smaller bodied species.

4. A scheme is proposed that relates modal amplitude distributions and sound pressure levels of song to body size and relative abundance of species. This four-way comparison, when applied to four sympatric species of Darwin's finches on Isla Genovesa, shows that smaller species, singing songs with higher "pitched" modal amplitudes, tend to have lower sound pressure levels and occur in greater relative abundance (and possibly defend smaller territories) than larger species.

5. Song dialects of *Geospiza conirostris* on islas Genovesa and Española are described and a correlation is made between the song bandwidth and the sound transmission peculiarities of their respective environments. The bandwidth is regulated by the sound attenuation characteristics of the vegetation so as to forestall the development of a frequency dependent disparity in sound pressure levels between highest and lowest song components that might be damaging to the integrity (information content) of the signal, long before it has travelled an effective communicating distance through the environment.

6. The Wolf Island environment is acoustically unique among those studied thus far in the Galápagos Archipelago because of the unusually high sound attenuation associated with the very dense vegetation. The latter causes a minimal disparity in rates of sound attenuation over unusually broad frequency spectra encompassed by the songs. The relatively high availability of foods has fostered a high population density of finches whose individual territories, when adjusted to differences in body size with conspecifics elsewhere, are, presumably, comparatively small and rendered acoustically compatable with the breeding ecology of the finches.

7. An ecoclinal shift in the song galaxy of *Camarhynchus parvulus* on the south side of Isla Santa Cruz is correlated with altitudinal differences in vegetation affecting sound transmission. The narrowband song most commonly heard in the humid highlands forest is less susceptable to frequency dependent disparity in sound transmission rates than would be the case with the wideband song of the lowlands, were it sung in the discordant highlands environment. There would appear to be little if any differential advantage of wideband song over narrowband song where they occur together in the lowlands environment of Isla Santa Cruz.

8. Several cases of parallel development of song structure by sympatric species of Darwin's finches may be due to selection favoring similar vocal responses to acoustically similar "sound niches".

Zusammenfassung

Anpassungsmorphologie in Gesangsdialekten bei Darwinfinken

1. Die Arbeit beschreibt die Struktur und funktionelle Bedeutung zahlreicher Gesangs-dialekte der Inselpopulationen bei Darwinfinken auf den Galapagos Inseln.

2. Folgende akustische Information wurde durch Tonbandaufnahmen im Freiland ermittelt:

a) Bandbreite der Frequenz, der Frequenz entsprechende Schallintensität, absoluter Schalldruckpegel (dB) der Gesänge.

b) Dämpfungscharakteristik des in verschiedenen Vegetationen gesendeten Breitbandspektrums eines Tongenerators.

Die Gesangsdaten sind graphisch als Frequenz/Schallintensität-Histogramme dargestellt und die Signal-Dämpfung als Isoplethen der Schallübertragung.

3. Ein Vergleich der Schallintensität der Gesangsfrequenzspektra mit Durchschnittsgrößen der Membrana tympaniformis interna in der Syrinx und mit durchschnittlichen Körpergewichten zeigt, daß größere Arten Gesänge besitzen mit der Höchstenergie in niederer Frequenz als kleinere Arten.

4. Ein Schema wird vorgeschlagen, welches Modalamplitudenverteilung und Schalldruckpegel der Gesänge mit Körpergröße und relativer Häufigkeit der Arten vergleicht. Dieser vierseitige Vergleich angewendet auf die vier zusammenlebenden Arten der Darwinfinken auf der Insel Genovesa zeigt, daß kleinere Arten, die mit Modalamplituden höherer Frequenz singen, zu niedrigerem Schalldruckpegel und zu höherer Abundanz neigen (möglicherweise auch kleinere Territorien verteidigen) als größere Arten.

5. Gesangsdialekte von *Geospiza conirostris* auf den Inseln Genovesa und Española werden beschrieben; das Verhältnis zwischen Bandbreite des Gesanges und Eigenheiten der Schallübertragung ihrer jeweiligen Umgebung ist dargestellt. Die Bandbreite wird durch die von der Vegetation verursachte Dämpfungscharakteristik der Schallübertragung reguliert, um von der Frequenz abhängige Ungleichheit des Schalldruckpegels zwischen höchsten und niedrigsten Gesangsteilen zu vermeiden, der den Informationsinhalt des Signals, lange ehe es eine effektive Kommunikationsentfernung erreicht hat, beschädigen könnte.

6. Der Biotop der Insel Wolf ist akustisch einzigartig unter den bisher untersuchten Inseln im Galapagos Archipel; er weist nämlich eine von der sehr dichten Vegetation abhängige ungewöhnlich hohe Schalldämpfung auf. Die Vegetation verursacht eine minimale Ungleichheit der Schalldämpfung über das ungewöhnlich breite Frequenzspektrum der Gesänge. Die relativ reichlich vorhandene Nahrung fördert eine hohe Siedlungsdichte der Finken. Ihre Territorien bezogen auf die Körpergröße verglichen mit Artgenossen auf anderen Inseln sind wahrscheinlich verhältnismäßig klein und akustisch der Brutökologie der Finken angepaßt.

7. Eine ökologische Verschiebung der Gesangscharakteristik von *Camarhynchus parvulus* im S der Insel Santa Cruz ist korreliert mit Höhenunterschieden in der Vegetation, die die Schallübertragung beeinflußt. Gesänge mit enger Bandbreite, die man gewöhnlich in den feuchten Höhenwäldern hört, sind weniger empfindlich gegen von Frequenz abhängige Ungleichheiten der Schallübertragung als die Breitbandgesänge des Tieflandes, wenn sie in der nicht passenden Hochlandumgebung gesungen würden. Ein möglicher kleiner Vorteil von Breitbandgesängen gegenüber Schmalbandgesängen spielt scheinbar keine Rolle in der Tieflandumgebung von Santa Cruz, wo beide Typen zusammen vorkommen.

8. Mehrere Fälle paralleler Entwicklung von Gesangstrukturen zusammenlebender Arten der Darwinfinken könnten durch Selektion verursacht worden sein, die ähnliche Stimmreaktionen in akustisch ähnlichen „Gesangsnischen" begünstigt.

Acknowledgements

Literature

ABBOTT, I., L. K. ABBOTT & P. R. GRANT (1977): Comparative ecology of Galápagos ground finches (*Geospiza* Gould): evaluation of the importance of floristic diversity and inter-specific competition. Ecol. Monogr. 47: 151—184. • BAPTISTA, L. F. (1975): Song dialects and demes in sedentary populations of the white-crowned sparrow (*Zonotrichia leucophrys nuttalli*). Univ. Calif. Publ. Zool. 105: 1—52. • BEEBE, W. (1924): Galapagos: world's end. G. P. Putnam's Sons, New York. • Ditto (1926): The Arcturus adventure. G. P. Putnam's Sons, New York. • BERGMANN, H.-H. (1976): Konstitutionsbedingte Merkmale in Gesängen und Rufen europäischer Grasmücken (Gattung: *Sylvia*). Z. Tierpsychol. 42: 315—329. • BILLEB, S. L. (1968): Song variation in three island populations of Galápagos warbler finch (*Certhidea olivacea* Gould). M. A. thesis, San Francisco State University. • BROWN, W. L. & E. O. WILSON (1956): Character displacement. Syst. Zool. 5: 49—64. • BOWMAN, R. I. (1961): Morphological differentiation and adaptation in the Galápagos finches. Univ. Calif. Publ. Zool. 58: 1—302. • Ditto (1963): Evolutionary patterns in Darwin's finches. Occas. Papers Calif. Acad. Sci. 44: 107—140. • Ditto (1980): The evolution of song in Darwin's finches. In BOWMAN, R. I. & A. E. LEVITON (Eds.): Patterns of evolution in Galápagos organism. Amer. Assoc. Adv. Sci. Pac. Div., San Francisco. • CHAPMAN, F. M. (1940): The post-glacial history of *Zonotrichia capensis*. Bull. Amer. Mus. Nat. Hist. 77: 381—438. • CHAPPUIS, C. (1971): Un example de l'influence du milieu sur les emission vocales des oiseaux: l'evolution des chants en foret equatoriale. Terre et Vie 25: 183—202. • CODY, M. L. (1969): Convergent characteristics in sympatric species: a possible relation to interspecific competition and aggression. Condor 71: 222—239. • Ditto (1973): Character displacement. Ann. Rev. Syst. Ecol. 4: 189—201. • Ditto (1974): Competition and the structure of bird communities. Princeton Univ. Press, Princeton. • Ditto & J. H. BROWN (1970): Character convergence in Mexican finches. Evolution 24: 304—310. • CURIO, E. & P. KRAMER (1965): *Geospiza conirostris* auf Abingdon und Wenman entdeckt. J. Orn. 106: 355—357. • CUTLER, B. D. (1970): Anatomical studies on the syrinx of Darwin's finches. M. A. thesis, San Francisco State University. • DOOLING, R. J., J. A. MULLIGAN & J. D. MILLER (1971): Auditory sensitivity and song spectrum on the common canary (*Serinus canarius*). J. Acoust. Soc. Amer. 50: 700—709. • GIFFORD, W. E. (1919): Field notes on the land birds of the Galápagos Islands and of Cocos Island, Costa Rica. Proc. Calif. Acad. Sci. 2: 189—258. • GRANT, P. R. (1966): The coexistence of two wren species of the genus *Thryothorus*. Wilson Bull. 78: 266—278. • GREENEWALT, C. H. (1968): Bird song: acoustics and physiology. Smithsonian Institution Press, Washington, D. C. • GRIMES, L. G. (1974): Dialects and geographical variation in the song of the splendid sunbird *Nectarinia coccinigaster*. Ibis 116: 314—329. • GULLEDGE, J. L. (1970): An analysis of song in the mockingbird genera *Nesomimus* and *Mimus*. M. A. thesis, San Francisco State University. • HARRIS, M. A. & R. R. LEMON (1972): Songs of song sparrows (*Melospiza melodia*); individual variation and dialects. Can. J. Zool. 50: 301—309. • HEUWINKEL, H. (1978): Der Gesang des Teichrohrsängers (*Acrocephalus scirpaceus*) unter besonderer Berücksichtigung der Schalldruckpegel ("Lautstärke"-) Verhält-nisse. J. Orn. 119: 450—461. • HOPE, S. (1976): Determinants of form in vocalizations of the Steller's jay. M. A. thesis, San Francisco State University. • INGÅRD, U. (1953): A review of the influence of meteorological conditions on sound propagation. J. Acoust. Soc. Amer. 25: 405—411. • JILKA, A. & B. LEISLER (1974): Die Einpassung dreier Rohrsängerarten (*Acrocephalus schoenobaenus, A. scirpaceus, A. arundinaceus*) in ihre Lebensräume in bezug auf das Frequenzspektrum ihrer Reviergesänge. J. Orn. 115: 192—212. • JO, N. (1979): Karyotypic analysis of Darwin's finches. In BOWMAN, R. I. & A. E. LEVITON (Eds.): Patterns of evolution in Galápagos organisms. Amer. Assoc. Adv. Sci. Pac. Div., San Francisco. • KING, J. R. (1972): Variation in the song of the rufous-collared sparrow, *Zonotrichia capensis*, in north-western Argentina. Z. Tierpsychol. 25: 155—169. • KONISHI, M. (1970 a): Comparative neuro-physiological studies of hearing and vocalizations in songbirds. Z. vergl. Physiol. 66: 257—272. • Ditto (1970 b): Evolution of design features in the coding of species-specificity. Amer. Zool. 10: 67—72. • Ditto (1973): Locatable and nonlocatable acoustic signals for

barn owls. Amer. Nat. 107: 775—785. • LACK, D. (1945): The Galápagos finches (Geospizinae): a study in variation. Occas. Papers Calif. Acad. Sci. 21: 1—152. • Ditto & H. N. SOUTHERN (1949): Birds of Tenerife. Ibis 91: 607—626. • LANYON, W. E. (1967): Revision and probable evolution of the *Myiarchus* flycatchers of the West Indies. Bull. Am. Mus. Nat. Hist. 136: 329—370. • Ditto (1978): Revision of the *Myiarchus* flycatchers of South America. Bull. Amer. Mus. Nat. Hist. 161: 427—628. • LEMON, R. E. (1971): Differentiation of song dialects in cardinals. Ibis 113: 373—377. • Ditto (1975): How birds develop song dialects. Condor 77: 385—406. • MARLER, P. (1955): Characteristics of some animal calls. Nature 176: 6—8. • Ditto (1960): Bird song and mate selection. In LANYON, W. E. & W. N. TAVOLGA (Eds.): Animal sounds and Communication. Amer. Inst. Biol. Sci. Publ. 7: 348—367. • Ditto (1970): A comparative approach to vocal learning. J. Comp. Physiol. Psychol. Monogr. 71: 1—25. • MARLER, P. & D. J. BOATMAN (1951): Observations on the birds of Pico, Azores. Ibis 93: 90—9. • Ditto & M. TAMURA (1962): Song "dialects" in three populations of white-crowned sparrows. Condor 64: 367—377. • MARTEN, K. & P. MARLER (1977): Sound transmission and its significance for animal vocalization. I. Temperate habitats. Behav. Ecol. Sociobiol. 2: 271—290. • Ditto, D. QUINE & P. MARLER (1977): Sound transmission and its significance for animal vocalization. II. Tropical forest habitats. Behav. Ecol. Sociobiol. 2: 291—302. • MAYR, E. (1942): Systematics and the origin of species. Columbia Univ. Press, New York. • MIRKSY, E. N. (1976): Song divergence in humingbird and junco populations on Guadalupe Island. Condor 78: 230—235. • MORTON, E. S. (1975): Ecological sources of selection on avian sounds. Amer. Nat. 109: 17—34. • NOTTEBOHM, F. (1972): The origin of vocal learning. Amer. Nat. 106: 116—140. • Ditto (1975): Continental patterns of song variability in *Zonotrichia capensis:* some possible ecological correlates. Amer. Nat. 109: 605—624. • OREJUELA, J. E. & M. L. MORTON (1975): Song dialects in several populations of mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*) in the Sierra Nevada. Condor 77: 145—153. • PETERSON, A. P. G. & E. E. GROSS (1972): Handbook of noise measurement, 7th edition. General Radio Company, Concord, Mass. • POLANS, N. O. (1980): Enzyme polymorphisms in Galápagos finches. In BOWMAN, R. I. & A. E. LEVITON (Eds.): Patterns of evolution in Galápagos organism. Amer. Assoc. Adv. Sci. Pac. Div., San Francisco. • ROTHSCHILD, W. & E. HARTERT (1899): A review of the ornithology of the Galapagos Islands. With notes on the Webster-Harris expedition. Novit. Zool. 6: 85—205. • Ditto (1902): Further notes on the fauna of the Galapagos Islands. Novit. Zool. 9: 373—418. • SIMKIN, G. (1973): Z. Zhurn. 52: 1261—1263. • SNODGRASS, R. E. & E. HELLER (1904): Papers from the Hopkins-Stanford Galapagos expedition, 1898—1899. XVI. Birds. Proc. Wash. Acad. Sci. 5: 231—372. • THIELCKE, G. (1965): Gesangsgeographische Variation des Gartenbaumläufers (*Certhia brachydactyla*) im Hinblick auf das Artbildungsproblem. Z. Tierpsychol. 22: 542—566. • Ditto (1969): Geographic variation in bird vocalizations. In R. A. HINDE (Ed.): Bird vocalizations, 311—339. Cambridge Univ. Press, Cambridge. • WARD, W. V. (1964): The songs of the apapane. Living Bird 3: 97—117. • WELTY, J. C. (1975): The life of birds. 2nd ed. Saunders, Philadelphia. • WITKIN, S. R. (1977): The importance of directional sound radiation in avian vocalization. Condor 79: 490—493. • WILSON, G. P. (1968): Instruction book for Galápagos Islands project: acoustical measuring equipment. Wilson, Ihrig & Assoc., Oakland, California. • WOOD, A. (1947): Acoustics. Interscience Publishers, Inc., New York.

Author's address: Department of Biological Sciences, San Francisco State University, 1600 Holloway Avenue, San Francisco, California, 94132, USA.