The Auk 111(1):87-103, 1994

SONG LEARNING AS EVIDENCED FROM SONG SHARING IN TWO HUMMINGBIRD SPECIES (*COLIBRI CORUSCANS* AND *C. THALASSINUS*)

SANDRA L. L. GAUNT,[1] LUIS F. BAPTISTA,[2] JULIO E. SÁNCHEZ,[3]
AND DANIEL HERNANDEZ[3]

[1]*Borror Laboratory of Bioacoustics, Department of Zoology, 1735 Neil Ave.,*
Ohio State University, Columbus, Ohio 43210, USA;
[2]*Department of Ornithology and Mammalogy, California Academy of Sciences,*
Golden Gate Park, San Francisco, California 94118, USA; and
[3]*Colección Nacional de Ornitología, Dept. de Historia Natural,*
Museo Nacional de Costa Rica, Apdo. 749-1000, San José, Costa Rica

ABSTRACT.—We have demonstrated that male hummingbirds in the genus *Colibri* share song types. The Sparkling Violet-ear (*C. coruscans*) from an Ecuadorian population and Green Violet-ear (*C. thalassinus*) from populations in Costa Rica form aggregates or neighborhoods. Males of a neighborhood sing the same song type and those of distant neighborhoods have different song types. The resultant geographic variation in song, we suggest, is due to cultural drift acquired through song learning. Song sharing was determined not only by traditional, visual examination of spectrograms of song but with a relatively new, digital cross-correlation method that permits statistical treatment. The statistical procedures included cluster analysis that reflects the distribution of songs in geographic space and an evaluation for randomness of that distribution by use of the Mantel test. *Received 13 May 1993, accepted 30 September 1993.*

ALTHOUGH SONG LEARNING and geographic variation in song are well known in oscines (Mundinger 1982), they are less well documented in nonpasserines. Indeed, it was once thought that, whereas song is acquired by imitation in songbirds, it is developed independent of learning in nonoscines (e.g. Konishi and Nottebohm 1969). However, learning of vocalizations, not just temporal patterning of notes, is also known in parrots (Baptista 1993). Oscines, parrots and hummingbirds, but few other birds, have in common a syrinx controlled by internal as well as external muscles, and Gaunt (1983) has suggested that, because of this shared trait, hummingbirds could be capable of song learning. However, there are few detailed studies of hummingbird vocalizations (Atwood et al. 1991).

The first direct evidence that some hummingbirds learned songs came from Skutch's (1972) observation of a Blue-chested Hummingbird (*Amazilia amabilis*) singing the song of a Rufous-tailed Hummingbird (*A. tzacatl*). Other indirect evidence of song learning comes from observations of song sharing by neighboring hummingbirds. Snow (1968) and Wiley (1971) found song sharing between neighbors in the leks of the Pygmy Hermit (*Phaethornis longuemareus*) in Trinidad. Snow (1974) discovered song sharing between neighbors of the Green Hermit (*P. guy*) within a lek, different song types between leks, and geographic differences between songs of individuals from Trinidad and Costa Rica (Snow 1977). Skutch (*in* Bent 1940) also described song sharing within singing assemblies of White-eared Hummingbirds (*Hylocharis leucotis*).

Mirsky (1976) found differences in songs between Anna's Hummingbirds (*Calypte anna*) from Isla Guadalupe, Mexico and those from mainland California. Baptista and Schuchmann (1990) documented song sharing between neighbors in this species and demonstrated by experiments that songs of Anna's Hummingbirds are the result of acquisition by vocal mimicry.

Although the Sparkling Violet-ear (*Colibri coruscans*) and the Green Violet-ear (*C. thalassinus*) are locally abundant and loquacious within their respective ranges, we know of no detailed studies on variation in their songs. There are, however, many onomatopoeic descriptions for the song of *C. thalassinus* and, although such descriptive representations of sounds produced by animals are notoriously unreliable, the extreme variation in the descriptions suggests song variation for this species (e.g. from Mexico, "hiut ti titati, hitu tita," [Wagner 1945]; from Guatamala, "k' chink chink k' chinky chink"

[Skutch 1967]; Andean populations, "tusup-chip" or "tsip-chup," sometimes combined with "rrt" notes [Fjeldsa and Krabbe 1990]; Costa Rican populations, "CHEEP chut, CHEEP-chup" [Stiles and Skutch 1989]). If these represent variation, the exact nature of the variation is unknown. It may be individual variation in song with no song sharing among members of a population or, alternatively, it may be in the form of regional song dialects.

In this study we describe a general pattern of song sharing among neighbors in these two species, the Green Violet-ear and the Sparkling Violet-ear. To test the hypothesis that song sharing occurs, we examined the relationship between song similarity and geographic distance; specifically, we predicted that if proximity promotes song sharing, then the songs of neighbors should be more similar than those of nonneighbors. In addition, we predicted that song similarity should be inversely related to distance between individuals.

In order to test these predictions we digitized the songs. We then used a cross-correlation procedure that compares the digitized spectrographs and returns a quantitative measure of song similarity (Clark et al. 1987). The results take the form of a matrix of song similarity for pairwise comparisons of all birds at a location. A linkage tree describing relationships within a matrix is generated using cluster analysis. The probability that these relationships are random is evaluated by comparing song similarity matrices with matrices of distance using the Mantel test (Manly 1991).

METHODS

Study areas.—This report is based on recordings of songs of 15 *C. coruscans* from Ecuador and 34 *C. thalassinus* from Costa Rica. Vocalizations of *C. coruscans* were recorded in the city of Quito, Ecuador in November 1991. Three individuals were recorded on the campus of the Universidad Católica, four were recorded 1 km S from the university, and eight individuals were recorded at two sites over 4 km SE from the university.

Three montane populations of *C. thalassinus* were observed in Costa Rica (Fig. 1) in February 1992. (1) In the Cordillera de Talamanca between Cerro Vueltas and Cerro de la Muerte, singing birds were recorded at two sites 10 km apart, Fila Zapotales (seven birds) and the Fila Pangolin (11 birds). (2) In the Cordillera Central, 11 birds were recorded along a 3-km transect on the southern slope of Volcán Irazu. This site is approximately 50 km from the Talamanca sites. (3) Five birds were recorded at or outside the Reserva Biológica Monteverde in the Cordillera de Tilarán. Monteverde is over 120 km from Volcán Irazu and 140 km from the Cordillera de Talamanca sites.

Field recording and sound analysis.—Vocalizations were recorded with either a Marantz PMD420 cassette recorder coupled with a Sennheiser ME20 omnidirectional microphone mounted in 46-cm plastic parabolic reflector, or with a Sony TC-D5 ProII cassette recorder coupled with an Audio-technica 815 directional microphone. Recordings are deposited in the archives of the Borror Laboratory of Bioacoustics and California Academy of Sciences.

Spectrograms were produced on a Kay Elemetrics model 5500 DSP Sona-graph (sample rate 44 kHz; frequency range of 16 kHz and transform size of 100 points [600 Hz]). These were visually inspected to obtain an initial note-type catalogue, which was used for comparing notes and phrases of the songs produced by individuals within and between localities. In these species, elements of a note may be separated by 1.0 to 1.8 ms of silence (Fig. 2); we treated these "note complexes" as single notes given that the cross-correlation analysis we used is insensitive to periods of silence of this magnitude. Furthermore, birds that have been tested cannot resolve temporal features shorter than 2.0 ms at or above 4.5 kHz, and resolution decreases with increasing frequency (Konishi 1969).

Digital sound acquisition, storage and analysis were performed on a Gateway 2000 microcomputer using Real-time Spectrogram (RTS) version 1.25 and SIGNAL version 2.27 programs and hardware (Beeman 1993). Four notes were extracted from four randomly selected song bouts recorded from each individual bird. Notes were stored as digitized waveforms in computer files using RTS (sample rate 25 or 33 kHz). Measures of frequency (Hz) and temporal (seconds) parameters were stored in an on-line log file from a digital cursor in RTS. Using a SIGNAL routine, the stored sounds were transformed into digital spectrograms (128- or 256-point Fast Fourier Transforms, 600 or 800 steps per signal) for cross-correlation.

Digital cross-correlations between pairs of note spectrograms were performed. Cross-correlation incrementally moves two digital spectrograms past each other in time. A digital spectrogram is a matrix of cells, each containing a value reflecting the amplitude for its particular row (frequency) and column (time). A cross-correlation coefficient is similar to a Pearson product-moment correlation coefficient of the amplitude values of corresponding cells of the matrices. Digital spectrograph matrices of equal length are offset, the last column of one overlapping the first column of the other, and a correlation coefficient is calculated. The matrices are then advanced one time step additional overlap, and another coefficient is calculated. A plot of correlation values versus the time offset is returned for the successive, discrete time offsets (Fig. 2). The peak correlation value from this

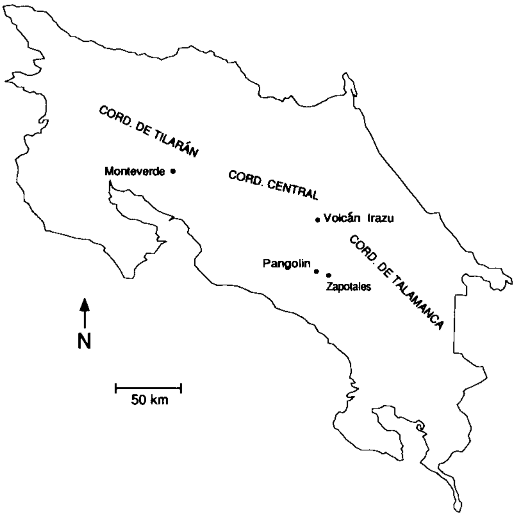

Fig. 1. Location of *C. thalassinus* sampling sites in Costa Rica. Monteverde is about 120 km from Volcán Irazu and Pangolin, whereas Pangolin and Zapotales are about 50 km from Volcán Irazu.

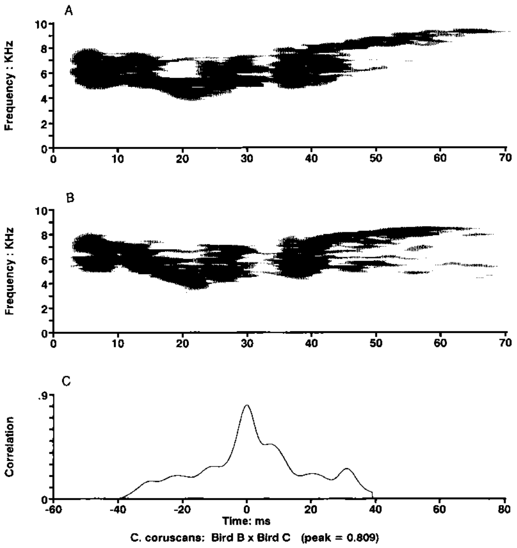

Fig. 2. (A and B) Notes from songs of *C. coruscans*, birds B and C, and curve of correlation coefficients obtained from cross-correlation of the two notes (C). The peak, or similarity, value of 0.809 occurs at or near maximum overlap (time 0).

curve of correlation coefficients is a measure of similarity between two spectrograms and is here referred to as a similarity value (the inverse is a dissimilarity value) between notes. The higher the value the greater the similarity. This procedure allows for the full representation of a sound's frequency and time structure, rather than a few discrete measures of these acoustic features, and is a sensitive measure of similarity between sounds.

A batch-processing routine in SIGNAL automates multiple cross-correlations of up to 64. The output of the peak correlation coefficients from all possible pairwise comparisons were stored in an $n \times n$ triangular matrix without diagonals (an $n \times n$ square matrix of these data is symmetrical about the diagonal, and the diagonal values are autocorrelations of no interest here; thus, only the lower left hand corner is calculated).

We have conducted sensitivity tests of SIGNAL's spectrogram cross-correlation calculation with sounds containing varying periods of silence, differences in duration, and amounts of background noise. The data from these tests will be presented elsewhere (Mauck et al. in prep.), but in all cases correlation coefficients were insensitive to the location of the high-amplitude cells within the grid. That is, SIGNAL's spectrogram cross-correlation is a matrix comparison routine that accurately measures the overlap of patches of gray and black on a white background. It is therefore not a magic box for comparing all features of sounds, but is useful for comparing the shapes of sounds that lack overtones, or the fundamental frequencies of sounds with overtones, particularly sounds that are of similar duration (Beeman 1993). *Colibri* notes have no overtones or only one, and are at or near the same frequency. They differ mainly in "shape," making them good candidates for spectrogram cross-correlation.

We used cluster analyses to describe the relationship between the notes of birds at each observation location. A cluster analysis was performed on the matrices of similarity values using average (UPGMA) hierarchical cluster analysis (SYSTAT 5.03; Wilkinson 1990). In the resulting linkage-tree diagrams, degree of similarity between notes is represented by the proximity of the branches, with the most similar notes closest to one another. These objective descriptions were compared to the subjective patterns obtained from visual spectrogram sorting and field observations of bird associations.

To test hypotheses about the association of song and groups, we used a method of matrix correspondence first described by Mantel (1967) and recommended by Manly (1991). The utility of this Mantel method for ethological problems was demonstrated with several examples by Schnell et al. (1985); one example, similar to ours, was a corroboration of microgeographic song variation in the Splendid Sunbird (*Nectarinia coccinigaster*) from Ghana (Payne 1978).

The Mantel method is a regression technique that tests for independence of two equal-dimension matrices. One matrix can be artificially constructed to specify a null hypothesis of interindividual association. The degree of correlation between two matrices is associated with a t-value, the Mantel statistic, that is compared to a standard normal distribution for significance testing. However, the Mantel statistic is only asymptotically normal and, for fewer than 20 individuals, valid *P*-values cannot be obtained in this manner. Significance of the Mantel statistic for our sample of fewer than 20 *C. coruscans* songs was estimated by performing a Monte Carlo, randomization simulation wherein rows and corresponding columns of one array are randomly rearranged and the Mantel statistic calculated for this new permutation. This randomization was carried out 5,000 times and the distribution of the resulting statistics was used to determine the level of significance to within 1% (Manly 1991). The Mantel test and the randomization simulations were generated by routines in SIGNAL.

For hypothesis testing with the Mantel method, three matrices were constructed for each *Colibri* species; one song similarity matrix then was compared to two distance matrices. In all matrices individual birds were arranged in the same order on the axes, and values in all cells were between zero and one.

To test the prediction that neighbor songs are more similar than those of nonneighbors, we constructed a "group matrix" in which a value of one was entered for each neighbor dyad (20–30 m between individuals) and a zero for nonneighbor dyads. A Mantel test between group and song similarity matrices tested the prediction that neighbor songs are more similar than nonneighbor songs against the null hypothesis of no difference.

To test the prediction that song similarity is negatively correlated with geographic distance, we constructed a geographic distance matrix in which the distance between members of a dyad was calculated by dividing each intra-dyad distance by the maximum intra-dyad distance. A Mantel test between geographic distance and song similarity matrices evaluated the prediction that song similarity is negatively correlated with geographic distance.

RESULTS

GENERAL DESCRIPTION OF DISPLAYS AND ASSOCIATED VOCALIZATIONS

In both species males delivered song bouts from one or more exposed perches in what has been termed a "static" display (Skutch *in* Bent 1940). Perches were at mid- to upper levels of tall trees. In the less disturbed, more intact habitat of the Cordillera de Talamanca and Volcán Irazu sites, *C. thalassinus* usually sang from posts high up in oak trees (*Quercus* sp.). At Monteverde, song posts were also high, but tree use was more variable, probably because all but one bird was recorded from disturbed areas outside the reserve. In the urban environment, *C. coruscans* was observed singing from tall ornamental trees. For both species, two or more birds within sight or sound of each other (20 to 30 m) formed singing assemblies or neighborhoods. Other aspects of the vocalizations, delivery and related behavior differ for the two species.

C. coruscans.—Song bouts delivered in the static display are relatively short, averaging 4.56 ± SD of 3.3 s ($n = 52$) in length, and are repeated at regular intervals. During song delivery the bill was pointed up at about 45° from the horizontal, and the head moved from side to side in rhythm with each song bout. Songs are composed of a single, repeated note or note complex, rarely a paired note phrase (see below).

Periodically, and without warning, a singing male engaged in an aerial display with song, the "dynamic" display (Skutch *in* Bent 1940). In this display the bird first flew up vertically and silently to a height of 6 to 10 m above its perch. About 0.5 m before reaching the apex of ascent the male spread its tail and, without pause at the peak of ascent, dove immediately with tail still spread at an angle with the vertical. During this dive phase, males produce a dynamic display song of a complex series of notes (Fjeldsa and Krabbe 1990) organized in three phrases (see below).

C. thalassinus.—Only static displays are performed by this species, and the songs or song bouts can continue uninterrupted for more than a minute. From our few tape samples with complete song bouts, the duration of a song was 7 to 125 s; Skutch (1967) documents an 11-min continuous song bout. Static songs, as in *C. coruscans*, are composed of note or note complexes with two or more fast frequency-modulated elements that can vary in direction, rate, and duration of modulation. Unlike *C. coruscans*, there are always two or more different notes in a song, and these are organized in repeated phrases (see below). When three notes form a phrase, two are usually a pair of similar notes; occasionally all three notes differ.

Although there is no dynamic display in this species, *C. thalassinus* males change singing perches with a display flight that traces an undulating path. During the flight the wings are spread and quivered for a few seconds before alighting.

SONG SHARING

All cluster analyses of song similarity returned linkage trees that grouped birds as they were geographically associated in the field and

TABLE 1. Similarity values from note comparison dyads in Figure 3 ($\bar{x}$ ± SD with n in parentheses).

	Same bird	Neighbor	Nonneighbor
C. coruscans	0.28 ± 0.05 (15)	0.70 ± 0.09 (12)	0.38 ± 0.07 (52)
C. thalassinus	0.84 ± 0.06 (29)	0.72 ± 0.08 (22)	0.40 ± 0.07 (81)

by spectrogram inspection except for two cases, one individual *C. coruscans* in a group of three birds and a pair of *C. thalassinus* from Monteverde (the sample from Monteverde was small and is not included in the cluster analyses, but is discussed below). Table 1 and Figure 3 summarize similarity values derived from cross-correlations of note pairs from different songs of the same bird, from neighboring birds, and for nonneighbors at each location. Clearly, notes compared from different songs of the same bird have values closest to unity (i.e. correlation of a note with itself), neighbors have similarity values broadly overlapping same-bird comparisons, and nonneighbors separate almost completely from neighbors. These assessments seem a strong indicator that neighbors are more likely to have similar, shared songs than nonneighbors.

Mantel tests supported this assessment of song sharing in our study populations. For both species, Mantel tests between the group matrix (neighbor vs. nonneighbor) and song similarity matrix were significant (*C. coruscans*, Mantel statistic = 5.14, $P = 0.0002$; *C. thalassinus*, Mantel statistic = 2.55, $P < 0.01$), suggesting that individuals' songs are influenced by the songs of neighbors. Mantel tests of correlation between geographic distance matrices and song similarity matrices were also significance (*C. coruscans*, Mantel statistic = −4.90, $P = 0.0002$; *C. thalassinus*, Mantel statistic = −3.14, $P < 0.01$), suggesting that as distance between individuals increases, their songs become less similar. Thus, our results support the hypothesis that song sharing occurs in these species and is promoted by geographic proximity.

Static display of C. coruscans.—Two clear assemblies were identified to be within hearing of each other at the university campus area and the area 1 km S. For the campus group I, visual inspection of spectrograms reveals that all three birds had chevron-shaped elements in the note makeup, and birds S at the university (group II) had repeated fast frequency-modulated elements forming a buzzy (vibrato) note (Fig. 4A). Cluster analysis on the note similarity matrix for groups I and II clearly link the birds of group II on a discrete branch, but places bird A of group I on its own branch and distant from birds B and C (Fig. 4A).

One discrete neighborhood of two birds was located and recorded 4 km from the university (group III) and about 1.25 km away a larger assembly of six birds was recorded (group IV). Group III birds sang songs consisting of inverted-chevron notes (Fig. 4B), and bird I delivered them singly or in pairs. Group IV birds all have repeated fast frequency-modulated elements similar to but slower than those of group II, and the note usually ended with a nonmodulated flag. The flag position was either near 7 kHz (birds J, L, N) or 5 kHz (M, K, O), forming two subgroups to group IV; the linkage tree of the similarity matrix for these groups places them on discrete branches (Fig. 4B). A linkage tree on the similarity matrix of all four groups retains each on discrete branches with bird A on its own, outlying branch. Sampling by re-

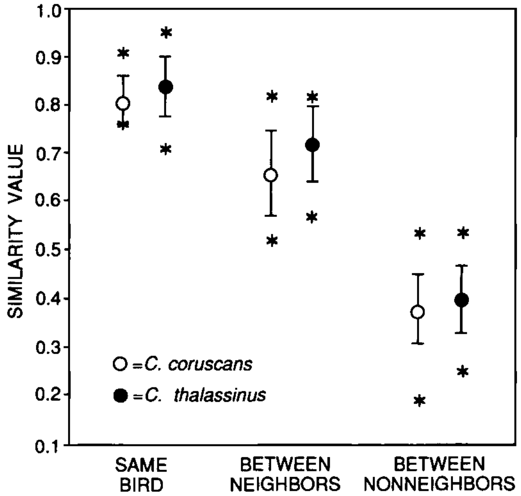

Fig. 3. Song similarity values from cross-correlation analysis. Songs compared for (1) same bird, (2) neighboring birds, and (3) nonneighboring bird dyads for each location. Circles indicate means (open for *C. coruscans*, closed for *C. thalassinus*), horizontal bars the standard deviation, and asterisks the range (see Table 1).

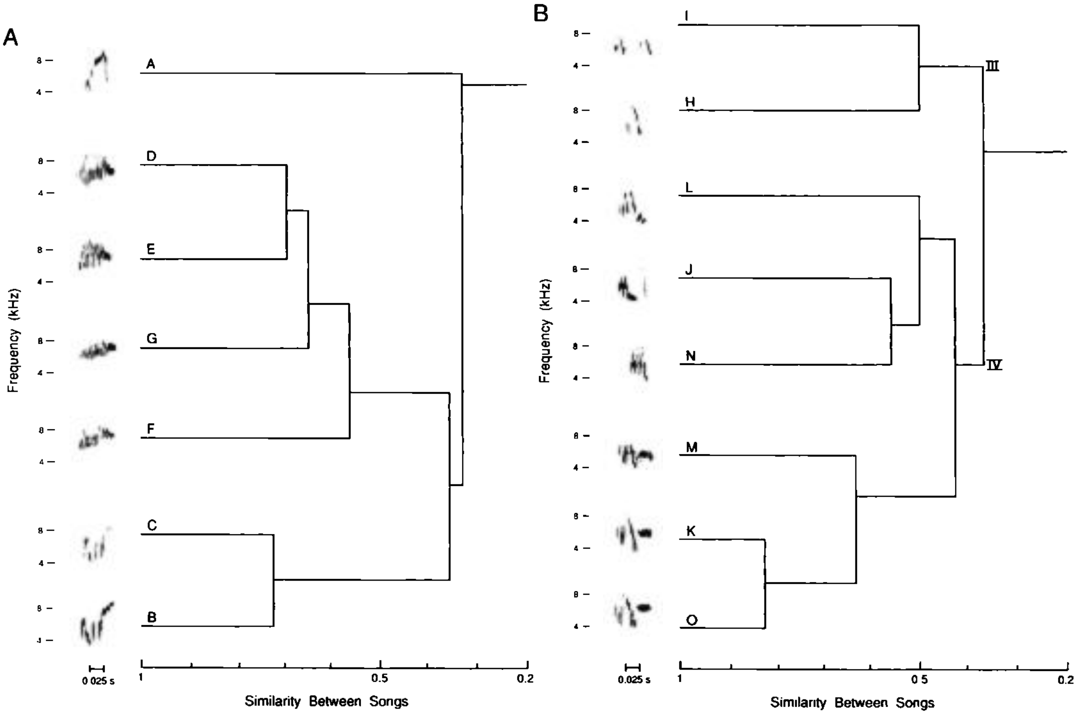

Fig. 4. Cluster analysis for *C. coruscans* from (A) vicinity of Universidad Católica, Quito, Ecuador and (B) 4+ km SE of Universidad Católica. Spectrograms from sound recordings deposited in Borror Laboratory of Bioacoustics (BLB): (bird A) BLB#18510; (B) BLB#18511; (C) BLB#18512; (D) BLB#18519; (E) BLB#18520; (F) BLB#18525; (G) BLB#18526; (H) BLB#18528; (I) BLB#18529; (J) BLB#18530; (K) BLB#18531; (L) BLB#18532; (M) BLB#18533; (N) BLB#18535; (O) BLB#18536. Bird I produced songs with single notes, as well as the double notes shown; analysis used the single-note renditions.

cording in none of the areas was exhaustive. Therefore, bird A may be in the assemblage with B and C with a variant song, an isolated bird, or may have a neighbor or neighbors with like songs that were not sampled.

Dynamic display of C. coruscans.—The dive portion of this aerial display is accompanied by a complex song. Samples of the song during the dynamic display were recorded from six birds, all of whom returned to static song delivery immediately after the dynamic display.

Dynamic songs are 1.93 ± 0.30 s ($n = 20$) in length and have three phrases (Fig. 5): an introductory phrase of "clicks" or single broad band notes of short duration; a middle phrase of a series of notes identical to those in the static display but delivered at a faster rate (static song-note interval 0.50 ± 0.01 s; dynamic interval 0.03 ± 0.007 s); and an ending phrase of a complex series of lower-amplitude notes, some of which are found in the dynamic song throughout the population (arrows, Fig. 5). All birds irrespective of neighborhood shared the ending phrase.

Birds also delivered partial dynamic display songs usually during activities involving close encounters between birds. Thus, in chases between birds, only the third, lower-amplitude phrase was used (Fig. 6A and B). One bird delivered the dynamic song without the introductory clicks while perched (Fig. 6C). These songs were loosely structured and were delivered more frequently than those from the other birds recorded (possibly subsong by immature bird).

Static display of C. thalassinus.—This species delivers song in phrases of notes, and cross-correlation analysis cannot be performed on the entire phrase. The cluster analyses in this discussion, therefore, were done using correlations between the first note of each phrase. Analyses using the last note of the phrase yielded similar results.

At the Zapotales site in the Cordillera de Tala-

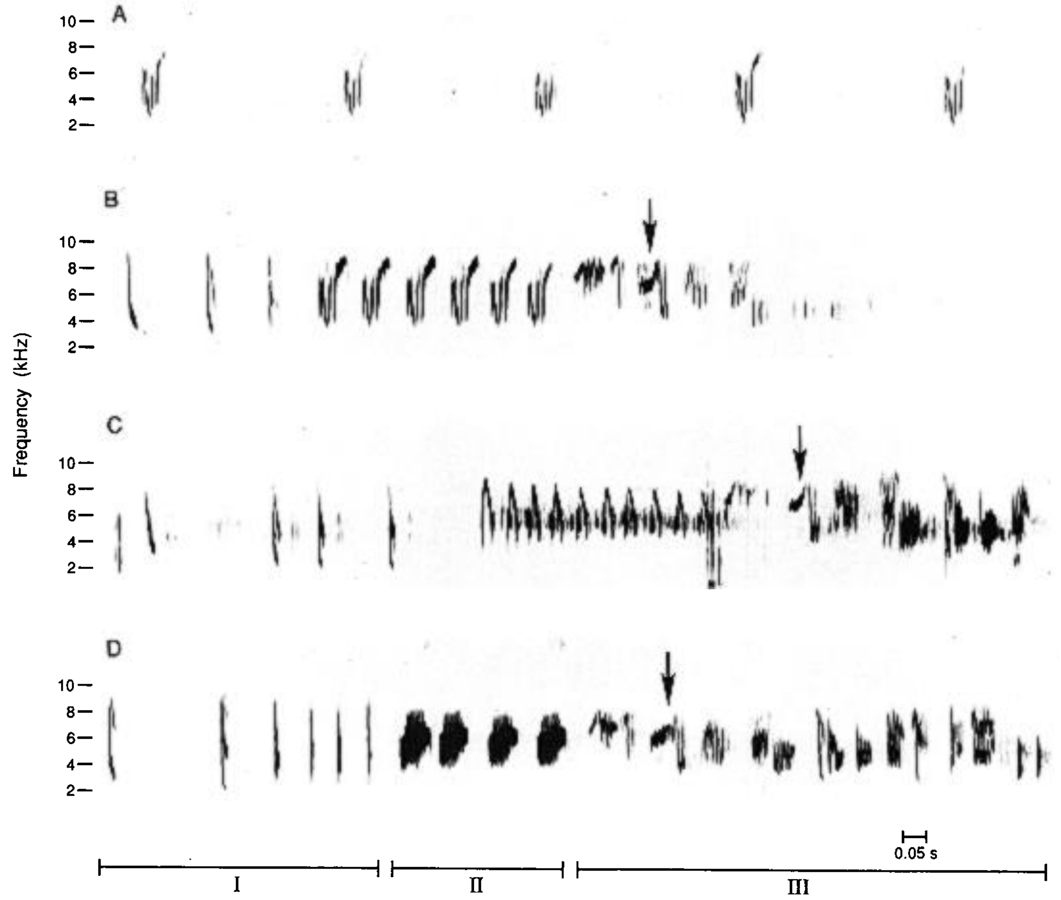

Fig. 5. *Colibri coruscans* songs. (A) One complete static song from bird B in Figure 4; (B) dynamic song for bird B; (C) dynamic song from bird H in Figure 4; (D) dynamic song from bird E in Figure 4. The dynamic song is composed of three phrases labeled I, II and III (see text); arrows indicate a note shared between birds in phrase III.

manca, two song assemblies within hearing of one another were located, one with two birds (group I) and the other with four birds (group II). A lone bird with no neighbor or with a neighbor not located by us was also recorded. Visual inspection and computer analysis clustered the groups similarly (Fig. 7). Group I birds had a first note with alternating down and up slurred, fast frequency-modulated elements with a *W*-shaped appearance on the spectrogram; group II birds had inverted-chevron notes with an overtone; the lone bird had three downslurred, fast frequency-modulated elements.

Although the songs of most birds were repeats of the same phrases, each male may vary the phrases. Individuals can vary their song by altering the number of notes or rhythm of notes in the phrases. Group I birds had no variation in phrases throughout song bouts. Group II birds varied phrases by having the first note single or paired (birds C, 42%; D, 100%; E, 88%; F, 90%).

The Pangolin site in the Cordillera de Talamanca was sampled along a transect of about 12 km. At the upper elevation of the transect, four birds formed a group (group I) and, although all four were within hearing of one another, an upper and lower dyad interacted with one another more closely. Group I was separated from a lower-elevation population by a gap with no *C. thalassinus*. The lower-elevation population had three groups within hearing; group II with three birds, and groups III and IV with two birds each. Visual inspection of spectrograms and statistical cluster analyses on similarity matrices confirmed these assemblages (Fig. 8). Group I had inverted chevrons

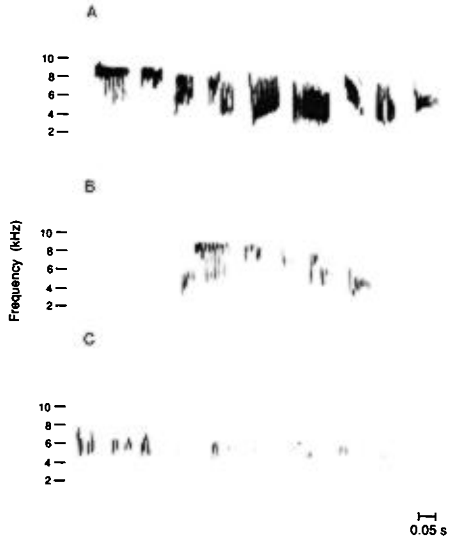

Fig. 6. Partial dynamic song given by two birds during a chase between (A) bird C and (B) bird B from sound recording BLB#18524. (C) Partial dynamic song from bird I.

with an overtone, but the peak of the chevron had a lower frequency in group Ib. The lower-elevation groups all had notes comprised of repeated fast frequency-modulated elements or buzz notes, and these varied between groups by seemingly slight differences in frequency range, rate, and/or direction of modulation.

Here also neighboring males often varied shared song by changing the number or arrangement of notes in the song phrases. For example, in group Ia, bird A had all phrases with paired first and single last notes (AA! B! AA! B!), whereas male B paired both the first the last notes in 35% of deliveries (AA! BB! AA! BB!). In group Ib, birds C and D had first notes similar to Ia, but the note paired with it resembled the last note (AB! B! AB! B!), and bird D gave long strings of the last note of a phrase before repeating the shared phrase. The lower-elevation groups had very little within-bird phrase variation.

There were three sites in the 3 km transect at Volcán Irazu. The middle site had two singing assemblages of two and four birds (Fig. 9A). Nonneighbors were recorded at the lower-elevation site (three birds) and at the upper-elevation site (two birds; Fig. 9B). For clarity, neighboring and nonneighboring birds are shown on separate trees; however, a tree with all Volcán Irazu birds clusters in the same way.

Variation and gradation of phrases in song bouts were the most pronounced in Irazu, group I of all assemblages recorded in Costa Rica. Notes used and temporal placement or rhythm were varied (Fig. 10) with bird F's rendition sounding syncopated.

Syllable sharing between locations in C. thalassinus.—At Volcán Irazu the cluster analyses of the nonneighboring birds (Fig. 9) most closely link birds A and J (similarity value 0.52), which were respectively at the lowest elevation (2,555 m) and highest elevation (2,795 m), separated by 3 km. These birds clearly were not within a song neighborhood. Visual inspection of spectrograms revealed three other cases of note similarity between distant populations (Fig. 11). Birds from the two Cordillera de Talamanca sites separated by 10 km had similar song phrases (Zapotales birds C, D, E, F and Pangolin birds A and B). Birds A and B of Zapotales, 50 km from bird C of Volcán Irazu, sing song bouts composed of the same phrase. Most remarkable is the similarity between phrases in Volcán Irazu group I and a bird from Monteverde, 120 km distant.

However, the similarity values from the cross-correlation of spectrograms of distant birds were always within the range observed for nonneighbors (Fig. 3): similarity value for the *W*-shaped note of neighbors at Volcán Irazu is 0.70, whereas between the locations the value is only 0.54; the value for neighbors at Zapotales was 0.82, at Pangolin 0.75 and between the sites only 0.40; the similarity value for the buzz notes from group I, Volcán Irazu is 0.68 and between Volcán Irazu and Monteverde only 0.32. Clearly, distant birds with similar song are more like nonneighbors than neighbors.

DISCUSSION

We document note and phrase sharing in song between neighbors of both *C. coruscans* and *C. thalassinus*. However, whereas the static song of *C. coruscans* consists of identical single or paired notes repeated in strings at regular rhythms (Figs. 4 and 5A), the song of *C. thalassinus* is more complex. In *C. thalassinus* there are phrases of two, three, or rarely four different notes shared by neighboring males (Figs. 7, 8 and 9). Different males in a neighborhood may deliver these notes at different interphrase rates and/or note combinations (Fig. 10).

Colibri coruscans also performs a dynamic flight

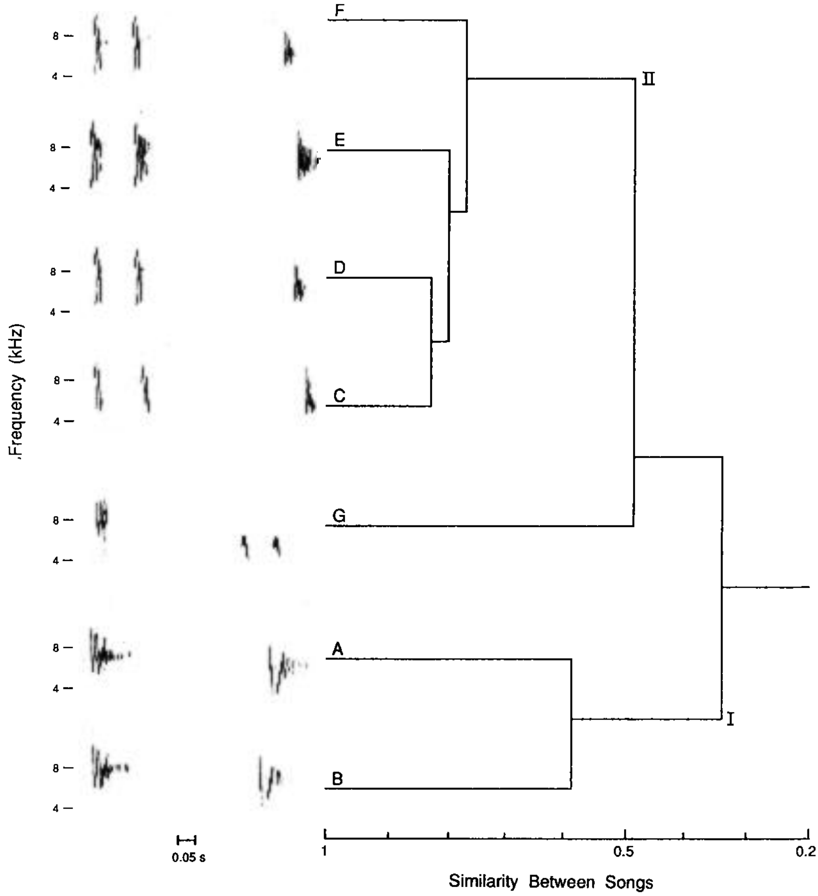

Fig. 7. Cluster analysis for *C. thalassinus*, Zapotales site. Spectrograms from: (bird A) BLB#18395.B; (B) BLB#18395; (C) BLB#18397.B; (D) BLB#18397; (E) BLB#18102; (F) BLB#18103.B; (G) BLB#188104.

display in which a more complex song is uttered. The shared, neighborhood notes of the static display song are inserted into the dynamic display song; these are preceded by click notes and followed by an array of softer, chattered notes that are shared by all individuals in the population (Fig. 5). This is reminiscent of song sharing in passerines such as White-crowned sparrows (*Zonotrichia leucophrys*; Baptista 1985, DeWolfe et al. 1989) in which nearest neighbors share introductory phrases and the population shares the penultimate trill.

Clicked sounds, such as found in *C. coruscans* dynamic song, increase the detectability and locatability of the sender by the receiver, especially in noisy environments (Wiley and Richards 1982). The dynamic song introduction, then, may alert potential receiver(s), the middle section may identify the neighborhood, and the softer end would be for receiver(s) in close proximity (i.e. for local consumption; sensu Smith 1991). Schmidt-Marloh and Schuchmann (1980) observed this species in Colombia and noted that the dynamic song was delivered after a territorial chase while the male was perched and during the precopulatory display. We did not observe this in our study area.

The North American Anna's Hummingbird (*Calypte anna*) also performs static and dynamic displays. However, in contrast to *Colibri coruscans*, it is in the static display that *Calypte anna* sings a longer complex song, and the dynamic display song has only two portions of the static display song (Wells et al. 1978, Baptista and Matsui 1979). Thus, there is no general tendency for dynamic songs to be complex and static songs to be simple among hummingbird species.

Is nearest-neighbor sharing of song as here documented for *Colibri* evidence for song learn-

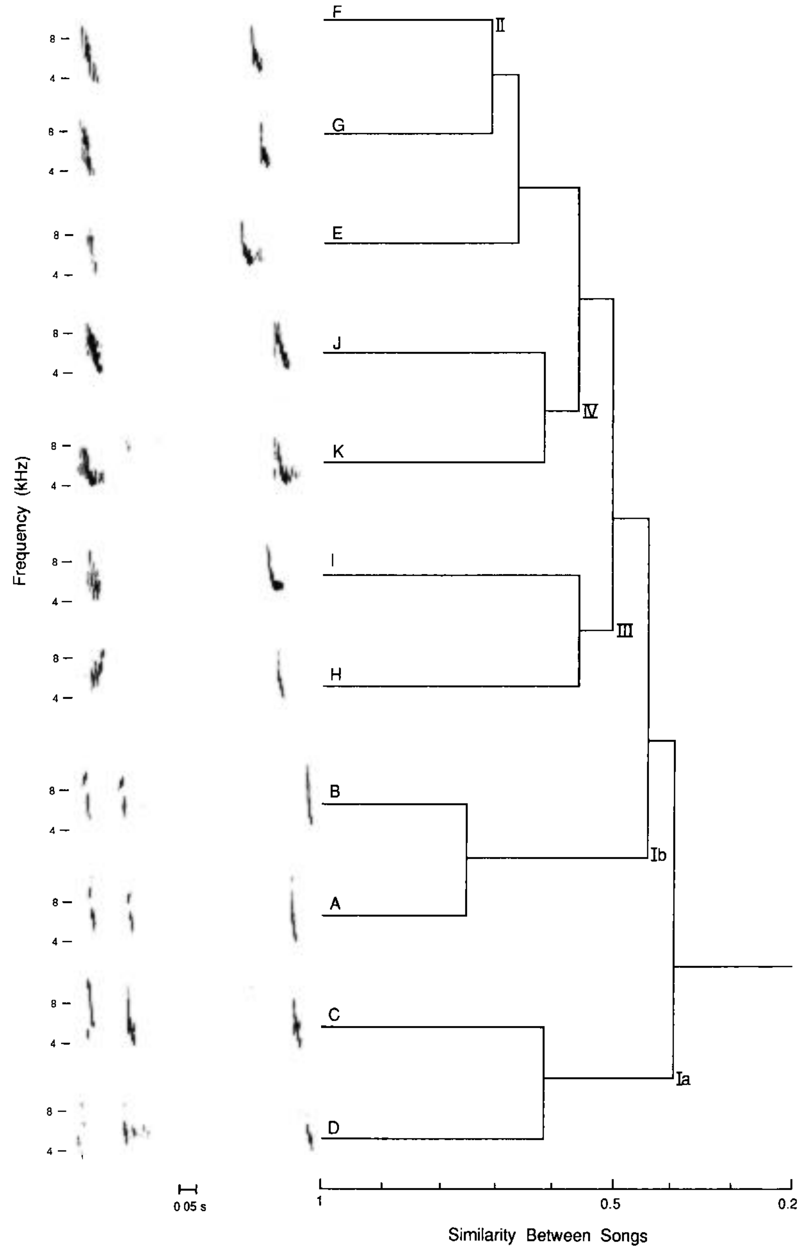

Fig. 8. Cluster analysis for *C. thalassinus*, Pangolin site. Spectrograms from: (bird A) BLB#18367.B; (B) BLB#18371.B; (C) BLB#18374.B; (D) BLB#18376; (E) BLB#18377; (F) BLB#18378.B; (G) BLB#18379; (H) BLB#18381; (I) BLB#18382; (J) BLB#18385.B; (K) BLB#18386.B.

ing? Such convergence in song structure among neighbors and resultant vocal dialects is generally accepted as indirect evidence for song learning in songbirds (Kroodsma 1982, Kroodsma and Baylis 1982), and we suggest that neighboring *Colibri* in this study are modifying their songs so as to mimic each other. Furthermore, although experiments on learning have not been done for *Colibri*, learning has been demonstrated in experiments with another hummingbird, *Calypte anna* (Baptista and Schuchmann 1990). An alternative explanation for song sharing is

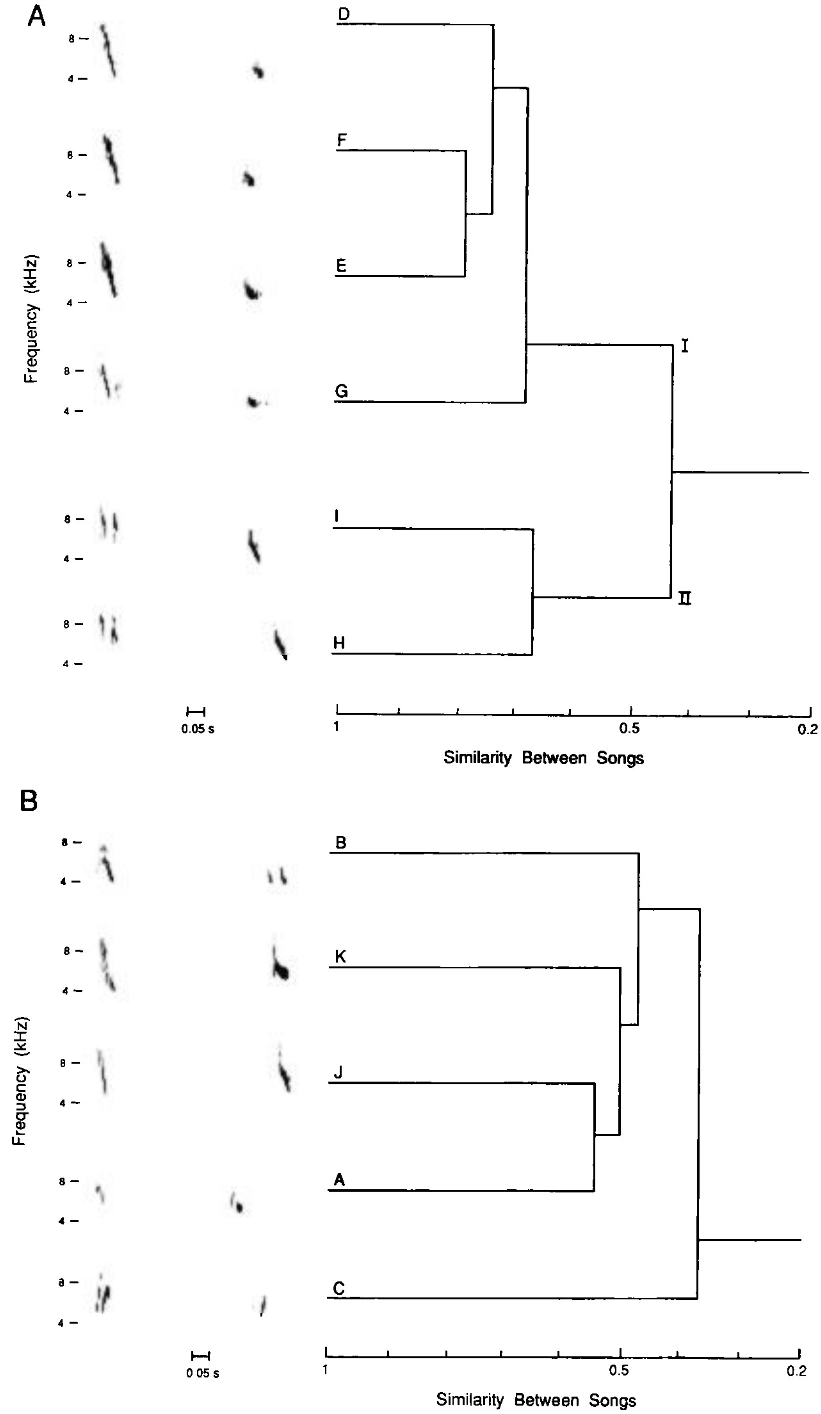

Fig. 9. Cluster analysis for *C. thalassinus* Volcán Irazu sites. (A) Mid-elevation birds (D, BLB#18108; E, BLB#18109; F, BLB#18110; G, BLB#18111.B; H, BLB#18112.B; I, BLB#18113.B). (B) Lower-elevation birds (A, BLB#18105.B; B, BLB#18106.B; C, BLB#18107), and upper-elevation birds (J, BLB#18114.B; K, BLB#18115.B).

that the birds are related and song is acquired by inheritance as has been demonstrated for the Northern Bobwhite (*Colinus virginianus;* Baker and Bailey 1987).

However, we judge that the breeding biology of these species makes it unlikely that song sharing is a consequence of relatedness between neighbors. Female *Colibri* build their nests in locations remote from male neighborhoods, which the females do not visit until nest construction is completed (Wagner 1945). Then females search out males, and Johnsgard (1983) suggested that "the far reaching call and display flights of males helps females locate them." Females lay only two eggs, and males do not aid in rearing young. Thus, two song-sharing males could be related if: (1) sons were recruited from nest areas located distant from and not necessarily nearest to the assemblage; or (2) both members of the clutch were male, both survived, and the brothers set up a neighborhood of two birds. The latter would not explain neighborhoods of three to four birds unless there was recruitment into a brother assembly of offspring of their mother (brothers or half brothers) over successive nestings. We intend to estimate relatedness among individuals and groups with DNA fingerprinting methods in the future (Queller et al. 1993, Parker et al. in press) and, in this case, we would expect no difference between neighbor dyads and nonneighbor dyads.

Each male's song area is associated with a patch or patches of flowers. Near Pension La Georgina in the Cordillera de Talamanca of Costa Rica, Colwell et al. (1974) observed *C. thalassinus* associated with patches of *Centropogon valerii.* At the Cordillera de Talamanca sites and at Volcán Irazu, males also defended patches of *Centropogon* ssp. Male assemblages in *Colibri* have been attributed to such food-plant association rather than to a tendency toward social interaction (Wagner 1945). If this were true, neighboring males should deliver their song randomly, and overlap or interference between songs should be common. However, we noted a lack of song interference between neighbors and

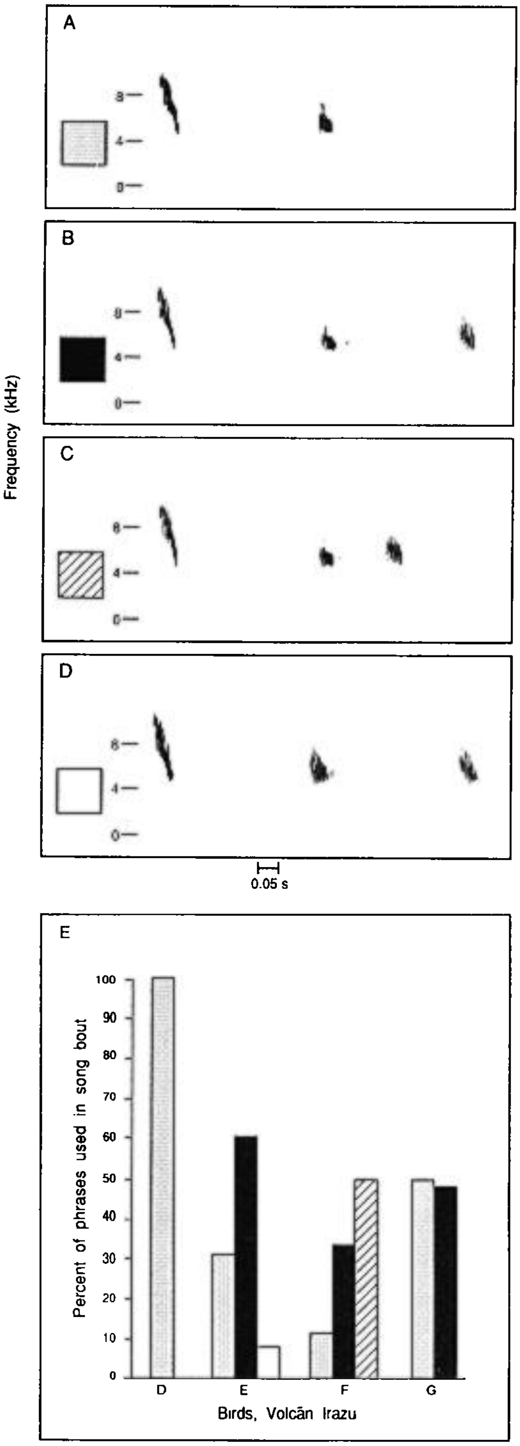

Fig. 10. Spectrograms (A, B, C and D) of phrase types in static songs of *C. thalassinus* group I birds (Fig. 9). To left of each spectrogram is code identifying phrase types depicted as histogram bars for each bird in E. All of songs of bird D consist of phrases shown in spectrogram A; bird F is only individual singing songs containing phrase shown in spectrogram C; and bird E is only individual singing songs with phrases shown in spectrogram D.

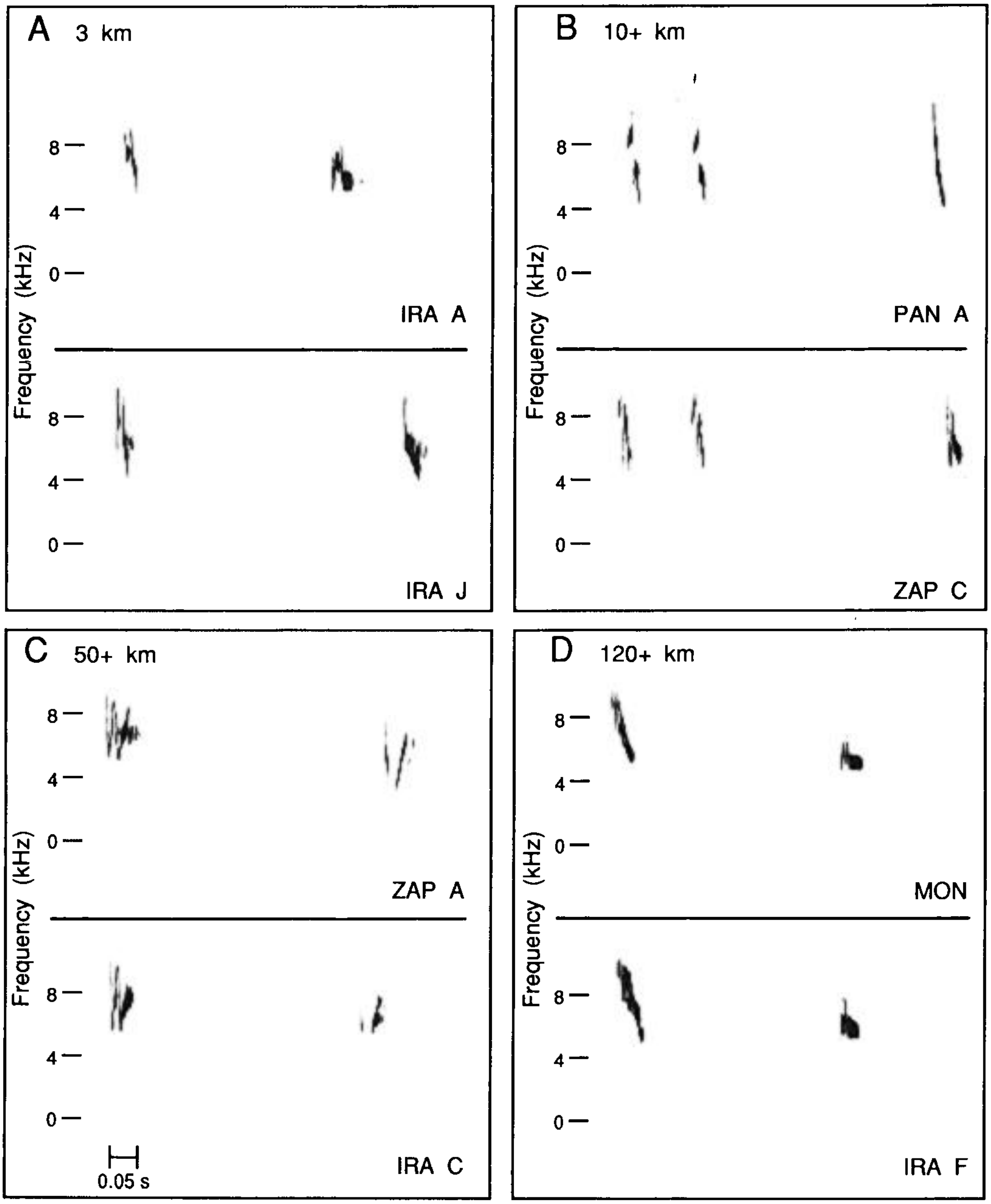

Fig. 11. Note and/or phrase similarity between birds from widely separated locations for *C. thalassinus.* (A) Volcán Irazu birds A and J that were 3 km apart. (B) Talamanca birds A from the Pangolin site and C from Zapotales site separated by 10 km. (C) Bird A from Zapotales and bird C from Volcán Irazu separated by 50 km. (D) Volcán Irazu bird F separated by 120 km from a bird at Monteverde.

suggest that social interaction is in fact occurring. Our recordings of a target male often captured the neighboring male(s) in the background, and notes of neighboring birds always fell in the silent intervals of the target bird with one exception, the Monteverde location. Here, two birds sang very different songs from perches within 30 m of one another. The unique songs of this pair of "neighbors" were delivered more rapidly and were in constant interference, suggesting that these birds were not behaving as neighbors. Song-delivery rate of all other neighbors approached that of the Monteverde birds only when a strange bird entered a territory.

When receptive to copulation, females must search for a beacon or beacons to locate males. Song can provide such a beacon and, if nearly continuous, would be likely to attract and direct the female. *Colibri* have been reported to devote up to 70% of the daily time budget to the song display (Johnsgard 1983). Such a continuous, rapidly delivered song display may be time and energy demanding. By cooperating with neighbors, individuals can afford to engage in activities other than singing, such as feeding, with some assurance that the song beacon will be little interrupted. In addition, when singing simultaneously but without note interference (i.e. notes are interdigitated), each male can sing slowly, and the "neighborhood song" sounds to us at a distance as being more rapid or nearly continuous. Individual males thus decrease the aerobic cost of displaying (Vehrencamp et al. 1989).

Assessment of individual males can occur when a female enters a lek. If rate of singing is important in female mate choice, individual males should increase their own song rate when females are within the neighborhood. Village Indigobirds (*Vidua chalybeata*) also aggregate forming dispersed leks, and Payne and Payne (1977) observed that the males obtaining the greatest number of female visits and copulations had the highest song rate. We observed only a few instances of strange birds of unknown sex entering a neighborhood, but song rate did increase on those occasions.

Size of assemblages may also be constrained by song interaction between birds. Larger assemblages would be counterproductive because of the increased probability of incurring song interference. Narins (1992) demonstrated such a threshold in neighborhood size for the Neotropical frog *Eleutherodactylus coqui* using modeling and a computer simulation based on computer-network algorithms. The simulations allowed for the evaluation of the various calling strategies available to an individual in a chorus with respect to chorus interactions and timing relations among frogs. The results agreed with the observation that an individual calling male should elect to vocally interact with only two of its neighbors. Neurological and physiological parameters would differ for hummingbirds, and the maximum number of birds in an assembly might differ.

Larger groups also may be at a disadvantage because some males would become central rather than edge birds and would have less opportunity to copulate with the female, who seems to mate with the first male she encounters (Wagner 1945). In *Colibri* each singing assembly then may represent a "dispersed lek" as has been postulated for some populations of Anna's Hummingbirds (Stiles 1982).

Learning a neighbor's song may confer other advantages. Margoliash (1986) has shown in oscine passerines that the brain nucleus necessary for and active during song production has auditory neurons that are most responsive to a bird's own song. If a neighbor's song matches the stored song image of one's own song, then an undegraded image of the neighbor's song is obtained. Morton (1982) has proposed that males can use such an image as a "standard" to judge degradation of the neighbor's song over distance. By doing so an individual could assess the distance of a singing neighbor and judge whether to ignore or threaten him by countersinging or attacking. Playback experiments by McGregor et al. (1983) and McGregor and Krebs (1984) with Great Tits (*Parus major*) support this hypothesis.

Songs of *C. thalassinus* between distant locations occasionally had notes and/or entire phrases in common (Fig. 11). Similar songs between distant males at Volcán Irazu (3 km) and the two Cordillera de Talamanca sites (10 km) are across distances where gene flow and exchange of memes might be expected. Finding similar songs between Volcán Irazu and the Cordillera Talamanca sites (50+ km) and Monteverde (120+ km) was unexpected.

Although the Green Violet-ear is a mobile species, Skutch (1967) found in Costa Rica that birds breed above 1,650 m and during the dry season move only to the mountain base at an altitude of 650 m. Individual males with distinctive vocalizations are reported to return to the same territory over subsequent years (over four years for one bird observed by Wagner [1945], but he was not aware of song sharing so this may not have been the same bird). Possibly, juvenile Green Violet-ears disperse great distances and bring with them learned song that results in "memeflow," or these hummingbirds may be capable of producing only a limited number of note types. In the latter case, learning involves the selection of notes from that limited set, and distant populations would end up with similar notes as argued by Marler and Pickert (1984) for Swamp Sparrows (*Melospiza georgiana*). Some of these phrase variants may be the result of cultural drift resulting in a mosaic distribution of note and/or phrase homologies. Such a situation has been described for homologous forms of Common Chaffinch (*Fringilla coelebs*) rain calls, which are distributed in a mosaic pattern across Europe so that similar variants may be separated by tens or hundreds of kilometers (Thielcke 1969, Baptista 1990).

Nevertheless, although distant birds have similar notes, the notes shared by neighbors are more similar. The differences between neighbors and distant birds are in the precision of mimicry neighbors seem to achieve in frequency modulation of elements within the note(s). Thus, neighbors are not only sharing notes, they are learning the internal, temporal elements of each other's notes, and the cross-correlation method of sound comparison is sensitive to these differences, which are visually difficult to resolve.

Analysis of syringeal function (Gaunt 1986) suggests that control of temporal features of vocalizations is primitive, and the ease with which temporal patterns can be varied suggests that these features could be culturally transmitted. Indeed, vocal learning of temporal features of calls has been documented in some Galliformes that have innate, stereotypic vocalizations (Sparling 1983). For birds with learned vocalizations, cues to both species (Becker 1982) and individual (Falls 1982) identification frequently include differences in temporal patterns of notes within song. Such control of learning by *Colibri* hummingbirds assumes that these birds can neurally resolve duration of within-note elements as well as control the syrinx to modulate them.

Colibri thalassinus has been suggested as the nearest relative to *C. coruscans* on the basis of plumage color and pattern similarities (Johnsgard 1983, Baptista pers. obs.). Both species construct notes of the song by varying the direction, rate and duration of the fast frequency-modulated elements, and the resulting notes are strikingly similar. Thus, shared notes, song delivery, and vocal learning may further reflect such a common ancestry.

ACKNOWLEDGMENTS

For assistance and hospitality in Costa Rica, we are grateful to the staffs of the Museo Nacional de Costa Rica, Servicio de Parques Nacionales, Ministerio de Recursos Naturales, Energia y Minas and The Tropical Science Center, Monteverde. We wish especially to thank Juan Diego Alfaro for his cooperation. In Ecuador, Baptista was assisted by Maria Sol Bajarano of the Universidad Católica, Quito and Michelle Brown of the University of Arizona, Tucson. For assistance with SIGNAL and statistical analyses we are greatly indebted to R. A. Mauck, R. Dettmers, and W. M. Masters, Ohio State University and E. Balaban, Harvard University. A. S. Gaunt, D. A. McCallum, R. B. Payne, S. M. Russell, G. D. Schnell and an anonymous reviewer gave helpful comments on the manuscript. The analysis was part of a preliminary test of SIGNAL for a project on parids supported by NSF funding to S.L.L.G. (NSF IBN-9212395).

LITERATURE CITED

ATWOOD, J. L., V. L. FITZ, AND J. E. BAMESBERGER. 1991. Temporal patterns of singing activity at leks of the White-bellied Emerald. Wilson Bull. 103:373–386.

BAKER, J. A., AND E. E. BAILEY. 1987. Sources of phenotypic variation in the separation call of Northern Bobwhite (*Colinus virginianus*). Can. J. Zool. 65:1010–1015.

BAPTISTA, L. F. 1985. The functional significance of song sharing in the White-crowned Sparrow. Can. J. Zool. 63:1741–1752.

BAPTISTA, L. F. 1990. Dialect variation in the rain call of the Chaffinch. Vogelwarte 35:249–256.

BAPTISTA, L. F. 1993. El estudio de la variación geográfico usando vocalizaciones y las bibliotecas de sonidos de aves neotropicales. Pages 15–30 *in* Curacion moderna de collecciones ornitologias (P. Escalante-Pliego, Ed.). Am. Ornithol. Union, Washington, D.C.

BAPTISTA, L. F., AND M. MATSUI. 1979. The source of dive-noise of the Anna's Hummingbird. Condor 81:87–89.

BAPTISTA L. F., AND K.-L. SCHUCHMANN. 1990. Song learning in the Anna Hummingbird (*Calypte anna*). Ethology 84:15–26.

BECKER, P. H. 1982. The coding of species-specific characteristics in bird sound. Pages 213–352 *in* Acoustic communication in birds, vol. 1 (D. E. Kroodsma and E. H. Miller, Eds.). Academic Press, New York.

BEEMAN, K. 1993. Signal users guide, version 2.2. Engineering Design, Belmont, Massachusetts.

BENT, A. C. 1940. Life histories of North American cuckoos, goatsuckers, hummingbirds and their allies. U.S. Natl. Mus. Bull. 176.

CLARK, C. W., P. MARLER, AND K. BEEMAN. 1987. Quantitative analysis of animal vocal phonology: An application to Swamp Sparrow song. Ethology 76:101-115.

COLWELL, R. K., B. J. BETTS, P. BUNELL, F. L. CARPENTER, AND P. FEINSINGER. 1974. Competition for the nectar of *Centropogon valerii* by the hummingbird *Colibri thallissinus* and the flower-pecker *Diglossa plumbea*, and its evolutionary implications. Condor 76: 447-452.

DEWOLFE, B. B., L. F. BAPTISTA, AND L. PETRINOVICH. 1989. Song learning and territory establishment in the Nuttall's White-crowned Sparrow. Condor 91:397-407.

FALLS, J. B. 1982. Individual recognition by sound in birds. Pages 237-278 *in* Acoustic communication in birds, vol. 2 (D. E. Kroodsma and E. H. Miller, Eds.). Academic Press, New York.

FJELDSA, J. AND N. KRABBE. 1990. Birds of the High Andes. Apollo Books, Svenberg, Denmark.

GAUNT, A. S. 1983. An hypothesis concerning the relationship of syringeal structure to vocal ability. Auk 100:853-862.

GAUNT, A. S. 1986. Interaction of syringeal structure and airflow in avian phonation. Pages 915-924 *in* Acta XIX Congressus Internationalis Ornithologici (H. Oellet, Ed.). Ottawa, Ontario 1986. National Museum of Natural Science, Ottawa.

JOHNSGARD, P. A. 1983. The hummingbirds of North America. Smithsonian Institution Press, Washington, D.C.

KONISHI, M. 1969. Time resolution by single auditory neurones in birds. Nature 222:566-567.

KONISHI, M., AND F. NOTTEBOHM. 1969. Experimental studies in the ontogeny of avian vocalizations. Pages 29-48 *in* Bird vocalizations (R. A. Hinde, Ed.). Cambridge Univ. Press, New York.

KROODSMA, D. E. 1982. Learning and the ontogeny of sound signals in birds. Pages 1-23 *in* Acoustic communication in birds, vol. 2 (D. E. Kroodsma and E. H. Miller, Eds.). Academic Press, New York.

KROODSMA, D. E., AND J. R. BAYLIS. 1982. Appendix: A world survey of evidence for vocal learning in birds. Pages 311-337 *in* Acoustic communication in birds, vol. 2 (D. E. Kroodsma and E. H. Miller, Eds.). Academic Press, New York.

MANLY, B. J. 1991. Randomization and Monte Carlo methods in biology. Chapman and Hall, New York.

MANTEL, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Res. 27:209-220.

MARGOLIASH, D. 1986. Preference for autogenous song by auditory neurons in a song system nucleus of the White-crowned Sparrow. J. Neurosci. 6:1643-1661.

MARLER, P., AND R. PICKERT. 1984. Species-universal microstructure in the learned song of the Swamp Sparrow (*Melospiza georgiana*). Anim. Behav. 32: 673-689.

MCGREGOR, P. K., AND J. R. KREBS. 1984. Sound degradation as a distance cue in Great Tit (*Parus major*) song. Behav. Ecol. Sociobiol. 16:49-56.

MCGREGOR, P. K., J. R. KREBS, AND L. M. RATCLIFF. 1983. The response of Great Tits (*Parus major*) to playback of degraded and undegraded songs: The effect of familiarity with the stimulus song type. Auk 100:898-906.

MIRSKY, E. N. 1976. Song divergence in hummingbird and junco populations on Guadalupe Island. Condor 78:230-235.

MORTON, E. S. 1982. Grading, discreteness, redundancy and motivational-structural rules. Pages 183-213 *in* Acoustic communication in birds, vol. 1 (D. E. Kroodsma and E. H. Miller, Eds.). Academic Press, New York

MUNDINGER, P. C. 1982. Microgeographic and macrogeographic variation in the acquired vocalizations of birds. Pages 147-208 *in* Acoustic communication in birds, vol. 2 (D. E. Kroodsma and E. H. Miller, Eds.). Academic Press, New York.

NARINS, P. M. 1992. Evolution of anuran chorus behavior: Neural and behavioral constraints. Am. Nat. 139:S90-S104.

PARKER, P. G., A. A. SNOW, M. D. SCHUG, G. C. BOOTON, AND P. A. FUERST. In press. Molecular markers for population biology. Q. Rev. Biol.

PAYNE, R. B. 1978. Microgeographic variation in songs of Splendid Sunbirds *Nectarinia coccinigaster*: Population phenetics, habitats and song dialects. Behaviour 65:282-308.

PAYNE, R. B., AND K. PAYNE. 1977. Social organization and mating success in local song populations of Village Indigobirds, *Vidua chalybeata*. Z. Tierpsychol. 45:113-173.

QUELLER, D. C., J. E. STRASSMANN, AND C. R. HUGHES. 1993. Microsatellites and kinship. Trends Ecol. & Evol. 8:285-288.

SCHMIDT-MARLOH, D., AND K.-L. SCHUCHMANN. 1980. Zur Biologie des Blauen Veilchenohr-Kolibris (*Colibri coruscans*). Bonn. Zool. Beitr. 31:61-77.

SCHNELL, G. D., D. J. WATT, AND M. E. DOUGLAS. 1985. Statistical comparison of proximity matrices: Applications in animal behaviour. Anim. Behav. 33: 239-253.

SKUTCH, A. F. 1967. Life histories of Central American highland birds. Nuttall Ornithol. Soc. Publ. 7.

SKUTCH, A. F. 1972. Studies of tropical American birds. Nuttall Ornithol. Publ. 10.

SMITH, W. J. 1991. Singing is based on two markedly different kinds of signalling. J. Theor. Biol. 152: 241-253.

SNOW, B. K. 1974. Lek behavior and breeding of Guy's Hermit Hummingbird, *Phaethornis guy*. Ibis 116:278-297.

SNOW, B. K. 1977. Comparison of the leks of Guy's Hermit Hummingbird, *Phaethornis guy*, in Costa Rica and Trinidad. Ibis 119:211-214.

SNOW, D. W. 1968. The singing assemblies of Little Hermits. Living Bird 7:47-55.

SPARLING, D. W. 1983. Quantitative analysis of prairie grouse vocalizations. Condor 85:30-42.

STILES, F. G. 1982. Aggressive and courtship displays of the male Anna's Hummingbird. Condor 84: 208-225.

STILES, F. G., AND A. F. SKUTCH. 1989. A guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, New York.

THIELCKE, G. 1969. Geographic variation in bird vocalizations. Pages 311-339 *in* Bird vocalizations (R. A. Hinds, Ed.). Aberdeen Univ. Press, Cambridge.

VEHRENCAMP, S. L., J. W. BRADBURY, AND R. M. GIBSON. 1989. The energetic cost of display in male Sage Grouse. Anim. Behav. 38:885-896.

WAGNER, H. O. 1945. Notes on the life history of the Mexican Violet-ear. Wilson Bull. 57:165-187.

WELLS, S., R. A. BRADLEY, AND L. F. BAPTISTA. 1978. Hybridization in *Calypte* hummingbirds. Auk 95: 537-549.

WILEY, R. H. 1971. Song groups in a singing assembly of Little Hermits. Condor 73:28-35.

WILEY, R. H., AND D. G. RICHARDS. 1982. Adaptations for acoustic communication in birds: Sound transmission and signal detection. Pages 131-181 *in* Acoustic communication in birds, vol. 1 (D. E. Kroodsma and E. H. Miller, Eds.). Academic Press, New York.

WILKINSON, L. 1990. SYSTAT: The system for statistics. SYSTAT, Inc., Evanston, Illinois.