

# SONGS OF THE COCOS FLYCATCHER: VOCAL BEHAVIOR OF A SUBOSCINE ON AN ISOLATED OCEANIC ISLAND<sup>1</sup>

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**Abstract.** The conservative song development of suboscine birds may make them better subjects than the song-learning oscines for studying the genetic evolution of vocal behaviors. We used the Cocos Flycatcher (*Nesotriccus ridgwayi*) from Cocos Island, about 500 km southwest of Costa Rica in the eastern Pacific Ocean, to test whether isolation in a depauperate avifauna has reduced song stereotypy. Males sang two song forms and females one form. Measures of both temporal and frequency parameters for the three song forms revealed that variability of songs within and among individuals was not different from that of either a close relative in species-rich South America or two distantly related *Empidonax* flycatchers in species-poor North America. Thus, the impoverished acoustic environment apparently has not markedly affected the song stereotypy of the Cocos Flycatcher. Singing behavior of the Cocos Flycatcher was unusual, however, in that the female initiated and concluded most singing interactions with her mate and sang about twice as many songs as did the male. The significance of this reversed singing role of the two sexes is unclear.

**Key words:** *Cocos Flycatcher; suboscine; vocalization; variability; songs; island; duetting.*

## INTRODUCTION

One of the least understood aspects of macrogeographic variation in bird song is the effect that avifaunal diversity, and hence the complexity of the sound environment, has on the design of vocal signals. In its simplest form, the "sound environment" hypothesis of Marler (1960) predicts a relaxation of species distinctiveness in depauperate avifaunas. There is, however, no convincing evidence of a relationship between vocal variability and species richness (Thielcke 1969, Bremond 1977, Brown 1977, Hunter and Krebs 1979, Miller 1982, Kroodsma 1985a).

One popular approach to testing this hypothesis has been to compare the songs of island birds with their closest relatives on the mainland, but the studies of Marler and Boatman (1951), Marler (1960), Thielcke (1969), Bitterbaum and Baptista (1979), and Becker et al. (1980) have not produced conclusive evidence relating vocal variability and avifaunal complexity. All bird subjects in these studies have been songbirds (oscines), species whose songs are generally learned

(Kroodsma 1982). But in songbirds both cultural and genetic evolution may occur simultaneously (Mundinger 1980, Dawkins 1982), perhaps obscuring the relative roles of each. In some songbirds "individuals are so extremely flexible at mimicking local dialects and even songs of other species that it raises the possibility that learning retards, rather than promotes, the . . . evolutionary (genetic) divergence of song" between populations (West-Eberhard 1983:175; see also Payne 1983).

We believe Marler's sound environment hypothesis should also be tested with suboscine species, such as flycatchers, whose vocal development is not dominated by song learning. Songs of flycatcher populations are less susceptible to sampling error, founder effects, and bottlenecks in population size than are the songs of a songbird (Thielcke 1983). For example, if a juvenile songbird colonizes an island before learning the species-typical song, it might imitate heterospecific song and initiate a song tradition based more on cultural accident than on natural selection. Such "errors" cannot occur with flycatchers like the Eastern Phoebe (*Sayornis phoebe*), Alder Flycatcher (*Empidonax alnorum*), or Willow Fly-

<sup>1</sup> Received 21 January 1986. Final acceptance 29 September 1986.

catcher (*Empidonax traillii*), because young birds do not have to learn songs from other adults in order to produce normal, wild-type songs (Kroodsma 1984, 1985b). Hence, any difference between mainland and insular songs would more likely result from natural selection than would the highly modifiable, plastic songs of songbirds.

We reexamine Marler's (1960) sound environment hypothesis by assessing the vocal variation in the subspecies Cocos Flycatcher (*Nesotriccus ridgwayi*), a resident of Cocos Island, Costa Rica. The only other passerine that occurs in abundance on the island is the Cocos Finch (*Pinaroloxias inornata*) (Slud 1967; Werner and Sherry, unpubl. data), and, as with other Darwin's finches, its songs are relatively simple (Bowman 1983). We then compare the songs of the Cocos Flycatcher to available songs of a close relative, the Mouse-colored Tyrannulet (*Phaeomyias murina*) (Lanyon 1984), in species-rich communities of Central and South America and to songs of two *Empidonax* flycatchers in species-poor North America. In addition, we document temporally coordinated singing by male and female *Nesotriccus* in which the female initiates and concludes the majority of interactions; duets dominated by females appear to be rare among other passerines (Levin 1983).

## METHODS

Cocos Island, Costa Rica, lies in the tropical eastern Pacific Ocean (5°32'57"N, 86°59'17"W), about 630 km northeast of the Galapagos Islands and 500 km southwest of Costa Rica. The island is 46.6 km<sup>2</sup> in area. The heavy rainfall, up to 8 m annually (Hogue and Miller 1981; Sherry and Werner, unpubl. data), and humid climate create a heavily-forested island.

During March and April of 1984 we recorded songs from 16 Cocos Flycatcher pairs. Using a Nagra IS-DT (7 1/2 ips) and Dan Gibson parabolic microphone (model EPM-200), we recorded twelve pairs (A to L) in forested habitat in the lower Rio Genio valley. On more remote Cerro Iglesias (approximately 6 to 7 km distant from and 460 m above Wafer Bay) we used a Sony WM-D6, the "Professional Walkman," with the Gibson parabola to record an additional four pairs (M, N, P, and Q). Because we recorded the flycatchers late in their reproductive cycle, they were singing at infrequent and unpredictable intervals; we therefore used song playback to stimulate singing.

Of these 32 birds, both individuals of pair J and M and one individual from pairs K (male), L (male), N (female), and Q (female) were color-banded for individual recognition. We could therefore be certain that individuals were not altering their behaviors during our recording sessions. Two birds collected on a previous expedition in March 1980 had both brood patches and ovaries, and, as in other flycatchers (Skutch 1960, 1975), apparently only the female incubates (Sherry and Werner, unpubl. data). In our present study the three birds with definite brood patches in pairs J, M, and N all sang the same song form III (see Results), and we therefore assumed that other birds singing song III were also females. We are confident of our indirect approach to sexing these birds, though these designations should in the future be confirmed with laparotomies (see also Sherry 1986).

We used a PAR 4512 spectrum analyzer and filmed the songs on 35 mm Kodak photographic paper. Selected songs were graphed on a Kay Elemetrics Model 7029A Sona-Graph with a Scale Magnifier. Temporal measures were made on wide-band sonograms (analyzing filter bandwidth, 300 Hz), and frequency was measured on narrow-band sonograms (filter bandwidth, 45 Hz). We prepared Figures 1, 2, 3, and 5 from ink tracings of the narrow-band sonograms.

## RESULTS

### SONGS OF THE COCOS FLYCATCHER

Males sang two different song forms, and females one song form, designated songs I, II, and III, respectively. These songs were often temporally coordinated as duets, with the female initiating and concluding most of them. After describing the three song forms, we then describe how the male and female interacted during a singing performance.

*Male song form I.* The loudest, most noticeable portion of this male song consisted of an explosive burst of six to nine syllables during approximately one quarter of a second (Fig. 1). The first syllable of this trill was loudest and of greatest duration; successive syllables dropped slightly in frequency and, especially after the second syllable, declined gradually in duration and markedly in intensity. Syllables loud enough to graph on a sonogram typically consisted of a note with a fundamental frequency between 1 and 2 kHz together with the second, third, and fourth

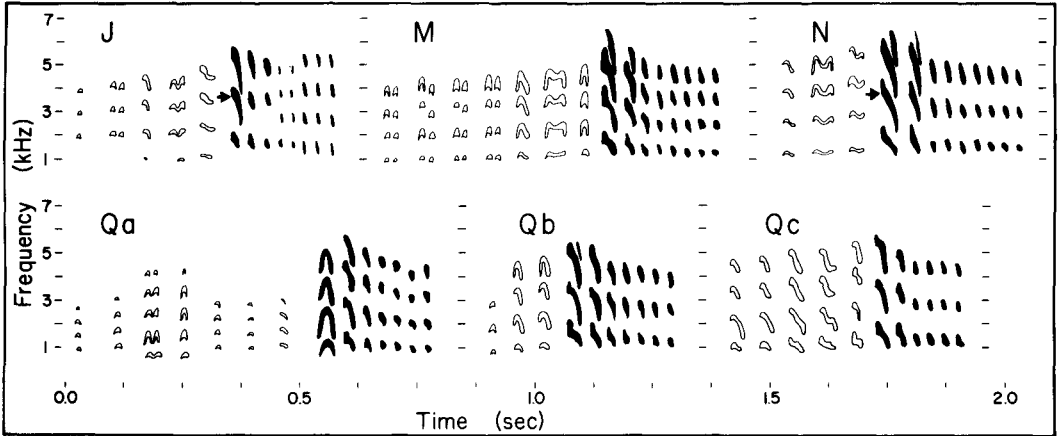


FIGURE 1. Song form I of the Cocos Flycatcher. We illustrate one example from male J, one from M, one from N, and three examples from male Q (Qa, Qb, Qc). The terminal trill (solid) is frequently given without the introductory notes (open). The small arrows on J and N indicate the frequency measure discussed in the text.

harmonics of that note. About half of the songs recorded from all males also began with a series of variable and low intensity introductory notes. These notes typically increased both in frequency and intensity, serving as an effective buildup to the first one or two loud notes of the terminal trill.

There was relatively little variability in this song form within and among males on Cocos Island. The variability consisted mostly of the form and number of introductory notes, though these notes seemed to be shared by all members

of the population. To quantify the variability in the terminal trill, we measured both temporal and frequency parameters (Table 1). The only frequency measure that we felt confident of measuring accurately was the lowest frequency at the onset of the second harmonic of the first syllable (arrows in Fig. 1). Temporal measures were made from the beginning of the first to the beginning of the third syllable, from the third to the fifth, from the fifth to the seventh, and from the first to the sixth syllable. Individual and population means, together with the low coefficients of vari-

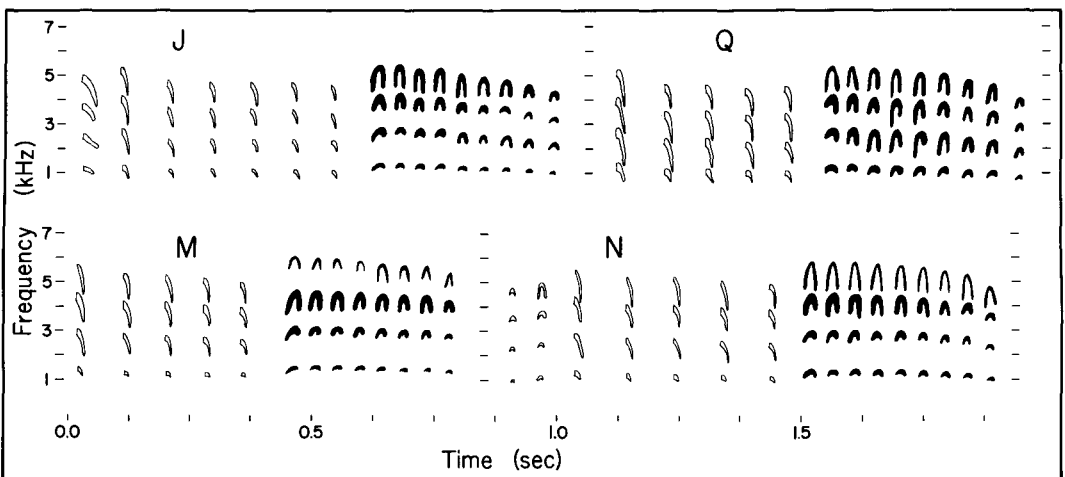


FIGURE 2. Song form II of the Cocos Flycatcher. One example from each of four males is illustrated. The introductory notes (open) and terminal trill (solid) always occurred together.

TABLE 1. Descriptive statistics for song form I of the Cocos Flycatcher.

Pair	Mean duration between syllables <sup>a</sup>				Mean frequency of first syllable <sup>b</sup>
	1-3	3-5	5-7	1-6	
J	0.070 (5.5)	0.057 (5.7)	0.051 (10.1)	0.151 (3.6)	3.53 (4.0)
M	0.081 (4.7)	0.057 (5.6)	0.054 (4.1)	0.165 (4.3)	3.43 (7.6)
N	0.096 (12.2)	0.058 (4.3)	0.056 (3.9)	0.181 (8.4)	3.73 (4.1)
Q	0.080 (4.4)	0.064 (2.4)	0.062 (2.5)	0.175 (2.0)	3.39 (4.9)
All pairs <sup>c</sup>	0.087 (12.0)	0.058 (5.7)	0.057 (9.3)	0.174 (6.3)	3.65 (8.6)

<sup>a</sup> Duration (sec) from the beginning of one syllable to beginning of next with the coefficient of variation (%) in parentheses. Sample sizes for Pairs J, M, N, and Q are 14, 15, 9, and 13, respectively.

<sup>b</sup> Measured at lowest frequency at onset of second harmonic (see Fig. 1 and text).

<sup>c</sup> One high quality song from each of the 16 pairs was chosen for these population statistics.

ation (Table 1), confirmed that this song form was very stereotyped.

*Male song form II.* All males also shared the same basic form of this second song (Fig. 2). The song began with low intensity introductory notes, and ended with a louder terminal trill of seven to ten syllables. As with song form I, the initial syllables in the trill were the loudest, and successive syllables declined in both frequency and intensity. The fundamental frequency was between 1.0 and 1.5 kHz, but most of the energy was contained in the second, third, and fourth harmonics. The overall rate of repetition of the syllables in the terminal trill was about 30% slower than in song form I. The decline in frequency and intensity of syllables was more gradual than in song I and there was no consistent shortening of successive syllables.

To quantify the variability in the terminal trill of this song form (Table 2), we measured the duration from the first to the fourth and from the fourth to the seventh syllable. In addition, we measured the maximum frequency of the second harmonic of the first, third, fifth, and seventh syllables. Successive renditions of this song form by the same male were stereotyped, with a me-

dian coefficient of variation of only 2.8% for all parameters. Variability among pairs was greater in the temporal measures (CV's of 9.0 and 21.5%), but ranged from only 2.5 to 4.5% for the four frequency measures.

*Female song form III.* The female had only one basic song form (Fig. 3). This song typically began with a series of nearly identical syllables, the first 9 to 10 of which gradually declined in frequency, duration, and, less noticeably, in intensity. After approximately 10 syllables, intensity and frequency dropped rapidly, often abruptly. If the male did not respond, the song would usually fade and stop after a single burst of singing (e.g., Fig. 3, females J, Q, and N). If the male was nearby and interacting vocally with the female, however, she usually sang two songs in rapid succession (e.g., Fig. 3, female M).

To assess the variability of this song we measured the maximum frequency of the second harmonic for every other syllable from 1 to 11 and the duration between the first and fifth, fifth and ninth, and ninth and thirteenth syllables (Table 3). As revealed by the similarity of the sonograms (Fig. 3), the similar means for temporal and frequency measures among the females (Table 3),

TABLE 2. Descriptive statistics for song form II of the Cocos Flycatcher.

Pair	Mean duration between syllables <sup>a</sup>		Mean frequency (kHz) for syllables in terminal phrase			
	1-4	4-7	Syllable number <sup>b</sup>			
			1	3	5	7
J	0.128 (4.7)	0.135 (3.7)	2.83 (1.9)	2.76 (2.1)	2.60 (1.6)	2.44 (3.1)
M	0.140 (2.0)	0.138 (2.5)	2.96 (6.0)	2.91 (6.3)	2.83 (6.9)	2.73 (7.4)
N	0.138 (2.8)	0.139 (3.0)	2.93 (4.1)	2.95 (2.8)	2.88 (4.2)	2.66 (7.1)
Q	0.130 (1.2)	0.146 (1.2)	2.88 (1.4)	2.82 (0.8)	2.70 (1.9)	2.50 (2.5)
All pairs <sup>c</sup>	0.139 (9.0)	0.131 (21.5)	2.87 (4.5)	2.83 (3.4)	2.67 (3.5)	2.49 (2.5)

<sup>a</sup> Duration (sec) with coefficient of variation in parentheses. Sample sizes for Pairs J, M, N, and Q are 11, 8, 3, and 5, respectively.

<sup>b</sup> Measured at the maximum frequency of the second harmonic.

<sup>c</sup> One song from each of 13 pairs (no song from E, H, or P) was chosen for these population statistics.

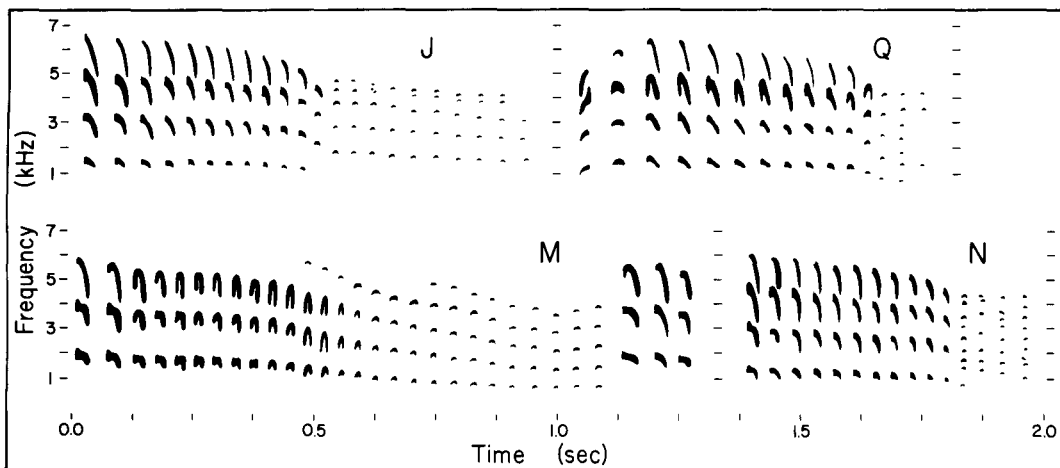


FIGURE 3. Song form III of the Cocos Flycatcher. We illustrate one example from each of four females. The song for female M is most typical, but it is abbreviated, for only the first three loud syllables of the second song are shown; as illustrated in Figure 4, the male's song (either I or II) would typically occur between 0.5 and 1.1 sec in this sequence.

and the low coefficients of variation both within and among females (Table 3), these song forms were also stereotyped within the population.

*Coordinated singing of male and female.* In our recordings, the female sang more than did the male (Table 4). Overall, from pairs J, M, and N, we recorded a total of 505 type III songs (footnote, Table 4). From the males we recorded 201 type I songs and only 60 type II songs. Thus, the females sang nearly twice as many songs as did the males. Furthermore, song form I of the male was much briefer than was song III of the female, and the impression that the female was doing most of the singing on the territory was therefore reinforced.

The relative number of male and female songs was in part a consequence of the style of singing interactions between the male and female. For example, from male J we recorded a total of 150 songs; 120 (80%) were single songs (89 of song form I and 31 of song form II, Table 4) occurring between two female songs. On only 26 occasions did the male appear to initiate an interaction, for no female song had occurred during the previous 5 sec. The data for pairs M and N, the other two pairs for which we had the most recordings, were similar to these data for pair J (Table 4).

Thus, in most examples the female initiated the singing interaction. She typically sang one of her songs, and while that song was fading the male contributed his song. His song in turn elic-

ited, in quick succession, a second song from the female (Fig. 4, Table 5). For pair J, for example, the female's first song typically began 1.40 sec before the terminal trill of the male's song I, but the second female song followed the beginning of the terminal trill of song I by only 0.37 sec (median times in Table 5). With pairs M and N the male typically uttered his song I less than a

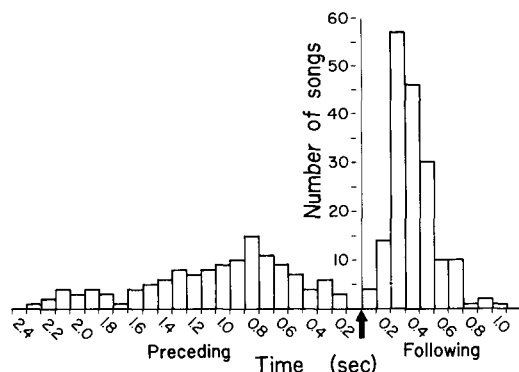


FIGURE 4. Temporal relationship of male song I and female song III in pairs J, M, and N (data combined) of the Cocos Flycatcher. The ordinate is the number of female songs. The reference point on the abscissa, time zero ("0") indicated by the arrow, is when the terminal trill of the male song begins, and the time (sec) indicates the preceding and following intervals (i.e., 0.2 references the interval 0.11 to 0.20) during which the female song began. There were 139 female songs preceding and 175 female songs following male song I during the intervals illustrated.

TABLE 3. Descriptive statistics for song form III of the Cocos Flycatcher.

Pair	Mean duration between syllables <sup>a</sup>				Frequency of syllables <sup>b</sup>				
	1-5	5-9	9-13	1	3	5	7	9	11
J	0.214 (8.1)	0.157 (5.2)	0.144 (3.1)	3.62 (5.6)	3.58 (4.6)	3.44 (3.9)	3.28 (5.9)	3.01 (10.3)	2.65 (16.5)
M	0.199 (5.7)	0.149 (5.8)	0.141 (3.0)	3.89 (8.2)	3.63 (7.3)	3.50 (9.0)	3.41 (10.1)	3.30 (10.3)	3.01 (16.0)
N	0.191 (6.9)	0.158 (2.8)	0.142 (3.6)	3.20 (3.4)	3.06 (2.1)	2.99 (2.0)	2.91 (1.9)	2.82 (3.0)	2.48 (14.0)
Q	0.232 (4.3)	0.166 (6.4)	0.144 (3.3) <sup>c</sup>	3.36 (3.9)	3.27 (2.5)	3.10 (3.2)	2.99 (2.8)	2.81 (5.0) <sup>d</sup>	2.24 (19.2) <sup>e</sup>
All pairs <sup>f</sup>	0.214 (8.9)	0.167 (10.4)	0.155 (7.4)	3.56 (7.6)	3.49 (7.3)	3.30 (10.0)	3.19 (11.4)	3.11 (7.5)	2.76 (12.2)

<sup>a</sup> Duration is in sec with coefficient of variation in parentheses. Sample sizes for Pairs J, M, N, and Q are 14, 11, 15, and 18 songs, respectively, except where indicated.

<sup>b</sup> Measured at maximum frequency of the second harmonic.

<sup>c-e</sup> Sample sizes for these data are as follows: c(16), d(17), e(14).

<sup>f</sup> One song from each of the 16 pairs was chosen for these population statistics.

TABLE 4. Use of song forms I and II by 3 male Cocos Flycatchers (J, M, and N).<sup>a</sup>

	Song form I			Song form II		
	J	M	N	J	M	N
Initiating the duet	23	9	2	3	2	1
Ending the duet	0	3	0	0	2	0
Between two female songs	89	50	19	31	15	6
Successive songs between two female songs <sup>b</sup>	4	2	0	0	0	0
Totals	116	64	21	34	19	7

<sup>a</sup> Females J, M, and N sang 300, 181, and 74 songs of form III, respectively, in this sample. Thus 30, 33, and 21 songs from females J, M, and N, respectively, were solo songs, i.e., unaccompanied by male song.

<sup>b</sup> Songs of form I given in rapid succession between two female songs.

second (0.96, 0.69 sec, respectively, compared to 1.40 sec for pair J) after the beginning of the first song III. We could discern no contextual differences in the use of the two male songs, and each of the two song forms was used in the duet with the same degree of synchrony (Table 5).

SONGS OF OTHER FLYCATCHERS

*Mouse-colored Tyrannulet.* To compare our recordings of the Cocos Flycatcher with the songs of the Mouse-colored Tyrannulet, we would ideally want recordings from several tyrannulet males at one locality or perhaps from two nearby localities. We could then compare both individual and population variability in the songs of the two species. We do not have this ideal combination of recordings, but we do have available Cuts 1 to 8 of the Schwartz collection at the Cornell Library of Natural Sounds. In this collection are nine excellent recordings of this species from Venezuela.

In most of these recordings, the bird (presumably the male) alternated between two basic call or song types. For example, two clearly distinct songs with different introductions but nearly identical concluding trills were alternated in the dawn song of Cut #1 (Fig. 5); much like the Eastern Phoebe in its dawn song (e.g., Smith 1977), this bird sang one to six renditions of one song type (A) before singing a single example of the other type (B). In six other recordings that Schwartz specifically labelled "dawn song" or simply "song" (Cuts 2, 3, 6a, 6b, 7, and 8), this same tendency to alternate between two song types with different introductory notes but identical concluding trills was evident. Even in "regular day-time calls" (Cut 4) this dichotomy per-

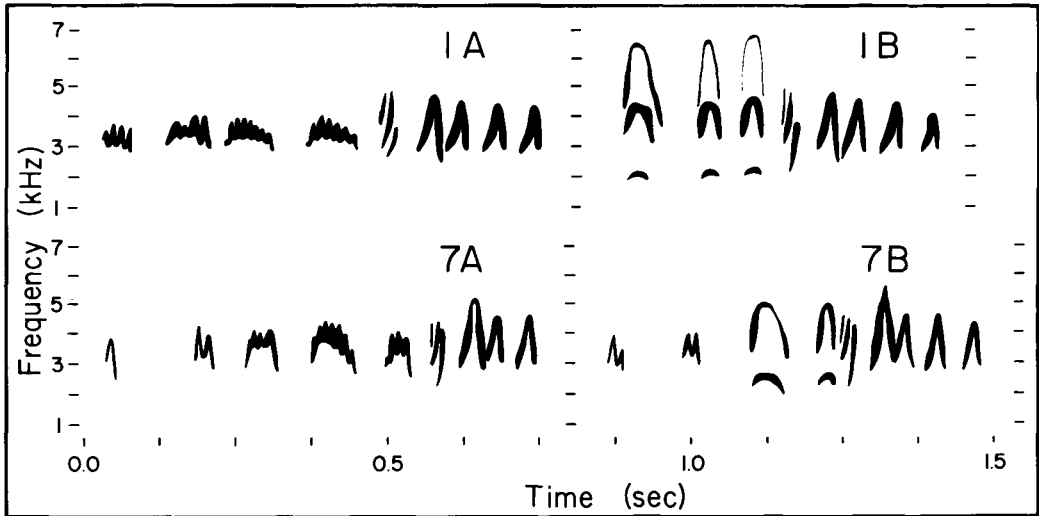


FIGURE 5. Two song forms (A and B) of the Mouse-colored Tyrannulet from Cuts 1 and 7 of the Paul Schwartz collection, housed in Cornell's Library of Natural Sounds.

sisted; the calls were somewhat like incomplete songs, with only the introductory notes to the two song forms being sung. One example of "evening song" contained only four vocalizations of one type; these appeared more similar to one of the calls in Cut 4 than to songs in other Cuts. In still other recordings, Theodore Parker (pers. comm.) has reported what appears to be duets in this species.

The relative brevity of the recordings (4 to 46 calls or songs) and the variety of songs and calls provide only a glimpse of the vocal behavior of this species, and our conclusions regarding population and individual variation are therefore limited. Like other flycatchers, though, birds from the same general area shared essentially identical song forms. Cuts 1, 2, 3, 7, and 8 from Caracas, Venezuela, and vicinity contained nearly identical examples of song A, and Cuts 1, 3, and 8 had nearly identical forms of the less frequently used song B (Fig. 5). Other Cuts seemed to con-

tain incomplete songs or to share similar call types.

To assess variation in successive renditions of songs by an individual, we compared temporal and frequency parameters of the two song forms of Cut 1 (1A and 1B in Fig. 5) and Cut 7 (7A, 7B). The CV's for the frequency of the first trill syllable in the four Mouse-colored Tyrannulet songs were 1.4% (1A,  $n = 11$ ), 1.9% (1B,  $n = 12$ ), 1.0% (7A,  $n = 13$ ), and 1.7% (7B,  $n = 8$ ); these values were significantly different from (i.e., smaller than) the CV's for the frequency of first syllables in the songs for individual Cocos Flycatchers reported in Tables 1 to 3 (2-tailed Mann-Whitney U-test;  $n_1 = 12$ ,  $n_2 = 4$ ,  $U = 45$ ,  $P = 0.01$ ; because the songs of male and female Cocos Flycatchers did not differ consistently in the variability of measured parameters, we combined data from the two sexes for these comparisons with other species). There was, however, no difference in variability of the third trill syllable;

TABLE 5. Number of seconds by which female song III preceded or followed songs I and II of the male Cocos Flycatcher.

Pair	Song I		Song II	
	Preceded by III	Followed by III	Preceded by III	Followed by III
J	1.40 (1.74, 56.0) <sup>a</sup>	0.37 (0.52, 92.5)	1.45 (1.71, 42.2)	0.45 (0.56, 58.3)
M	0.96 (1.42, 89.3)	0.38 (0.64, 139.3)	1.08 (1.49, 67.5)	0.30 (0.30, 40.6)
N	0.69 (0.91, 83.3)	0.34 (0.47, 109.0)	1.93 (1.87, 46.3)	0.32 (0.32, 28.9)

<sup>a</sup> Median, with mean and coefficient of variation in parentheses. Sample sizes for male songs uttered "between two female songs" are given in Table 4.

CV's for songs 1A (1.0%, sample sizes as above), 1B (7.2%), 7A (4.6%), and 7B (1.4%) were comparable to those listed in Tables 2 and 3 for the Cocos Flycatcher (2-tailed test,  $n_1 = 8$ ,  $n_2 = 4$ ,  $U = 18$ ,  $P > 0.2$ ). Nor was there a difference in variability of the duration from the beginning of the first trill syllable to the beginning of the third or fourth trill syllable; CV's for songs 1A (1.3%), 1B (2.1%), 7A (4.9%), and 7B (4.1%) were not different from those listed in Tables 1 to 3 for the Cocos Flycatcher (2-tailed test,  $n_1 = 12$ ,  $n_2 = 4$ ,  $U = 35$ ,  $P > 0.2$ ). Overall, then, in only one out of three measures did we find that individual Cocos Flycatchers sang more variable songs than did individuals of this close relative on the mainland (see Discussion on how to interpret this difference).

*Empidonax flycatchers.* Data on song variability among males, but not within males, were available for the *fee-bee-o* song of the Alder Flycatcher and the *fizz-bew* and *fizz-bew* songs of the Willow Flycatcher from western Massachusetts (Kroodsma 1984). Median coefficients of variation for duration measures in these three song forms were 15.2% ( $n = 13$  CV's; each CV was obtained by measuring a representative song from each of 15 birds), 8.9% (8 CV's, 23 birds), and 10.1% (8 CV's, 23 birds), respectively (from tables 1, 2, and 3 in Kroodsma 1984). For the Cocos Flycatcher, the median CV for nine measures of duration (from Tables 1 to 3) was 9.0%. There was no significant difference in song variability in these measures of duration (2-tailed Mann-Whitney U-test,  $n_1 = 29$ ,  $n_2 = 9$ ,  $U = 163$ ,  $P > 0.2$ ), though the Cocos Flycatcher songs tended to be less variable.

For each of the three *Empidonax* songs two measures of frequency were available. The median CV's for the three songs were 5.0, 15.0, and 13.6, respectively, while the median CV for 11 frequency measures of the Cocos Flycatcher songs was 7.5. Again, the measures for the Cocos Flycatcher songs tended to be less variable than those for the two *Empidonax* species (2-tailed Mann-Whitney,  $n_1 = 11$ ,  $n_2 = 6$ ,  $U = 50$ ,  $P = 0.1$ ).

## DISCUSSION

During its period of isolation on Cocos Island, the Cocos Flycatcher has diverged both morphologically and behaviorally from its mainland relatives (Sherry 1985). Thus, there has been sufficient time for genetic evolution to occur. The song of this flycatcher is unique as well, though

experienced tropical biologists have "remarked on the great similarity between the vocalizations of *Nesotriccus* and *Phaeomyias*" (Lanyon 1984).

In comparison to songs of other flycatchers, songs of the Cocos Flycatcher are neither elaborate nor especially simple. Males share two relatively simple song forms (I and II) with one another, and females also sing a highly stereotyped pattern (III) that is shared with other females. Intra- and inter-individual variation are comparable to the variation in songs found among *Phaeomyias* populations in Venezuela and *Empidonax* populations in the northeastern United States. When comparing individual variability we found that one of three measures of *Nesotriccus* songs was more variable than in the *Phaeomyias* songs; in population variability both duration and frequency measures of the *Nesotriccus* songs tended to be less variable than the *Empidonax* songs. Some added variability in the *Nesotriccus* songs was undoubtedly due to recording techniques: songs of *Nesotriccus* individuals were recorded after occasional playback over a period of several hours to several days, and we can expect these songs to be somewhat more variable than songs recorded during several minutes of an undisturbed singing sequence, as in the *Phaeomyias* flycatchers. We also realize that there are hazards in comparing songs that are dissimilar in structure and in measuring relatively few parameters on song features for which we do not know the function (e.g., whether used in individual, population, or species recognition); there is no easy solution to this difficult problem. Yet, because our quantitative analyses substantiated our qualitative impressions of these songs, we are confident of our overall conclusions. There are certainly no striking differences in song variability among these flycatcher species, and our belabored attempts to detect slight but consistent differences in variability have not been greatly successful. We therefore conclude that songs of the Cocos Flycatcher are typical, stereotyped tyrannid songs, and that the depauperate avifauna of Cocos Island has not affected variability in the songs of this species.

Adaptation to the physical "acoustical environment," i.e., the sound transmission properties of the Cocos Island habitat, may have helped shape the present day song of the Cocos Flycatcher. Bowman (1979, 1983) finds this explanation for the "adaptive morphology" of bird song more tenable than any character or variance



shifts (see Miller 1982) occurring as a result of avifaunal complexity. The song of the Cocos Finch does vary throughout the island (Werner and Sherry, unpubl. observ.), perhaps in a manner consistent with this hypothesis. Yet *Nesotriccus* lives in rainforest on Cocos Island, while *Phaeomyias*, whose songs are quite similar, lives in xeric scrub habitats on mainland Central and South America. Such evolutionary flexibility in matching vocal patterns to habitat types may occur in song-learning oscines (Bowman 1979, Gish and Morton 1981, Wiley and Richards 1982), but these adaptations remain to be demonstrated for species, such as flycatchers, in which vocal development is less flexible and songs are not learned from other adults.

Song variability in the Cocos Flycatcher is not strikingly different from that of other flycatchers, and the duetting mode of interaction between the sexes is also not unique. Many other suboscines duet, although ours is the first quantitative study of this behavior in the group. Farabaugh (1982) lists from Panama one furnariid, 18 formicariids, three cotingids, and 15 additional tyrannids that "duet" by her definition. Theodore A. Parker (unpubl. data) lists an additional 11 tyrannids that sing synchronized duets: *Octhoeca leucophrys*, *O. rufipectoralis*, *O. cinnamomeiventris*, *Ochthornis littoralis*, *Myiozetetes similis*, *Todirostrum calopterygum*, *T. maculatum*, *Capsiempis flaveola*, *Stigmaturota budytoides*, *S. napensis*, and *Serpophaga cinerea*. Thomas (1979) also describes duetting in a tyrannid (*Conopias inornata*) from Venezuela, and Skutch (1960) confirms duetting in several of the above species.

The dominant singing role of the female appears to be an intriguing reversal from that described for other suboscines and oscines. About 80 percent of the male songs in our samples appear to occur as a response to the female song. Most singing sessions with no playbacks contained this same style of female-male interaction, so we do not believe that our results are an artifact of our recording techniques. One recording, for example, consisted of a session during the afternoon when an isolated female, apparently near her nest, uttered many single songs with no response from her mate. We never heard males solo singing like this. In general it seems as though the female invites the male to sing; if he does not sing, she stops with a single song, but once he responds to her, she replies immediately with

another song. By using occasional playbacks of both male and female songs to stimulate singing, we were essentially simulating a territorial intrusion. It was our impression during these playbacks that the female approached the speaker as closely as and often more closely than the male. Taken together, these data and observations suggest that, at least during that part of the season during which we studied these birds, the female has an aggressive and dominant role in singing and territory defense.

A review of the literature indicates that there are few studies in which the birds were actually marked and sexed, and therefore we find it difficult to assess the uniqueness of our Cocos Flycatcher singing patterns. Only in the Bay Wren (*Thryothorus nigricapillus*) do females appear to initiate a duet routinely (Levin 1983), though the similarities to the female-initiated duets in Bornean gibbons (*Hylobates muelleri*) are intriguing (Mitani 1984, 1985). Before singing patterns and aggressive behaviors of passerines can be fully understood, we will need additional data on both male and female song throughout the reproductive cycle, from different taxonomic groups, and across different ecologies and social systems.

#### ACKNOWLEDGMENTS

For generous support, without which this and other Cocos Island studies would not have been possible, TKW and TWS acknowledge the National Geographic Society, EARTHWATCH and the Center for Field Research, the Frank M. Chapman Memorial Fund, the Alexander Wetmore Fund, the George D. Harris Foundation, the Western Foundation of Vertebrate Zoology, and the Univ. of Massachusetts Department of Zoology for financial support; Johnson Camping Inc., The Coleman Company, Woolrich, Pelican Products, and the United States National Museum (Divisions of Birds and Mammals) for equipment loans and donations; the Servicio de Parques Nacionales de Costa Rica (especially F. Cortés) for permission to work on Cocos Island; and the Organization for Tropical Studies and Stewart L. Carse (TI2SLC) for help with logistics. In addition, we thank the Cornell Library of Natural Sounds (especially Jim Gullede and Andrea Priori) for generous help; Gene Morton, Theodore Parker, Betsy Thomas, and especially Rachel Levin for sharing unpublished data and ideas; Susan Peters (PHS BRSG SO7RR07065) for filming flycatcher songs; George Drake, Tod Highsmith, and David Spector for help with logistics; Rachel Bereson and Tony Masuck for help with analyses; and the National Science Foundation (BNS 820185 and 8506996 to DEK) for financial support.

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