The Condor 94:680–691

SONG CHARACTERISTICS AND VARIATION IN A POPULATION OF BANANAQUITS ON PUERTO RICO[1]

JOSEPH M. WUNDERLE, JR.[2]
Department of Biology, University of Puerto Rico, Cayey, Puerto Rico 00633 and
Institute of Tropical Forestry, Southern Forest Experiment Station, USDA Forest Service,
P.O. Box B, Palmer, Puerto Rico 00721

RAFAEL A. CORTES AND WILLIAM CARROMERO
Department of Biology, University of Puerto Rico, Cayey, Puerto Rico 00633

Abstract.—Bananaquits (*Coereba flaveola*) in a high density island population with small permanent territories, numerous intraspecific interactions, and polygyny, showed many of the song characteristics expected for species with these life history traits. These song characteristics included high singing rates, relatively large song repertoires (120–340 song types per male); predominance of rare song types; and sequence of song types presented with a pattern approaching immediate variety. Note arrangement within a song was indeterminate and nonrandom; the probabilities of occurrence of a specific note type depended on at least the immediately preceding note. Nine males uttered 10 different note types, of which 9 were shared by all; nonetheless, few song types were shared by neighbors. Different song types were produced primarily by the addition or deletion of notes at the end of a song, whereas the introductory notes were less variable. Males differed from each other in note usage and song types, but produced similar levels of song variation. No consistent relationship was found between singing continuity and song versatility. Songs of two juveniles (4–5 months), a yearling (10–11 months), and older (> 1 yr) males indicated that song variation declines with age until at least the second year, when the sequence of notes in a song becomes more predictable.

Key words: Vocalizations; Bananaquit; Coereba flaveola; *Puerto Rico; island.*

INTRODUCTION

Comparative studies of vocal behavior of North American wrens (Troglodytidae) and European warblers (Sylviidae) have revealed correlations between repertoire size and the ecology of closely related species (Kroodsma 1977, Catchpole 1980). These studies indicate that complexity of song repertoires is closely related to intraspecific population density (Kroodsma 1983). The association of large vocal repertoires and elevated singing rates with high intraspecific population density may arise because high densities may result in frequent interactions. These interactions may increase singing rates and eventually contribute to a more elaborate repertoire which maintains a stimulating vocal performance (Kroodsma 1990). Typical of species that exhibit this behavior are Sedge Wrens (*Cistothorus platensis*) in which males exhibit relatively large song repertoires, little immediate repetition of song types, high singing rates, and a tendency for song versatility to increase with an increase in singing rates (Kroodsma and Verner 1978). Factors such as polygyny and opportunistic breeding also may contribute to the evolution of these song characteristics (Kroodsma 1977).

Small territory sizes, high conspecific densities, frequent intraspecific interactions, polygyny and opportunistic breeding are characteristic of many island populations of Bananaquits, *Coereba flaveola* (Wunderle 1982, 1984). If such traits influence the evolution of singing behavior of passerines, then the singing behavior of Bananaquits should be similar to that of unrelated species exhibiting similar life history characteristics. Our paper describes song variation and repertoire size within and among individuals and examines the effect of age on song variation in a population of Bananaquits on the Caribbean island of Puerto Rico.

STUDY AREA AND METHODS

This study was conducted on the campus of the University of Puerto Rico in Cayey at an altitude

---

[1] Received 18 November 1991. Accepted 12 March 1992.

[2] Present address: Institute of Tropical Forestry, Southern Forest Experiment Station, USDA Forest Service, P.O. Box B, Palmer, Puerto Rico 00721.

of 460 m. The 1.5 ha study site, located in an arboretum, contains a mixture of variably spaced ornamental trees (12–14 m tall) in the genera *Tabebuia, Pithecellobium, Delonix, Calophyllum, Eucalyptus,* and *Mangifera.*

Mist nets were used to capture Bananaquits in August 1988. Each adult (≥1 year of age) was marked with a unique combination of three color-bands and a U.S. Fish and Wildlife Service band. Juveniles were banded only with U.S. Fish and Wildlife Service bands. The locations and boundaries of each male's territory and the status of his mate were determined by monthly observations from October 1988 to May 1991.

All vocalizations were recorded using either a microphone mounted on a Dan Gibson Parabolic reflector or a ME 88 head on a K3U Sennheiser microphone with a Sony TCM 5000 tape recorder. Songs were analyzed using a Kay Elemetrics Corp. DSP Sona-Graph, Model 5500, with both wide and narrow bands at the high shape setting. For purposes of this study, a sound producing a continuous mark on a spectrograph was designated as a note, whereas songs usually consisted of a group of notes in which the time interval between the notes was shorter than the time interval between songs. However, males often uttered an extended solo "A" note, which for convenience, we have designated as a song type when produced with a gap between subsequent renditions (>3 sec) comparable to the inter-song interval in a normal sequence of songs. A song bout was defined as continuous singing uninterrupted by silence longer than 30 sec. Songs per bout provided a more accurate measure of a male's uninterrupted singing activity, because males occasionally left the territories for several minutes at a time or were involved in chases or fights in which only call notes were uttered.

A focal individual sampling technique (e.g., Altmann 1974) was used. Vocalizations of territorial males were recorded and additional behavior noted during 30 min observation periods starting at 06:30, 07:30, 08:30, 09:30, and 10:30 hr respectively. Between observation periods, we searched for nests and sought to determine the reproductive status of individuals. We recorded vocalizations of color-banded males during all observation periods and stages of the nesting cycle (Wunderle et al., ms) to document overall repertoire size during the breeding season. However, detailed analyses of song characteristics and variation within and among males were restricted to songs produced during a two week period prior to clutch initiation (i.e., pre-breeding stage). Because Bananaquits are multi-brooded, pre-breeding periods can occur 3–4 times during a breeding season, depending upon the number of breeding attempts. We excluded songs produced while the focal male was fighting or chasing an intruding male.

The vocal behavior of nine adult males was documented from January through June 1989. One of these males was also observed during the same period in 1990. All adult males were in at least their second breeding season and older than one year of age, as indicated by plumage (Wunderle, unpubl. data). These males were observed with their color-banded mates at least three months prior to the breeding season.

A different male was observed during each 30 min observation period. Males were observed for an average of 10 (range 4–26) observation periods. Although recordings were obtained from nine adults, we did not obtain sufficient samples from all time periods for five males. Therefore, we used four adult males (WW-XR, $n = 406$ songs, $n = 29$ bouts; BW-RX, $n = 161$ songs, $n = 23$ bouts; BX-YW, $n = 357$ songs, $n = 31$ bouts; XB, $n = 976$ songs, $n = 65$ bouts) with adequate samples for the analyses involving time of day and for the more detailed analyses requiring large samples during the pre-breeding period.

Male XB was first captured on 5 August 1988, with juvenile plumage (7–8 months of age). Subsequently he was observed establishing a territory (with a female already present) on 23 October 1988. This individual was intensively recorded during both its first (January–June 1989; designated yearling) and second (January–June 1990; designated adult) breeding seasons. A sequence of 64 songs was recorded from an unbanded juvenile Bananaquit on 20 June 1989 (designated as Juvenile 1) and 94 songs, from a second individual on the opposite side of the study site (designated as Juvenile 2) on 23 June 1989. Both juveniles had plumage characteristics indicating ages of 4–5 months (Wunderle, unpubl. data). Because both juveniles sang one continuous bout each, it was not possible to analyze juvenile song variation among song bouts.

To test for differences in singing versatility among adult males, we calculated several measures. Each measure was divided by the total number of songs in a bout, thereby providing a proportional value which enabled the comparison of bouts of different sizes. For example, we calculated the proportion of song types per bout and the proportion of transitions between different song types per bout. As a measure of total versatility, we calculated the product of the total song types in the bout by the number of transitions among song types in the same bout (after Kroodsma and Verner 1978). The degree of uncertainty with which a specific song type was found within a bout was quantified using the Shannon-Wiener information measure (Margalef 1958). For any given number of song types in a bout, the information measure is greatest when all song types are equally abundant. The Beta turnover index (Wilson and Shmida 1984) was used to measure differences in the use of song types between consecutive bouts. The higher this index, the greater the turnover between bouts.

We also examined the relation of several measures of versatility to song rates and percent performance time (see Kroodsma and Verner 1978). This was accomplished by determining song type versatility, transition versatility, total versatility, number of renditions of a song type, song length, and percentage performance time in samples of 10 consecutive songs. We also determined recurrence numbers, the number of songs between successive repetitions of song type (see Kroodsma and Verner 1978).

Our analysis involved various statistical tests (see Sokal and Rohlf 1981). Homogeneity of variances was established with Bartlett's Test before Analysis of Variance (ANOVA) was used. Two-way ANOVA without replication was used to compare song variation among males and among time periods; two-way ANOVA with replication was used to compare an individual's song variation among time periods and dates. A two-level nested ANOVA (mixed model) was used to compare song variation between adults and juveniles and among individuals within age groups. Categorical data were analyzed using several tests. A Log-Linear Model was used to examine the interaction among adult males, time periods, and note types. A Row × Column Test of Independence was used to test for independence among note types and time periods. A Chi-Square Goodness of Fit Test was used to determine if observed note transitions differed significantly from expected transitions. An Unplanned Test for Homogeneity was used with replicates tested for goodness of fit to examine preference for different note types between the two juveniles and among adults. Pearson correlation coefficients were used to establish association between two variables, and are reported in the text only when significant. A probability of type I error of 0.05 or less was accepted as significant, but we show greater values for descriptive purposes. Standard deviations are used to describe variation around the mean.

RESULTS

ADULT SONG CHARACTERISTICS AND VARIATION

Singing rates. Four males sang at a rate of 70.5 ± 52.1 songs per half hour. Although song rates varied among time periods for a single male (e.g., male XB rate ranged from 5 to 101), no significant differences in song rates were found either among males (2-Way ANOVA, $F_{3,12} = 0.77$, $P = 0.542$) or among time periods ($F_{4,12} = 0.89$, $P = 0.130$). These males produced an average of 4.6 ± 2.9 bouts per half hour, with no significant differences among males in bouts per half hour (2-Way ANOVA, $F_{3,12} = 1.44$, $P = 0.257$) or among the five time periods ($F_{4,12} = 1.53$, $P = 0.271$). Bouts consisted of 18.9 ± 16.6 songs, with no significant differences among males (2-Way ANOVA, $F_{3,12} = 0.94$, $P = 0.421$) or among time periods ($F_{4,12} = 1.41$, $P = 0.29$). Songs were uttered at an average rate of 11.9 ± 1.8 songs per min within bouts, with no significant differences among males (2-Way ANOVA, $F_{3,12} = 0.83$, $P = 0.127$) or among time periods ($F_{4,12} = 1.50$, $P = 0.269$).

Number of notes per song. Four males produced songs with an average of 5.7 ± 2.2 notes (range 1–18 notes), with a mode of four notes. The four males differed significantly (2-Way ANOVA, $F_{3,12} = 40.21$, $P < 0.001$) in average number of notes per song, but this average did not vary significantly (2-Way ANOVA, $F_{4,12} = 0.27$, $P > 0.75$) among the five time periods.

Variation in number of notes per song was sometimes complex, as determined for male XB, recorded during all five time periods and during four different pre-breeding periods (21 Jan.–1 Feb.; 22–26 Mar.; 23–26 April; 2–8 May 1990). The significant 2-way interaction between time of day and date in the ANOVA of this male's song ($F = 11.38$, $P < 0.001$) indicates that the pattern in which the number of notes per song varies with time of day is dependent upon date

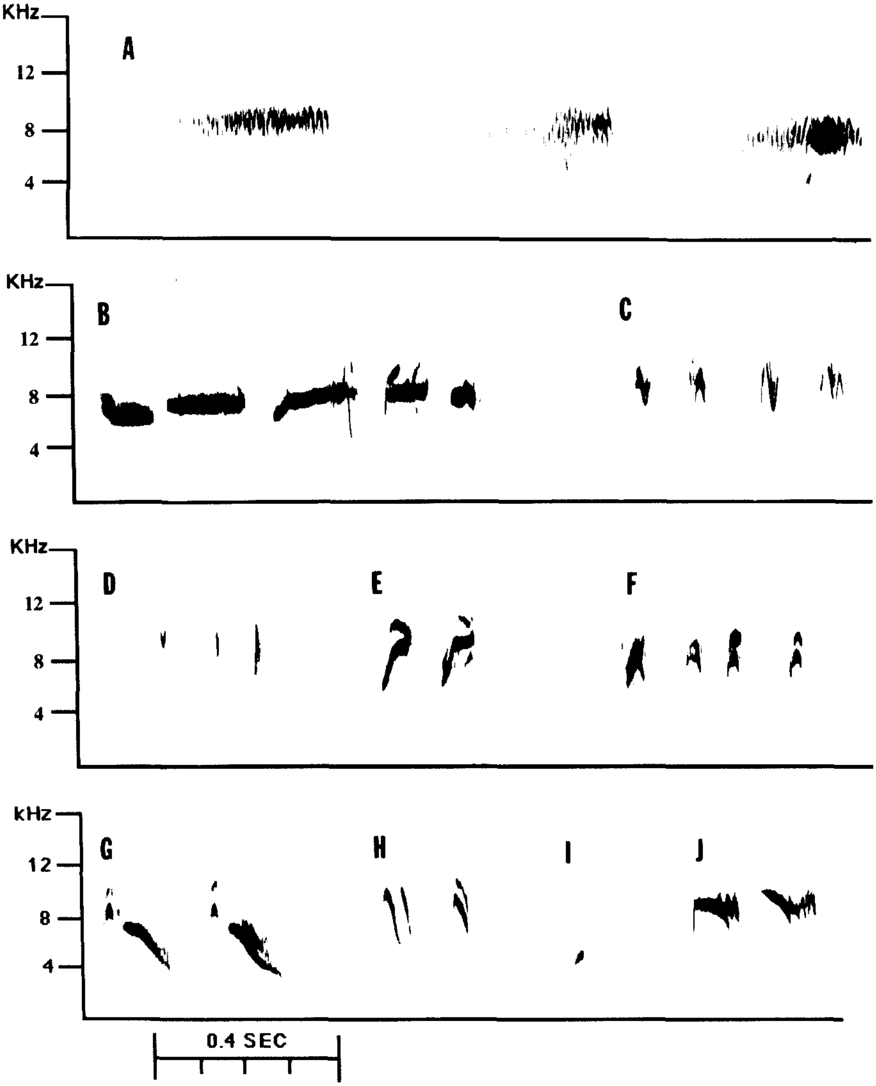

FIGURE 1. Characteristic note types of adult male Bananaquits in a population in Cayey, Puerto Rico. Each letter designates a note type and the extent of its variation found among nine males.

in the season. The significant main treatment effects (time of day, 2-Way ANOVA, $F_{4,12} = 6.71$, $P < 0.001$; date in the season, $F_{3,12} = 75.06$, $P < 0.001$) suggest that the pattern of differences in notes per song is more accentuated during some dates than others. Thus the number of notes in a Bananaquit song can vary with hour in the day and date in the breeding season, but the variation is not consistent.

Note types. Nine males in our population produced 10 different note types, with note types exhibiting both inter- and intra-individual variation (Figs. 1, 2). Nine of the 10 note types were common to all males. An introductory "A" was the most frequently used note and was found in 99.5–100.0% of all songs. An "I" was the rarest note and was present in only three (1.1%) of the 262 songs of one male.

The preference for different note types was highly variable within and among males. Analysis of note use by four males during the five sample periods revealed a significant three-way interaction among males, time, and note types (Log-Linear Model, $\chi^2 = 135.00$, df = 32, $P <$

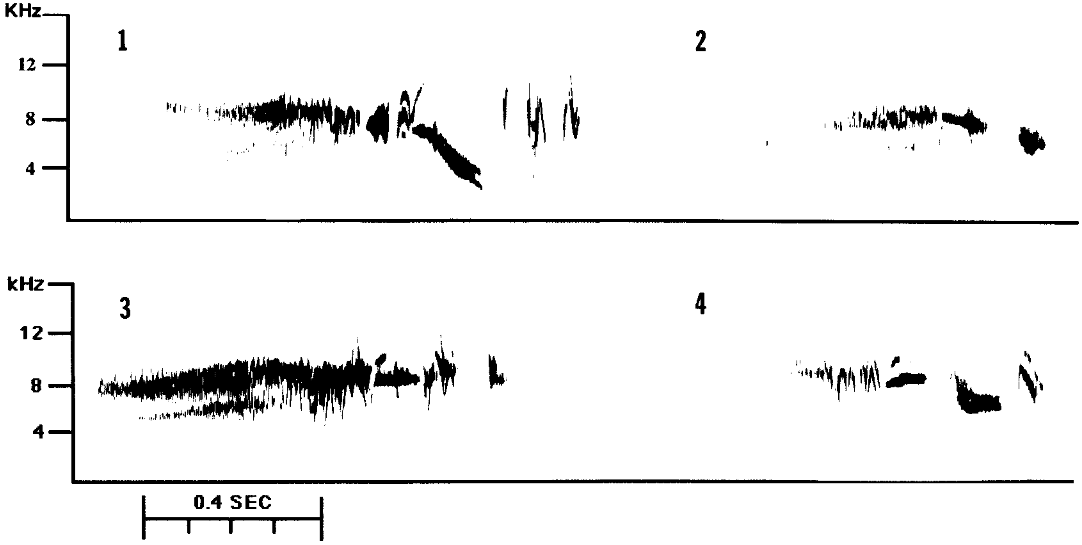

FIGURE 2. The most common song types used by individual male Bananaquits in a population in Cayey, Puerto Rico. Each number indicates the song of a different male: 1, male XB, type AFGDCC; 2, male WW-XR, type AJB; 3, male BX-YW, type ABCD; 4, male RX-YB, type ABBH.

0.001). For each male, the use of note types differed significantly among the time periods. For example, "A" was the most frequently uttered note by WW-XR at 06:30 (29.3% of 352 notes); "E" (21.1% of 318 notes) at 08:30, and "A" (35.1% of 94 notes) was again the most common at 10:30. This reflects the significant difference in note usage among time periods (Row × Column Test of Independence, $G = 761.74$, $df = 36$, $P < 0.001$). Likewise, note usage differed among time periods for male BX-YW (Row × Column Test of Independence, $G = 185.55$, $df = 28$, $P < 0.001$), male RX-YB ($G = 133.64$, $df = 32$, $P < 0.001$), and male XB ($G = 292.01$, $df = 32$, $P < 0.001$).

Note usage also differed among the pre-breeding stages at different times of the year. For example, the songs uttered by XB showed a significant interaction among time of day, time of year, and note type (Log-linear $\chi^2 = 894.04$, $df = 96$, $P < 0.001$). Within each time period, differences in note use were found among the four pre-breeding stages in the same breeding season. For example, significant differences in note usage were found among the four repeated stages in the season during the 06:30 period (Row × Column Test of Independence, $G = 96.95$, $df = 24$, $P < 0.001$), the 07:30 period ($G = 108.4$, $df = 24$, $P < 0.001$), 08:30 period ($G = 507.88$, $df = 24$, $P < 0.001$), 09:30 period ($G = 427.77$, $df = 24$, $P < 0.001$), and 10:30 period ($G = 263.35$, $df = 24$, $P < 0.001$). Thus, the note composition of songs uttered by individual males varied among hours of the morning and among dates in the breeding season.

Sequential organization of notes in a song. The sequence of notes in Bananaquit songs was nonrandom, as found in transition matrices of the preceding and following notes in songs. For example, in an analysis of the first 100 songs of male BW-RX, the 305 note transitions were limited to only 19 of the 81 possible cells of the matrix (Table 1). In this male's matrix, the limited number of cells occupied by note transitions was significantly different from random (Chi-Square Goodness of Fit Test, $\chi^2 = 626.88$, $df = 47$, $P < 0.001$), as found in the songs of the eight other males. Most of the entries in the matrix fell into cells to the right and left of the major diagonal (from upper left to lower right), indicating that repetition of notes was not an important feature of the song. The presence of an approximately equivalent number of entries in the cells to the right and left of the major diagonal indicates that the note sequence in Bananaquit songs is highly indeterminate. Although males always produced songs with a nonrandom sequence of preceding and following notes in a song,

TABLE 1. Transition matrix of the preceding and following notes from 100 songs of male Bananaquit BW-RX.

Preceding note	Following note A	B	C	D	E	F	G
A	—	74	1	—	—	3	—
B	—	—	69	—	1	4	—
C	—	2	—	4	1	30	—
D	—	—	3	15	—	18	—
E	—	20	—	—	8	—	—
F	9	13	—	4	—	—	—
G	—	26	—	—	—	—	—

this sequence showed considerable variation within individual males, often varying significantly among consecutive song bouts. Thus, the organization of notes in a song was indeterminate and nonrandom, and the probabilities of occurrence of a specific note type depended on at least the immediately preceding note.

Size of song repertoire. We identified 300 different song types in the repertoire of four males. From males BX-YW, RX-YB, WW-XR, and XB, we recorded 59, 76, 85, and 101 song types, respectively. When the cumulative number of song types of adults was graphed against the total number of sampled songs, the curves asymptotically approached the total repertoire size (Fig. 3). After about 140–175 songs the curves of all four adult males leveled off at approximately 35–40 song types, although males continued to add new song types. Even after pre-breeding, new song types continued to be added to each male's repertoire, so that by the end of the breeding season, a large repertoire was documented for each male (BX-YW 120 song types in 859 total songs; RX-YB 155 types in 897 songs; WW-XR 269 types in 845 songs; XB 340 types in 3,680 songs).

Much of the variation among song types was produced by a singer's addition, deletion, substitution, or repetition of notes at the end of songs, while the first few notes of each song were repeated in consecutive songs. For instance, male RX-YB uttered the following typical sequence of

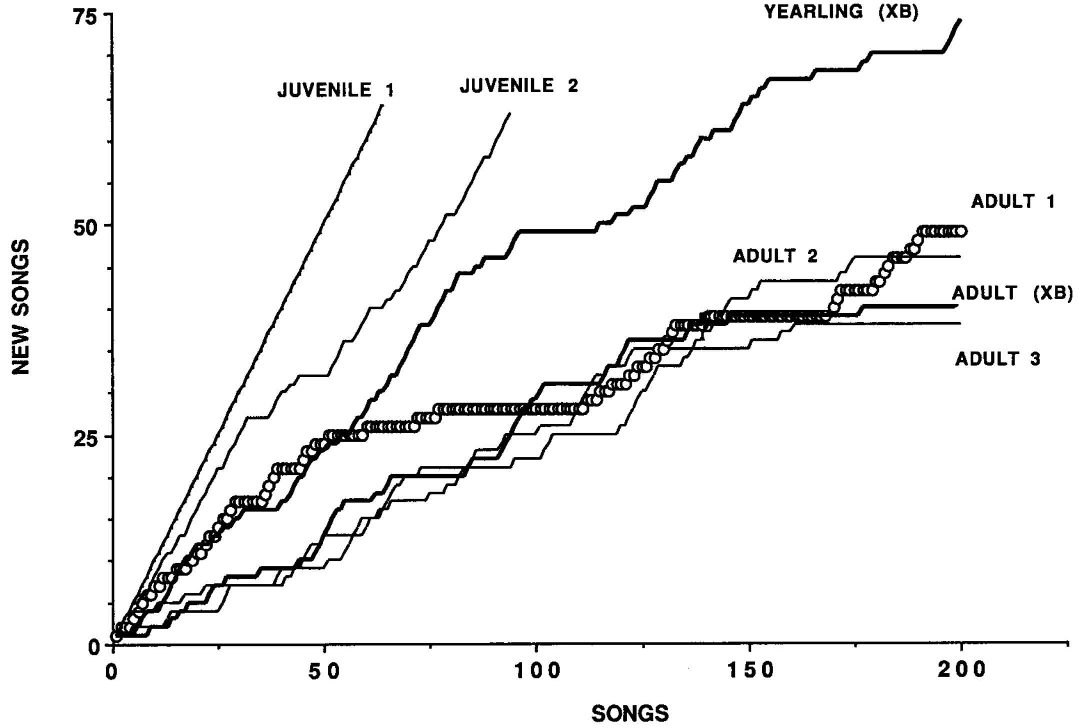

FIGURE 3. Cumulative number of new songs versus total songs in samples obtained from two juveniles, one yearling, and four adult male Bananaquits in Cayey, Puerto Rico. Male XB was recorded as both a yearling and then again as an adult in its second year. Adult 1 corresponds to male WW-XR; adult 2 corresponds to male BX-YW; adult 3 corresponds to male RX-YB.

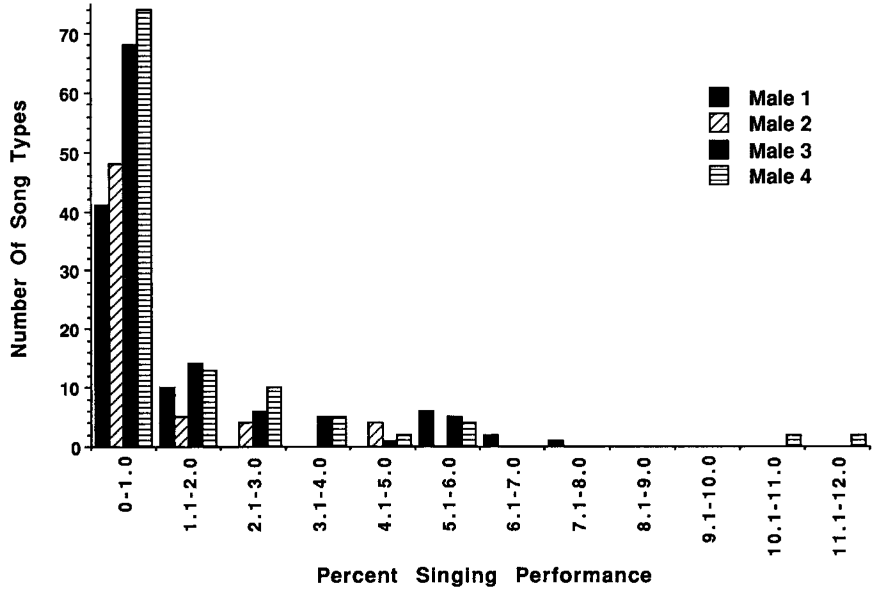

FIGURE 4. Percentage of the total singing performance devoted to different song types in four male Bananaquits. Male 1 corresponds to WW-XR; male 2 to BX-YW; male 3 to RX-YB; male 4 to XB (second year).

songs during a bout on 8 March 1989: AJBIF, AJBIF, AJBI, AJBIIIE, AJBIID, AJBI, AJBIFD-AHC, AJBIC, AJBI, AJBF, AJBI.

Most song types used by a male were rare, accounting for 1% or less of the male's singing performance (Fig. 4). Even favorite song types rarely accounted for more than 12% of a male's singing performance. After a male introduced a song type, if it re-occurred, it was most likely to be immediately repeated before disappearing from the repertoire for some time. For example, we determined the recurrence numbers for song types which were sung two or more times by a male. This analysis was restricted to the four males, when each produced more than 120 songs in a single morning. Of song types sung two or more times, most (61.0% ± 4.3) were uttered immediately after the first appearance, with fewer recurrences after one (12.8% ± 6.4), two (4.0% ± 2.4) or three (4.3% ± 1.5) intervening songs. No significant differences were found among the males in the proportion of song types with recurrence values of 0 to 10 (Row × Column Test of Independence, $\chi^2 = 39.86$, df $= 30$, $P = 0.108$). Thus, once introduced, a song type might be repeated several times in sequence, with an occasional intervening song type or two, before disappearing for 100 or more songs, when it might again be repeated.

The conservative nature of the first few notes of Bananaquit songs is illustrated by a song classification based on the first two notes which yielded only six different song types in the songs of the four pre-breeding males. Song types with the first two notes AA, AB, and AJ were found in the repertoires of all four males, songs starting with AF were used by three males, while songs starting with AC or AH were found in the songs of two males. However, when song types were classified on the basis of all notes, adult males shared few song types—only song types AB and ABC were found in the repertoires of all four adults. Among any two adult males, an average of 8.2% ± 1.7 of the song types were shared (Table 2).

Variation within song bouts. The average proportion of different song types per bout was 0.33 ± 0.19 (or 33 song types per bout of 100 songs) for the four males. No significant differences were found in average proportion of song types per bout either among males (2-Way ANOVA, $F_{3,12} = 0.60$, $P = 0.616$) or among time periods ($F_{4,12} = 1.00$, $P = 0.08$).

The average proportion of transitions among unlike song types was 0.39 ± 0.26, or 39 transitions per bout of 100 songs. This indicates that a song type was repeated an average of 2.56 times in a bout of 100 songs before the singer switched

TABLE 2. Percentage of song types shared between any two male Bananaquits. Male XB was recorded as a yearling (12–13 months) and in the following year as an adult (≥2 years). Juveniles 1 and 2 (Juv.) were 4–5 months of age at time of recording; all other adults were ≥2 years of age.

		Juveniles		Yearling	Adults			
Males	Song types	Juv. 1	Juv. 2	XB	XB	WW-XR	RX-YB	BX-YW
Juv. 1	64	—	3.1	1.6	1.6	1.6	3.1	1.6
Juv. 2	59	3.4	—	1.7	1.7	1.7	1.7	1.7
XB(Year)	71	1.4	1.4	—	29.6	8.4	8.4	4.2
XB(Ad.)	101	1.0	1.0	20.8	—	7.9	7.9	4.9
WW-XR	85	1.2	1.2	7.1	9.4	—	9.4	5.9
RX-YB	76	1.3	1.3	7.8	10.5	10.5	—	6.5
BX-YW	59	1.7	1.7	5.1	8.5	8.5	8.5	—

to the next song type. No significant differences were found in average proportion of transitions per bout either among males (2-Way ANOVA, $F_{3,12} = 0.08$, $P = 0.271$) or among time periods ($F_{4,12} = 0.25$, $P > 0.500$).

The versatility index, as a proportion of the number of songs in a bout, averaged 2.86 ± 3.33 for the four males. No significant differences were found in the proportional versatility index either among males (2-Way ANOVA, $F_{3,12} = 0.94$, $P = 0.427$) or among time periods ($F_{4,12} = 0.27$, $P > 0.75$).

Finally, the Shannon-Weiner Index did not vary significantly either among males (2-Way ANOVA, $F_{3,12} = 1.34$, $P = 0.269$) or among time periods ($F_{4,12} = 1.60$, $P > 0.25$). The average index per bout for the four males was 0.53 ± 0.27; this represents a moderate level of uncertainty in predicting the presence of a specific song type in a bout.

Versatility and different song parameters. No consistent pattern was found among the four males in song rates and the different measures of versatility (Table 3). In contrast, all four males showed a positive correlation between percentage performance time and song length. However, the relationship between performance time and other measures of versatility was not as strong. For example, percentage performance time was positively correlated with song type versatility and total versatility in only two of the males.

For three males, positive correlations were found between song length and measures of transition versatility, song type versatility, and total versatility. The relationship between song length and number of renditions per song type differed between two males, as one showed a positive correlation, the other a negative correlation.

All measures of versatility were significantly correlated with each other. These relationships were expected because the different measures of versatility were not independent, but rather represented different ways of measuring variation in the same singing behavior.

Variation between consecutive song bouts. The turnover of different song types among consecutive song bouts, as measured by the Beta turnover index, showed no significant variation among the four males (2-Way ANOVA, $F_{3,12} = 2.40$, $P = 0.119$) or among the five time periods ($\mathrm{F}_{4,12} = 0.97$ $P = 0.460$). The average Beta turnover index value was 1.43 ± 0.67 for the four males. On average, only 0.94 ± 0.86 song types were shared among consecutive song bouts of five or more songs.

SONG VARIATION WITH AGE

Comparison of first and second breeding seasons of male XB. Male XB produced more song types as a yearling than as an adult (Figure 3). The mean proportion of song types per bout was 0.47 ± 0.232 as a yearling and 0.29 ± 0.111 in the second year. This difference was significant (2-Way ANOVA, $F_{1,4} = 19.85$, $P < 0.001$), whereas no significant differences were found among time periods ($F_{4,4} = 1.17$, $P = 0.334$). Similarly, the average number of transitions between unlike songs within a bout was higher as a yearling (0.49 ± 0.25) than in the second year (0.36 ± 0.31). This difference was also significant (2-Way ANOVA, $F_{1,4} = 4.74$, $P = 0.034$), whereas no significant differences were found among time periods ($F_{4,4} = 1.06$, $P = 0.384$). Finally, as a consequence of a greater variety of song types and more transitions, the versatility index as a proportion of songs in a bout was higher as a yearling (3.18 ± 3.21) than as an adult (2.37 ± 3.07). Versatility differed significantly with age

TABLE 3. Correlations between different measures of singing behavior for four Bananaquits in Cayey, Puerto Rico. See text for definition of singing behavior measures.

Male	Percentage performance time	Song length	Renditions/ song type	Transition versatility	Song type versatility	Total versatility
Song rate						
XB	−0.35	−0.80**	+0.60**	−0.58*	−0.64*	−0.61
RX-YB	+0.39	−0.35	+0.14	−0.27	−0.25	−0.30
BX-YW	+0.78**	+0.79**	+0.10	−0.23	−0.16	−0.19
WW-XR	+0.58	−0.22	+0.24	−0.20	−0.29	−0.25
Percent performance time						
XB		+0.83**	−0.36	+0.70**	+0.71**	+0.79**
RX-YB		+0.71**	−0.37	+0.44	+0.47*	+0.50*
BX-YW		+0.71**	−0.10	−0.10	+0.03	−0.06
WW-XR		+0.66**	+0.02	−0.03	−0.13	−0.11
Song length						
XB			+0.60*	+0.72**	+0.81**	+0.83**
RX-YB			−0.48*	+0.65**	+0.69**	+0.74**
BX-YW			−0.36	+0.68**	+0.69**	+0.67**
WW-XR			−0.18	+0.13	+0.09	+0.12
Reditions/song type						
XB				−0.77**	−0.70**	−0.62*
RX-YB				−0.90**	−0.85**	−0.77**
BX-YW				−0.79**	−0.95**	−0.88**
WW-XR				−0.72**	−0.86**	−0.71**
Transition versatility						
XB					+0.71**	+0.78**
RX-YB					+0.94**	+0.94**
BX-YW					+0.79**	+0.94**
WW-XR					+0.63**	+0.88**
Song type versatility						
XB						+0.98**
RX-YB						+0.97**
BX-YW						+0.94**
WW-XR						+0.85**

* $P < 0.05$; ** $P < 0.01$.

(2-Way ANOVA, $F_{1,4} = 11.6$, $P = 0.001$), but not among time periods ($F_{4,4} = 1.39$, $P = 0.249$).

The degree of uncertainty with which a song type was produced within a bout did not differ between years, with nearly identical average Shannon-Weiner Information measures obtained from bouts uttered as a yearling (0.52 ± 0.27) and as an adult (0.51 ± 0.29). Therefore, no significant differences were found between the average information measures calculated for the two years (2-Way ANOVA, $F_{1,4} = 0.02$, $P = 0.903$); although a suggestive, but not significant difference in average information measures was found among time periods ($F_{4,4} = 2.17$, $P = 0.083$).

Turnover of song types within bouts (beta turnover index) varied with age in male XB. Average turnover values were higher between bouts sung by XB as a yearling (3.96 ± 1.27) than between those produced in the second year (1.29 ± 0.49). This difference was significant (2-Way ANOVA, $F_{1,4} = 21.92$, $P = 0.009$), but no significant differences were found among time periods ($F_{4,4} = 1.26$, $P = 0.414$). An average of 0.52 ± 0.65 song types were shared between consecutive bouts (of five or more songs) during XB's first year compared with 0.67 ± 0.66 song types in the second year.

Of the 71 different song types uttered by XB as a yearling, 29.6% were still in his repertoire the following year. As a yearling, XB shared song types with the other adults at levels comparable to which adults shared song types with each other (Table 2).

SONGS OF JUVENILE BANANAQUITS

Number of notes per song. Juveniles 1 and 2 uttered songs with an average of 11.9 ± 2.5 notes per song and 6.8 ± 3.11 notes per song, respectively. Significant differences were found between age classes in number of notes per song (Mixed Model, Nested ANOVA, $F_{1,1419} = 297.74$, $P < 0.001$), with the two juveniles singing longer songs (9.4 ± 3.7 notes per song) than the four adults (5.7 ± 4.8). Moreover, significant heterogeneity in number of notes per song was found among the individuals within the two age classes (Mixed Model, Nested ANOVA, $F_{4,1419} = 84.93$, $P < 0.001$).

Note types. The note types produced by the two juveniles occurred within the range of variation in frequency and time span observed in the adult population. Both juveniles used nine of the ten notes found in the repertoires of adults. As with all but one adult, the juveniles did not use the "I" note. Use of the nine note types by the two juveniles varied significantly (Unplanned Tests of the Homogeneity of Replicates Tested for Goodness of Fit, $G = 161.72$, df = 40, $P < 0.001$) as well as between each juvenile and each of the four adults (all pairwise comparisons $P < 0.001$). The most commonly produced note of Juvenile 1 was "A" (37% of his 505 notes), while the most common note of Juvenile 2 was "D" (32% of 1,003 notes).

Sequence of notes in a song. As with adults, the sequence of notes in the songs of juveniles was nonrandom and indeterminate. Transition matrices showed that not all of the potential note transitions actually occurred, indicating that the composition of dyads was a consequence of a nonrandom assortment of uttered notes (Chi-Square Goodness of Fit Test, $\chi^2 = 317.61$, df = 47, $P < 0.001$ and $\chi^2 = 345.12$, df = 47, $P < 0.001$ for Juveniles 1 and 2, respectively).

Juveniles differed from adults by not "favoring" particular note transitions in their songs. For example, 60 different note transitions were found in the 64 songs of Juvenile 1 and each note transition occurred with an average frequency of 1.8% ± 1.9; and 59 different note transitions were found in the 94 songs of Juvenile 2 and each note transition occurred with an average frequency of 1.7% ± 2.5. In contrast, each note transition of the four adults (based on 100 songs for each male) occurred with an average of 5.4% ± 2.52. Thus, the two age classes differed significantly (Mixed Model, Nested ANOVA, $F_{1,194} = 25.91$, $P < 0.001$) in the average frequency of each note transition. However, significant heterogeneity occurred among males in the average frequency of note transitions (Mixed Model, Nested ANOVA, $F_{4,194} = 2.78$, $P = 0.028$), indicating that adults produce songs with more predictable note sequences than juveniles.

Song types. Both juveniles added new song types to their repertoires at rates above those of the yearling and adults (Fig. 3). A total of 121 song types was produced by the two juveniles in a relatively small sample of songs. Juvenile 1 uttered 65 songs and only one song type was repeated. Juvenile 2 repeated song types more frequently in the sequence of 94 songs (59 song types)—"A" note (with time interval equivalent to inter-song interval), 14 times; A-A, 13 times; A-A-A, 6 times; A-A-A-A, 2 times.

Very few song types were shared. All birds used a single "A" note as an individual "song." The juveniles shared only the AHGA song. In addition to the A song type, adult male RX-YB and Juvenile 2 shared the AH song type. Thus, the two juveniles shared approximately 3% of their song types whereas juveniles shared an average of 1.8% ± 0.5 of their song types with adults (Table 2).

DISCUSSION

The life history traits of Caribbean Bananaquits are consistent with those believed to be important in shaping singing behavior in other species with high population densities (Kroodsma 1983). For example, Bananaquits are usually abundant in depauperate island bird communities (MacArthur and Wilson 1967) where densities can be as high as 12 birds per hectare (Wunderle 1984). Territories are small (100–550 m^2) and encompass an individual's sleeping dormitory, which is defended throughout the year. Bananaquits routinely leave their own territories to feed, often intruding on territories of neighbors. These intrusions may result in numerous chases and agonistic interactions (Gross 1958). Bananaquits breed opportunistically depending upon rainfall. Furthermore, polygyny occurs in some populations (Wunderle 1984).

As in other species with high population densities and numerous intraspecific interactions (Kroodsma 1983), Bananaquit song rates are higher than other Caribbean warblers, tanagers, and finches, which never obtain the population densities characteristic of Bananaquits (Wunderle, unpubl. data). In our study, song rates did not decline during the morning sampling periods, as found in other Caribbean species (Wunderle, unpubl. data). Furthermore, in contrast to most other Caribbean species, Bananaquits sing during non-breeding periods, albeit at a reduced rate (Wunderle et al., ms).

Song rates increase with the intensity of intraspecific interactions in high density populations (Kroodsma 1983); as a result, the overall singing versatility of a male may increase, presumably to maintain listener attention and interest (e.g., Kroodsma and Verner 1978, Kroodsma 1983). This follows from the "monotony-threshold hypothesis," which predicts that the rapid production of a signal may become monotonous unless the singer produces successive songs that are different (Hartshorne 1956, 1973). Therefore, a relationship may exist between continuity (quantity of song relative to silent intervals) and song versatility. A singer can produce song versatility in a variety of different ways. For example, a rich repertoire of song types can partially contribute to versatility, although this measure alone is not sufficient (Kroodsma and Verner, 1978). Even though the Bananaquit repertoire (120–340 song types per male) is only moderately high in comparison to other passerines, the most favored song types account for only a relatively small proportion (e.g., 12% in Bananaquits) of the vocal performance. However, Bananaquit songs are relatively short and simple in structure.

Versatility can be further enhanced by altering the sequential arrangement of song types within a singing bout (Hartshorne 1973). For example, a rapidly singing male could produce a sequence of songs in which a different song type follows another in sequence (e.g., ABCD, immediate variety). This would provide greater versatility than the other extreme in which the male repeats a single song type prior to switching to a different type (e.g., AAAABBBB, eventual variety). Obviously these two extremes are theoretical, with the songs of most species characterized by intermediate variety (Kroodsma 1982). Pre-breeding Bananaquits produce songs approaching immediate variety by occasionally uttering song types which are not repeated (e.g., ABBBCDDE). However, if a song type is repeated it is uttered about 2.6 times in sequence before switching to a different type. This description overstates the extent of their sequential variety, as Bananaquits usually alter only a few terminal notes in successive songs, thereby uttering the same introductory note sequence for almost all songs. This stereotypy of introductory notes is also found in high density populations of Sedge Wrens which rarely alter the introduction, but regularly vary the ending notes to produce songs of immediate variety (Kroodsma and Verner 1978).

The expected relationship between continuity and song versatility was not found in our pre-breeding males. For instance, no consistent correlations were found between song rates and percent performance time, song length, renditions, transition versatility, song type versatility, or total versatility. In fact, for the one male that showed significant correlations with song rates and different measures of versatility, the direction of the relationships was opposite that predicted. Similarly, the expected relationship between performance time and the various measures of versatility was not much stronger; at best, only two of the four males showed significant positive correlations between percent performance time and song type versatility or total versatility. These findings contrast with those found in Sedge Wrens, in which many of the measures of versatility were correlated with song rates and percent performance time (Kroodsma and Verner 1978). However, a relationship between continuity and versatility may not occur in many species (e.g., Parulinae, Weary and Lemon 1988); although controversy exists regarding what constitutes the appropriate measures of continuity and versatility (Kroodsma 1990, Weary and Lemon 1990).

Although our study was not designed to determine the factors affecting the ontogeny of song in Bananaquits, the following observations suggest a likely pattern of song development. The widespread introductory "A" note appears to develop in the absence of adult tutors. For example, nestlings raised together in acoustical isolation from 7–10 days of age produced only the introductory "A" note, even after two years of captivity (Wunderle, unpubl. data). This suggests that the remaining notes are acquired from other members of the population. Apparently by the age of 4–5 months, juveniles had acquired all of the note types typical of adults. This was observed in songs with characteristics of "plastic song"—long highly variable songs with less predictable note sequences, and song sequences of immediate variety (Marler and Peters 1982). Although all note types were present prior to territory establishment, it is unknown whether juveniles acquired these note types from their fathers or from interaction with other males while attempting to establish a territory. Songs were "crystalized" by 12 months of age in the one male we studied in its first breeding season. At this time, a highly diverse repertoire was produced; however, this might be attributed to the acquisition of a new territory and mate, rather than a consequence of age alone. By the second year, the male's repertoire was comparable to that of older (>2 year) neighboring males.

Males in our population shared virtually all note types, but few song types (average of 8.2%) were shared between neighbors. It appears that the use of similar note types, rather than song types, characterizes different populations of Bananaquits. This is supported by preliminary observations of vocalizations of other populations, that indicate that it is the sharing of unique note types, rather than song types, which characterizes members of different Bananaquit populations on Puerto Rico (Wunderle, unpubl.).

Differences in life history traits may account for the absence of consistent trends in song complexity and repertoire size among island passerines (Miller 1982). For example, the simple vocalizations of Christmas Island Warblers (*Acrocephalus aequinoctialis*) are attributed to low population density, large permanent territory size, few intraspecific interactions, and monogamy (Milder and Schreiber 1989). Our island Bananaquit population displayed the opposite life history traits (i.e., high density, small territories, numerous intraspecific interactions, and polygyny), which presumably favors their relatively complex songs and large repertoire sizes. If we have correctly identified the selective forces responsible for Bananaquit vocal behavior on Puerto Rico, then future studies should find lower song rates, reduced song complexity, and smaller repertoires in the low density populations characteristic of mainland Bananaquits.

ACKNOWLEDGMENTS

We gratefully acknowledge the field and lab assistance provided by Nydia I. Ramos and Oscar J. Vazquez, and the administrative help from José Velazquez and Robert Ross. We also thank the college's chancellor, Dr. Margarita Benitez, for her support and encouragement. Statistical advice was provided by Michael R. Willig and Andrew Gillespie. Two anonymous reviewers provided helpful comments. Funding was provided by the National Institute of Health, Minority Biomedical Research Support program.

LITERATURE CITED

ALTMANN, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–267.

CATCHPOLE, C. K. 1980. Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. Behaviour 74: 149–166.

GROSS, A. O. 1958. Life history of the Bananaquit of Tobago Island. Wilson Bull. 70:257–279.

HARTSHORNE, C. 1956. The monotony threshold in singing birds. Auk 73:176–192.

HARTSHORNE, C. 1973. Born to sing. Indiana Univ. Press, Bloomington, IN.

KROODSMA, D. E. 1977. Correlates of song organization among North American wrens. Am. Nat. 111:995–1008.

KROODSMA, D. E. 1983. The ecology of avian vocal learning. BioScience 33:165–171.

KROODSMA, D. E. 1990. Patterns in songbird singing behaviour: Hartshorne vindicated. Anim. Behav. 39:994–996.

KROODSMA, D. E., AND J. VERNER. 1978. Complex singing behaviors among *Cistothorus* wrens. Auk 95:703–716.

MACARTHUR, R. H., AND E. O. WILSON. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, NJ.

MARGALEF, D. R. 1958. Information theory in ecology. Gen. Syst. 3:36–71.

MARLER, P., AND S. PETERS. 1982. Subsong and plastic song: their role in the vocal learning process, p. 25–50. *In* D. E. Kroodsma and E. H. Miller [ed.], Acoustic communication in birds. Academic Press, New York.

MILDER, S. L., AND R. W. SCHREIBER. 1989. The vocalizations of the Christmas Island warbler *Acrocephalus aequinoctialis*, an island endemic. Ibis 131:99–111.

MILLER, E. H. 1982. Character and variance shifts in acoustic signals of birds, p. 253–295. *In* D. E. Kroodsma and E. H. Miller [ed.], Acoustic communication in birds. Academic Press, New York.

SKUTCH, A. F. 1954. Life histories of Central American birds. Pac. Coast Avif. No. 31.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. W. H. Freeman, San Francisco, CA.

WEARY, D. M., AND R. E. LEMON. 1988. Evidence against the continuity-versatility relationship in bird song. Anim. Behav. 36:1379–1383.

WEARY, D. M., AND R. E. LEMON. 1990. Kroodsma refuted. Anim. Behav. 39:996–998.

WILSON, M. V., AND A. SHMIDA. 1984. Measuring beta diversity with presence-absence data. J. Ecology 72:1055–1064.

WUNDERLE, J. M. 1982. The timing of the breeding season in the Bananaquit (*Coereba flaveola*) on the island of Grenada, W.I. Biotropica 14:124–131.

WUNDERLE, J. M. 1984. Mate switching and a seasonal increase in polygyny in the Bananaquit. Behaviour 88:123–144.

WUNDERLE, J. M., N. I. RAMOS, AND O. J. VASQUEZ. ms. Singing behavior in a population of Bananaquits on Puerto Rico.