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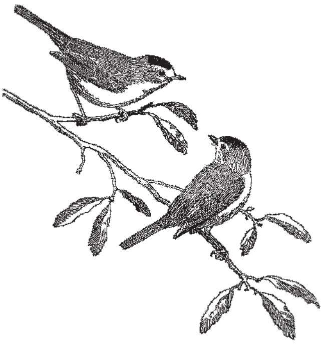

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BEHAVIORAL EVIDENCE FOR SONG LEARNING IN THE SUBOSCINE BELLBIRDS (*PROCNIAS* SPP.; COTINGIDAE)

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ABSTRACT.—Why vocal learning has evolved in songbirds, parrots, and hummingbirds but not in other avian groups remains an unanswered question. The difficulty in providing an answer stems not only from the challenge of reconstructing the conditions that favored vocal learning among ancestors of these groups but also from our incomplete knowledge of extant birds. Here we provide multiple lines of evidence for a previously undocumented, evolutionarily independent origin of vocal learning among the suboscine passerines. Working with bellbirds (*Procnias* spp.), we show that (1) a captive-reared Bare-throated Bellbird (*P. nudicollis*) deprived of conspecific song not only developed abnormal conspecific songs but also learned the calls of a Chopi Blackbird (*Gnorimopsar chopi*) near which it was housed; (2) songs of Three-wattled Bellbirds (*P. tricarunculata*) occur in three geographically distinct dialects (from north to south: Nicaragua, Monteverde, and Talamanca); (3) Three-wattled Bellbirds at Monteverde, Costa Rica, are often bilingual, having learned the complete song repertoire of both the Monteverde and Talamanca dialects; (4) immature bellbirds have an extended period of song development, lasting the 6 years in which they are in subadult plumage; and (5) adult male Three-wattled Bellbirds continually relearn their songs, visiting each others' song perches and adjusting their songs to track population-wide changes. Perhaps female preferences and strong sexual selection have favored vocal learning among bellbirds, and additional surveys for vocal learning among other lekking cotingas and other suboscines may reveal patterns that help determine the conditions that promote the evolution of vocal learning. *Received 21 February 2012. Accepted 13 July 2012.*

Key words: bellbird, birdsong, Contingidae, dialects, evolution, *Procnias*, vocal learning.

One of the most frequently asked but unanswered questions among those who study birdsong is why vocal learning evolved among parrots, hummingbirds, and passerines but not other species groups, and within the passerines why in oscine songbirds but not in their sister group the suboscines (Baptista and Kroodsma

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2001). Our fascination with this question no doubt lies in our own human elaboration of vocal learning through speech, and the absence of such elaborated vocal learning in our close primate relatives (but see Crockford et al. 2004). Vocal learning also occurs among some other mammals, such as certain whales (Noad et al. 2000) and bats (Boughman 1998, Knornschild et al. 2010).

Such evolutionary questions are difficult to answer, not only because vocal learning arose so far back in time that we cannot reconstruct the conditions under which selection for this trait occurred, but also because surveys for vocal learning among extant animal groups are incomplete. Among birds, for example, lack of vocal learning among suboscines is often inferred for the entire group from studies of only a few species (Raposo and Höfling 2003).

Here we provide behavioral evidence for song learning among *Procnias* bellbirds, cotingas that are firmly embedded within the suboscine Tyranni. Among birds, this is a more recent origin of vocal learning than occurred among ancestral songbirds, parrots, or hummingbirds, giving hope that a comparative survey among the suboscine cotingas may help reveal the conditions under which vocal learning evolved.

METHODS

During July 1999–2002, and again in 2011, male Three-wattled Bellbirds (*Procnias tricarunculata*) were recorded intensively at Monteverde, Costa Rica. Each recorded bird was classified by plumage into one of three groups: two or three years old (with yellowish-green streaked plumage); four, five, or six years old (with increasing amounts of white and chestnut plumage); or adult, with pure chestnut and white plumage and long wattles. (The aging scheme is based on plumage changes in banded birds from hatching to at least seven years, when males reach adult plumage; D. Hamilton, unpubl. data.) We did not analyze recordings of unseen birds.

During each year of intensive sampling, we took care to include each male only once in the analyses. A number of birds were banded and could always be identified as individuals (at least eight in our recorded samples, out of 151 that had been caught in canopy nets and banded at Monteverde; for methods, see Powell and Bjork 2004). Others were identified by location and favorite singing perches, often well-separated from other singers. Other times we could walk from one bird to the next along a transect, insuring that each new bird was different from the one before. Most of our analyses are based on males who sang the ''Monteverde dialect'' (see below), and the number of adult males with Monteverde songs that were recorded throughout the years was: 1974 (5), 1981 (1), 1985 (7), 1986 (2), 1987 (1), 1988 (9), 1989 (1), 1991 (2), 1998 (3), 1999 (4), 2000 (15), 2001 (19), 2002 (14), 2006 (3), 2011 (14). Of particular interest in these Monteverde songs was the frequency of their intensely loud tonal notes (hereafter 'Whistles'); the number of Whistles measured for each male ranged from 2-191 (mean 31.7).

A variety of recorders and microphones was used, but when we needed precise temporal and frequency measurements, we used primarily digital recordings made on an HHB Portadat PDR-1000 (1999–2002) and a Sound Devices 722 (2011). Parabolic microphones were essential to record the exceptionally soft elements in the songs, and from 1999–2002 we used a Telinga Pro5W parabolic microphone, and during 2011 a Telinga Universal with a Sennheiser MKH20.

Other recordings used in this study came from a variety of sources. Those from the British Library included recordings archived by Barbara Snow in 1974; the Macaulay Library at the Cornell Laboratory of Ornithology provided a number, including those by Trainer from the 1980s. For these recordings, professional analog recorders were used, and the recorded birds were identified and described; slightly varying analog tape speeds could have introduced small errors into these recordings, and we are mindful of that as we interpret song differences over time. In Nicaragua during July 2001, we used Sony TCD5ProII analog recorders and Telinga Pro5W microphones to record four males. At Monteverde during April 2006, Kroodsma used a Sony MZN-707 minidisc and Sennheiser ME66 to record three adult males.

As an index of how the songs of the Monteverde dialect changed from 1974 to 2011, we measured the frequency of the songs' loud Whistles with the 'Max Frequency' (frequency of peak power) feature on Raven software (with ''spectrogram window size'' of 66,536, yielding a frequency resolution of <1 Hz). Song components other than the loud whistles also changed over the years, and we describe them where we can, but we found it difficult to characterize

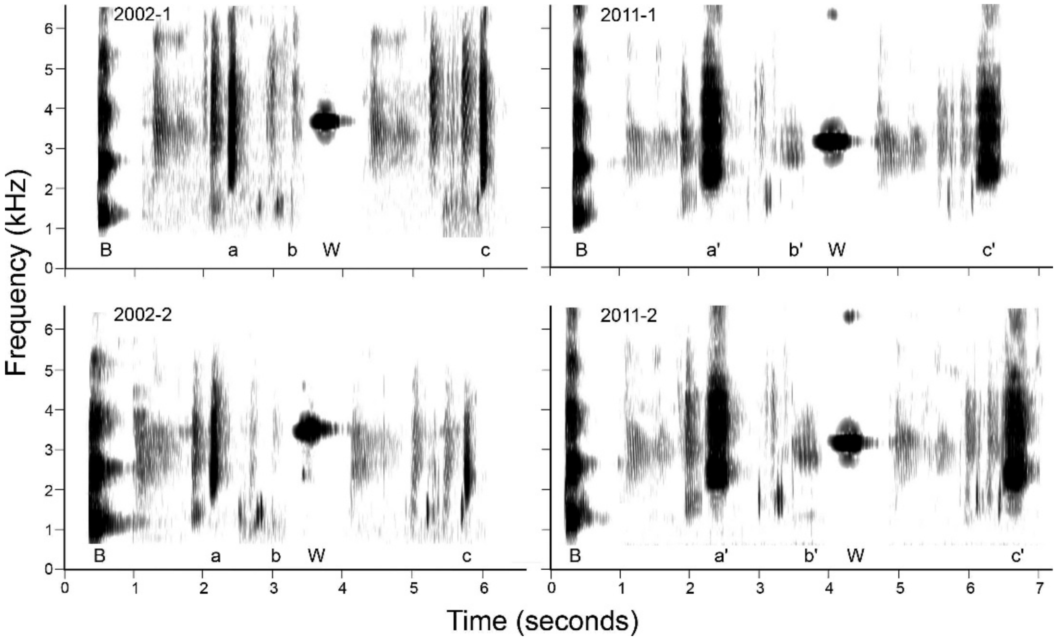

FIG. 1. The '*Bonk*-swish-Whistle-swish' song of the Monteverde dialect of the Three-wattled Bellbird. The basic form of the song has stayed the same from 2002–2011: songs begin with a loud *Bonk* (B), contain a loud Whistle (W) mid-way, and have soft swishing elements before and after the Whistle. Songs from the two males within each year are essentially identical to each other, but notable changes occurred from 2002 to 2011: By 2011, the Whistle is about 450 Hz lower in frequency; elements a, b, and c have been extended to about three times the duration (designated by a 'prime' in 2011); and element b has been transformed in quality. Another song of the Monteverde dialect ('*Bonk*-swish-swish') omits the section after note 'a' through the loud Whistle. In typical sonagrams, the louder the song element the darker the image, but in these and other sonagrams the especially quiet elements (all those not designated with a capital letter) have had to be darkened so that they would show.

satisfactorily and systematically changes in either the loud, complex *Bonk*s of the Monteverde dialect or the songs' softer sounds that are so difficult to record.

In Arapongas, Brazil, Fandiño-Mariño walked the streets of town during 1998, listening to sounds of captive Bare-throated Bellbirds (*Procnias nudicollis*) that many aviculturists kept in the town. Given our suspicion that bellbirds learned their songs, we reasoned that he might find a bird that had developed atypical songs or perhaps had even learned the songs of another species with which it had been raised, because such atypical songs are often found in the repertoires of song-learning birds that are reared in isolation from songs of their own species. He found one such male bellbird, and after recording this bird over several days, together with a normal-sounding Bare-throated Bellbird in another cage in the same courtyard, Fandiño-Mariño traced the history of the odd singer.

RESULTS

Description of Adult Bellbird Songs

The 'Monteverde Dialect.'—At Monteverde, Costa Rica, during July of the years 1999–2002 and 2011, about three-quarters of adult males (73 of 101 encountered, or 72%) sang only what has come to be called the 'Monteverde dialect.' Among all banded adults for whom the dialect was known from 1991–2011, 52 of 75 (69%) were of the Monteverde dialect. This Monteverde dialect consisted of four basic songs.

Undoubtedly the loudest, most striking sound, carrying for great distances, was a harsh, strident '*Bonk*' (designated B in song formulas, the capitalized letter indicating its relative loudness; Fig. 1). The *Bonk* was often given singly, but sometimes in a string of 2–3 in rapid succession.

The *Bonk* also introduced two longer, more complex songs. One song we referred to as the '*Bonk*-swish-Whistle-swish' song (Fig. 1). In this

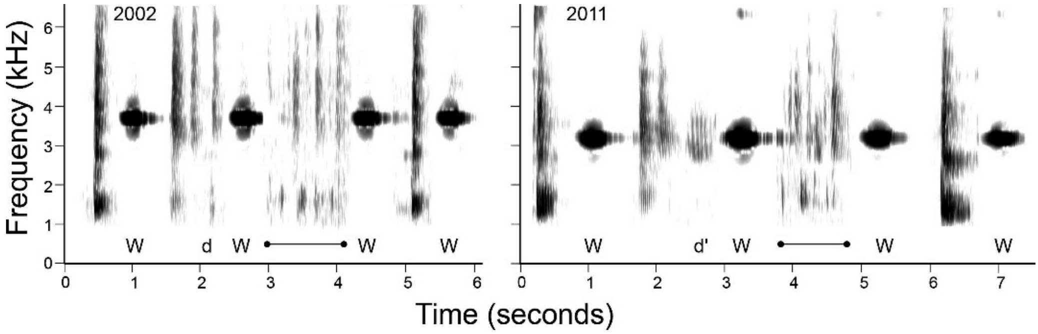

FIG. 2. The ‘four-Whistle’ song. The basic form of the song in 2002 and 2011 consisted of a series of four loud Whistles; a single softer element preceded the first and fourth whistle, with more complex swishing sounds before the second and third whistles (section marked with underline is illustrated in Fig. 3). The whistle frequency dropped about 450 Hz over these nine years, and the total duration of the song increased by about 18%. To the human ear, the change in note ‘d’ from 2002 to 2011 is also easily detected, and appears to be the same change that note ‘b’ has undergone in the *Bonk*-swish-Whistle-swish song (Fig. 1).

song, a loud, pure-toned Whistle (W) occurred near the mid-point, with the rest of the song consisting of soft, muted, atonal notes, typically with 40–50 dB less power than either the loud *Bonk* or Whistle (as measured in Raven software). The second song was similar, except that it omitted a brief section in the middle of the song (the loud Whistle and the notes during the preceding second); we referred to this

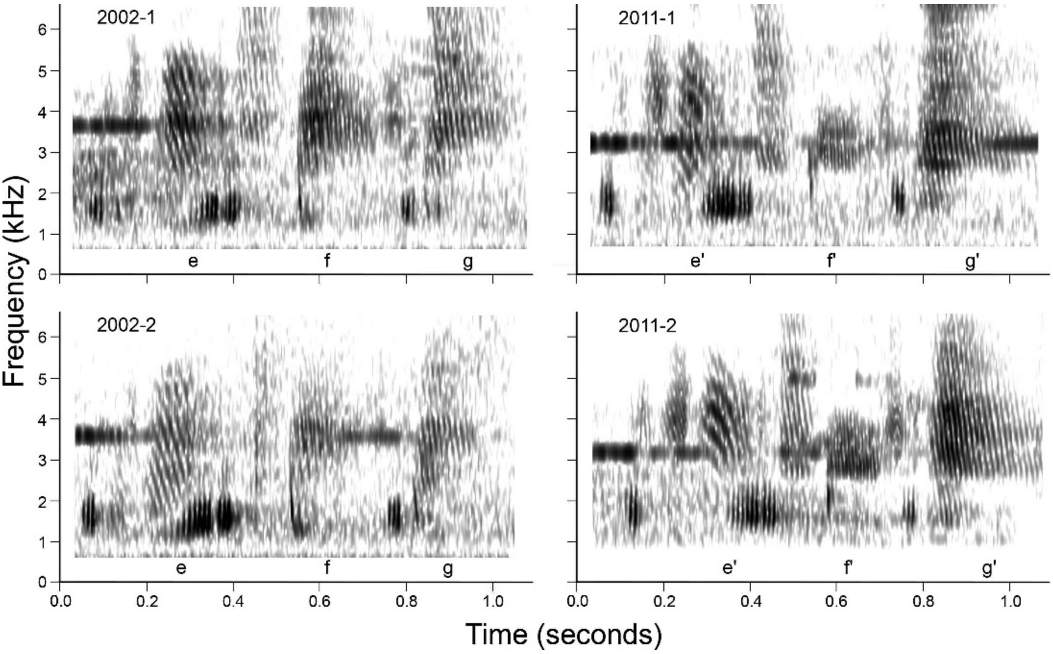

FIG. 3. An expanded view of the soft, swishing elements between the second and third whistles of the four-Whistle song. Within each year, song elements from different males are essentially identical (compare two examples from each year), but significant changes have occurred between 2002 and 2011. In the 2002 songs, for example, one hears (and sees in the sonagrams) three conspicuous, similar notes (e f g), but by 2011 that distinctive rhythm has been lost, perhaps most affected by the transformation in note f and lengthening of note g. These softer elements are 40–50 dB quieter than the loud Whistles (as measured with ‘Max Power’ in Raven software), the reverberation of which can be seen in the broad bands at ~3,600 Hz in 2002 and at ~3,150 Hz in 2011.

song as the ''*Bonk*-swish-swish'' song. These two song variations were used by most males for which we had extended recordings, as if the two were alternate ''song types.''

A fourth typical song of the Monteverde dialect contained four loud Whistles together with characteristic muted notes—the 'four-Whistle song' (Fig. 2). During July, when we recorded the birds, many of these songs were incomplete, often stopping after the third loud whistle, or even after the second. To our ears, this song had a distinctive rhythm, as we heard a single note preceding the first and fourth whistle, and three notes preceding the second and third whistles. Closer analysis, however, especially of the soft notes between the second and third whistle, revealed far more complexity (Fig. 3).

Data from a 10-min recording of one male provide a representative sequence in which the four songs described above were used. Designating the four as 1, 2, 3, and 4, respectively, with ''1'' a *Bonk* and ''4'' the four-Whistle song, the sequence of songs was as follows: 2 1 1 4 1 2 1 4 1 1 2 1 4 1 1 2 1 2 1 4 3 1 2 1 4 1 2 1 2 1 1 4 2 1 2 1 2 1 1 4 2. Typically, as in this sequence, the *Bonk* (''1'') is the most frequently used song, the *Bonk*-swish-swish (''3'') the least used.

From 1974–2011, the 38-year period for which we have recordings, the basic form of the four Monteverde songs has remained the same. Both *Bonk*s and Whistles occur throughout these years, for example, and the four different songs are readily identifiable. Many of the details in these songs, however, have changed, some slightly, some markedly (e.g., in Figs. 1–3, for 2002–2011, compare notes a–d, f). More than a dozen qualitative changes are evident to the ear over the years, such as the presence or absence of certain swishing notes, their relative emphasis, or the overall timing and rhythm of the songs; analysis of sonagrams reveals many more changes. Remarkably, however, the recorded males largely agree on the subtle features that constitute the songs in any given year.

The frequency change in the loud Whistles is a good index not only of how much these songs have changed from 1974 to 2011 but also of how closely each male tracked the population-wide changes (Fig. 4). In 1974, the frequency of the whistle was 5,575 ± 19 Hz (mean ± SD, $n = 5$ adults), but by 2011 it had plummeted to 3,129 ± 20 Hz ($n = 14$ adults), an average of 66 Hz/year. Whistle frequency declined at a surprisingly constant rate, resulting in a highly linear relationship between frequency and recording year. This continual change over time is all the more remarkable given that males routinely live up to 16 years (about 10 years as an adult; see Hamilton et al. 2003), and many of the same banded, adult birds are represented in successive years from

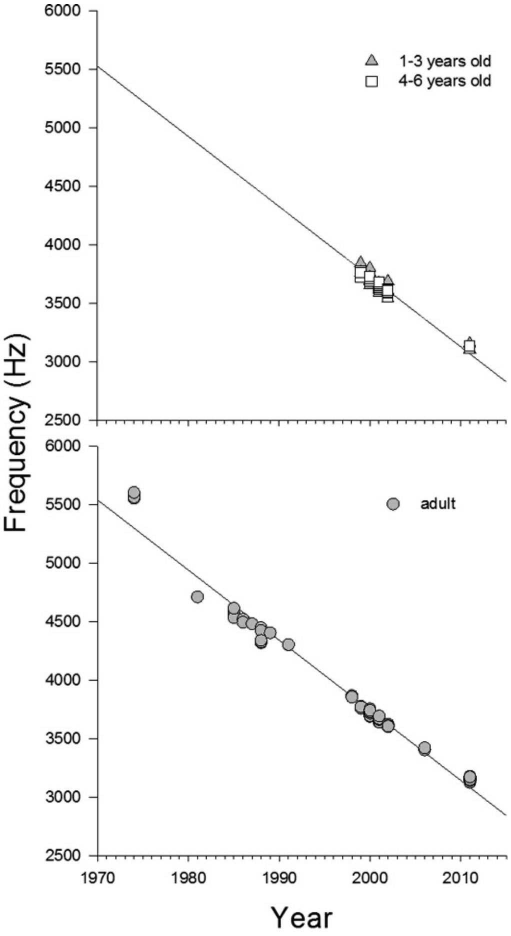

FIG. 4. The mean Whistle frequency for Monteverde singers from 1974–2011, revealing a strikingly linear decline over time (least squares regression $R^2 = 0.98$, $P < 0.001$, df = 175). Frequency declined in both subadults (top) and adults (bottom; the two age classes are shown separately for better visualization, but the regression line is the same in both graphs and represents all birds combined). Males can live 15–20 years and must relearn their songs each year to track the population change shown here. Each point in the graph represents the mean frequency of a single male's songs (2–188 Whistles/bird, mean = 31.7); number of adult males in annual samples is given in Methods, and numbers of subadult males during 1999, 2000, 2001, 2002, and 2011 were 11, 13, 35, 13, and 5, respectively.

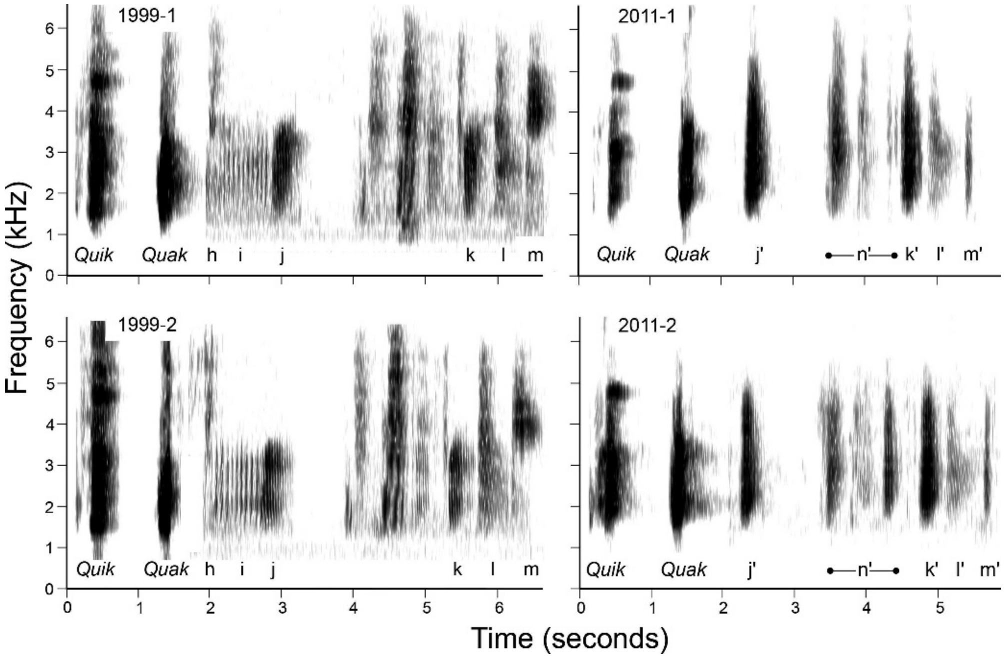

FIG. 5. The *Quik-Quak* song of the Talamanca dialect. Songs begin with the same two loud elements in 1999 and 2011. Within years, the softer swishing elements from different males are essentially identical, but these elements have been overhauled considerably in 12 years: Elements h-i-j in 1999 have been replaced in 2011 with a single, emphasized note (j′), and the three distinctively rising terminal notes (k l m) of 1999 are absent in 2011, replaced by three notes (k′ l′ m′) with a very different quality and rhythm. Two song variants are shown for 2011 (compare subtle differences in section denoted n′). The *Quak* is the loudest element, with other elements far quieter (e.g., *Quik*, −15 dB; k, l, and m ranging from −30 to −50 dB).

1999–2002 as each male changes his song to match the population changes in whistle frequency. (Note: The expected small differences in tape speed for analog recorders that were used before 1998 would have no meaningful effect on the pattern depicted in Fig. 4.)

As suggested by the sonagrams in Figures 1 and 2, the duration of the songs has also changed over the years. Over the 10 years from 2001–2011, for example, the three complex songs have all increased in duration: The four-Whistle song increased by 18% (as measured from the beginning of the song to the beginning of the third whistle; median 3.8 sec during 2001, 4.5 sec during 2011), the *Bonk*-swish-Whistle-swish by 18% (total duration of song; median 5.4 sec during 2001, 6.4 sec during 2011), the *Bonk*-swish-swish song by 15% (total duration of song; median 3.9 sec during 2001, 4.5 sec during 2011). The range of song durations in the 2001 sample did not overlap with the 2011 range for any of the three songs, and the differences between median durations in the two years were statistically significant for all three songs (Mann-Whitney U-test, two-tailed $P < 0.002$ for all three songs, $n_{2001} = 10$ males, $n_{2011} = 5$).

The 'Talamanca Dialect.'—During recording sessions at Monteverde during July 1999–2002 and 2011, about a quarter of the adult males (24 of 101, or 24%) we encountered sang only what we came to call the 'Talamanca dialect.' Of 75 banded adults for whom the dialect was known from 1991–2011, 19 (25%) were Talamanca singers. This dialect is so named because these songs occur primarily in the Talamanca mountain range that runs from central Costa Rica into Panama. During multiple visits to the Las Tablas, Costa Rica region on the border with Panama (1997, 1998, 2000, and 2001), songs of only the Talamanca dialect were heard from well over 100 birds. Songs of this dialect, like those of the Monteverde dialect, consist of a combination of exceptionally loud notes and soft, muted sounds but do not contain the loud whistles of the Monteverde dialect.

Three loud notes were distinctive and especially harsh, more discordant even than the *Bonk* of the Monteverde dialect. One was often given by itself, a sharp, explosive *Kokk*; the two others often occurred together, the first higher pitched than the second, a bit like *Quik Quak* (Fig. 5). The *Quak* also occurred in another context, with a single introductory note.

Although these harsh notes were often used alone, they were also used to introduce two highly stereotyped songs shared by the Talamanca males during 1999–2002. One song version was introduced by the *Quik Quak*, followed immediately by a distinctive three-note sequence (notes h i j; see Fig. 5); after a brief pause, the song concluded with a nearly 3 sec sequence of stereotyped muted notes, the last three of which rose in a distinctive emphasis and rhythm (notes k l m). The second song was introduced by all three loud song elements, *Kokk Quik Quak*; notes h i j were then omitted, and after a brief pause, this song concluded with the same 3 sec sequence of notes as the first song.

The basic form of these Talamanca songs remained stable from 2002–2011. The three loud sounds were readily identifiable in all sampled years, and the two complex songs were still introduced by the same loud sounds in 2011 (either *Quik Quak* or *Kokk Quik Quak*). The muted sections of these Talamanca songs, however, had been revised extensively in the intervening years (Fig. 5). By 2011, the distinctive and ubiquitous three-note ending (k l m) of 1999–2002 had disappeared in all 10 Talamanca singers that we sampled. Also conspicuously absent in 2011 were notes h and i, and note j had become isolated and emphasized. The 2011 songs were also briefer than those 10 years earlier (for the *Quik Quak* song: median 6.3 sec in 2001 and 2002, median 5.2 sec in 2011, ranges do not overlap; Mann-Whitney *U*-test, two-tailed $P = 0.004$, $n_{2001\text{–}2002} = 5$ males, $n_{2011} = 6$). These major changes were unanimous among the 2011 males, but some minor changes were not (see Fig. 5). Given these extensive changes over 10 years, it is possible the very different song recorded by Eugene Morton in Chiriqui, Panama, during 1966 (Macaulay Library Audio # 7288; macaulaylibrary.org) is not a different dialect but instead could actually be an earlier version of the Talamanca dialect, with so much change having occurred over 30 years that the dialect became unrecognizable.

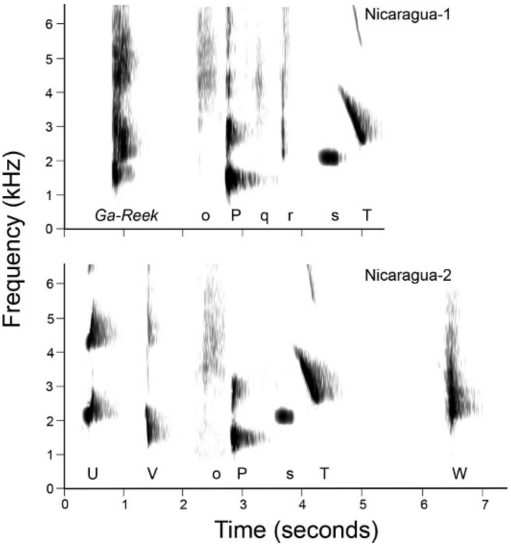

FIG. 6. Two songs of the Nicaragua dialect, showing the loud slurred tonal notes that are unique to this dialect (e.g., notes T U V). As is typical of the Monteverde and Talamanca dialects, some elements are exceptionally loud (within 10 dB of the loudest note; *Ga-Reek*, P, T, U, V, W) and others especially quiet (30 to 40 dB quieter than the louder notes; o q r s), and the same song elements occur in more than one song (e.g., o P s T).

The 'Nicaragua Dialect.'—This most northern dialect, recorded in 2001 at Selva Negra in Matagalpa, also consisted of songs with exceptionally loud and soft notes. One of the loudest sounds was a discordant, quarter second *Ga-Reek*, rising stepwise from about 1,700 Hz to 2,350 Hz (Fig. 6). This note was given either alone or as the first note in a 4 sec song that ended in a loud whistle slurred from roughly 4,100 Hz to 2,500 Hz (Fig. 6, top).

Another song began with a loud whistle (U) slurred upward, from roughly 2,000–2,900 Hz, with harmonics stacked above this fundamental; this song contained some of the same elements as the first song (o P s T; Fig. 6), and concluded after 6 sec with a discordant note (W) tacked onto the end. The two males most thoroughly recorded in 2001 also shared another song that substituted a single unique note for elements o, P, s, and T in song 2. Our recordings are insufficient to document long-term changes that have probably also occurred in this Nicaragua dialect (see especially J. W. Hardy's recordings from 1969, Macaulay Library Audio #7289, 7290; macaulay-library.org).

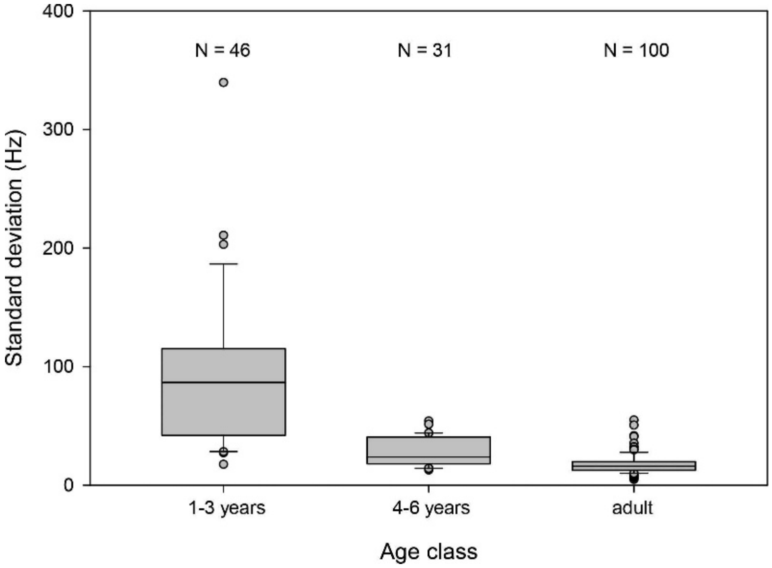

FIG. 7. Variation in whistle frequency declines with age. The plot compares the standard deviations of whistle frequency of 177 males in three age classes. The lower and upper boundaries of each box indicate 25th and 75th percentiles; the line within each box marks the median value. The whiskers below and above a box span the 10th to 90th percentiles; the additional points shown are outliers.

A Possible Panama Dialect.—A possible fourth dialect of the Three-wattled Bellbird may occur on the Azuero Peninsula of Panama (Hamilton et al. 2003). It has been described as a series of squeaky whistles, but we have not recorded or confirmed the existence of this possible dialect.

Song Development among Free-living Birds

Many greenish, streaked immature bellbirds which were 3 and possibly 2 years old already sang complete song repertoires, with all of the song elements for either the Monteverde or Talamanca dialect. Many of these immature birds, in fact, sang most or all song elements for *both* dialects—see the section on bilingual birds, below. The quality of the songs improved with age, with the songs of many greenish 2- to 3-year-olds especially rudimentary, and those of older subadults more adult-like, though still imperfect. First-year birds (and possibly some second-year birds) are not capable of making the *Bonk* call even though they struggle with open bills to force air out.

To quantify this gradual improvement with age, we measured the frequency of greatest intensity for Whistles of non-adults who sang the Monteverde song components during the years 1999–2002 and 2011. From when they first begin singing, the young males are already focused on the appropriate whistle frequency for a given year, as the mean frequency of 1–3-year-olds is already similar to that of the adults (see Fig. 4). Those early attempts at the pure whistled notes often emerge as a shriek, however, and often sound more like a parrot than a bellbird; as the birds age, they gradually improve their songs, reducing the variability from one rendition to the next, so by the time they are adults the Whistle frequencies are remarkably consistent (Fig. 7).

Our surveys at Monteverde for 1999–2002 revealed that many young birds were bilingual, with songs of both the Monteverde and Talamanca dialects, but that fewer bilingual birds were found in the older age classes. Among the streaked, greenish 2- to 3-year-olds, about 40% were bilingual (25 of 64), but among 4-, 5-, and 6-year-olds, the subadults with some white and chestnut in their plumage, only 10% were bilingual (four of 40). Bilingual birds in full adult plumage were even rarer, with only one bird (of 84 over the 4 years; about 1%) heard to sing song components of both dialects. During 2011, however, three of 17 visually confirmed adults were bilingual (18%), suggesting that bilingual adults were more common in 2011 than in the earlier period (Fisher's exact test, two-tailed $P = 0.015$). Overall, it seems that many young birds learn the songs of both the Monteverde and Talamanca dialects, much like many song-learning songbirds ''overproduce'' during song development, but then choose to specialize on one or the other dialect as they age (for similar behavior among White-crowned Sparrows, *Zonotrichia leucophrys*, see Nelson 2000).

Fairly typical is this example of a greenish bilingual bird, perhaps 3 years old. In a 6 min recording, during which he was about 10 m distant and in plain view, he sang the loud notes of both dialects (the *Bonk* and Whistle of the Monteverde dialect as well as the three harsh quacks *Kokk Quik Quak* of the Talamanca dialect) and typical renditions of the two complex Talamanca songs and the three complex Monteverde songs. In our samples, he never quite completed his four-Whistle song (stopping after the third whistle), and he inserted an extra note of unknown origin just before the third whistle. Most of his songs were either pure Monteverde or pure Talamanca, but some songs had dual sources, such as when he occasionally substituted the Talamanca *Kokk* for a Monteverde *Bonk* in the *Bonk*-swish-Whistle-swish song. Although most song notes were clearly recognizable, at times his rhythm was off, extra notes were included in a song, or an occasional loud note could not be confidently identified.

The only adult bilingual bird during 1999–2002 was recorded in both 2001 and 2002 (and heard again in 2005), as he was recognizable not only by his unique singing but also by his unique combination of leg bands. He had been banded as a 4- or 5-year-old subadult in a mixture of green, brown, and white plumage in July 1995 and was in adult plumage 2 years later, in 1997.

His songs in 2001 and 2002 differed little, and were clearly a mix of both the Monteverde and Talamanca dialects. His Talamanca song repertoire was complete, as he sang all elements and the full songs expected from a pure Talamanca singer. Other songs were largely of the Monteverde dialect, but he was clearly less proficient with these Monteverde songs. One song routinely began with loud Talamanca elements (*Quik Quak*) and ended with components of two different Monteverde songs. Another was an abbreviated four-Whistle song, missing the third whistle and the swishing sounds before it. Still another song combined elements from two different Monteverde songs, and he seemed to be missing some Monteverde notes, such as the *Bonk*. The most noticeable change from 2001 to 2002 was an improvement in notes h-i-j (Fig. 5), as he enunciated them far more clearly in 2002; he also tracked the population changes in the frequency of the Monteverde Whistle, lowering his median frequency by 54 Hz over the 1 year span (from 3,666 Hz down to 3,612 Hz, as measured in one session for each year).

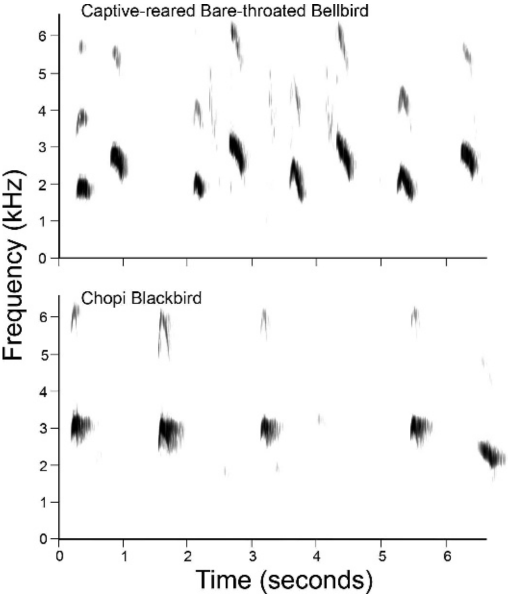

FIG. 8. A captive-reared Bare-throated Bellbird learned the tonal notes of the female Chopi Blackbird near which he was housed.

The one bilingual adult for which we had the most recordings in 2011 sang essentially the complete set of songs for both the Monteverde and Talamanca dialects. In one 18-min session, for example, he sang all of the Talamanca vocalizations: the isolated *Kokk* (two times), the single loud *Quak* note (together with a muted introductory note; three times), the complete *Quik Quak* song (10), and the complete *Kokk Quik Quak* song (3). Most of his vocalizations were of the Monteverde dialect: the loud *Bonk* (15), the four-Whistle song (8), and the *Bonk*-swish-Whistle-swish song (26). All of his Talamanca songs were sung through to completion, but all of the Monteverde songs (other than the simple *Bonk*) were incomplete. In 45 additional recorded minutes, we did find one complete *Bonk*-swish-Whistle-swish song but never a complete *Bonk*-swish-swish or four-Whistle song (he never continued beyond the third whistle). The incomplete songs are not atypical of some pure

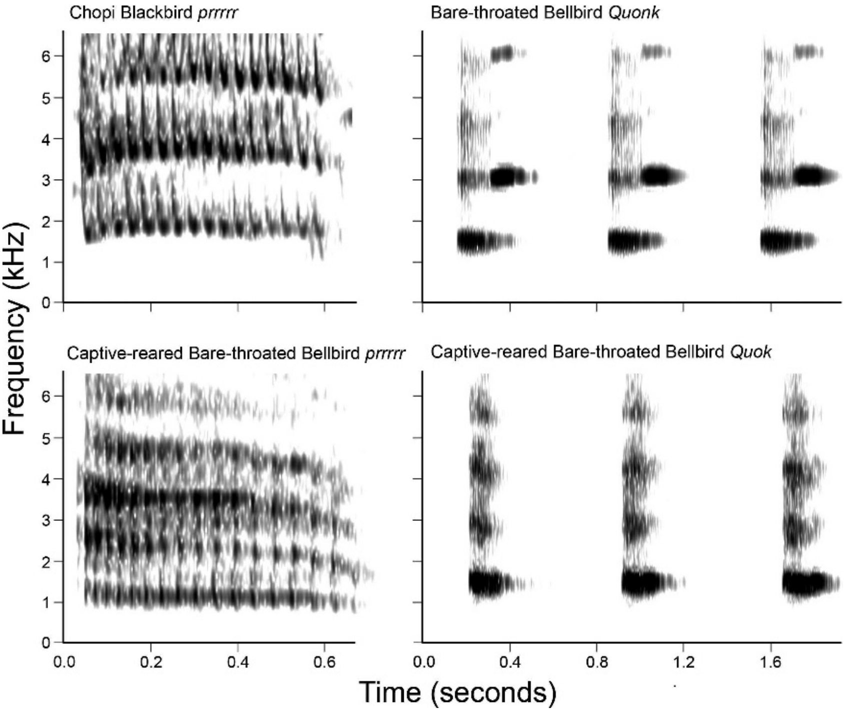

FIG. 9. Further evidence of song learning in the captive-reared Bare-throated Bellbird. The bellbird (lower left) learned the purring *prrrrr* call of the female Chopi Blackbird (upper left) near which it was housed. Also, the captive-reared bellbird, raised initially without hearing conspecific song, never developed a normal conspecific song, instead singing only the harsh, repeated *Quok* (lower right), never mastering the intense ringing note that follows at 3 kHz in the normal *Quonk* call of the Bare-throated Bellbird (upper right).

Monteverde singers that, under what might be low motivation, also sing mostly incomplete songs.

Song Development by a Captive Bare-throated Bellbird

Evidence of song learning among bellbirds is bolstered by data from a captive-reared Bare-throated Bellbird in Brazil. This young male was purchased in 1994 by an avicultural hobbyist (Mr. Ivo Porvani) near the town of Arapongas, Paraná, Brazil. (‘Arapongas’ is probably the name for ‘bellbird’ in the Guarani language of the area’s native inhabitants, and is also the name of the main street through town. Aviculture is a historically popular hobby in Arapongas, and all the streets there are named for birds common in the area). In 1994, this bird was in juvenile plumage, grayish with typical streaks on its breast. For 6 months, this young bellbird was caged beside a female Chopi Blackbird (*Gnorimopsar chopi*); after 2 years, however, Porvani tired of a bellbird that sang like a blackbird, and he sold the bird to an another aviculturist in Arapongas, where the bird was discovered by Fandiño-Mariño in 1998. At that time this bellbird was in fully white, adult plumage.

When first encountered as an adult in Arapongas, the bellbird had a repertoire of three basic sounds, two of blackbird origin and one of bellbird origin (Figs. 8, 9). One class of blackbird sounds consisted of a variety of low frequency whistles, with a fundamental roughly between 2–3 kHz (Fig. 8); according to the account of the original owner, the young bellbird and the female blackbird with whom he was raised used these whistles during frequent counter-calling during the 6 months they were together. The bellbird also learned the female blackbird’s purring *prrrrr* note, which consisted of a series of repeated elements delivered at the rate of about 28 notes/sec (Fig. 9).

The third sound of the captive bellbird was of bellbird origin, but deficient, suggesting that this bird’s early isolation from typical Bare-throated

Bellbird sounds had a lasting effect on this learned vocalization. Wild birds produce two basic sounds (Snow 1973). One is a harsh *Quok* (Snow's ''*Bock*''), usually delivered singly, with a fundamental note about 1,500 Hz and with multiple harmonics (Fig. 9). The second is more of a *Quonk*, given in a long series of about one call per second, and is ''a less loud but otherwise apparently identical version of the [*Quok*] … followed … by a very loud and pure high-pitched note … an octave above the fundamental frequency of the first note. The two different and partly overlapping notes give the impression of a hammer striking an anvil a glancing blow so that it rings'' (Snow 1978: 159; see Fig. 9). This ringing note was never sung by the captive-reared bellbird, so that he sang both isolated *Quok*s and repeated *Quok*s, but never the repeated *Quonk*s with the ringing note.

By December 2000 through February 2002, when this bellbird was at least 6–8 years old, he no longer sang the blackbird whistles or *prrrr*s, only the *Quok*s of bellbirds. He died shortly thereafter, never having learned the ringing note to produce a normal, repeated *Quonk*, even though as an adult he was caged adjacent to a normal singing Bare-throated Bellbird for several months during 1998.

DISCUSSION

The behavioral evidence for song learning among these suboscine bellbirds is extensive. We review and evaluate the evidence here.

First, a young captive-reared bellbird, initially isolated from songs of its own species, acquired (i.e., learned) the vocalizations of the Chopi Blackbird with which it was raised *and* sang an abnormal bellbird song as an adult. Under similar, ''deprived'' conditions, young songbirds often learn songs of other species and/or develop abnormal songs (e.g., Baptista and Petrinovich 1986, Eriksen et al. 2009). The behavior of this bellbird and songbirds contrasts sharply with that of suboscines that do not learn their songs (i.e., have ''innate'' songs): Deafened Eastern Phoebes (*Sayornis phoebe*) that are deprived of auditory feedback still develop normal phoebe songs (Kroodsma and Konishi 1991), and Alder and Willow flycatchers (*Empidonax alnorum* and *E. traillii*) in cross-fostering experiments, exposed only to songs of the other species, still develop normal songs (Kroodsma 1984). Furthermore, as with some other non-learning suboscines, fledgling Alder Flycatchers just out of the nest already use a vocalization that is a rudimentary form of the adult song (Kroodsma 1984, 2005). For these suboscine flycatchers, the developmental trajectory leads directly from juvenile vocalizations to adult songs, never digressing to produce (i.e., learn) the sounds of other species encountered along the way.

Second, many young Three-wattled Bellbirds, as well as a few adults, are completely bilingual, singing the entire set of both Monteverde and Talamanca songs. If these songs were innate and not learned, as is believed to be the case among most suboscines, then the Monteverde and Talamanca singers would most likely be different species (Isler et al. 1998) and no individual would possess a song repertoire that combined both putative species' full sets of songs. But if the Monteverde and Talamanca singers really were separate species with innate songs, hybrids of Monteverde and Talamanca singers would produce intermediate, hybrid sounds, as in doves and pigeons (de Kort et al. 2002) or flycatchers (Pieplow et al. 2008). A pure Monteverde *Bonk* singer crossed with a pure Talamanca *Kokk* singer might produce a hybrid *Konk* singer, for example. In any case, a recent genetic analysis revealed that the populations using the different song variants are only weakly genetically differentiated, and are not distinct taxa (Saranathan et al. 2007). Given that the Nicaragua, Monteverde, and Talamanca geographic variants do not represent different bellbird species, throughout this paper we refer to the variants as song ''dialects,'' three culturally transmitted song groups distributed about the highlands of Central America much like any system of dialects in the song-learning songbirds.

Third, many features of songs change from one year to the next, with our annual snapshots during July revealing the changes that had accumulated over the prior year. These population changes are tracked by long-lived adults with remarkable precision, and subadult birds also focus on learning the details of the songs in any given year. Part of the display behavior of the males readily lends itself to this careful listening, as males visit each other on their singing perches, the resident bird often singing both his ear-shattering and his soft swishing sounds directly into the ears of the visitor. No known innate, learning-free mechanism would enable the kinds of coordinated, intricate song changes over time that we observed. A far more parsimonious explanation is that the males simply listen carefully to each other and continuously relearn their songs; such continuous relearning and reshaping of song also occurs in humpback whales (*Megaptera novaeangliae*) and Yellow-rumped Caciques (*Cacicus cela*) (Payne et al. 1983, Trainer 1989, Noad et al. 2000), but not in most songbirds, which show only the typical between-generation cultural evolution (e.g., Indigo Buntings, *Passerina cyanea*, Payne 1996).

The above three lines of evidence constitute, in our minds, unequivocal confirmation for song learning in these suboscine bellbirds. A fourth line of evidence consistent with song learning is that young male bellbirds ''babble,'' taking 6 years or more to perfect their songs, just as they take 6 years or more to acquire their adult plumage. (Throughout their development, of course, they are also tracking the annual population changes in song.) Although this extended period of plastic, developmental song is consistent with song learning, and such developmental song also occurs among song-learning songbirds (Trainer and Parsons 2002), it is conceivable that non-learned song could take many years to mature, with no ''learning'' required. We therefore accept this extended babbling phase as only suggestive, non-confirming evidence of song learning in the bellbirds.

Our study extends the field observations of Barbara Snow (1970, 1973, 1977), who first suggested that suboscine bellbirds may learn their songs. Her conclusion was based on several lines of evidence, including the extended period of song development by young birds, the geographic song variants of the Three-wattled Bellbird, an apparent bilingual singer (a Monteverde singer with what may have been the note of a Nicaraguan singer), and apparent change over time of the songs of the Bearded Bellbird (*Procnias averano*) in Trinidad. And our study complements that by Saranathan et al. (2007), who showed great genetic similarity among the Monteverde and Talamanca singers and populations; such a lack of genetic differentiation between birds of the two dialects strongly implicates song learning rather than a wholly genetic origin of songs.

Overall, these data reveal a previously undocumented, independent evolutionary origin of vocal learning in birds, in addition to learning that occurs in songbirds, hummingbirds, and parrots. The bellbird genus *Procnias* is clearly imbedded within the Cotingidae (Prum 2000, Ohlson et al. 2006, Ohlson et al. 2007), a family which in turn is clearly imbedded within the suboscines (Barker et al. 2004, Ericson et al. 2006). No vocal learning has been documented among other suboscines, and many suboscines apparently require no vocal learning for songs to develop normally (Kroodsma 1984, Kroodsma and Konishi 1991). The most parsimonious conclusion is that vocal learning has arisen independently in bellbirds, rather than their having retained this trait from some shared, common ancestor among the song-learning oscines.

The origin of vocal learning in bellbirds is either the third or fourth well-documented, evolutionarily independent origin of vocal learning in birds. It would be the third if parrots and passerines are sister taxa, as suggested by Hackett et al. (2008), and if vocal learning arose in the common ancestor of these two groups and was lost by the mainstream suboscines until it was reinvented by bellbirds. Or it would be the fourth if vocal learning arose independently in the psittacine and oscine lineages, as well as in hummingbirds and bellbirds.

We cannot be sure how vocal learning evolved among *Procnias* suboscine bellbirds in general, or why Three-wattled Bellbirds continually relearn their songs to track population changes, but we suspect that strong sexual selection has played a role, as suggested by Aoki (1989). Male Three-wattled Bellbirds invest an enormous amount of time singing throughout the day from prominent display perches (Snow 1977), both during the breeding season and outside the breeding season as they migrate up to Nicaragua and throughout Costa Rica (Powell and Bjork 2004). Males appear to be highly attentive to the nuances of songs produced by their competitors, as both immatures and adults visit each others' display perches, listening there for up to several minutes at a time. We suggest that the males use these listening bouts to monitor and learn song and song changes in the population. Females visit the display perches and mate with a selected male at a nearby, more protected perch inside the canopy, and then raise the young completely on their own, indicating a polygynous mating system with strong sexual selection. We suspect that a link between strong sexual selection and vocal learning would be supported in a survey for evidence of vocal learning among other cotingas and suboscines in which strong sexual selection is suspected.

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