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REPERTOIRE SIZE AND SYLLABLE SHARING IN THE SONG OF THE CLAY-COLORED THRUSH (*TURDUS GRAYI*)

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ABSTRACT.—Song repertoire size and extent of song sharing provide information about social interactions that occur in songbird species. We recorded the songs of eight male Clay-colored Thrushes (*Turdus grayi*) in San José, Costa Rica during the 2008 breeding season. We classified 695 songs and 5,032 syllables using visual inspection of spectrograms and spectrogram correlation analysis to measure repertoire size and syllable sharing among a local group of males. Male repertoire size was 10–17 syllable types. Males shared on average 28 ± 15% (SD) syllable types from their repertoires with other males, but a larger proportion of syllable types remained unique to particular males. Extent of repertoire sharing and distance between singing males were not related. Presence of shared and individually unique syllables in the repertoires indicate that imitation, and perhaps improvisation, contribute to development of the song of Clay-colored Thrushes.
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Bird song is used in territorial defense and female attraction (Krebs et al. 1978, Catchpole 1987, Catchpole and Slater 1995). Some songbird species accomplish both purposes with a single song or phrase type throughout their lives (Kroodsma 1996), but in many species the song repertoire is much larger ranging from a few (Krebs et al. 1978) to hundreds (Todt and Hultsch 1996) or even thousands of song types (Kroodsma and Parker 1977).

Songbird species also differ in the extent of song sharing between individuals of a given population (Johnson 2006, Nicholson et al. 2007). Song sharing within a population is thought to be a result of learning, in which young individuals produce accurate imitations of previously heard adult con-specific songs (Marler 1970, Marler and Peters 1981, Kroodsma 1982). Usually, only part of the repertoire is shared among individuals (Catchpole and Slater 1995). Thus, repertoire size and extent of song sharing are behavioral characters that provide information about social interactions and the song learning process of a songbird species (Baker et al. 1986, Searcy and Andersson 1986, Beecher et al. 2000, Beecher and Burt 2004).

Thrushes (Turdidae) in general are known for their long, varied, and melodious songs. The song of Clay-colored Thrushes (*Turdus grayi*) consists of a sequence of syllables highly variable in length. Our objectives were to: (1) describe the temporal structure of songs of the Clay-colored Thrush, (2) identify individual repertoire size, and (3) estimate the extent of syllable sharing between neighboring males to better understand the social interactions that occur among neighbors of this thrush.

METHODS

Study Area.—We conducted this study on the campus of the Universidad de Costa Rica (UCR), San José Province, Costa Rica (09° 56′ N, 84° 02′ W; 1,200 m asl). The campus has large open areas with scattered trees and bushes near a stream that crosses the campus. There are also two old-second growth forest patches of 1 and 0.5 ha, respectively. Female Clay-colored Thrushes nest principally on trees in open areas or human-made structures, while males defend a small territory around the nest.

Procedures.—The Clay-colored Thrush breeds from March to June at this location. We recorded songs of eight adult males from March to May in 2008, of which four were banded with a unique combination of colors and another had a unique mark on his chest. We recorded one banded male on 4 different days, three other males (2 of which were banded) on 3 different days, and the rest of the males (2 were marked) during a single day. Some males were unbanded, but we were able to identify each male through time by its territory location and presence of individual syllable types in its repertoire. We obtained most songs between 0450 and 0930 hrs, but we also used recordings from other times of the day.

Song Recording.—We used a Sony M-635VK tape recorder and a Sennheiser ME66/K6 shotgun microphone to record songs. We digitized the recordings at a sample rate of 44.1 kHz and a resolution of 16 bits with Adobe Audition 1.0 software (Adobe Systems Inc., San Jose, CA,

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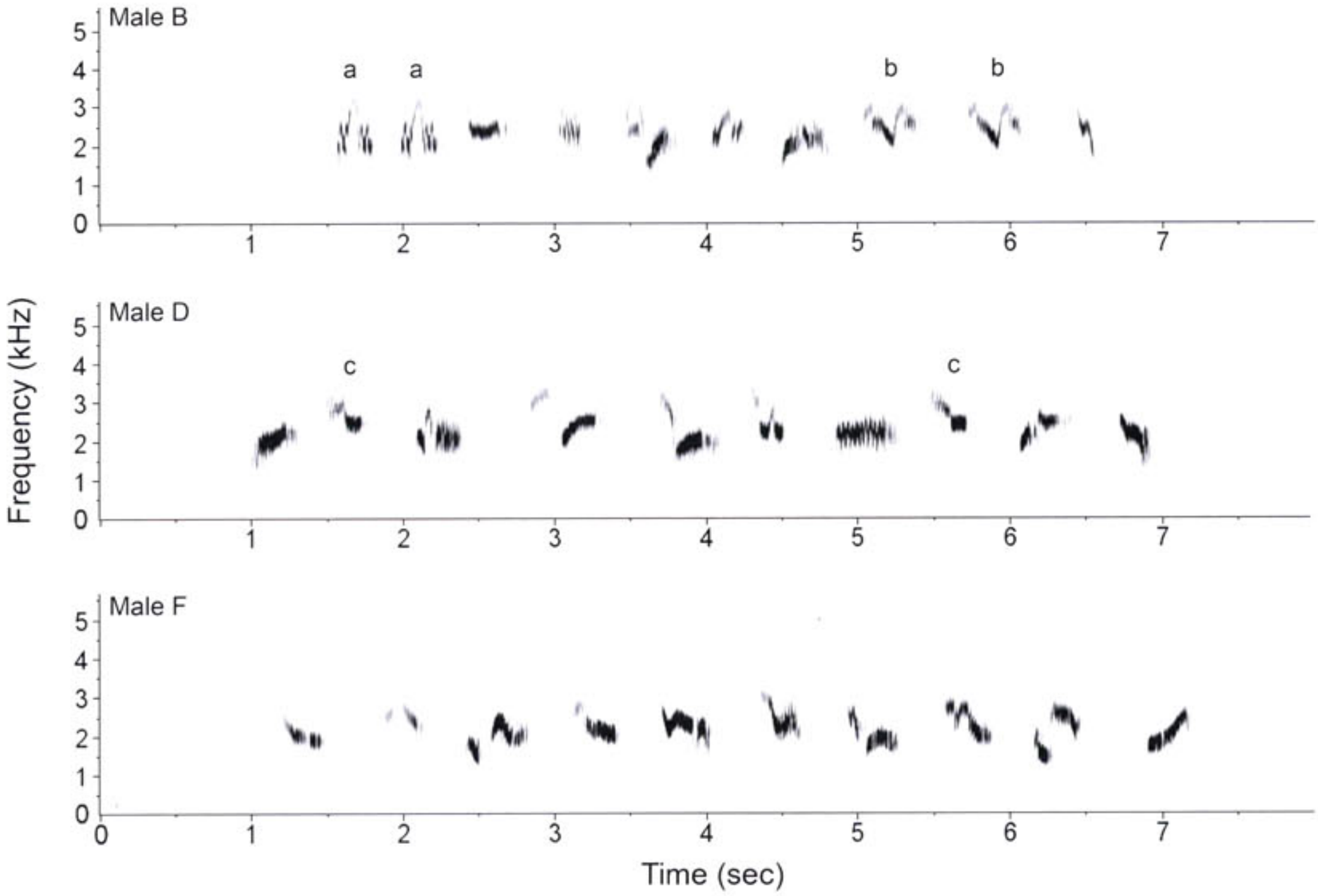

FIG. 1. Spectrograms of the songs of three male Clay-colored Thrushes recorded during 2008 in San José, Costa Rica. Each of these songs is composed of 10 syllables in total, but males may sing songs ranging from one syllable to more than a hundred syllables. Songs with equal number of syllables usually vary in syllable sequence. The songs of male B, D, and F have 8, 9, and 10 different syllable types, respectively. Lower case letters a, b, and c indicate syllables of the same types. Syllables are 0.29 ± 0.07 sec in length and separated by comparable silent intervals of 0.28 ± 0.07 sec in length (mean ± SD, $n = 8$ males, 54–125 syllables from 10 random songs/male were measured). Syllables have a sound frequency range of 1100 to 5400 Hz and complex frequency modulations that may include buzzes or trills.

USA) to produce .wav sound files. We used Raven Pro 1.4 software (Cornell Laboratory of Ornithology, Ithaca, NY, USA) for sound spectrogram production and analysis.

Song Measurements.—Each song is composed of a sequence of syllables, which are the minimal structural units of a song (Fig. 1). Some syllables are single notes that appear as a continous trace in the spectrogram, but other syllables are comprised of multiple notes. Consecutive songs in a song bout are separated by silent intervals ≥1 sec. We measured the number of syllables per song, song duration, inter-song silent intervals, and song tempo (number of syllables/sec) in 695 songs (range: 44–150 songs/male). We randomly selected 10 songs from each male to measure syllable duration and inter-syllable silent intervals.

The song of the Clay-colored Thrush, as in other thrushes, contains two syllable categories: whistles (or loud syllables) and soft syllables. The latter in other thrushes have been termed 'hisselly' or 'whisper' elements (Grabowski 1979, Rasmussen and Dabelsteen 2002, Johnson 2006). Soft syllables are sung at a lower amplitude and have a more complex structure than whistles. A given male Clay-colored Thrush sings at least two times as many soft syllable types as whistle syllable types (LEV, unpubl. data). Soft song in other songbird species is used in close-range communication, primarily during aggressive interactions, courtship displays, or both, depending upon the species (Dabelsteen et al. 1998, Searcy and Beecher 2009). However, soft syllables are rare in the spontaneous 'loud' songs that we analyzed here. We recorded a total of 5,188 syllables of which 5,032 were whistles and only 3% were soft syllables. Thus, we included soft syllables in the song-level measurements but we excluded them from the syllable repertoire size estimation and syllable sharing analysis.

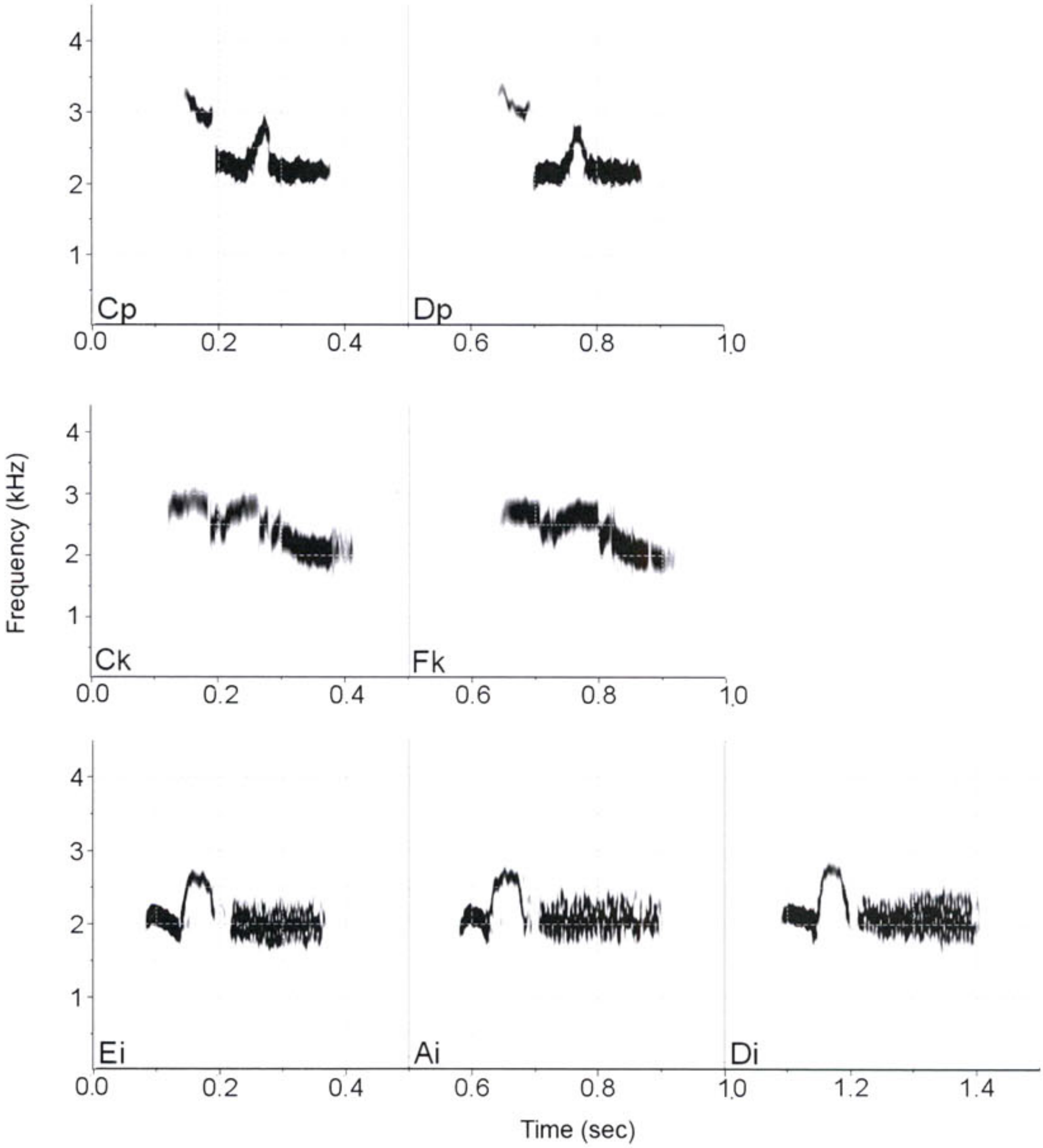

FIG. 2. Shared syllable types between male Clay-colored Thrushes during the 2008 breeding season in San José, Costa Rica. Syllable 'p' is shared among the repertoires of males C and D, syllable 'k' is shared between males C and F, and syllable 'i' is shared by males, E, A, and D. Mean spectrogram correlation values are: Cp-Dp = 0.86, Ck-Fk = 0.76, Ei-Ai = 0.66, Ai-Di = 0.70, and Ei-Di = 0.69.

Syllable Repertoire Size.—We printed spectrograms of the recordings using a fixed scale and visually identified each syllable type to produce a catalogue of the repertoires of all males. Clear differences in the frequency-temporal pattern of the different syllables facilitated the visual classification process (Fig. 1). We measured repertoire size as the total number of different syllable types in the songs of a given male. We also constructed cumulative plots of new syllable types per every 10 recorded syllables to verify that we had obtained complete repertoires.

Syllable Sharing.—We based identification of shared syllables between males by the similarity of the frequency-temporal patterns (Fig. 2) using a similar procedure as other studies analyzing

syllable or song type sharing (Mundinger 1982, Hughes et al. 1998, Molles and Vehrencamp 1999, Rasmussen and Dabelsteen 2002, Nicholson et al. 2007). We printed spectrograms of each syllable type in the repertoire of all males and mixed them into a single syllable pool. Three different observers blindly looked for matches between syllable types. A pair of syllables from two different males was considered to be a shared type only if all observers agreed on that match.

We re-examined similarity of shared types using the spectrogram correlator tool of Raven Pro 1.4 software (Cornell Laboratory of Ornithology, Ithaca, NY, USA). The correlator compares two syllables to each other and provides a correlation value based on the similarity of the frequency-temporal pattern of the sounds. We applied a 900–6,000 Hz band pass filter and selected the normalize and linear power options in the correlator configuration settings. We randomly selected 10 different renditions of that syllable type from each male for each pair of shared syllables, and ran the correlator using those sets of renditions to obtain 100 correlation values. We used the largest number of renditions available if the number of renditions of a given syllable type sung by one male was <10 (2 cases). We also selected 10 syllables for each pair of males at random from both males and compared those random sets to obtain 100 additional correlation values. Mean spectrogram correlations of shared and random syllables were later analyzed in a paired comparison.

We calculated the proportion of repertoire sharing between pairs of males using the formula: $2N_s/(R_1 + R_2)$, following McGregor and Krebs (1982). N_s is the number of shared syllable types among two males and R_1 and R_2 are the repertoire sizes of each male, respectively. We substracted the proportion of repertoire sharing from 1 to obtain a dissimilarity measure of the repertoires between pairs of males.

Statistical Analysis.—We used a paired *t*-test to examine whether males have as many types of shared syllables as individual syllables (exclusive to each male) in their repertoires. We used a *t*-test to examine if the relative frequency of individual and shared syllables in the songs was not different from that expected by the proportion of individual and shared types in the repertoires. All tests were two-tailed; assumptions of normality and homogeneity of variance were met (Zar 1996). We conducted a Mantel test using repertoire dissimilarity values and distance between song perches to test if males that were closer to each other shared a higher proportion of their repertoires (Sokal and Rohlf 1995). The *P*-value of the Mantel test correlation was calculated from 9,999 permutations. We used R 2.14.0 (R Development Core Team, Vienna, Austria) to conduct statistical tests.

RESULTS

The song of Clay-colored Thrushes consists of a sequence of syllables that is highly variable in length. Overall variation of number of syllables per song (mean = 7 syllables, CV range = 30–94%), song length (mean = 4.07 sec, CV range = 31–101%), and silent intervals between songs (mean = 3.94 sec, CV range = 58–131%) was high within and across individuals, but song tempo had low variation (mean = 1.9 syllables/sec, CV range = 7–11%) (n = 8 males, 44–150 songs/male).

We identified 91 different syllable types from all birds. Male repertoire size ranged from 10 to 17 syllable types (Table 1). The cumulative plots of syllable types all clearly reached asymptotes, demostrating that complete repertoires were detected for all males during the time of the study (Fig. 3). Males sang a given syllable type only once during the study period in few cases.

Only single syllables were shared among males rather than complete songs. There were 51 matches considered as shared syllable types between pairs of males by at least one observer. Seventeen of these 51 possible matches were identified as shared types by all three observers (Table 1). These final matches consisted of 13 different syllable types. Comparisons within pairs of males showed that mean spectrogram correlations were constantly higher for shared types than for random syllables (Table 2).

Most of the males (6/8) shared syllables with three or more males (Table 1). Males shared on average (± SD) 4 ± 2 syllables, which correspond to 25 ± 16% of their repertoires (Table 1). Repertoires were composed of more individual syllable types (syllables exclusive to each male) than shared syllable types ($t_7 = 4.689$, $P = 0.002$) (Table 1). The frequency of individual and shared syllables in songs did not differ from that expected by chance according to the proportion of individual and shared types in the repertoires ($t_7 = 0.047$, $P = 0.96$) (Fig. 4). Males that had closer song perches did not have more similar repertoires ($Z = -0.036$, $P = 0.48$) (Table 1).

TABLE 1. Distance (m) between territories (upper half) of eight male *Turdus grayi* (A-H) and number of shared syllables between males (lower half) during the 2008 breeding season in San José, Costa Rica. Male syllable repertoire size is shown in parenthesis.

Male	A (12)	B (11)	C (14)	D (13)	E (10)	F (17)	G (12)	H (17)
A	—	55	149	209	271	32	135	125
B	0	—	96	181	325	29	84	75
C	0	0	—	140	420	118	68	33
D	2	0	1	—	452	181	205	124
E	1	0	1	1	—	303	394	395
F	1	0	2	1	1	—	113	93
G	0	0	1	0	0	0	—	82
H	1	0	3	1	0	0	0	—
Totals[a]	4	0	7	5	2	4	1	5

[a] Total number of different shared syllable types. A male may share the same syllable type with more than one other male.

DISCUSSION

Songs of Clay-colored Thrushes are highly variable in length and number of syllables within and between males. Variation between males in song length and syllable number could be the result of individual differences in neuromuscular development that constrain song duration and performance (Lambrechts 1996, Suthers et al. 1999). For example, male Zebra Finches (*Taeniopygia guttata*) with longer and more complex songs have greater reproductive success (Woodgate et al. 2012). Thus, song length and syllable number are traits that could provide females with valuable information regarding male quality. In turn, variation in song length (Weary et al. 1988) and song tempo (Cooper and Goller 2006) within males could be affected by the motivational state of the singing bird. However, song tempo in our study was considerably steady.

Male Clay-colored Thrushes have a repertoire of 10–17 syllable types. This repertoire size is within the range that has been observed for other thrushes of the genus *Turdus*, which have repertoires composed of 6 to 25 syllable types

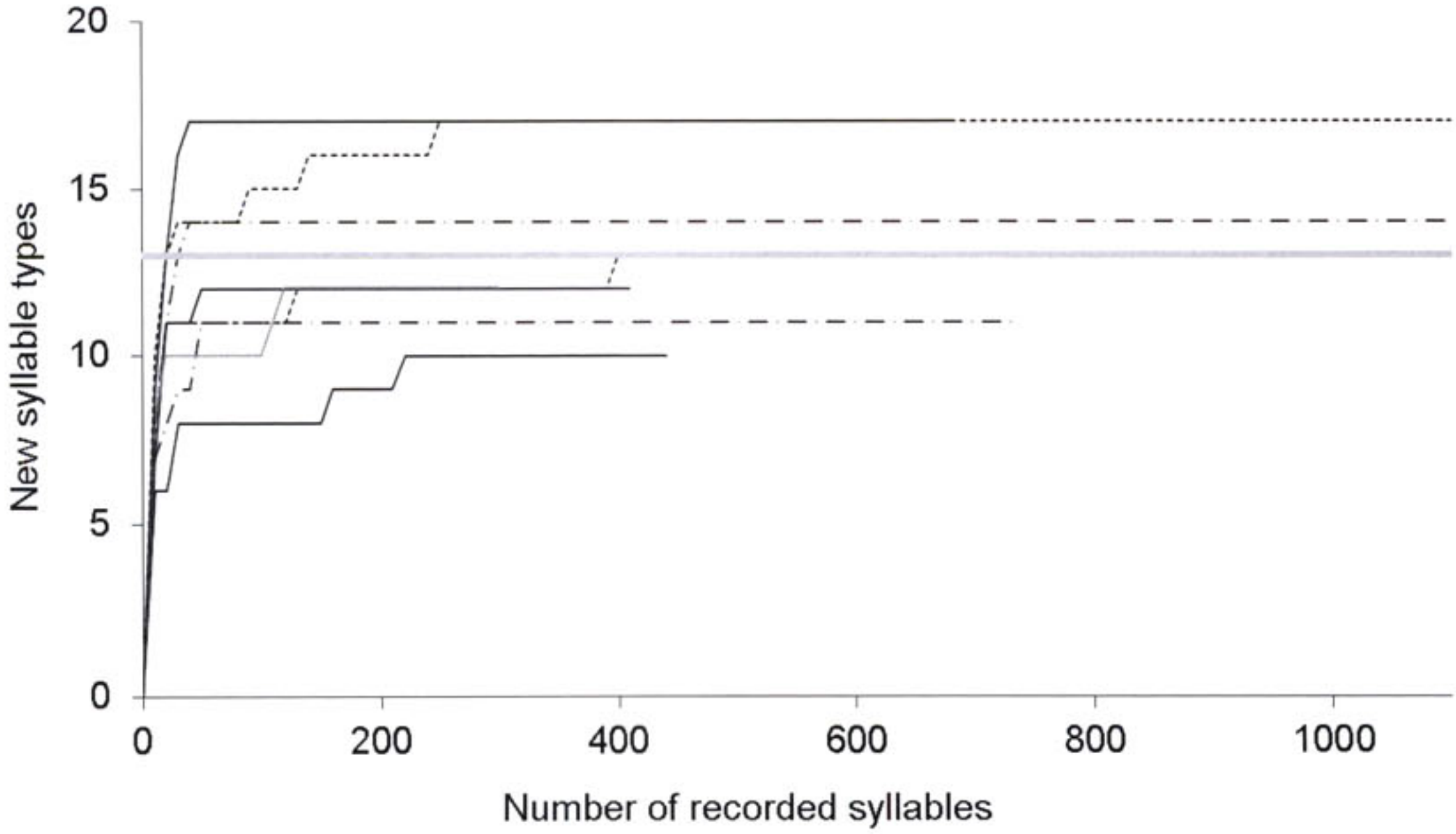

FIG. 3. Cumulative syllable repertoire size by number of recorded syllables of Clay-colored Thrushes during the 2008 breeding season in San José, Costa Rica. The solid gray line indicates mean repertoire size = 13 syllable types (n = 8 males).

TABLE 2. Mean spectrogram correlations for shared syllable types and one set of random syllables from the songs of eight male *Turdus grayi* by male pair. Each value represents the average of 100 spectrogram correlations, except for male pairs A-F and D-H, which are based on 10 and 70 correlations, respectively.

	Shared type			
Male pair	First	Second	Third	Random
A-D	0.75	0.70	—	0.33
A-E	0.66	—	—	0.18
A-F	0.68	—	—	0.34
A-H	0.70	—	—	0.29
C-D	0.86	—	—	0.31
C-E	0.64	—	—	0.10
C-F	0.64	0.76	—	0.27
C-G	0.60	—	—	0.27
C-H	0.62	0.55	0.65	0.35
D-E	0.69	—	—	0.21
D-F	0.55	—	—	0.30
D-H	0.63	—	—	0.29
E-F	0.73	—	—	0.16

(Rufous-backed Thrush [*T. rufopalliatus*] in Grabowski 1979, American Robin [*T. migratorius*] in Johnson 2006, Japanese Thrush [*T. cardis*] in Tooru 2006). Common Blackbirds (*T. merula*) in contrast have a larger repertoire of motifs (Rasmussen and Dabelsteen 2002) than the syllable repertoires of Clay-colored Thrushes, but this species has a different song structure.

The repertoire of the Clay-colored Thrush is composed of a set of individually unique syllable types and a smaller number of syllable types that are shared with neighbors. A larger fraction of individual syllables comprising the repertoires probably facilitates individual recognition (Falls 1982, Beecher et al. 1994), although unique

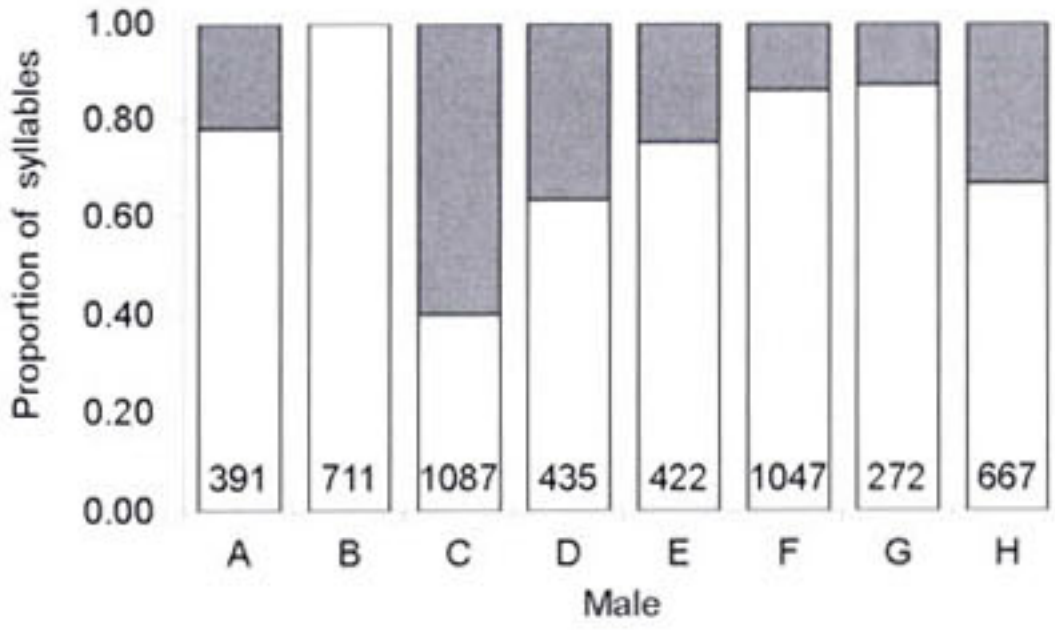

FIG. 4. Proportion of individual (white) and shared (gray) syllables sung by each male Clay-colored Thrush during 2008 in San José, Costa Rica. Total number of recorded syllables is at the base of each bar.

syllables or song types may not be necessary to accomplish individual recognition (Weary and Krebs 1992). Individual syllables could be invented, improvised or learned elsewhere (Marler and Peters 1982, Payne 1996, Kroodsma et al. 1999). Johnson (2006) observed that most of the elements (75–82%) in the repertoires of hand-reared American Robins were acquired by invention. The high and similar proportion of individual syllables that we found in the repertoires of Clay-colored Thrushes suggests that at least part of these syllables are invented as well.

Shared syllables in turn reflect social learning among neighboring males (Payne 1981, Baptista and Petrinovich 1984, Beecher and Burt 2004). Only single syllables were shared among males, suggesting that syllables are the unit of imitation. Shared song components are maintained through time in a local population if vocal learning occurs early in life (e.g., as nestlings) followed by short natal dispersal or if song learning occurs after young males disperse and interact with local neighbors in a new area (Kroodsma 1974, Lynch 1996, Payne 1996). Generally, the extent of repertoire sharing decreases with increasing distance between territorial males (Bertram 1970, McGregor and Krebs 1982). However, we did not find a relationship between repertoire sharing and song perch distance. Such a relationship would not be expected if Clay-colored Thrushes disperse relatively long distances before setting up their first territory. Unfortunately, natal dispersal distance of Clay-colored Thrushes is only known for one male that we found defending a territory about 130 m distant from where it was banded as a nestling. Alternatively, Clay-colored Thrushes could follow a different pattern of repertoire sharing with increasing distance, similar to that of Common Blackbirds and Common Nightingales (*Luscinia megarhynchos*), which are more likely to share components of their repertoires with other males at intermediate distances (>100 m) rather than with closer neighbors (Hultsch and Todt 1981).

Local repertoire sharing has an important role in territory possession (Beecher et al. 2000) and song discrimination by females (Searcy 1990, Searcy et al. 2002). The relative importance of song sharing in Clay-colored Thrushes for different social functions needs further investigation. Future research on population dynamics, especially natal dispersal, as well as on the critical period for song learning is required to better

understand song development and function in this and other species of thrushes.

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