



Individual Distinctiveness in the Fine Structural Features and Repertoire Characteristics of the Songs of White-eared Ground-sparrows

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Abstract

Communication between social animals is often more effective when signals facilitate individual recognition. Two critical requirements for individual recognition are the occurrence of characteristics that are unique to each individual, and the consistency of these characteristics through time. In some animals, characteristics of acoustic signals are known to vary over time due to changes in a variety of factors, including physiological and environmental features. Such temporal variation requires careful evaluation when exploring the individual distinctiveness of animal signals. In this study, we evaluate individual distinctiveness in the songs of male white-eared ground-sparrows *Melospiza leucotis* and the persistence of distinctive characteristics over time. We collected focal recordings from populations of banded ground-sparrows during two consecutive breeding seasons, including multiple recording sessions within each breeding season. We evaluated individual distinctiveness in fine structural acoustic features of songs. We also extended our analysis to repertoire characteristics, focusing on whether the relative frequency of song type use may provide cues to individual identity. We found that each male white-eared ground-sparrow sang individually distinctive songs, although their fine structural features varied between recording sessions. We found the frequency with which males sang different song types was also individually distinctive, and this feature varied little between recording sessions. Receivers may be able to use these distinctive characteristics to differentiate individuals over extended time periods; this may be especially important for species that engage in long-term social interactions, such as tropical birds that defend territories against rival conspecific animals throughout the year.

Introduction

A prerequisite for individual recognition is the occurrence of features that are unique to each individual, a characteristic that is common to many animals (Barnard & Burk 1979; Dale et al. 2001; Tibbetts & Dale 2007). In social groups, signals of identity allow receivers to distinguish between different signallers, making social interactions direct and efficient (Beecher 1982; Dale et al. 2001; Ellis 2008). For example, a receiver can judge if the signal comes from a

competitor, a familiar neighbour, a breeding partner, a non-threatening juvenile or a relative, and then respond according to the signaller's identity (van Rhijn & Vodegel 1980; Whitfield 1986; Tibbetts & Dale 2007; Wilson & Mennill 2010).

Individual-specific components of signals have been measured across a wide variety of animal species and multiple signalling modalities, including chemical, visual and acoustic signals (Ptacek 2000; Tibbetts & Dale 2007; Grether et al. 2009; Ord & Stamps 2009; Grether 2011; Ord et al. 2011). Individually distinctive

acoustic signals have been documented in amphibians (e.g. Bee et al. 2001; Feng et al. 2009; Gasser et al. 2009), mammals (e.g. Dallmann & Geissmann 2001; Blumstein & Munos 2005; Vannoni & McElligott 2007) and birds (e.g. Harris & Lemon 1972; Lovell & Lein 2004; Barrantes et al. 2008). Within birds, individually distinctive vocalizations have been reported in both song-learning species (e.g. Nelson & Poesel 2007; Ellis 2008; Benedict & McEntee 2009) and those with innate vocalizations (e.g. Lengagne et al. 2000; Fitzsimmons et al. 2008; Sandoval & Escalante 2011; Garcia et al. 2012). Individually distinctive vocalizations are thought to be more pronounced in song-learning species (Mennill 2011), especially because the learning process leads to small changes in acoustic structure, introducing 'mistakes' and improvisations into the songs of each individual for song-learning species (Hultsch & Todt 2004; Catchpole & Slater 2008).

Another important component of individual recognition is the consistency of the individually distinctive features of signals through time. There is much evidence of signal consistency and of changes in signal characteristics over time, in many different avian taxa and other animal taxa (reviewed by Ellis 2008). In some bird species, fine structural characteristics of vocalizations may vary over time owing to morphological or physiological changes in the signaller (Nottebohm et al. 1987; Gil & Gahr 2002), or changes in the physical environment that serves as the transmission medium for the vocalizations (Forrest 1994; Slabekoom et al. 2002). Beyond fine structural features, broader characteristics of vocalizations may vary over time because of ontogenetic changes in repertoire size (e.g. Adret-Hausberger et al. 1990; Vargas-Castro et al. 2012) or changes in social status or breeding stage (e.g. Topp & Mennill 2008; Hennin et al. 2009). Consequently, it is important to measure temporal variation when evaluating the individuality of animal signals, especially in species that have more than one song type.

There are few studies that evaluate temporal variation in individually distinctive acoustic signals. Investigations of species with small repertoires have compared the fine structural acoustic characteristics of songs between recording sessions (e.g. Riebel & Salter 2003; Leitão et al. 2004; Ellis 2008; Wilson & Mennill 2010). Investigations of species with large repertoires have compared repertoire consistency through time (e.g. Adret-Hausberger et al. 1990; Todt & Hultsch 1998; Vargas-Castro et al. 2012). We were motivated by an interest in evaluating individual distinctiveness in a species with an intermediate to small repertoire size, to contrast two categories of vocal

characteristics—fine structural features and repertoire characteristics—and gain a deeper understanding of individual distinctiveness in animal vocal signals.

In this study, we test whether male white-eared ground-sparrows *Melospiza leucotis* sing with individual distinctiveness, and whether this distinctiveness is found in the fine structural acoustic features of their songs, or the broader characteristics of their repertoires or both. Secondly, we analyze whether individually distinctive characteristics persist over time. White-eared ground-sparrows are year-round territorial songbirds that inhabit dense thickets, shade coffee plantations and areas with early successional vegetation in Central America (Stiles & Skutch 1989; Sandoval & Mennill 2012). The visually occluded nature of their habitat makes vocal signals the principal form of conspecific interaction for this species. Male white-eared ground-sparrows sing near their territory boundaries starting just before sunrise and continue singing at a lower level throughout the course of the day; male solo songs have been associated with territory defence and mate attraction in this and other closely related species (Benedict & McEntee 2009; Sandoval & Mennill 2012; Sandoval et al. 2013). If fine structural acoustic features or characteristics of their vocal repertoires are important for individual recognition, we expected that each male would exhibit unique fine structural features or repertoire characteristics. Furthermore, if their acoustic features or repertoire characteristics are important in individual recognition, we expected them to remain consistent over time.

Methods

We recorded songs from 38 male white-eared ground-sparrows in four locations within Costa Rica (Fig. 1): north of Heredia, Heredia province (10°01'N, 84°05'W; elevation: 1200–1500 m; n = 14 males); Universidad de Costa Rica campus, San José province (09°56'N, 84°05'W; elevation: 1200 m; n = 9); Lankester Botanical Garden, Cartago province (09°50'N, 83°53'W; elevation: 1400 m; n = 6); and Estación Biológica Monteverde, Puntarenas province (10°18'N, 84°48'W; elevation: 1600 m; n = 9). Although white-eared ground-sparrows produce solo songs, duets and calls, we focus on male solo songs here because these vocalizations are the most prominent for this species, and these vocalizations could be readily assigned to one individual.

We collected recordings between Apr. and Aug. 2011 and between Mar. and Jun. 2012, during this species' breeding season (Sandoval & Mennill 2012).

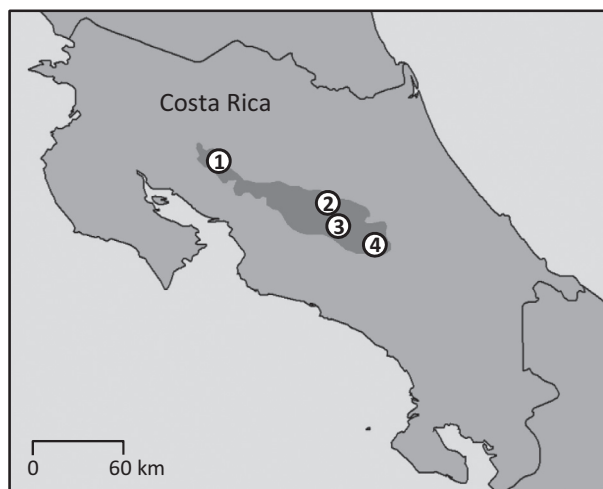


Fig. 1: Map showing four populations of white-eared ground-sparrows in Costa Rica where male songs were recorded for analyses of individual distinctiveness: (1) Monteverde (MTV); (2) north of Heredia (HDIA); (3) the campus of Universidad de Costa Rica (UCR); and (4) Lankester Botanical Garden (JBL). Shaded grey region shows the species' range in Costa Rica.

Recordings were collected prior to egg laying, during incubation and while the parents had hatchlings. For most of the birds sampled, we were not able to calculate the exact stage of breeding because the dense thicket habitat at our study sites made finding nests and observing breeding behaviour difficult (e.g. in 8 yr of studying this species, we have found only ten nests; Sandoval & Mennill 2012). For 12 pairs in the current study, however, we observed the adults exhibiting nesting behaviour (adults carrying nesting materials or food) or we observed chicks directly, confirming that our recordings were collected during the breeding period.

We recorded each male starting between 0450 and 0600 h. We banded 35 of the 38 males with a unique combination of coloured leg bands. These individually marked males allowed us to record the same individuals on different days during the same year and between years (the three unbanded males were recorded on a single day and are included only in our comparison of repertoire characteristics between males). We collected these recordings using a Marantz PMD660 or PMD661 digital recorder and a Sennheiser ME66/K6 shotgun microphone (recording format: WAVE; sampling rate: 44.1 kHz; accuracy: 16 bits). Twenty-one males were recorded during a single session in 2012; eleven males were recorded during two sessions in 2011 and one session in 2012; four males were recorded during three sessions in 2011 and one session in 2012; one male was recorded during two

sessions in 2011; and one male was recorded during one session in each of 2011 and 2012. Each focal recording session lasted from 40 to 75 min (average \pm SE: 59 ± 1 min). We complemented the repertoire size description for 10 males with recordings obtained using autonomous digital recorders (model: Song Meter SM2; Wildlife Acoustics Inc., Concord, MA, USA) placed in the middle of the white-eared ground-sparrow territories. The location of these recorders in the middle of the birds' territories reduced the chance of our recording vocalizations from non-target individuals, particularly since ground-sparrow songs attenuate and degrade rapidly in this habitat, often in less than the width of one territory (LS & DJM unpubl. data). Each automated recording session lasted from 720 to 2160 min (average \pm SE: 1368 ± 168 min).

Song Classification and Measurements

We classified song types visually based on their appearance on sound spectrograms (as in Franco & Slabbekoorn 2009; for example), focusing on the number of different types of elements and the overall shape of each element. All songs were compared to a library of song types that we developed for white-eared ground-sparrows. Within song types that share most of their features, we found subtle variation in the total number of elements; different birds added or omitted elements from the introductory component of the song or varied the number of elements in the terminal trill. Songs that varied only in the number of repeats of introductory elements and terminal trill elements but were otherwise similar in their fine structural details, we classified as the same song type (see Fig. 2 for examples).

We measured two repertoire characteristics: the number of song types and the frequency of use of each song type. We included, in the comparisons, only males with more than 20 songs recorded per male (average \pm SE: 94.8 ± 11.1 songs per male, $n = 38$ males) and between recording sessions of the same male with more than 12 songs within each session within and between years (54.8 ± 7.1 songs per session, $n = 13$ males). We calculated male repertoire size following the curve-fitting method with the Wildenthal equation (Wildenthal 1965). We conducted these repertoire size estimations for 19 males where we had recorded 80 or more recorded songs. We used Excel 2007 to implement the curve-fitting method, and we reported the estimated repertoire size from the asymptote of the curve.

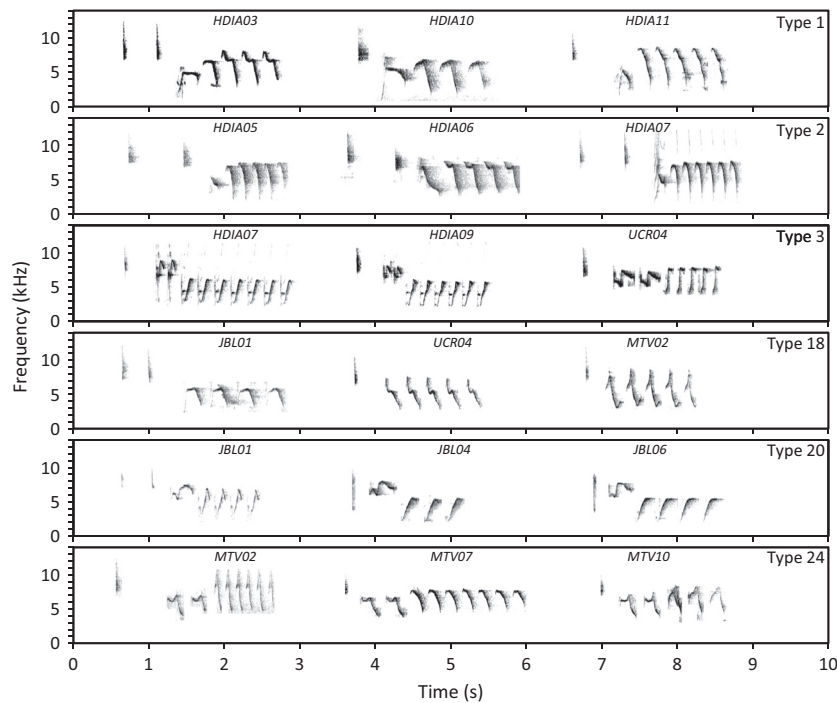


Fig. 2: Sound spectrograms representing six common solo song types, with examples from three different male white-eared ground-sparrows for each type. Songs were classified visually according to similarities between the elements before the final trill and overall song structure. Male identity is shown above each song, coded by the population of origin (HDIA: north of Heredia, JBL: Lankester Botanical Garden, MTV: Monteverde, and UCR: Universidad de Costa Rica campus) and a number to represent each individual.

For each song, we measured seventeen fine structural acoustic features (Fig. 3) using Raven Pro 1.4 sound analysis software (Cornell Lab of Ornithology, Ithaca, NY, USA). We measured duration, number of elements, lowest and highest frequency and frequency of maximum amplitude for the entire song, the middle section of the song and the terminal trill. In addition, we measured the number of inflections for elements in the middle portion of the song and the terminal trill (Fig. 3). We used a combination of spectrograms (to identify the songs), power spectra (to measure frequency) and waveforms (to measure duration) to collect these 17 measurements. We used a temporal resolution of 5.8 ms and a frequency resolution of 188 Hz with the following settings: Hann window, 50% overlap, 256 kHz sampling. We collected these measurements in a subset of vocalizations from all of the vocalizations available from each male, selecting the first eight songs per song type per recording session for each male, skipping recordings that had prominent background sounds.

Statistical Analysis

Different males often share the same song types between their repertoires, but they might sing these shared song types in different proportions, giving rise to a behaviour that may be individually distinctive. Hereafter, we refer to this behaviour of producing

song types in similar proportions over time as 'repertoire-use similarity'. To measure whether repertoire-use similarity can provide a cue of individual identity, we calculated the Morisita index of similarity (Morisita 1959), to quantify the frequency of use of each song type, both between males and within males between recording sessions. We calculated the index according to the equation presented by Morisita (1959; p. 75); this index has values from 0 to 1, where values close to zero indicate 0% similarity between a pair of recordings and values close to one indicate 100% similarity between a pair of recordings. For example, imagine three different birds that sing three song types (A, B and C). If bird 1 sings type A 80% of the time, type B 20% of the time, and type C 0% of the time; bird 2 sings type A 60% of the time, type B 35% of the time, and type C 5% of the time; and bird 3 sings type A 20% of the time, type B 20% of the time, and type C 60% of the time; then bird 1 vs. 2 has a Morisita similarity score of 0.94, bird 1 vs. 3 has a Morisita similarity score of 0.36, and bird 2 vs. 3 has a Morisita similarity score of 0.48. We used cluster analysis to depict the pattern of repertoire-use similarity based on the Morisita scores. We evaluated repertoire-use similarity between populations and between recording sessions within males using one-way analysis of similarities (ANOSIM; Clarke 1993; Hammer 2012), where we used Morisita indices of similarity as the distance measurement.

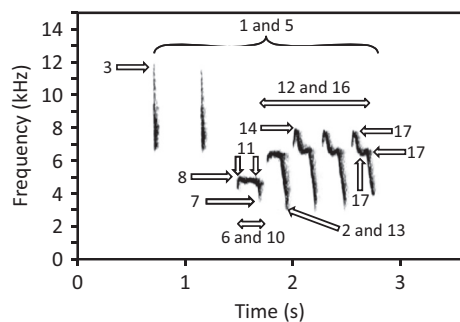


Fig. 3: Sound spectrogram of a typical white-eared ground-sparrow song showing the 17 fine structural features we measured: (1) the duration of the whole song, in seconds; (2) the lowest frequency of the whole song, in Hz; (3) the highest frequency of the whole song, in Hz; (4) the frequency of maximum amplitude for the whole song (not shown); (5) the total number of elements of the whole song; (6) duration of middle section of the song (defined as the portion of the song following the high-pitched introductory notes and the start of the terminal trill), in seconds; (7) the lowest frequency of the middle section, in Hz; (8) the highest frequency of the middle section, in Hz; (9) the frequency of maximum amplitude for the middle section (not shown); (10) the total number of elements of the middle section; (11) the number of inflections points in the middle section; (12) the duration of the terminal trill, in seconds; (13) the lowest frequency of the terminal trill, in Hz; (14) the highest frequency of the terminal trill, in Hz; (15) the frequency of maximum amplitude for the terminal trill (not shown); (16) the total number of elements in the terminal trill; and (17) the number of inflection points in one syllable in the terminal trill.

We also conducted a Mantel test (using 10 000 permutations) to evaluate the relationship between the geographic distances between the centre of males' territories (using Euclidian distance) and repertoire-use similarity scores (i.e. Morisita similarity scores). To analyze whether repertoire-use similarity between sessions is an effect of correlation in recording length, we ran an additional ANOSIM using Jaccard's index of similarity as the distance measurement. Jaccard's index of similarity compares only the repertoire size within males across recording sessions without taking into account the number of songs recorded in each session (as in Lapierre et al. 2011; for example). We used the following equation implemented in PAST (Hammer 2012):

$$J_i = \frac{M}{M + N}$$

where M is the number of songs shared by two males, and N is the total number of songs sang just by one male.

Following the approach used by Ellis (2008), we used a discriminant function analysis to compare differences in the seventeen fine structural acoustic features between males. We used an interactive backward stepwise discriminant analysis to find the

fewest possible acoustic features to explain the largest possible amount of variation between individuals. Using SYSTAT (version 11.00.01; SYSTAT Software, Chicago, IL, USA) we started with a model that included all 17 measurements; we excluded from the discriminant analysis the variable with the lowest F-to-remove value; after each exclusion, we cross-validated the model (see below for description of cross-validation approach) and we continued excluding variables until we obtained a model with the fewest variables that still provided the same or higher percentage of correct assignments relative to the original model that included all acoustic features. This analysis was conducted for each song type that was shared by more than five males and that was sung eight or more times by each male; six song types satisfied these criteria. We report classification accuracy from the discriminant function analysis based on the leave-one-out approach to cross-validation (Krebs 1999). We used a binomial test to compare whether the classification accuracy determined by the discriminant function analysis is higher than the classification expected by chance. Chance expectations were calculated by dividing one by the number of males included in each particular DFA.

We complement the discriminant analysis approach by calculating the Potential for Individual Coding scores (PIC scores; Vignal et al. 2004; Robisson et al. 1993) on the six song types used in the discriminant function analysis mentioned above. This approach estimates the coefficient of variation in the song characteristics between males (CV_b) and within males (CV_w). We estimated the PIC as the ratio between the two coefficients of variation (CV_b/CV_w), where CV_w is the mean value of the CV_w of all individuals. When PIC scores are >1.0 , the measured feature will have the potential for individual distinctiveness. We compare whether the variability in song measurements was different between CV_b and CV_w using analysis of variance. For this analysis, we pooled together all recording sessions for each male.

We used multiple analysis of variance (MANOVA) to explore whether fine structural features varied between recording sessions of the same song type. We focused on the fine structural features that were detected by the discriminant function analysis as being important for individual distinctiveness. In these analyses, we used only males that sang the same song type in more than one recording session. For this analysis, we nested recording session within male identity and used the fine structural measurements of songs as dependent variables. We only conducted this analysis for song types that were present in five or

more males in two or more recording sessions; three song types satisfied these criteria. For each MANOVA, we present the details of the whole model as well as recording session nested within male (i.e. Recording session [Male]) and between males.

We used PAST (version 2.17; Øyvind Hammer, Natural History Museum, University of Oslo, Norway) for ANOSIM, Mantel tests and cluster analyses. All other analyses were conducted in SYSTAT. Throughout, values are reported as means \pm SE. We considered our results significant at $p = 0.05$, except for the analyses that included multiple comparisons (see Results) when we reported significance based on exact Bonferroni corrections.

Results

We collected recordings from 38 male white-eared ground-sparrows from four different populations in Costa Rica during two consecutive breeding seasons. For 19 males where we had 80 or more song recorded, the repertoires varied in size from two to eight song types, with an average repertoire size of 3.5 ± 0.3 song types.

Fine Structure Analysis

We found 32 unique song types in our recordings of the 38 recorded males, although the six most common song types dominated our recordings (2282 of 3627, or 62.9% of all recorded songs, were the six song types depicted in Fig. 2). The fine structural acoustic features of the six most common male song types of white-eared ground-sparrows showed substantial between-male variation. Six discriminant analyses, one for each of the six most common song types, consistently assigned songs to the correct male at levels that exceeded chance expectations (Table 1). The

lowest percentage of correctly-assigned songs during cross-validation for the six song types analyzed was 72%. This high level of distinctiveness was reached with a subset of acoustic features, varying from four to eight features, as shown in Table 1. These features varied among the six song types, although some of them (e.g. structural feature 14, the highest frequency of the terminal trill) were important in all six song types.

For the six most common song types, we found PIC scores greater than 1.0 (Tables S1–S6) for most of the fine structural features (88–100% of features in Tables S1–S6), indicating a high level of individual distinctiveness in male white-eared ground-sparrow songs. Following correction for multiple comparisons, four features showed the highest levels of individual distinctiveness across the six song types, according to the PIC analysis: the duration of the middle section ($p < 0.001$ for all comparisons), the lowest frequency of the middle section ($p < 0.001$ for all comparisons), the highest frequency of the middle frequency ($p < 0.01$ for all comparisons) and the lowest frequency of the trill ($p < 0.001$ for all comparisons).

Repertoire-Use Similarity

Male white-eared ground-sparrows share song types between individuals and between populations. We found substantial variation between males in repertoire-use similarity (i.e. the relative proportion in which different song types are produced over time). Six males received a Morisita score for repertoire-use similarity ≤ 0.50 , indicating that their patterns of repertoire use were dissimilar from all other males. Eight males received a Morisita score for repertoire-use similarity of 0.51–0.75, indicating that their song repertoire use was moderately similar. Seventeen males received a Morisita score for repertoire-use

Table 1: Results of six discriminant function analyses (DFA) used to evaluate individual distinctiveness in male white-eared ground-sparrow songs. The analyses were conducted on six song types that were found in the repertoire of ≥ 5 males and that were sung ≥ 8 times for each male. Sample size (n) shows the total number of males that sang each song type in the analysis. The Wilks λ and F values show the results of backwards DFA with cross-validation and $p < 0.001$ for the six analyses. The p-values show the results of a binomial test comparing the percent of correct classification based on chance (i.e. one over n). The features retained in the backwards DFA correspond to the seventeen numbered fine structural features outlined in Figure 3

| Song Type | n | Percent correct classification (%) | Wilks' λ | F_{df} | p | Features retained in backwards DFA |
|-----------|----|------------------------------------|------------------|------------------------|--------|------------------------------------|
| Type 1 | 10 | 88 | <0.001 | 36.6 _{72,634} | <0.001 | 2, 8, 11, 12, 13, 14, 16, 17 |
| Type 2 | 11 | 83 | <0.001 | 27.5 _{80,636} | <0.001 | 2, 6, 7, 8, 11, 13, 14, 16 |
| Type 3 | 10 | 80 | <0.001 | 28.8 _{72,731} | <0.001 | 6, 7, 8, 12, 14, 15, 16, 17 |
| Type 18 | 13 | 72 | <0.001 | 30.4 _{60,621} | <0.001 | 2, 5, 14, 16, 17 |
| Type 20 | 6 | 96 | <0.001 | 31.9 _{35,250} | <0.001 | 4, 6, 7, 8, 12, 14, 16 |
| Type 24 | 7 | 86 | <0.001 | 76.2 _{24,165} | <0.001 | 2, 6, 8, 14 |

similarity between 0.76 and 0.95 indicating that their repertoire use was moderately to-highly similar. Eight males received a Morisita score for repertoire-use similarity higher than 0.95, indicating that repertoire use was highly similar (Fig. 4). Interestingly, although all eight males with the highest similarity shared territory boundaries (i.e. two pairs of males in adjacent territories and four males in a cluster from one population), not all males that shared territory boundaries showed this high degree in repertoire similarity. These differences in repertoire-use similarity indicate that the repetition patterns used by males may provide cues for distinguishing between individuals (Fig. 4). Nearby males (males within each population) were more similar in their patterns of repertoire-use similarity when compared to males from other populations (ANOSIM: $R = 0.77$, $p < 0.001$, Fig. 4). This pattern was also true when we analyzed the relationship between geographic distance and repertoire-use similarity (Mantel test: $R = 0.40$, $p = 0.001$).

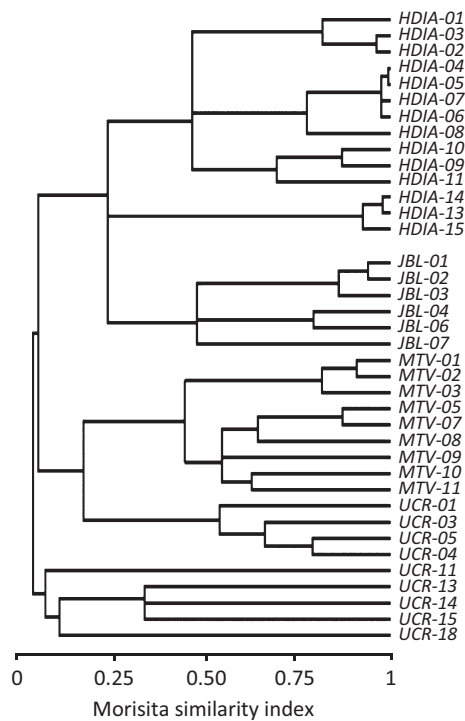


Fig. 4: Comparison between male solo song repertoire-use similarity in white-eared ground-sparrows, using the Morisita index of similarity, comparing shared song types and the frequency of utilization of each song type ($N = 38$). The tips of each branch show a letter code for the population where the bird was recorded (HDIA: north of Heredia, JBL: Lankester Botanical Garden, MTV: Monteverde, and UCR: Universidad de Costa Rica campus) and a number that represents the individual's identity. When individuals are clustered at the end of branches, it means they show similar patterns of repertoire use.

Consistency Over Time

We analyzed consistency in fine structural features of male songs for the three most common song types. The fine structural characteristics of song types varied both between males and between recording sessions within males for the three common song types that we analyzed, including song type 1 (whole model, $F_{78,1163} = 128.91$, $p < 0.001$; recording session [male], $F_{48,1037} = 17.20$, $p < 0.001$; males, $F_{24,733} = 28.90$, $p < 0.001$), song type 3 (whole model, $F_{78,855} = 75.53$, $p < 0.001$; recording session [male], $F_{48,761} = 9.17$, $p < 0.001$; males, $F_{24,538} = 6.12$, $p < 0.001$) and song type 18 (whole model, $F_{156,1251} = 49.56$, $p < 0.001$; recording event [male], $F_{102,1215} = 2.40$, $p < 0.001$; males, $F_{48,1047} = 9.69$, $p < 0.001$). In other words, for all three song types analyzed, we found significant variation in fine structural features between males and between sessions of the same male.

We compared repertoire-use similarity between recording sessions for 13 male white-eared ground-sparrows. Patterns of repertoire use were more similar within different recording sessions of the same male than between recording sessions of different males. This was true when we took into account the number of songs recorded (ANOSIM using Morisita scores: $R = 0.83$, $p < 0.001$, Fig. 5). The same pattern held true when we analyzed the number of song types detected independently of the number of songs recorded (ANOSIM using Jaccard indices: $R = 0.55$, $p < 0.001$).

Discussion

Male white-eared ground-sparrows have individually distinctive songs and singing styles. Both the fine structural features of male songs as well as the proportion of time spent singing each song type vary more between individuals than within individuals. This distinctiveness is evident when we compared between multiple recording sessions of the same male, although there was also significant variation between recording sessions. We also found that males recorded in the same population share similar patterns of repertoire used in comparison to males from other populations.

Our results suggest that the solo song repertoire (song types and frequency of use) encode sufficient information to distinguish male white-eared ground-sparrow identity, at both the population level and the individual level. This pattern has also been reported in other bird species such as common blackbird (*Turdus merula*; Rasmussen & Dabelsteen 2002), white-crowned

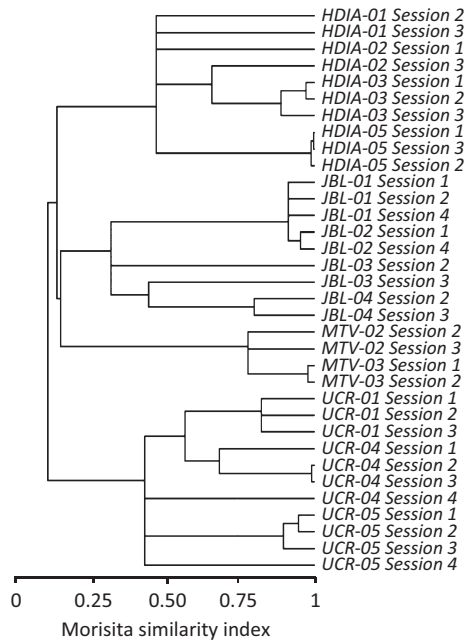


Fig. 5: Comparison between recording sessions of male solo song repertoire in white-eared ground-sparrows, using the Morisita index of similarity, comparing shared song types and the frequency of utilization of each song type within males ($N = 13$). The tips of each branch show a letter code for the population where the bird was recorded (HDIA: north of Heredia, JBL: Lankester Botanical Garden, MTV: Monteverde, and UCR: Universidad de Costa Rica campus) and a number that represents the individual's identity.

sparrow (*Zonotrichia leucophrys*; Nelson & Poesel 2007) and skylark (*Alauda arvensis*; Briefer et al. 2009). In these examples, one component of male songs or singing behaviour is understood to encode individuality, and another component is thought to encode geographic or group affiliation. In our study of white-eared ground-sparrows, the group level might be encoded in the features that are shared between the males in the same population (e.g. repertoire-use similarity), and individual distinctiveness might be encoded in features that vary most between individuals (e.g. fine structural features).

We found that the fine structural features of male songs were individually distinctive in white-eared ground-sparrows. The structural features that contributed most strongly to individual distinctiveness in the discriminant analysis were frequency measurements of the songs and the number of elements and inflections within the trills (Table 1). Not all of the structural features we measured encode sufficient information to distinguish males. For the six most widespread song types that we measured, only four to eight of the seventeen fine structural measure-

ments were included in our backwards discriminant analysis, suggesting that a subset of fine structural features may be most useful for encoding identity. As in previous studies (e.g. Robisson et al. 1993; Tripp & Otter 2006; Garcia et al. 2012), a combination of frequency and temporal measures were the most individually distinctive components. We found significant differences in fine structural measurements between recording sessions of the same male, as has also been found in previous studies (see Ellis 2008). For example, black-capped chickadees exhibit significant variation between recording sessions in individually distinctive song features, and their responses to playback reveal that they perceive playback songs from different recording sessions as the same male (Wilson & Mennill 2010). We expect white-eared ground-sparrows would behave in the same fashion, given the significant PIC scores across recording sessions and the significant effect of the singer's identity in our analyses; playback experiments will be required to confirm this expectation.

Repertoire characteristics (such as repertoire-use similarity or repertoire size) might be inefficient for individual recognition (Kroodsmá 1976; McGregor & Avery 1986; Botero et al. 2007) because they would require assessment over long periods. Indeed, if identity can be assessed from the fine structural features of a single song, this will necessarily be more efficient than assessing multiple songs. However, repertoire characteristics might provide additional information in individual discrimination that complements or enhances individual distinctiveness of fine structural features (Hartshorne 1956; Krebs 1977; Hultsch & Todt 1981; Searcy & Andersson 1986). Our results support the idea that patterns of repertoire use may enhance individual recognition within this ground-sparrow species, and that potential receivers (e.g., neighbours, other rival males, potential mates) might use these acoustic features to distinguish between males. Playback experiments could help to test this idea by independently altering the fine structural features of playback songs and the simulated pattern of repertoire use.

Consistency of individual signals through time may be a common feature for species where individuals have long-term and stable social interactions with other individuals, particularly in species where individuals live in social groups (Jones et al. 1993; Riesch et al. 2006; Wright et al. 2008). White-eared ground-sparrows defend territories year-round (Sandoval & Mennill 2012), often occupying the same territory for several years (L. Sandoval, pers. obs.), so that neighbourhoods have stable long-term membership.

White-eared ground-sparrows will benefit from individual recognition because they may defend territories against familiar rivals year after year, and it is beneficial to display less aggressive responses against stable neighbours as predicted by the dear enemy hypothesis (Fisher 1954).

In the tropics, early successional habitats may pose challenges for signal transmission because of high attenuation rates due to the dense vegetation (McGregor & Krebs 1984; Wiley 1991; Slabbekoorn & Smith 2002; Dingle et al. 2008). In contrast to the predictions of the acoustic adaptation hypothesis, the songs of male white-eared ground-sparrows do not appear to be well adapted for long distance transmission through the dense vegetation of their native habitat. Male solo songs have broad-bandwidth frequency modulations and consistently feature trills (Fig. 1). These characteristics are more often associated with open habitats, rather than habitats with dense vegetation (Morton 1975; Wiley 1991); these features would be expected to show more substantial degradation and attenuation in dense vegetation compared to narrow bandwidth song elements or non-trilled songs (Blumstein & Turner 2005; Boncoraglio & Saino 2006). Evaluation of the transmission properties of male songs through the white-eared ground-sparrow's native thicket habitat and whether the individually distinctive components persist over long transmission distances (as in Christie et al. 2004) is important for assessing whether the individually distinctive components identified here can withstand attenuation and degradation.

In conclusion, our results demonstrate that both the fine structural acoustic features of ground-sparrow songs and their patterns of repertoire use encode individual distinctiveness. Playback will be required to determine whether white-eared ground-sparrows use these individually distinctive acoustic features in individual recognition. This study also reveals that the individually distinctive characteristics show little variation over time, as is predicted for species that are engaged in long-term social interactions including year-round territorial interactions, a common feature for many species of tropical birds. Using a Morisita index of similarity, we found that patterns of repertoire delivery by white-eared ground-sparrow males reveal individual identity and these patterns are consistent over time. This feature has rarely been investigated in birds because individuals would require integration over long periods of time to assess the repertoire composition. Nevertheless, we encourage other investigators to look at higher-order cues of individual distinctiveness and their consistency over time.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1: Fine-scale song measurements for song type 1 shared between White-eared Ground-sparrow males; coefficients of variation between males (CV_b) and within males (CV_w), potential for individual coding (PIC) and results of analysis of variance comparing the coefficients of variation for each song measurement.

Table S2: Fine-scale song measurements for song type 2 shared between White-eared Ground-sparrow males; coefficients of variation between males (CV_b) and within males (CV_w), potential for individual coding (PIC) and results of analysis of variance comparing the coefficients of variation for each song measurement.

Table S3: Fine-scale song measurements for song type 3 shared between White-eared Ground-sparrow males; coefficients of variation between males (CV_b) and within males (CV_w), potential for individual coding (PIC) and results of analysis of variance comparing the coefficients of variation for each song measurement.

Table S4: Fine-scale song measurements for song type 18 shared between White-eared Ground-sparrow males; coefficients of variation between males (CV_b) and within males (CV_w), potential for individual coding (PIC) and results of analysis of variance comparing the coefficients of variation for each song measurement.

Table S5: Fine-scale song measurements for song type 20 shared between White-eared Ground-sparrow males; coefficients of variation between males (CV_b) and within males (CV_w), potential for individual coding (PIC), and results of analysis of variance comparing the coefficients of variation for each song measurement.

Table S6: Fine-scale song measurements for song type 24 shared between White-eared Ground-sparrow males; coefficients of variation between males (CV_b) and within males (CV_w), potential for individual coding (PIC) and results of analysis of variance comparing the coefficients of variation for each song measurement.