ENTROPY CALCULATIONS FOR MEASURING BIRD SONG DIVERSITY: THE CASE OF THE WHITE-VENTED VIOLET-EAR (*COLIBRI SERRIROSTRIS*) (AVES, TROCHILIDAE)

RAČUNANJE ENTROPIJE KOT MERILO RAZNOVRSTNOSTI PTIČJEGA PETJA: PRIMER KOLIBRIJA VRSTE *COLIBRI SERRIROSTRIS* (AVES, TROCHILIDAE)

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ABSTRACT

Entropy calculations for measuring bird song diversity: The case of the White-vented Violet-ear (*Colibri serrirostris*) (Aves, Trochilidae)

The White-vented Violet-ear (*Colibri serrirostris*) is a common and brilliantly colored Brazilian hummingbird that sings a series of high-pitched and evenly spaced short notes with a repertoire size of 3 to 5 note types. We analyzed the song of 17 individuals from 10 localities in relation to note types, repertoire size and non-conditioned and conditioned entropy. Despite the small repertoire size, each singer presented different note types and sequences. Neighbors can share note types, but maintain distinct sequences and entropy values. The entropy values were useful to objectively differentiate between more or less versatile songs with the same repertoire size. Conditioned entropy, a calculation that shows the distribution of the combinations of two consecutive notes, revealed the more versatile singers, which were not evident from the repertoire size only nor the non-conditioned entropy. Despite the rare presence of note sharing in our sample, we did not find any cue of dialects or geographic patterns of variation, but individual variation. The variability of *C. serrirostris* song in note structures, sequences and entropy is evidence of vocal learning and creative capacity, a poorly described communication strategy in non passerine birds.

Key words: Birds, Brazil, repertoire size, song versatility, vocal learning.

IZVLEČEK

Računanje entropije kot merilo raznovrstnosti ptičjega petja: primer kolibrija vrste *Colibri serrirostris* (Aves, Trochilidae)

Kolibri vrste *Colibri serrirostris* je pogost brazilski kolibri lesketajočih se barv katerega napev sestavljajo zaporedja visokih in kratkih tonov, ki obsegajo 3 do 5 različnih zvokov. Analizirali smo napeve 17 osebkov iz 10 lokalitet s posebnim ozirom na značilnosti zvokov, velikost reperoarja (nabora) in nepogojne ali pogojne entropije. Kljub majhnemu naboru zvokov se je izkazalo, da je vsak osebek oddajal različne tipe zvokov in njihovega zaporedja. Sosednje živali imajo lahko enak nabor zvokov, vendar ima vsak drugačno zaporedje in vrednosti entropije. Vrednosti entropije so se izkazale za koristno merilo za razlikovanje bolj ali manj zapletenih napevov z enako velikostjo repertoarja. Pogojena entropija, izračun, ki kaže razporeditev kombinacij dveh zaporednih tonov, je prikazala bolj zapletene (napredne) pevce, ki jih ni bilo mogoče razlikovati po velikosti repertoarja ali z nepogojeno entropijo. Čeprav so bili v našem vzorcu redki primeri istih zvokov, nismo našli nobenih znakov za dialekte ali geografsko pogojene razlike, temveč le razlike med osebki. Variabilnost napevov kolibrija *C. serrirostris* v strukturi zvokov, njihovem zaporedju in entropiji so dokaz za učenje napevov in kreativne sposobnosti, komunikacijsko strategijo, ki je slabo poznana in opisana pri pticah nepevkah.

Ključne besede: ptiči, Brazilija, zvočni repertoar, spremenljivost napeva, vokalno učenje.

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INTRODUCTION

Two important biological questions are addressed intensively through the study of oscine bird song properties. They are sexual selection and vocal learning. Recently, non oscine birds have appeared to be also valuable models, especially hummingbirds whose neural capacities of learning have been proved (JARVIS et al. 2000). New tools of investigation into complex communication signals, particularly entropy values derived from the information theory (SHANNON & WEAVER 1949), have also recently been introduced and allowed for a more accurate quantitative approach of highly variable acoustic signals, as in the Rufous-bellied Thrush (*Turdus rufiventris*) (SILVA et al. 2000) or the Bottlenose Dolphin (*Tursiops truncatus*) (MCCOWAN et al. 1999).

We will present here an analysis of the song of a species of hummingbird, the White-vented Violet-ear (*Colibri serrirostris*), that shows individual variations which may be related to sexual selection and vocal learning. Applying information theory, we will calculate entropy values for evaluating song structure and its correlation with sexual selection capacity and vocal learning ability.

For a long time, hummingbird songs were neglected, in part because of their high-pitched and rapidly modulated frequencies, in part because of the general thought that hummingbirds use predominantly visual signals to communicate, particularly for mate attraction. Hummingbirds are now known to produce well elaborated songs and distinct calls. For instance, the Amethyst-throated Hummingbird (*Lampornis amethystinus*) has a song composed of an introductory phrase and a variety of notes arranged into four to nine complex phrases, besides three different calls emitted under different behavioral contexts (ORNELAS et al. 2002). VIELLIARD (1983) presented the vocalizations of various Brazilian species, showing a large diversity of song and call structures, some stereotyped others versatile. Indirect evidences of song learning through song sharing between neighbors and geographic differences between individuals have been gathered on Little Hermit (*Phaethornis longuemareus*) and Green Hermit (*P. guy*) (WILEY 1971, SNOW 1977), Anna's Hummingbird (*Calypte anna*) (MIRSKY 1976, BAPTISTA & SCHUCHMANN 1990), Scale-throated Hermit (*P. eurynome*), Planalto Hermit (*P. pretrei*), *C. serrirostris* and Hooded Visor-bearer (*Augastes lumachellus*) (VIELLIARD 1983), Sparkling Violet-ear (*Colibri coruscans*) and Green Violet-ear (*C. thalassinus*) (GAUNT et al. 1994) and Blue-throated Hummingbird (*Lampornis clemenciae*) (FICKEN et al. 2000). Vocal learning was also revealed by using behaviorally driven gene expression in Rufous-breasted Hermit (*Glaucis hirsuta*) and Sombre Hummingbird (*Aphantochroa cirrhochloris*) (JARVIS et al. 2000).

In hummingbirds, females take care of the whole reproductive process, from nest building to the feeding of the fledglings, selecting their mates presumably in part to their song and singing behavior. Since male hummingbirds are dedicated only to mate attraction, the study of their attributes in relation to sexual selection made by the females would be a valid approach. In oscine birds, mating success has been related to song repertoire size (CATCHPOLE 1980, SEARCY 1992, SEARCY & YASUKAWA 1996, NOLLAN & HILL 2004). However, the number of vocal unit (note or phrase) types emitted by a singer is a value

that is dependent on the size of the sample and that does not reflect the differences in the frequency of emission of each unit, nor their more or less versatile sequencing. Therefore, the repertoire size, besides its inherent imprecision, is inadequate for measuring the degree of monotony or diversity of the song, i.e. the capacity to attract the attention of potential mates. Taking *C. serrirostris* song as an example, we will show that repertoire size is not reliable to predict entropy values.

MATERIAL AND METHODS

The White-vented Violet-ear (*C. serrirostris*) is a relatively large hummingbird commonly found in the savanna-like habitats of Central Brazil and adjacent countries. Its plumage is brilliantly colored and sexually monomorphic, but it is assumed that only males sing, defending an individual territory where he tries to attract a mate by persistent singing. The song is composed of an individually variable sequence of discrete notes. Notes are emitted at frequencies between 2.0 to 10.0 kHz in series of variable duration, but at quite regular and well spaced rhythm: average rhythm is 2.34 notes per second, notes have short duration (mean = 60 ms) and the interval between the notes is relatively long (mean = 385 ms).

Our sample consists of recordings from 17 males of *C. serrirostris* from 10 different localities in Brazil (Table 1). Recordings were made with various recorders and microphones and are deposited in the Arquivo Sonoro Neotropical (UNICAMP, Campinas, SP, Brazil). The song units, or notes, were identified visually on sonograms produced by Avisoft-SASLab Pro version 4.3 software (Fig. 1 and 2). For each individual, we named the notes in alphabet order according to the sequence of their emission. We obtained the individual repertoire and the sequences of notes. Considering the probability p_i assigned to each symbol as its relative frequency of occurrence in the recording, we define the individual information of each symbol I_i (SHANNON & WEAVER 1949) as:

$$I_i = \log_2 \left(\frac{1}{p_i} \right) \qquad (1)$$

For all the N symbols emitted, we can calculate the values of I_i from 1 to N and the informational entropy (E) is given by:

$$E = \sum_{i=1}^{N} p_i I_i \qquad (2)$$

The entropy is given in bits per symbol, here represented by the notes. We calculated the first order informational entropy or non-conditioned entropy (E_1) considering the individual repertoire and according to equation (2).

To evaluate the sequence structure of the song, we also calculate the second order informational entropy or conditioned entropy (E_2), considering the combination of two

consecutive notes. These combinations reflect the versatility of the sequence: if one note type is always followed by the same other note type it will result in a single combination and a higher monotony of song; if it can be followed by various other note types, it will result in as many combinations and make the song versatile. For example, in the sequence **abcaba**, we found the combinations **ab** (2 times), **bc** (1), **ca** (1) and **ba** (1), where **a** is always followed by **b** but **b** can be followed by either **a** or **c**; once the proportions of these combinations are established, we proceeded to calculate E_2 according to equation (2).

RESULTS

The 17 analyzed singers presented great inter-individual variation in note structures and repertoire sequencing (Fig. 1 and 2). Because of these great individual differences in the complexity of note sequences and in spite of the small repertoire, entropy values, i.e. degrees of monotony or diversity, are quite variable from one singer to another.

The observed values are given in Table 1 and plotted on Fig. 3 in order of increasing repertoire size, then double notes repertoire and entropy (E_1 and E_2) values. The mean value, standard error and standard deviation of the cited parameters are shown on Fig. 4.

Repertoire size and entropy

The repertoire size is small: 6 singers (ind. 4, 5, 7, 8, 14 and 15) were using 3 note types, 10 (ind. 1, 2, 6, 9, 10, 11, 12, 13, 16 and 17) 4 note types and one (ind. 3) 5 note types.

The values of non-conditioned entropy (E_1) varied from 0.88 (ind. 10) to 1.92 (ind. 1), i.e. a coefficient of variation (CV) of more than 100% (precisely 118%). However, the value calculated for individual 10 on the 1014 notes recorded includes a very long series of A and B notes instead of the full repertoire of 4 note types, thus reducing strongly the diversity of its song; considering only the beginning of the recording, when the bird sang its 4 note types repertoire, E_1 would be 1.17 (notes 1 to 286). It seems that the insistent presence of the recordist provoked some perturbation to the singer. Thus the lowest E_1 value becomes that of individual 15 (1.07) and the CV is only 79%.

The highest values of E_1 were obtained with individuals 1 (1.92), 3 (1.91), 16 (1.90) and 2 (1.89). This strong tight suggests a specific maximum of song diversity. These values were attained by singers with 4 or 5 note types. However, the repertoire size is not a reliable predictor of non-conditioned entropy: for instance, individuals 4, 7, 8 and 14 have 3 note types and their E_1 values (1.55 to 1.58) are similar to that of individual 6 (E_1=1.56), which has 4 note types.

The values of conditioned entropy (E_2) varied from 1.60 (ind. 10 again) to 3.26 (ind. 3) with a CV of 104%. As for E_1, calculation of E_2 in the song of individual 10 rises to 2.26 if we consider only the initial, presumably less perturbed, part of the recording (notes 1 to 286). Then, the lowest value becomes that of individual 14, that has a medium E_1, but is the less versatile with only 4 double notes combinations, hence low E_2 (1.75; CV=86%).

The highest value of E_2 is from individual 3 (3.26), well above the following ones: 7 individuals with E_2 of 2.90 to 3.07. Both individuals 3 and 9 emitted the highest number of double notes combinations (12), but in less balanced proportions by the latter, resulting in much lower E_2 (2.90). That same E_2 value was obtained by individual 13 with only half that number of double notes combinations. This makes clear that, although the repertoire of double notes is more informative than the note types repertoire, it is the conditioned entropy that discriminate the more versatile singers.

Sequencing and notes sharing

Neighbors can share some note types, but they emit them in different sequences, as we observed in the 3 following cases.

Individuals 10 and 11 were recorded a few km apart; they have the same repertoire size but different sequences and entropy values and share one note type (Fig. 2), whereas individuals 12 and 13 in the same period and perimeter have distinct note structures.

Singers 4, 16 and 17 were recorded the same day, the last two in direct contact, the first one a few km farther; individual 4 presented a 3-note types song with a mostly regular sequencing (Fig. 1A), whereas individuals 16 and 17 have 4 note types and high entropy values. These last two individuals share the same structure of their 4 note types, although they use them in different sequences; VIELLIARD (1983) published a sonogram of individual 17 and described its sequencing as "ABACABDAC" with variations in the position of D (generally following C), whereas the sequence of these same 4 notes was given as "ABDCABDACADCA" in individual 16.

Another case of note sharing was observed in Serro, MG (18°37'04" S, 43°22'51" W), where 3 interacting singers were recorded; sonographic analysis revealed 4 note types that were apparently shared by these 3 individuals, however the recording is not clear and long enough to determine the individual sequences.

DISCUSSION

Although the White-vented Violet-ear song is high-pitched, with short and rapidly modulated notes that do not catch the attention of human ears, it shows a complex structure at different levels of organization: shape of the song units, individual repertoire, sequences and predictability. We have found variation at all these different aspects that allow us to recognize an individual by his song. The species-specific recognition is maintained by the similar overall structure of the notes and their quite regular rhythm. Individual recognition is made by the fine structure of the notes and their sequences, highly variable even with such small repertoire size.

The song of Brown Violet-ear (*Colibri delphinae*) is known by a single recording of a captive male of the *greenewalti* population; it shows an organization similar to that of *C. serrirostris* with a somewhat larger repertoire and more variable note structures (VIELLIARD 1983). *Colibri coruscans* and *C. thalassinus* present a quite different singing behavior, the former emitting a three-parts phrase in flight, the latter a continuous and

repetitive series of a few notes; in both species the variation is not individual, but geographic (GAUNT et al. 1994).

Other species of hummingbirds present complex songs. Complexity can be attained by different means, for instance (sonograms in VIELLIARD 1983): sophisticated phrase and note structures as in Ruby-topaz Hummingbird (*Chrysolampis mosquitus*), elaborated phrase as in Reddish Hermit (*Phaethornis ruber*), varied phrase as in *G. hirsuta*, versatile note sequencing as in *A. lumachellus*, in addition to *C. serrirostris*. The most complex song described so far is that of *L. clemenciae*, that combine complex phrases with versatile note sequencing (FICKEN et al. 2000).

The ability to share complex note types is an evidence of vocal learning, as already stressed by VIELLIARD (1983), who considered that the similarity of note structures between neighbors 16 and 17 could be obtained only by learning from the same model. However our sample shows only a few cases of note sharing between neighbors, while several singers from the same area and date present totally different note structures, as individual 4 (Fig 1A) in comparison with individuals 16 and 17. No pattern of geographic variation is apparent; instead, differences are clearly individual. Even the males sharing note structures can be distinguished by their note sequences.

Vocal learning would imply some pattern of local similarity, as in *C. coruscans* and *C. thalassinus* (GAUNT et al. 1994), and the coexistence of note sharing with individual variation is difficult to explain. We must take into account the spatial distribution of the species: *C. serrirostris* is nomadic and establish its singing posts only during the breeding season, when singers are well scattered and rarely in auditory contact. This pattern of distribution would be responsible for the mixing of singers with different models of song. Another factor is suggested by the fact that note sequencing is different even between singers sharing notes: individual creativity would explain how birds learning the same repertoire may use it in distinct sequences.

CONCLUSIONS

The application of the information theory to bird song permits us to introduce entropy values as an objective measure of their structural complexity. It is clear that repertoire size do not bring relevant information about the structure of complex song: with the same repertoire, more varied singers reach higher informational entropy (E). This occurs on two levels. The first order or non-conditioned entropy (E_1) reflects not only the number of sound units in the repertoire, but also the proportion of their use; thus, a singer may have a larger repertoire than another, but if it makes little use of some of theses elements, its entropy will be lower than that of the other, which utters each of its note types more equally, hence showing higher variety. The second order or conditioned entropy (E_2) reflects the versatility of the song, i.e. the number and proportion of combinations of two consecutive notes; thus, singers that are more monotonous, i.e. whose note types are in more repetitive order, will show lower values.

These analyses are evidence that song unit structures are different between individuals as is their sequencing. These characteristics permit individual recognition by their

song. Song sharing is rare, but exists and implies vocal learning. The individual variability of note type sequencing implies a creative capacity, a poorly known ability among birds.

These conclusions, obtained from *C. serrirostris* song analysis, are valid for any complex communication signal.

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Table 1: Recorded individuals listed by localities, from North to South, with the number of notes analyzed, number of note types and double notes combinations, and values of entropy.
Individuals 16 and 17 were singing side by side, ind. 4 a few km apart the same day; ind. 10-13 were recorded within a few days and same area, but were not in auditory contact; the same is true also for ind. 5-6 and 14-15.

| ind.	locality	coordinates	notes	types	double notes	E_1	E_2
4	Palmeiras, BA	12° 30'58.2'' S 41° 34'00.4'' W	339	3	7	1.57	2.61
16	-	-	58	4	10	1.90	2.99
17	-	-	267	4	10	1.87	2.98
10	Mucugê, BA	12° 59'58.5' S 41° 22'57.9'' W	1014	4	6	0.88	1.60
11	-	-	339	4	8	1.79	2.97
12	-	-	337	4	8	1.62	2.37
13	-	-	756	4	6	1.79	2.90
8	Brasilia, DF	15° 49'13.1'' S 47° 59'17.8'' W	120	3	6	1.55	2.26
5	Diamantina, BA	18° 14'53.8'' S 43° 36'17.1'' W	721	3	8	1.40	2.56
6	-	-	108	4	9	1.56	2.44
14	Mineiros, GO	17° 33'56.8'' S 52° 33'55.5'' W	57	3	4	1.58	1.75
15	-	-	92	3	7	1.07	1.88
3	Santa Teresa, ES	19° 54'55.7'' S 40° 35'59.9'' W	75	5	12	1.91	3.26
2	Santa Leopoldina, ES	20° 05'58.2' S 40° 32'02.6'' W	136	4	11	1.89	3.02
1	Itatiaia, RJ	22° 30'00.0'' S 44° 33'57.7'' W	78	4	9	1.92	3.07
7	Campinas, SP	22° 51'05.6'' S 47° 06'33.7'' W	331	3	8	1.55	2.57
9	Palmeira, PR	25° 25'00.7'' S 49° 59'55.6'' W	210	4	12	1.71	2.90
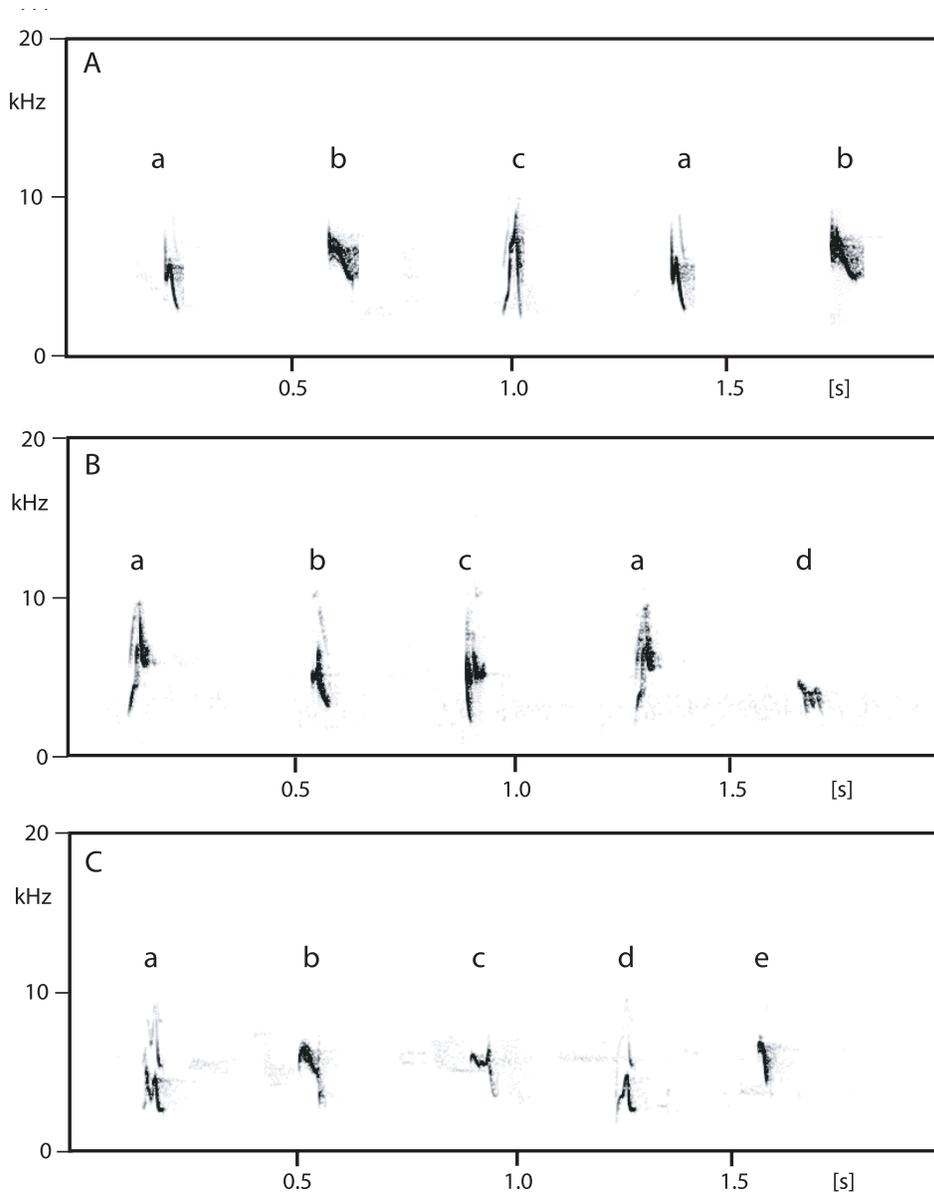
Figure 1: Sonograms of the song of *Colibri serrirostris* showing diverse note types and sequences. A: ind. 4 with 3 note types and mostly regular sequence. B: ind. 1 with 4 note types and varied sequence. C: ind. 3 with 5 note types and highly versatile sequence. Note the fine structure of each note type and its great diversity intra- and inter-individually, without note sharing. Patterns of sequencing do not appear on these small segments of the series uttered.
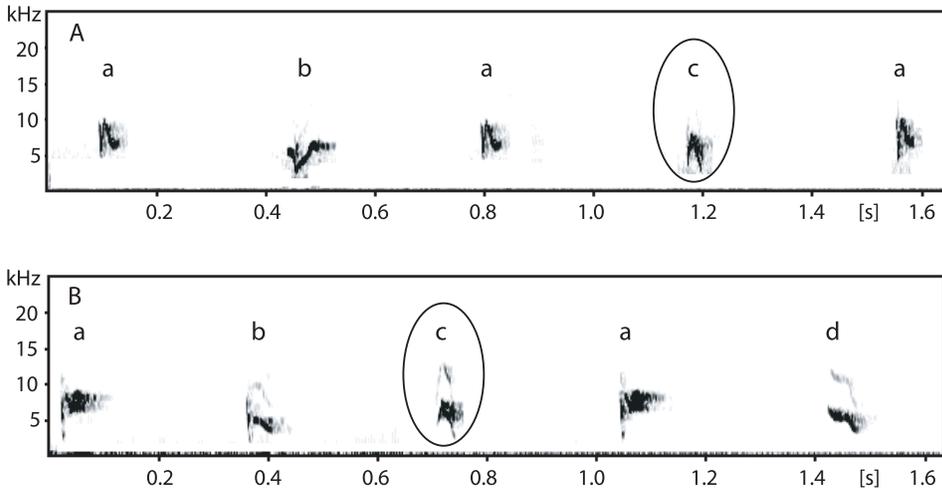
Figure 2: Sonograms of the song of *Colibri serrirostris* showing one note sharing in the repertoire of individuals 10 and 11. Note that these two singers were recorded a few km apart.
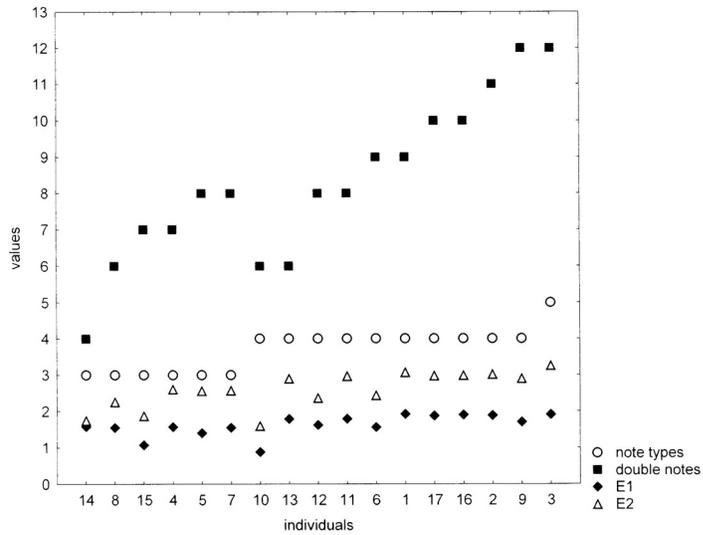

Figure 3: Individual values of repertoire size, double notes repertoire and entropy, in increasing order of number of note types, then number of double notes combinations and values of non-conditioned entropy (E_1) and conditioned entropy (E_2).
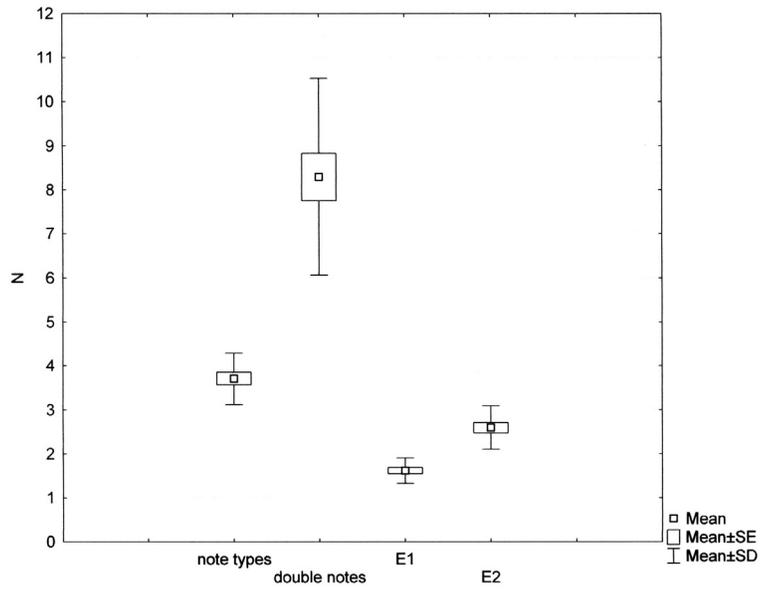
Figure 4: Note types repertoire, double notes repertoire, E_1 and E_2 values: mean, standard error and standard deviation. N=17 individuals.