



Using Shannon Entropy on Measuring the Individual Variability in the Rufous-bellied Thrush *Turdus rufiventris* Vocal Communication

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We applied the information theory concepts to notes repertoire characteristics combined with temporal parameters of the Rufous-bellied thrush *Turdus rufiventris* song, using this particular case to test a new method of analysing quantitatively complex animal communication systems. Like most *Turdus* thrushes, Rufous-bellied thrushes are remarkable for their long, varied and melodious songs. For the analysis of the species repertoire, we used recordings of 44 individuals from 24 localities covering its full geographical range. We measured the repertoire size, note duration and rhythm (frequency of note utterance), and combined these parameters with the Shannon entropy values calculated for each individual. Although individuals maintain species-specific recognition capacity, we find a large variation between their song parameters and show that the information theory can be useful to analyse large and varied animal vocal repertoires. We are introducing two new parameters, temporal average entropy (E_t) and utterance frequency average entropy (E_f), for measuring such communication systems.

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Introduction

There are many books on the use of information theory applied to communication (Shannon & Weaver, 1949; Khinchin, 1957; Culmann *et al.*, 1967; Guiassu & Theodorescu, 1968) and papers and book chapters trying to apply that theory to biological problems (Blumenfeld, 1981; Kugler & Turvey, 1987; Weber *et al.*, 1988; Piqueira, 1994; McCowan *et al.*, 1999). In this context, we are studying the song of birds and its variability by identifying the frequency of occurrence of the sound units, that we call notes. Those relative

frequencies are assumed to be probabilities, and thus an individual information value can be assigned to each note. The mean value of the song information for each individual is defined as informational entropy (E). The maximum entropy (E_m) would be obtained if all the notes had the same probability.

Most *Turdus* thrushes are remarkable for their long, varied and melodious songs. The species-specific song of the Rufous-bellied thrush *Turdus rufiventris* is composed of whistles and trills of medium pitch (frequency range between 1 and 4 kHz). The phrases are uttered in long sequences of regularly spaced notes (Silva, 1997).

We looked at the individual localities to eventually find peculiar population characteristics.

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Sick (1993) reports a different *Turdus rufiventris* song in Rio de Janeiro city describing it as “simple and monotonous, (...) constituting a degraded form of song, a sort of dialect (...)”. However, later data of song analyses (Silva, 1997) do not demonstrate song populational differences, in either repertoire size, notes structure or sequence.

Rufous-bellied thrush is a good species to study complex varied songs because it is abundant and widespread, allowing the study of many individuals from different localities. Like the majority of Oscines that have songs with populational or even individual variations (Mundinger, 1982; Marler, 1997; Kroodsma, 1982, 1996; Canady *et al.*, 1984; Baker & Cunningham, 1985; Todt & Hultsch, 1996), thrushes show inter- and intra-individual variations. Those variations represent indirect evidences of a learning process during song ontogenesis (Vielliard, 1987).

In order to normalize the entropy measures it is important to define new quantities that consider the temporal parameters of note emission in analogy to the idea of necessary capacity of the channel required for communication. So we have defined the entropy average rate in two different ways: the rate considering the average duration of the notes or “temporal average entropy” (E_t) and the rate considering the average frequency or rhythm of notes emission, the “utterance frequency average entropy” (E_f).

We present the following measures for each individual: entropy (E) based on relative frequency of notes occurrence, the mean value of duration of notes, the mean value of notes utterance frequency and two different combinations of these parameters, temporal average entropy (E_t) and utterance frequency average entropy (E_f). These analyses produced several sets of data, permitting to test the methodology developed and to propose, as a result, some biological inferences.

Our goal is to define an easy way to calculate single index, that represents the variability of complex vocal communication signals.

Entropy Calculations

Let us consider some kind of alphabet, composed by N symbols and let us consider the

probability p_i assigned to each symbol as a number calculated according to its relative frequency, observed experimentally. Under those conditions, we can define individual information of each symbol I_i (Shannon & Weaver, 1949) as

$$I_i = \log_2(1/p_i). \quad (1)$$

Considering all the N symbols emitted, we can define the mean value of I_i and call it informational entropy (E):

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

It is important to note that the individual information (I_i) is given in bits and the entropy (E) is given in bits per symbol.

Because the results obtained applying eqs (1) and (2) to our data were highly heterogeneous, and in order to compare individuals with different repertoire size (number of note types), we introduced two new equations for calculating average entropy rates, as defined in the following parameters.

Temporal average entropy rate (E_t) can be defined as

$$E_t = \frac{E}{\tau} \times 1000. \quad (3)$$

with τ being the mean value of duration of the note in ms:

$$\tau = \sum_{i=1}^N \tau_i p_i. \quad (4)$$

Utterance frequency (rhythm) average entropy rate (E_f) can be defined as

$$E_f = E\Phi \quad (5)$$

with Φ being the mean value of the number of notes emitted per second in Hz:

$$\Phi = \sum_{i=1}^N \Phi_i p_i. \quad (6)$$

E_t and E_f units are bits per second (bps) in both cases.

Material and Methods

In all of our experiments we considered only songs uttered in typical advertising conditions, which is the best match to our concept of the “species-specific recognition function of the acoustic communication signal” or functional song; *sensu* Vielliard (1987). Then, we selected the best available recordings in the Arquivo Sonoro Neotropical, 75 recordings of 44 individuals from 24 different localities, which correspond to the full geographical distribution of *Turdus rufiventris*. The individuals were identified by a number from 1 to 44, and the corresponding localities classified into four major regions as shown in Table 1.

These recordings are of high fidelity and technical quality and were analysed on UNISCAN II digital sonograph in the Laboratory of Bioacoustics at the University of Campinas (Unicamp), São Paulo, Brazil.

The sonograms were used to define the song units that we call notes. Each note was identified visually, and named with an alphabet order ac-

ording to the sequence of its emission. The notes were then classified into sound types, and organized in clusters according to their shape and kind of modulation, allowing us to recognize the notes shared by different individuals.

For each individual, we measured the duration (τ) and rhythm (Φ) of each note, as shown in Fig. 1. After obtaining the individual repertoire, we calculated the frequency of occurrence of each of the note types making its repertoire. From these data, we calculated E , E_r and E_f for each individual.

Results

The individual repertoire size varied from 1 to 36 note types (mean = 14, S.D. = 7.46; $N = 44$) and the entropy values varied from 0 to 4.55 (mean = 3.19, S.D. = 0.9; $N = 44$). Figure 2 shows the distribution of the mean values and the correlation between repertoire size and entropy.

Most of the notes of our sample are gently modulated pure sounds. We found 592 note types

TABLE 1
Sample localities and individual designation, presented from north to south (NE = North-east, CW = Central-west, SE = south-east, S = South)

No. locality	Region	Locality	Individual
I	NE	Crato, CE	2
II	NE	Caruaru, PE	1
III	NE	Formosa do Rio Preto, BA	9
IV	NE	Morro do Chapéu, BA	3
V	NE	Itabuna, BA	4, 5, 6, 7 and 10
VI	CW	Brasília, DF	19
VII	CW	Poconé, MT	16
VIII	SE	Piracanjuba, GO	21
IX	SE	Rio Miranda, MS	29
X	SE	Santa Teresa, ES	40 and 41
XI	SE	Rio de Janeiro, RJ	11
XII	SE	Piracicaba, SP	17 and 18
XIII	SE	Cunha, SP	35, 36, 37 and 38
XIV	SE	Picinguaba, SP	20
XV	SE	Caraguatatuba, SP	31, 42, 43 and 44
XVI	SE	Boracéia, SP	15
XVII	SE	São Paulo, SP	8, 28, 30, 32, 33 and 34
XVIII	SE	Sete Barras, SP	22
XIX	SE	Ilha do Cardoso, SP	14
XX	S	La Cornisa de Jujuy, Salta-ARG	23
XXI	S	Palmas, PR	12 and 13
XXII	S	Pelotas, RS	39
XXIII	S	Reserva Costanera Sur, B. Aires, AR	27
XXIV	S	Estancia El Destino, Magdalena, AR	24, 25 and 26

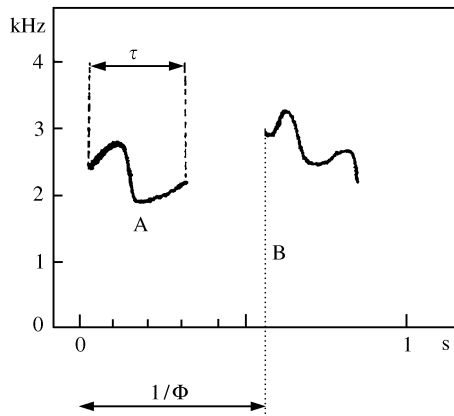


FIG 1. Schematic representation of two different sequential notes A and B, indicating the duration of the note (τ) and the period of emission ($1/\Phi$).

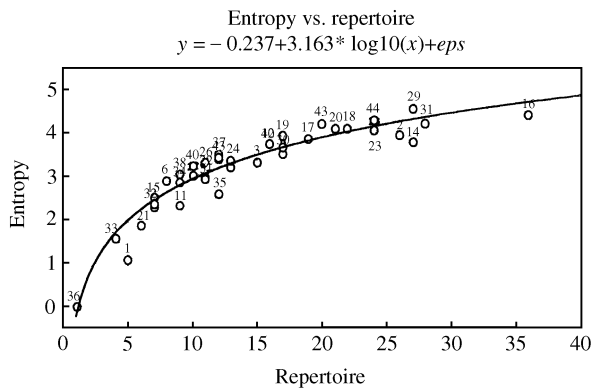


FIG 2. Entropy vs. repertoire size (E).

in the whole sample, of which 24 (4.05%) were shared by different individuals. Of the shared notes, 12 (50%) were between males from the same locality, and only one between neighbour males (individuals 40 and 41 from Santa Teresa, Espírito Santo state).

The mean value of the duration of the notes varied between the individuals analysed from 134 to 356 ms (mean = 259, S.D. = 49; $N = 44$). We calculated E_t using eqn (3) and plotted these values in correlation with the repertoire size in Fig. 3.

The rhythm was obtained in Hz or notes per second and the mean value varied individually between 1.62 and 3.13 Hz (mean = 2.44, S.D. = 0.36; $N = 44$). We calculated E_f using eqn (5) and these values were plotted in correlation with repertoire size in Fig. 4.

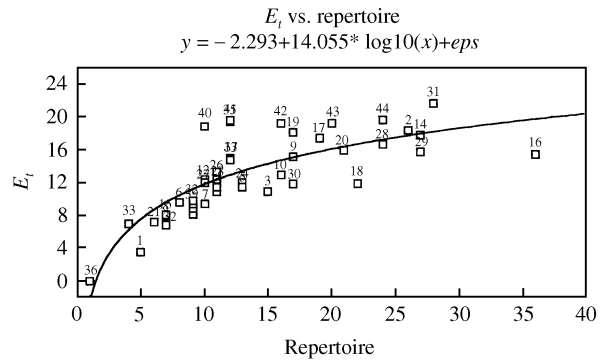


FIG 3. Temporal average entropy (E_t) vs. repertoire size.

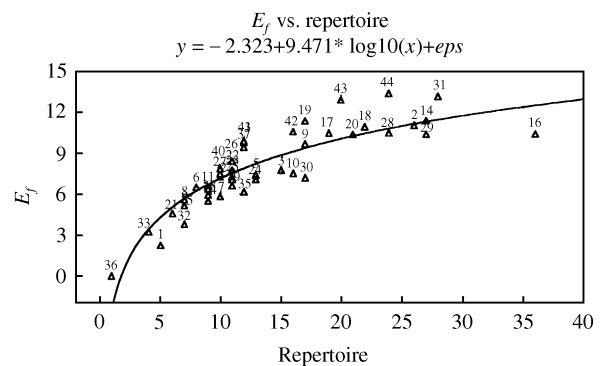


FIG 4. Utterance frequency average entropy (E_f) vs. repertoire size.

The different entropy mean values, with their standard deviation and standard error where more than one individual has been analysed, are presented according to the locality in Fig. 5 for E , Fig. 6 for E_t and Fig. 7 for E_f .

The localities were grouped into four major regions, North-east, Central-west, South-east and South, and the entropy (E) mean values, with their standard deviation, standard error and extralimital values plotted as in Fig. 8.

Discussion

These results corroborate our early descriptive study of the *Turdus rufiventris* song (Silva, 1997) in its most prominent feature: its quite large and remarkable inter-individual variation. However, although our sample included some individuals presenting extreme repertoire size values, most of them presented similar information quantity in their song. Individual 36, with its repertoire

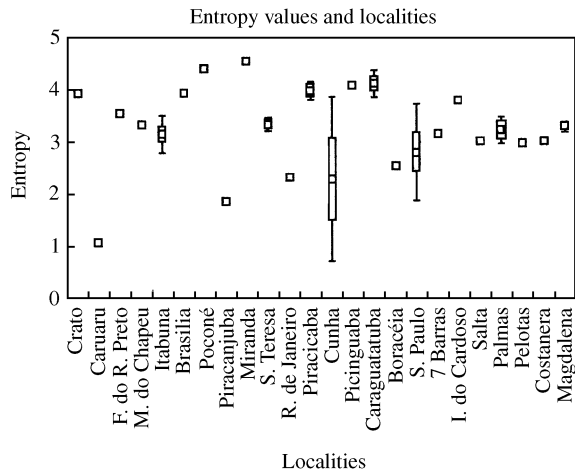


FIG 5. Distribution of entropy (E) mean values, with their standard deviation and standard error where more than one individual has been analysed, according to the locality: (⊕) mean + S.D., mean - S.D.; (⊖) mean + S.E., mean - S.E.; (□) mean.

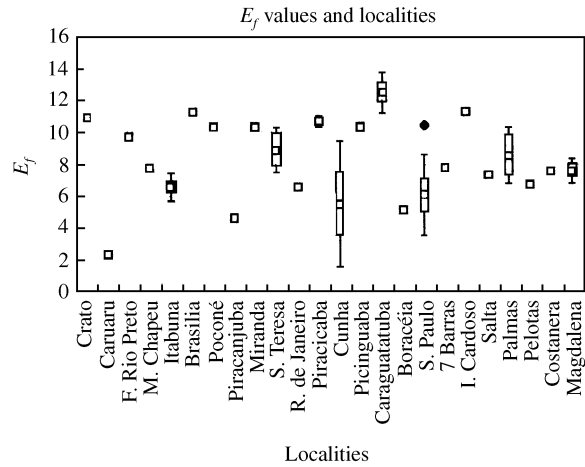


FIG 7. Distribution of E_f mean values, with their standard deviation and standard error where more than one individual has been analysed, according to the locality: (⊕) mean + S.D., mean - S.D.; (⊖) mean + S.E., mean - S.E.; (□) mean; (●) outliers.

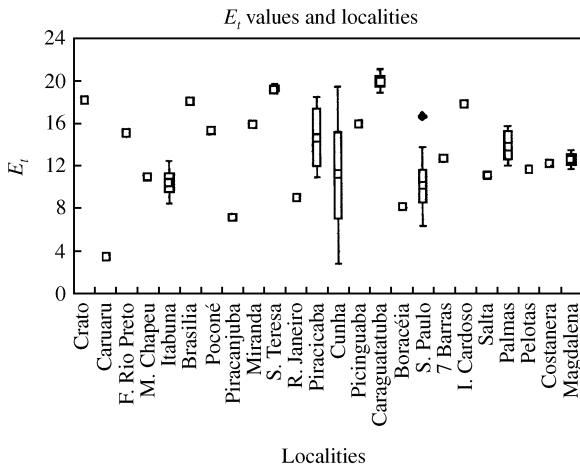


FIG 6. Distribution of E_t mean values, with their standard deviation and standard error where more than one individual has been analysed, according to the locality: (⊕) mean + S.D., mean - S.D.; (⊖) mean + S.E., mean - S.E.; (□) mean; (●) outliers.

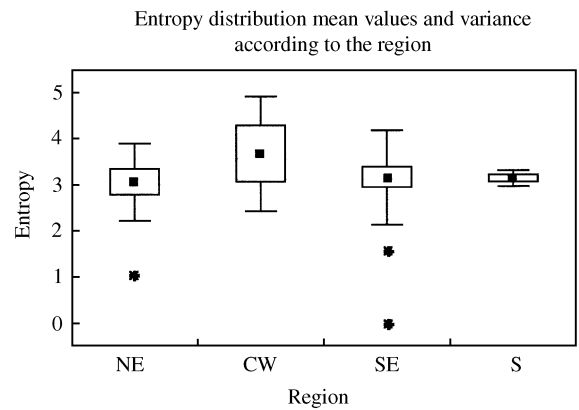


FIG 8. Distribution of the entropy mean values with their standard deviation, standard error and extralimital values according to the localities which were grouped in four major regions, north-east (NE), central-west (CW), south-east (SE) and south (S): (⊕) mean + S.D., mean - S.D.; (⊖) mean + S.E., mean - S.E.; (■) mean; (●) extremes.

reduced to a single note type, emits a song with no entropy, whereas individual 16 exhibits an extraordinarily large repertoire of 36 note types which would allow it to the highest entropy. Nevertheless, individual 36 appeared to communicate effectively, and individual 16 had not used its full potential and presented an entropy value lower than individuals with smaller repertoires (equivalent to individual 44 with only 24

note types). The entropy has a relation with the repertoire size, but that relation may be significantly altered, particularly when the repertoire size value is outside the core of the sample.

The temporal organization is defined by the parameters with lesser variation in the song of *Turdus rufiventris* (Silva, 1997) and is possibly a species-specific character. The frequency of note utterance represents the combination of

note duration and silence interval, which means the song rhythm; its variation in the sample is still smaller than that of the note duration. The entropy values calculated in combination with these parameters, E_t taking into account the duration of the notes and E_f their rhythm, put into evidence further individual variations between entropy and repertoire size. Besides the confirmation of extreme individual values, these correlations discriminate more distinctively those individuals forming the core of the sample, than simple entropy had permitted. Interestingly, individuals depart differently from their original position (as defined by repertoire size and entropy E) if we introduce one or another temporal parameter. For instance, individual 18, with 22 note types, presents an entropy in accord with its repertoire size (Fig. 2); in relation to E_f , its value continues near the regression line of the sample (Fig. 4), but not when the correlation is with E_t (Fig. 3). Looking at other individuals, we can find the other kind of deviations.

The entropy values did not show any correlation with the localities of the sampled individuals, impeding us to evidence any populational patterns. Even in the cases where we analysed several neighbouring birds, no similarities appeared, which would indicate the possibility of a local dialect. As the only learning process known in the ontogenesis of bird song is through vocal mimicry, it remains a mystery how *Turdus rufiventris* singers manage to learn their repertoire without sharing it with their neighbours.

If we are, for now, unable to say from where *Turdus rufiventris* singers learn their normally large repertoire of different note types, we can say that individual entropy values vary considerably from one locality to another (Figs 5–7). As with the repertoire, the correlations of the localities with the entropy show interesting variation depending on its calculation method: crude or in combination with duration or rhythm of the signal (note type). A visual comparison of Figs 5–7 will show potentially instructive discrepancies. For instance, the two individuals from Santa Teresa are very similar if we look at E and E_t , but not for E_f , whereas the two individuals from Piracicaba are similar for E and E_f but not for E_t .

Despite these strong variations between individuals and even between localities, an overall analysis dividing the sample into four regions shows much less entropy variation in the South region (Fig. 8). It is interesting to note that although the mean values are not significantly different between the four regions, the variation remains high in each, except for the South. A biological explanation we could suggest is that the southern population of *Turdus rufiventris* is made of relatively recent colonizers, derived from a reduced genetical or cultural pool, exhibiting therefore a lesser heterogeneity.

The large individual variability demonstrated by *Turdus rufiventris* in its song needs to be measured not only by the number of different note types each singer may utter, but also by the informational entropy it may emit. Because bird song represents an acoustic signal of communication, using a sound channel for transmitting the information it carries and it becomes necessary to measure the flow of that information. This is the reason what we are proposing here to introduce the two average rates of entropy, both in linear proportion to temporal parameters: duration of the units or notes for E_t , rhythm of delivery of these units for E_f .

The comparison of the repertoire size, which determine the maximum entropy that an individual singer has the potential to deliver, with the entropy of the song it effectively emits shows that individuals depart differently from their maximum entropy, and that most of the individuals analysed utter songs whose entropy remains near the mean of the sample. Our data show that repertoire size and overall entropy are not varying in the same proportion. A study of the rate of departure from the maximum entropy might reveal unsuspected patterns.

By introducing the temporal (E_t) and utterance frequency (E_f) average entropy rates, we further discovered the individual discrepancies, which need to be analysed in detail. It would be necessary to choose one entropy value, in order to establish, together with the repertoire size, a kind of index of individual variation. Since it incorporates a more heuristic concept of the temporal flow of information, E_f would be the best candidate. However, more comparisons are needed to

understand the significance of the differences observed here.

Conclusions

Biological conclusions are still premature, but unexpected interesting suggestions can be made. Variability in the song of *Turdus rufiventris* is confirmed to be individual, not populational. However, that variability, as expressed by the individual entropy, consisted of a strange pattern of variation: a high deviation from the mean over the geographical range, except in the south. Since the mean is not significantly different between the southern individuals and the rest of the sample, biological hypothesis must incorporate various theories to explain such a complex situation.

Sick (1993) used his common sense to interpret *Turdus rufiventris* monotonous song from the city of Rio de Janeiro as a dialect, but our single recording is well within the rest of the sample. Although more data from that population might reveal the microgeographic patterns of variation, it is clear that empirical evaluations based on aural impressions are misleading, especially when the song is complex and highly variable.

If we admit that the colonization of *Turdus rufiventris* comes from the north, the southern population could be more recent and should have had less time to present variation of the entropy of its song. To have some idea on how this could happen, we would need to know how young birds learn and disperse in natural conditions.

These results are preliminary but demonstrated that quantitative tools have a great potential to evaluate complex vocal communication systems and to compare their informational structure with biological evolutionary processes. We will continue to study the *Turdus rufiventris* song database, trying to find correlations between entropy and environmental factors.

Even if, for the moment, our analysis is bringing more unexpected questions than answers, it is clear that the use of entropy values has a great importance for the characterization and understanding of biological communication systems with high natural complexity. In the case of *Turdus rufiventris*, we still need to develop and

incorporate an index derived from the sequencing of the signal units. In that species, as in few other birds, the song is not only variable through the individual diversity of signal units or notes, but is said to be versatile for the order of utterance of these notes is also variable and even, in part, unpredictable.

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