How a simple and stereotyped acoustic signal transmits individual information: the song of the White-browed Warbler *Basileuterus leucoblepharus*

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ABSTRACT

The White-browed Warbler *Basileuterus leucoblepharus*, a common bird of the Brazilian Atlantic forest, emits only one distinct song type in the context of territorial defense. Individual or neighbor-stranger recognition may be more difficult when birds share similar songs. In fact, the analysis of songs of different individuals reveals slight differences in the temporal and the frequency domains. Effectively, a careful examination of the signals of different individuals (21) by 5 complementary methods of analysis reveals first, that one or two gaps in frequency occur between two successive notes at different moments of the song, and second, that their temporal and frequency positions are stereotyped for each individual. Playback experiments confirm these findings. By propagation experiments, we show that this individual information can be only transmitted at short range (< 100 m) in the forest. In regard to the size and the repartition of territories, this communication process appears efficient and adaptive.

Key words: bird acoustic communication, individual information, tropical forest.

INTRODUCTION

In tropical forests, visual communication is limited by obstacles and birds use mainly the acoustic channel to communicate at long range (Chappuis 1971, Marten et al. 1977, Waides and Narins 1988). However, in a dense vegetation, sounds are strongly modified during transmission over distance (Wiley and Richards 1982, Michelsen and Larsen 1983, Heuwinkel 1990, Dabelsteen et al. 1993). To be effective, information transfer may rely upon parameters resistant to degradation (Gish and Morton 1981, Brenowitz 1982, Mathevon and Aubin 1997, 2001).

A typical and abundant understory bird of the Brazilian Atlantic forest, the White-browed Warbler *Basileuterus leucoblepharus* produces a territorial song which consists of a very simple signal: a succession of similar notes slowly decreasing in frequency. In previous playback experiments (Aubin et al. 2004), we have shown that, for species-specific recognition, birds use mainly one feature resistant

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to the degradation, the slow decreasing frequency modulation, and ignore parameters sensitive to propagation. With this common and stereotyped feature, birds transmit specific information at long range. But how are individuals able to distinguish each other with a so simple signal and in a so constraining environment? To answer this question, we have made (1) acoustic analysis of songs of several individuals to bring out the different possibilities of vocal signatures, (2) propagation experiments to evaluate the active space of the information, and (3) playback experiments to understand the individual coding-decoding process.

MATERIALS AND METHODS

SUBJECTS AND LOCATION

The experiments were performed in an Atlantic forest of South-eastern Brazil, at Morro Grande State Reserve, during November 2000 and 2001, i.e. during the peak of the breeding season of the White-browed Warbler.

In the forest, the birds were distributed in patches of two to ten more or less contiguous territories. Male territories were first spotted and then mapped by a global positioning system (GPS) and territorial songs of the corresponding birds were recorded. According to our observations, the territories corresponded roughly to a circle of 100 m diameter.

RECORDING AND PLAYBACK INSTRUMENTATION

Songs were recorded using an ultra-directional Sennheiser MKH 816 microphone and a Sony TCD-D10 DAT recorder (sampling frequency: 48 kHz; frequency response: flat within the range 20-20000 Hz) and subsequently digitized at a sampling frequency of 22 kHz. For propagation and playback experiments, the emission chain was constituted of a Sony TCD-D7 DAT recorder connected to an autonomous 10W amplifier equipped with an Audax loudspeaker (frequency response 100-8600 Hz ± 2.5 dB). As reception chain for propagation experiments, we used an omni-directional Beyer Dynamic

M-69 microphone (± 2dB for frequency range 150-15000 Hz) connected to a Sony TCD-D10 DAT recorder.

METHODS OF ANALYSIS

To identify the acoustic parameters likely to carry information on individual identity, we have analyzed the songs of 21 individuals using 5 complementary methods of analysis: a classification by artificial neural network (ANN), a coefficient of variation calculation (Cv), a principal component analysis (PCA), an entropy calculation (2^H) and a time and spectral decomposition examination.

ANN: this method is now widely used as a powerful classification technique in bioacoustics (Reby et al. 1997). In the present study, we have used a ZiscLab system (Durr and Sarton 2001) consisting of a fully classical parallel architecture with 3 layers. The principle was to analyze the shape of the instantaneous frequency, calculated with the Hilbert transform (see Mbu Nyamsi et al. 1994, for the method), of the entire song of different individuals. A learning phase was first computed by an algorithm updating the connection weights between neurons so as to obtain the correct discrimination of a set of signals for which the identity of the individual was known. Once the learning phase was achieved, connection weights were definitively fixed and the classification by ANN could run with a set of test songs.

CV and PCA calculations: acoustic features of 125 songs from 21 individuals were analyzed in the temporal and the frequency domains (Fig. 1). The chosen acoustic parameters were (1) in the temporal domain: the mean duration of notes (mDurn), the mean duration of silences (mDurs), the total duration of the song (TotDur), the elapsed time between the beginning of the signal and the main gap in frequency (TGap), the elapsed time between the first and the second note (Tn1), and the elapsed time between the first and the third note (Tn2); (2) in the frequency domain: the maximum frequency (Fmax), the minimum frequency (Fmin), the frequency of the last
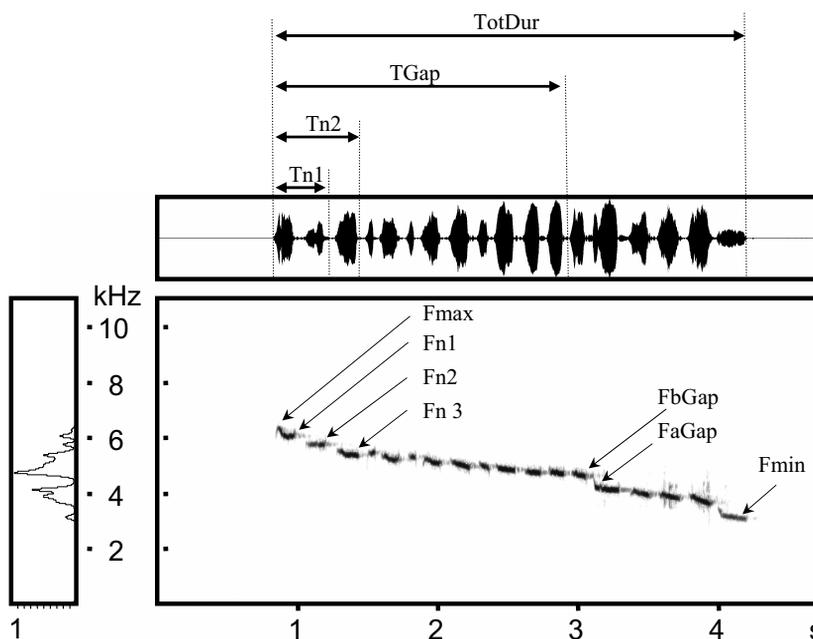
Fig. 1 – Typical territorial song of *Basileuterus leucoblepharus* and measures done in the temporal and frequency domains (abbreviations: see text).

note before the main gap (FbGap), the frequency of the first note after the main gap (FaGap), the frequencies of the first (Fn1), second (Fn2) and third (Fn3) notes, and the frequency value of the main gap (FGap); (3) in both domains: the total number of notes (Totn), the number of notes before the main gap (nGap), the mean slope of the whole song (TotSlope), and the mean slope of the song before the gap (GapSlope).

Coefficients of variation for mean values of each acoustic feature were calculated for each individual (mean CV_i). An inter-individual coefficient of variation (CV_b) was also calculated using mean characteristics of the songs from each of the individuals analyzed. CV_i and CV_b were calculated from the formula $CV = 100*(1 + 1/4n)*sd/\overline{x}$ (Scherrer 1984). Ratios CV_b/mean CV_i were then calculated.

2^H: on the basis of the theory of information (Shannon and Weaver 1949), Beecher (1982, 1989) developed a method to assess the efficiency of a vocal signature in animal communication systems. The aim of this method, mainly based upon the analysis of variances made on acoustic parameters, was to provide an information capacity measure (H) of an individual signature. H is expressed as:

$$H = \log_2 \left(\frac{\sigma_b}{\sigma_i} \right) = \log_2 \left(\sqrt{\frac{F_n(k-1)}{k(n-k)}} \right)$$

with F corresponding to the ANOVA Fisher's value, n to the number of calls and k to the number of individuals.

Then, 2^H gives a theoretical estimate of the number of potential signatures achievable for a given parameter.

Time and frequency decomposition: this method (Lengagne et al. 1997) allows a separate analysis of the two different domains where the species might code the individual signature: the temporal and the spectral domains. In a first step, the energy profiles of the different signals were compared frame by frame (of equal length) on the envelopes and the spectra. In a second step, the energy profiles between signals coming from the same individual (Et_i

and Ef_i, for respectively the temporal and the frequency domains) were compared to those coming from different individuals (Et_b and Ef_b). The advantage of this method is that no acoustic parameters were ''a priori'' selected by the observer, except the temporal and frequency bandwidths (frames) used in calculation.

PROPAGATION PROCEDURE

To assess the modifications of signals during propagation through the natural habitat, a typical song of the species was broadcast repetitively (10 signals separated by 6 s of silence) and recorded at different distances. The test sequence was transmitted along a 100 m transect through an area representative of the natural habitat of the White-browed Warbler. The speaker and microphone heights (6 m) were chosen so as to represent the natural song perches and receiver locations. Four microphone-loudspeaker distances were tested: 1.5 m, 25 m, 50 m, 100 m. These distances represent common distances between interacting birds. The signal was broadcast at a natural Sound Pressure Level (SPL), i.e. on average 90 dB_{SPL} measured at 1m from the loudspeaker.

Among the ten propagated signals, recorded songs with overlapping foreign signals in the vicinity of the microphone were first eliminated. Then, among the remaining signals, only 3 were chosen at random for subsequent analysis. The spectrograms corresponding to the 3 selected signals were averaged using Avisoft SasLab Pro software and the averaged spectrograms corresponding to the different distances of propagation were then compared.

PLAYBACK PROCEDURE

Before playback experiments, two loudspeakers were positioned, one at the center of the territory near the main song post of the territory holder and the second 25 m ahead, inside the territory. The song of a stranger was broadcast by the first loudspeaker in order to attract the bird towards the center of his territory. Five minutes later, another signal (the song of a neighbor or the modified song of this neighbor) was played-back with the second loudspeaker and the behavior of the bird was noted. Typically, in natural conditions, a territory holder replies to the song of a stranger by a song followed by an approach to the song source. When it heard a neighbor's song from the neighbor's territory, the territory holder being tested sometimes sang in reply and sometimes not, but did not approach the sound source. In our playback experiments, the first behavior, typical when hearing a stranger's song, was indicated by ''+'' and the second behavior, corresponding to hearing the neighbor's song, was indicated by ''−'' when the tested bird sang and ''− −'' when it did not sing. To avoid habituation, each tested bird received only one treatment. Moreover, neighbors were tested with different experimental songs. To minimize the effect of possible eavesdropping (Dabelsteen et al. 1997), neighbors were subjected to playback on different days. As for the propagation experiments, signals were played-back at the natural intensity level of 90 dB_{SPL}.

RESULTS

SONG ANALYSIS

ANN: with 20% of the signals learned (17 signals), the ANN is able to correctly classify 92% of the songs, i.e. to attribute a given signal to the right individual.

CV: the CVs have been calculated for each of the 18 selected parameters (Fig. 2). All frequency and temporal parameters appear to be specific to the individual ($CVb/meanCV_i > 1$, ranging from 1.42 to 24.18). The higher values are obtained for parameters depicting the main frequency gap: Tgap, FaGap, nGap.

PCA: the PCA, performed on the 18 acoustic parameters chosen for the CV calculation, identified four factors as explaining 80% of the total variance. The first two factors accounted for 54% of the variance. Figure 3a is a representation of the results of the PCA, taking into account the two axes corresponding to these two factors. On this basis, the
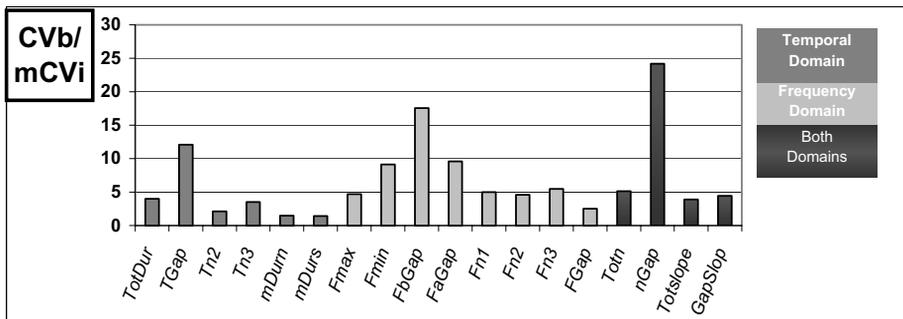
Fig. 2 – Results corresponding to the ratio between the inter-individual coefficient of variation (CV_b) and the mean intra-individual coefficient of variation (mean CV_i) calculated for 18 acoustic parameters of the song. Higher values correspond to parameters linked to the main gap: Tgap, FaGap, nGap.

PCA still separated 71% of the 21 individuals analyzed. A further analysis by a correlation circle (Fig. 3b) allows identification of the acoustic parameters which may support the individual signature. The axis corresponding to factor 1 (responsible of 33% of the total variance) is strongly correlated or inversely correlated to the variables describing the main gap: TGap, nGap, FaGap, FbGap. Other correlation values are relatively high if factors 1 and 2 are considered together. They correspond to the parameters describing the secondary gaps situated at the beginning of the signal: Fmax, Fn2, Fn3.

2^H: the number of individuals that could be potentially discriminated was calculated for each of the studied parameters. The higher values obtained are 41 for FbGap and 29 for Tgap (Fig. 4). However, the 2^H values of the various measured parameters cannot be summed, since they are not always fully independent from each other, and the calculation of the quantity of information would be overestimated.

Time and frequency decomposition: the ratio between the mean energy profiles of the population (the 21 individuals studied) and the mean energy profiles of each individual was calculated for the envelopes and for the spectra. Their values are respectively: $Et_b/Et_i = 1.28$, $Ef_b/Ef_i = 3.70$. That means that the envelope, and consequently the shape of the amplitude modulation of the song, seems to contain

less potential for individual coding, than the spectrum.

SONG PROPAGATION

The examination of the averaged spectrograms corresponding to the signals recorded at different distances of propagation (Fig. 5) reveals that the first third of the signal, corresponding to the higher frequencies, is embedded in the background noise after only 50 m of propagation. This proportion grows to more than half the song after 100 m of propagation.

PLAYBACK EXPERIMENTS

The responses of birds to a neighbor's song, whose main gap was shifted in time or frequency, is given on Table I. For both modifications, it appears that the signal is perceived as the song of a stranger and not of a neighbor by the birds living in the immediate vicinity.

DISCUSSION AND CONCLUSION

That birds can recognize one another by voice alone has been demonstrated repeatedly. Considerable effort has been expended to determine the specific features of song that facilitate individual recognition in territorial birds, especially in species with variable song syntaxes and song type repertoires (Falls 1982, Lambrechts and Dhondt 1995, Stoddard 1996). Individual recognition may be more difficult
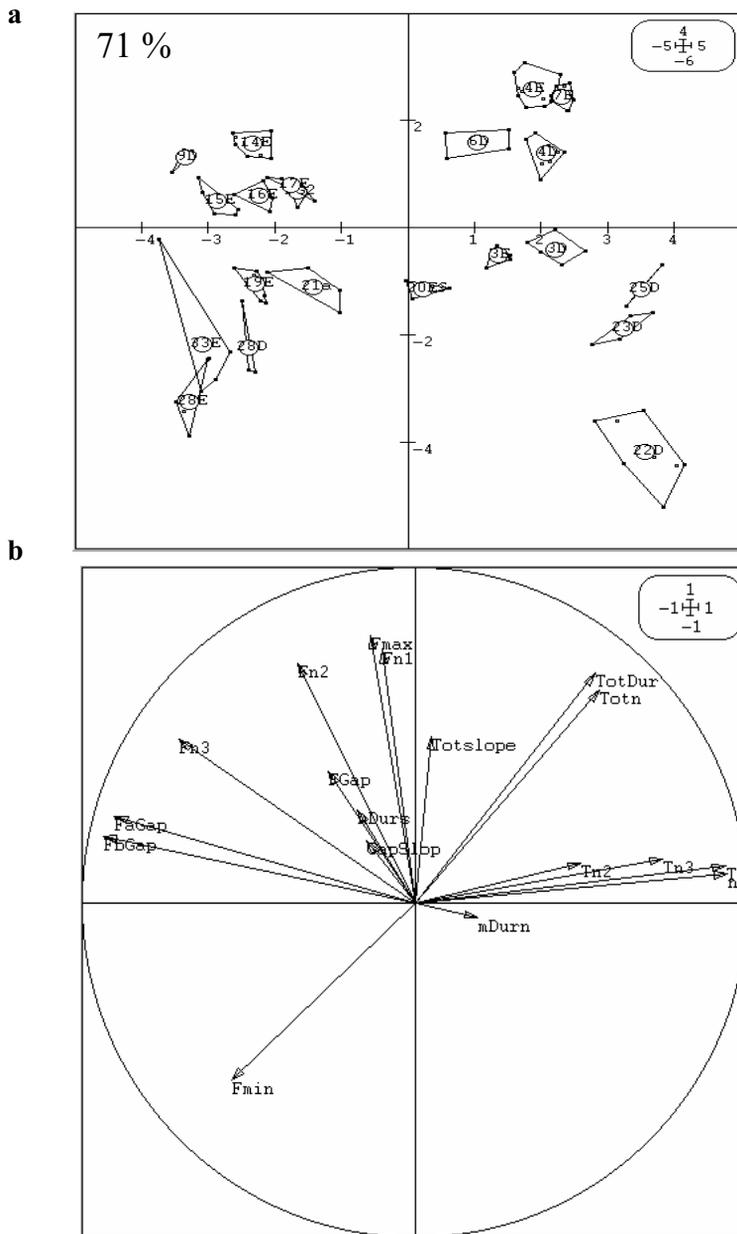
Fig. 3 – PCA analysis taking into account 2 factors (54% of the total variance) and based upon 18 acoustic parameters. On this basis, the PCA (**a**) separates 71% of the 21 individuals analyzed (each number corresponds to 1 individual). A correlation circle (**b**) identifies the parameters responsible for these variances.

when birds of a given species share similar songs, as it is the case for the species studied here. This would mean that species having single song repertoires are sensitive to relatively subtle differences in songs. Effectively, an artificial neural network (ANN) analysis, based upon the examination of the overall frequency modulation of the signal, seems to take into account these subtle differences to sep-
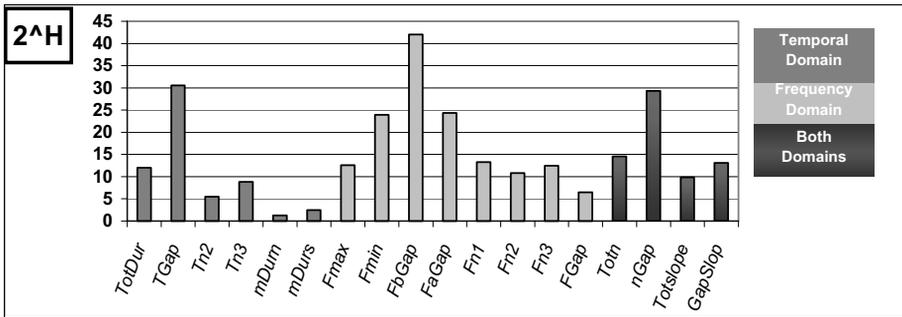
Fig. 4 – Number of individuals that can be potentially discriminated for each of the 18 parameters of the song. Calculation was realized on the basis of the 2^H measure (with H: quantity of information). Higher values are obtained with parameters linked to the main gap: Tgap, FbGap, nGap.

TABLE I

Responses of territorial males *Basileuterus leucoblepharus* to a neighbor song or to a neighbor signal with the main frequency gap modified in the time domain (n=6) or in the frequency domain (n=4).

Frequency gap	Signals	Intensity of responses					
Shifted in time	Neighbor	– –	– –	– –	–	– –	–
	Modified	+	+	+	+	+	+
Shifted in frequency	Neighbor	– –	–	– –	– –		
	Modified	–	+	+	+		

+ : song in reply and approach; – : song in reply but no approach; – – : no song, no approach.

arate with success the different individuals. Further analysis allows detection of the parameters responsible of these differences between individuals. A first analysis with the coefficients of variation (CV) reveals that the differences between individuals are mainly due to a gap in frequency between two successive notes occurring at the end of the first half of the signal. Another analysis by frequency and time decomposition of the energy of the song shows that, contrary to the frequency gaps, the shape of the amplitude modulation of the song contains a low potential for individual coding. An analysis by PCA confirms these findings and reveals also that smaller frequency gaps, situated at the beginning of the song, could be responsible for the inter-individual differ-

ences. Thus, it appears that the individual recognition process could be multi-parametric, i.e. not based upon only one key parameter. Nevertheless, if we take into account only the main gap in frequency, the quantity of information calculation (2^H) reveals that it is possible to distinguish at least 40 individuals. This value seems low in regard to those estimated for other species with wide repertoires (Silva et al. 2000), but seems quite sufficient in regard to the spatial distribution of territories observed in the field and consequently in regard to the number of potential neighbors.

It can be pointed out that the potential cues responsible for the individual signature in this species have been found in the first half of the signal.
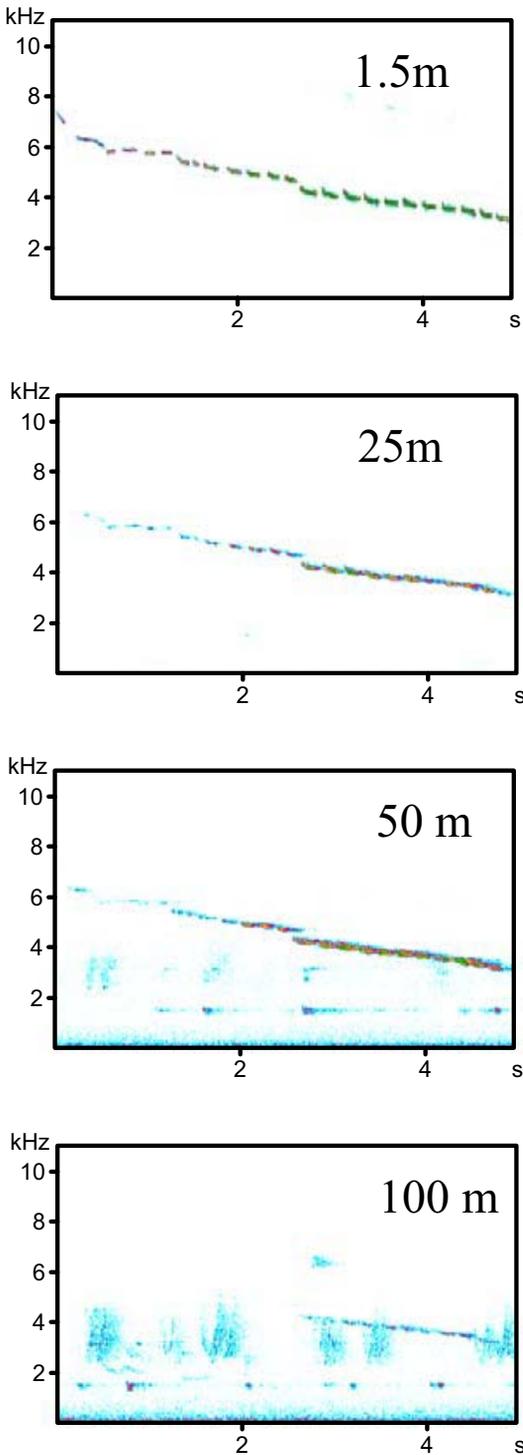
Fig. 5 – Averaged (n=3) spectrograms of a song played-back and
recorded at 4 distances in the forest.

A study on two other songbird species (Elfström
1990) also found that the features used in individual recognition are at the beginning of a song, while
those used in species recognition are at the end. This
organization of the information could be considered as an adaptation, if territorial defense requires
fast individual recognition of con-specific neighbors
rather than fast species recognition. Such an organization has another consequence: the privacy of
the individual information. Effectively, in the case
of the White-browed Warbler, we have shown by
experiments, that after more than 100 m of propagation, the first half of the signal, and consequently the
potential vocal signature, disappears into the background noise. A short range propagation of the individual information seems fully adapted to the size
and the distribution of the territories for this species.
It also reduces aggressive responses to unfamiliar
birds and consequently limits useless energy consumption in territorial defense.

Knowing that it is possible to distinguish the
songs of individuals statistically does not tell us
how birds do it. By playback experiments, we have
demonstrated that there not only exists a neighbor-stranger song discrimination (males responding
non-aggressively to neighbors and aggressively to
unfamiliar song), but also a discrimination between
songs of neighbors. By moving the main frequency
gap back and forth in the temporal domain or up
and down in the frequency domain, and by playing-back these synthetic songs, it is possible to impede
the recognition of neighbors. Thus, the gaps in frequency distributed along the signal support the individual identity in this species.

Then, in spite of the simplicity of the acoustic
structure, of the propagation problems linked to the
constraining environment of a tropical forest, and of
the necessity to transmit a common species-specific
information, the song of the White-browed Warbler satisfies an important requirement of territoriality: neighbor identification. Thus, we have demonstrated with this species that a neighbor-stranger
discrimination process can exist in birds having a

simple and stereotyped single song.

RESUMO

O Pula-pula-assobiador *Basileuterus leucoblepharus*, um pássaro comum da Mata Atlântica, emite um único e distintivo tipo de canto para defesa territorial. O reconhecimento individual ou entre vizinho e estranho pode ser mais difícil quando as aves compartilham cantos semelhantes. De fato, a análise dos cantos de diferentes indivíduos revelou ligeiras diferenças nos domínios temporal e das freqüências. Efetivamente, um exame cuidadoso dos sinais de 21 indivíduos diferentes por 5 métodos complementares de análise revelou que, primeiro, um ou dois espaços na série tonal ocorrem entre duas notas sucessivas em determinados momentos do canto e, segundo, ocupam posições em tempo e freqüência estereotipadas para cada indivíduo. Experiências de ''play-back'' confirmam esses dados. Através de experiências de propagação, mostramos que esta informação individual pode ser transmitida somente a curta distância (< 100 m) na mata. Considerando o tamanho e a repartição dos territórios, este processo de comunicação mostra-se eficiente e bem adaptado.

Palavras-chave: comunicação acústica em aves, informação individual, floresta tropical.

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