Individuality of contact calls in the Greater Flamingo *Phoenicopterus ruber* and the problem of background noise in a colony

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Acoustic communication has great importance in social relationships and especially in individual recognition in the Greater Flamingo *Phoenicopterus ruber*. However, it is constrained by the noisy environment of the colony. I performed an analysis of both the temporal and frequency patterns of contact calls and showed that the use of both is essential for discrimination between individuals. I made a search for the acoustic parameters which are used by the flamingos. It appears that the call duration, the slow amplitude modulation, the spectrum bandwidth and the repartition of energy among harmonics exhibit individuality. Recognition between the birds must be based on a multiparametric analysis, taking into account both spectral and temporal features of the calls. Indeed, no single parameter was sufficient to discriminate between individual birds used in my research. In the noisy environment of the colony, the transmission of individuality in a message is improved by this multiparametric coding, which can be considered as an adaptation to these extreme acoustic conditions. Moreover, the study revealed numerous acoustic convergences with another colonial bird species, the Emperor Penguin *Aptenodytes forsteri*, and both species seemed to use the same method to encode individuality in their vocalizations.

The Greater Flamingo *Phoenicopterus ruber* breeds in large and dense colonies, often of thousands of individuals. They are noisy birds, and vocalizations are very important in their social relationships (Brown 1958, Studer-Thiersch 1967, 1974, Cramp 1977). Vocal communication may allow individual recognition, especially during breeding (Studer-Thiersch 1974, Cramp 1977).

The aim of this study was to determine which parameters could be used for individual recognition by sounds by these birds. Particular attention was given to the contact call, described as a nasal double honk *ka-ha* by Brown (1958) and named “2-s call” by Studer-Thiersch (1974). It is uttered often by paired adults. If an individual emits this call, its mate responds with the same call, even if they cannot see each other (Studer-Thiersch 1974).

The individual-specific features must be adapted to the environmental acoustic constraints imposed by colonial life, i.e. the difficult transmission of highly precise information through an acoustically obstructed and noisy medium (Wiley & Richards 1982, Robisson *et al.* 1993, Aubin & Mattevon 1995). This difficulty of communicating in the continuous background sounds of other birds is similar to the “cocktail party effect” described in psychophysics (Cherry 1966, Wiley & Richards 1982). A previous study made in this laboratory of another colonial bird, the Emperor Penguin *Aptenodytes forsteri*, has shown that to successfully transmit individual information, the birds must use several features in the call: no single feature is sufficient to assure the absolute identification of the emitter by the receiver. In the case of the Emperor Penguin, the parameters which are used for individual recognition are temporal parameters (duration of call syllables and amplitude modulation) and frequency parameters (values of the fundamental frequencies of the two voices; Robisson *et al.* 1993). Taking into account these results from the Emperor Penguin, I examined whether another colonial bird, the Greater Flamingo, also used several features to encode individuality in its contact calls. I performed an extensive analysis of both the temporal and frequency patterns of the call in order to determine whether they were specific to individuals and which pattern, temporal or frequency, is the more informative for individual characterization.

MATERIALS AND METHODS

Recordings

The recordings were made on a captive flock of 25 Greater Flamingos at the Parc Zoologique de Paris, France. When being recorded, the birds were in an area of about 40 m². All the recordings were made at less than 5 m from the birds. A Sennheiser MD211N omnidirectional microphone connected to a Sony TCD-D10 PROII DAT recorder was...
Sound analysis

Taped calls were digitized with a 16-bit acquisition card at 11 kHz sample rate with an anti-aliasing filter (low-pass filter, fc = 9.2 kHz, -120 dB/octave) and then examined using software written in our laboratory (T. Aubin, unpubl.).

The contact call was spread over a wide frequency band with a slow frequency modulation extended over a narrow range (Fig. 1). A precise analysis of frequency features showed that there were two fundamentals with their respective harmonic series, characterizing a two-voices phenomenon, which is very common among bird calls (Aubin 1986). There were large fluctuations of amplitude, with rapid and slow rates of amplitude modulation. Because of these characteristics, individuality might be encoded by temporal or frequency features.

To determine if the contact calls of the flamingo were specific to each individual and whether temporal or frequency pattern was the more informative concerning individuality, I compared the amplitude functions and the amplitude spectra of several calls of various individuals by means of principal component analysis (PCA).

The analysis of the amplitude modulations was performed using the envelopes of the calls. The duration of calls differs, and to compare envelopes of exactly the same duration, I took into account only the first 0.145 s of each call because this value corresponds to the duration of the shortest analysed call. Envelopes of 0.145 s were described by 1458 points distributed along the temporal axis, allowing a great precision in time domain (one point every 0.1 ms).

The amplitude spectrum of each call was computed using fast Fourier transform (FFT) with a 4096 window size, which overlay the duration of the whole call and allowed a great precision in frequency domain (interval between two points = 2.7 Hz). This spectrum was examined between 502 Hz and 5497 Hz, which represents 1861 points distributed equally along the frequency axis.

I used PCA (Escoufier & Pages 1990) to perform the statistical comparisons between the amplitude envelopes and between the amplitude spectra. For statistical calculations, I used STATISTICA package software. In addition, I selected a set of parameters and searched to isolate the main individual-specific features of the calls which could be used by the birds to identify each other (Fig. 1). I chose a limited number of parameters which objectively described the call structure. These were temporal parameters—call duration, slow amplitude modulation (calculated from the envelope by a digital filtering 0–150 Hz using short-term Fourier transform)—and frequency parameters—spectrum bandwidth, frequency with the greatest energy, first frequency of the spectrum. Because the frequency with the greatest energy is sometimes isolated in the spectrum, while much of the energy is distributed in another part of the spectrum, I defined another spectrum parameter—the main energy portion of the spectrum (the spectrum is divided into 10 intervals of 500 Hz from 0.5 kHz to 5.5 kHz; the main energy portion is the 500-Hz interval which contains most of the signal energy). For each parameter, I used the formula coeff. var. = 100 × (1 + 1/4n) × s.d./mean (Scherrer 1984) to compute the between-individual (coeff. var. b) and within-individual coefficients of variation (coeff. var. i). The mean coeff. var. i was calculated for each bird, and the ratio coeff. var. b/mean coeff. var. i indicates how great the between-individual variation was relative to the within-individual variation. I then performed a univariate analysis of variance (Scherrer 1984).

RESULTS

Comparison of the amplitude envelopes

The PCA identified four factors which explained 80% of the total variance. The first factor accounted for 59.6% of the variance. On the basis of only the differences between the patterns of the envelopes, most of the individuals can be discriminated by means of their calls. Figure 2 is a representation of the results of the PCA, taking into account the two axes corresponding to the factors explaining most variance. The individuals E, D and C are well discriminated since they are separated on the graph. The individuals A and B overlap with each other but they are differentiated from the other individuals. Therefore, amplitude envelopes can be considered as being individual markers. The temporal pattern of amplitude modulation shows much more variability between birds than within a given bird.

Comparison of the amplitude spectra

The first three factors given by the PCA accounted for only 25.7% of the variance, so amplitude spectrum seems to be a less reliable parameter for individuality. However, by taking into account the first three factors, discrimination between the cluster of points is easy (Fig. 3), and most of the individuals are correctly identified by means of amplitude spectra. Individuals B and C are clearly separated from the others, and there is also a good separation of individuals D and E. Thus, the pattern of the amplitude spectrum could be important in characterizing an individual. However, the calls of individual A are only partially isolated from those of individuals D and E.

If both the amplitude envelopes and the amplitude spectra are considered, all the birds are separated since those with similar temporal patterns differ in frequency distribution. The use of both characteristics appears to be essential to discriminate among individuals. In the second step of the study, I searched to identify the acoustic parameters which may be used by the flamingos to discriminate each other.

Analyses of selected variables

Means and standard deviations of the call parameters are shown for each individual in Table 1. All the considered
parameters appear to be specific to the individuals (coeff. var. b/mean coeff. var. i > 1). However, the degree of individuality varies considerably from one parameter to another (Table 2). Indeed, the ratio coeff. var. b/mean coeff. var. i ranges from 2.02 (slow amplitude modulation) to more than 12 (first frequency of the spectrum).

The most useful parameters concerning individuality are frequency ones: the first frequency of the spectrum and the frequency with the highest energy. The spectrum width and the principal portion of the spectrum are also informative. Degrees of individuality of temporal features are less important although they are substantial: call duration and slow amplitude modulation have a degree of individuality superior to 2. All the selected parameters show significant differences between means of each individual (Table 2). However, multiple comparison tests indicate that no one parameter is sufficient to discriminate among the five individuals (Table 2).

**DISCUSSION**

The results show that the identity of an individual can be encoded in the flamingo contact calls. The combination of various frequency and temporal parameters allows the birds to discriminate each other. A multiparametric analysis appears useful for individual recognition in other colonial species of birds, such as Emperor Penguin and Barnacle Goose *Branis bernicla* (Robisson *et al.* 1993, Hausberger *et al.* 1994). The necessary combination of various frequency and time parameters for individual distinctiveness is asserted for many bird species (Hutchison *et al.* 1968, Sieber 1985, Beecher *et al.* 1986, Jones *et al.* 1987). My analysis reveals that most individual features of the calls are frequency ones: the value of the first lower frequency of the spectrum and the spectrum portion with the highest energy. Individuality of these parameters may result from anatomical structures, such as the length of the tracheal tract and the syrinx con-
formation, which are linked to the individual genetic pool and therefore vary from one individual to another (Michelson 1983). Because these characteristics are probably constant in adults, they may be reliable over time. Temporal features such as amplitude modulation are also very informative concerning individuality. The periodic fluctuations of amplitude characterize a beat phenomenon generated by the interaction of two frequencies (Brommond et al. 1990, Robisson et al. 1993).

Acoustic communication must be accurate to manage with the important acoustic constraints arising from colonial life. To improve the reliability of information transmission, flamingos must encode individuality in several call parameters, both frequency and temporal, which counteract these acoustic constraints. A comparison of the results of this study with the previous works done in this laboratory on the Emperor Penguin (Robisson et al. 1993) provides several convergences concerning call structure: a virtual absence of frequency modulation, a wide spectrum (two voices and harmonics) with the energy concentrated in low frequencies and a beat phenomenon generating important amplitude fluctuations. These characteristics appear to be well adapted to the acoustic constraints of colonial life in particular, because low frequencies can propagate through the medium of birds' bodies better than higher ones, and because the amplitude modulation generated by beats is likely to resist to propagation at the opposite of an amplitude modulation sensu stricto (Robisson et al. 1993, Aubin & Mathevon 1995). Moreover, according to the mathematical theory of communication (Shannon & Weaver 1949), the information passed through the transmission channel is improved by repetition. The flamingos use this possibility since the calls are most often emitted sequentially.

The results of this study indicate that individual recognition based on calls in flamingos is possible. This acoustic recognition certainly plays a major role in social relationships. The colonial life requires an accurate recognition process between mates, and the acoustic features of vocalizations provide sufficient information on individuality to allow

### Table 1. Mean ± s.d. for selected call parameters for Greater Flamingo individuals A to E

<table>
<thead>
<tr>
<th>Individual</th>
<th>Call duration (s)</th>
<th>Slow amplitude modulation (Hz)</th>
<th>Spectrum bandwidth (Hz)</th>
<th>Frequency with the greatest energy (Hz)</th>
<th>First frequency (Hz)</th>
<th>Main energy portion of the spectrum (arbitrary unit)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A (n = 7)</td>
<td>0.215 ± 0.021</td>
<td>82.8 ± 6.7</td>
<td>3500 ± 445</td>
<td>2588 ± 314</td>
<td>838 ± 172</td>
<td>5.14 ± 1.46</td>
</tr>
<tr>
<td>B (n = 5)</td>
<td>0.205 ± 0.015</td>
<td>77.5 ± 2.9</td>
<td>3660 ± 127</td>
<td>887 ± 15</td>
<td>419 ± 2</td>
<td>2 ± 0.0</td>
</tr>
<tr>
<td>C (n = 8)</td>
<td>0.214 ± 0.032</td>
<td>78.3 ± 3.3</td>
<td>3750 ± 578</td>
<td>963 ± 245</td>
<td>411 ± 9</td>
<td>2.25 ± 0.43</td>
</tr>
<tr>
<td>D (n = 4)</td>
<td>0.145 ± 0.020</td>
<td>123.9 ± 8.7</td>
<td>1377 ± 175</td>
<td>2583 ± 105</td>
<td>2414 ± 51</td>
<td>5.57 ± 0.43</td>
</tr>
<tr>
<td>E (n = 5)</td>
<td>0.327 ± 0.086</td>
<td>72.9 ± 2.1</td>
<td>3980 ± 219</td>
<td>1538 ± 653</td>
<td>773 ± 42</td>
<td>4.2 ± 1.6</td>
</tr>
</tbody>
</table>

* The number of calls examined for each individual is shown in parentheses.

### Table 2. The coeff. var. b/mean coeff. var. i and analysis of vari the studied variables for Greater Flamingo individuals A to E

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coeff. var. b/ mean coeff. var. i</th>
<th>ANOVA Kruskal-Wallis Multiple comparisons</th>
</tr>
</thead>
<tbody>
<tr>
<td>Call duration</td>
<td>2.19 18.0* (D)(B-A-C)(E)</td>
<td></td>
</tr>
<tr>
<td>Slow amplitude modulation</td>
<td>2.02 15.4* (D)(A-B)(B-E-C)</td>
<td></td>
</tr>
<tr>
<td>Spectrum bandwidth</td>
<td>2.60 15.3* (D)(B-A)(E-C)</td>
<td></td>
</tr>
<tr>
<td>Frequency with the greatest energy</td>
<td>2.80 20.9** (B-C)(E-D-A)</td>
<td></td>
</tr>
<tr>
<td>First frequency</td>
<td>12.04 24.3** (B-C)(E-D-A)</td>
<td></td>
</tr>
<tr>
<td>Main energy portion of the spectrum</td>
<td>2.51 18.0* (B-C)(E-D-A)</td>
<td></td>
</tr>
</tbody>
</table>

* P < 0.01, ** P < 0.001.
individual discrimination. However, a role of visual cues, such as postures, is not incompatible.

A few days after hatching, the chicks gather together in large creches of hundreds or thousands of birds. Each chick is fed by its own parents, and then a mutual recognition between the parents and their chick seems to be necessary. The flamingo chicks have the possibility to recognize their parents using the acoustic features identified by this analysis. Indeed, it has been reported that when a chick leaves its nest, the parents follow it, emitting the call I have investigated (Studer-Thiersch 1974). This recognition between adults and their offspring may have several biological interpretations in terms of adaptation significance. First, by feeding exclusively their own chick, parents promote their own gene pool. Second, chicks begging only from their parents for feeding may avoid conflict with other adults.

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REFERENCES


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