A method of independent time and frequency decomposition of bioacoustic signals: inter-individual recognition in four species of penguins

Une méthode de décomposition temporelle et spectrale des signaux bioacoustiques : reconnaissance individuelle chez quatre espèces de manchots

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RÉSUMÉ

L'objet de cette publication est de présenter une méthode de décomposition temporelle et fréquentielle des signaux sonores qui permet d'étudier le potentiel de codage de l'information individuelle. Cette analyse s'effectue à la fois dans le domaine temporel (rythme d'émission du chant indépendamment de son contenu spectral) et dans le domaine fréquentiel (contenu spectral indépendamment des paramètres temporels). Cette méthode est ensuite appliquée à une étude comparative de quatre espèces de manchots chez lesquelles le problème de la reconnaissance individuelle se pose de manière sensiblement différente. Chez ces espèces, nous avons montré qu'un fort potentiel de codage de l'information individuelle est directement lié aux difficultés des retrouvailles entre oiseaux.

***Mots clés :** reconnaissance individuelle, manchot, communication acoustique*

ABSTRACT

The aim of this paper is to introduce a method for analyzing acoustic signals capable of assessing the potential for individual coding information. Signals are analysed both in the time domain (rhythm of emission of the song independent of its frequency content) and in the spectral domain (spectral content of the song independent of the rhythm of emission). The method is then applied to a comparative study of four penguin species, where the problem posed by inter-individual recognition differs from species to species. A direct relationship was shown between the potential of individual coding and the difficulty in partner identification.

Key words: individual recognition, penguin, acoustic communication

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VERSION ABRÉGÉE

Cette publication présente une méthode d'analyse des signaux acoustiques capable d'examiner les variabilités intra- et interindividuelle séparément dans le domaine temporel (étude du rythme d'émission du signal, énergie versus temps) et dans le domaine fréquentiel (étude du spectre du signal, énergie versus fréquence). Cette méthode est ensuite appliquée à l'étude des signaux acoustiques utilisés partiellement ou exclusivement pour la reconnaissance individuelle par quatre espèces de manchots : le manchot royal (*Aptenodytes patagonicus*), le manchot empereur (*Aptenodytes forsteri*), le manchot Adélie (*Pygoscelis adeliae*) et le gorfou macaroni (*Eudyptes chrysolophus*).

Pour l'analyse temporelle du signal on calcule le profil d'énergie de chacun des signaux enregistrés. La ressemblance entre profils est mesurée par le r non paramétrique de Spearman. On obtient ainsi à la fois des corrélations intra-individuelles (comparaisons des chants d'un même individu) et interindividuelles (comparaisons des chants de deux individus). Chez les quatre espèces étudiées, la médiane des coefficients de corrélation intra-individuels (m1) est supérieure à celle des coefficients interindividuels (m2), les différences étant toujours très hautement significatives. On peut calculer, espèce par espèce le rapport des deux médianes m1/m2. Les valeurs les plus élevées sont rencontrées chez les espèces dont le rythme d'émission du chant est à la fois homogène pour un individu donné (m1 élevée) et faiblement ressemblant avec celui des congénères (m2 faible). Le rapport m1/m2 traduit finalement le potentiel de codage dans le domaine temporel. Les valeurs les plus fortes (supérieures ou égales à 1,7) sont observées chez le manchot royal et le manchot empereur, les plus faibles (égales à 1,2) sont observées chez le manchot Adélie et le gorfou macaroni.

L'analyse fréquentielle est basée sur le calcul du spectre moyen par la méthode de Welch. Après élimination de la première bande de fréquence (0–174 Hz) qui contient principalement du bruit de fond, les données sont soumises espèce par espèce à une analyse discriminante progressive en vue d'éprouver la séparation des individus. Chez les quatre espèces considérées, chaque individu possède un profil de fréquence caractéristique, distinct de celui de ses congénères. La signature acoustique dans le domaine spectral est donc non ambiguë. Néanmoins, les espèces diffèrent sur le nombre de bandes de fréquences nécessaires à l'établissement de cette séparation. Une mesure du potentiel de codage peut être définie par l'inverse du rapport : nombre de bandes spectrales nécessaires à la discrimination des individus sur le nombre de bandes disponibles sur l'ensemble du spectre. Ce potentiel est maximum chez le manchot empereur (1,6), intermédiaire chez le manchot royal et le gorfou (1,2) et faible chez le manchot Adélie (1,0).

Chez les quatre espèces étudiées, le problème de la reconnaissance individuelle se pose de manière sensiblement différente. Les potentiels de codage fréquentiels et temporels ont des valeurs élevées chez le manchot empereur et le manchot royal, espèces où la reconnaissance du partenaire ne peut être facilitée par des repères topographiques comme la présence d'un nid ou d'un territoire aux contours bien délimités. Chez les deux autres espèces de manchots étudiées, le nid et le territoire agissent comme des points de rendez-vous précis, les retrouvailles entre partenaires ne dépendent donc plus entièrement des émissions sonores. C'est précisément chez ces espèces que les potentiels de codage, fréquentiel comme temporel, sont les plus faibles.

Il semble donc exister une relation directe entre l'efficacité du codage acoustique de l'information individuelle et l'absence de repères visuels ou topographiques capable d'orienter la recherche du partenaire. Par contraste avec les méthodes précédemment utilisées on peut réaliser facilement des comparaisons inter-spécifiques: la méthode proposée ici pour l'analyse du chant est identique quels que soient les individus ou les espèces. Elle permet de révéler des signatures acoustiques individuelles, lorsqu'elles existent, et se prête facilement à l'évaluation comparative des potentiels de codage.

Introduction

Individual recognition (IR) assumes that the emitter is able to produce a signal of fixed or only slightly varying structure between successive emissions. Furthermore, the signal must be different from those emitted by conspecific individuals. Acoustic IR also assumes that the receiver is able to recognize, discriminate and memorize signals. The acoustic signature of an emitter can be coded in the time domain (rhythm of signal emission), in the spectral domain (frequency content) or simultaneously in both. In all cases it is expected that the parameters that will characterize the rhythm of signal emission or its spectral content exhibit an intra-individual variability much lower than the inter-individual variability [1]. The ratio of these two variabilities could help define a potential for individual coding (PIC). However, until now, the problem of

separately estimating the time PIC and the spectral PIC has proved difficult to solve. Most commonly, measures have been analysed on sound spectrograms (energy versus time and versus frequency) [2–6]. However, owing to the uncertainty principle [7], precision in both the time and frequency domains could not be obtained simultaneously, making it impossible to obtain precise measurements in both domains from the same spectrograms [8].

The aim of this paper is to introduce a method for analysing acoustic signals able to separately assess the PICs both in the time domain (PIC of the temporal distribution of energy) and in the spectral domain (PIC of the frequency distribution of energy). The method is then applied to the comparative study of four penguin species, where the problem of individual recognition faced by each species is known to be slightly different from that found in the others. The species studied are the Adelie

penguin (*Pygoscelis adeliae*), the Macaroni penguin (*Eudyptes chrysolophus*), the King penguin (*Aptenodytes patagonicus*) and the Emperor penguin (*Aptenodytes forsteri*). They are known for partially or exclusively using acoustic signals for IR [9].

In the four species under study, both parents take turns in rearing the young, as found in most marine birds: one parent spends its time fishing at sea while the other broods or protects the chicks. The shifts practised by parents assumes that they are able to recognize each other among all the conspecifics found in the colony.

The simplest situation, as well as the most frequently met in marine birds, is found in the Adelie penguin and the Macaroni penguin. Individuals of both species own nests at fixed locations and well-defined small territories. The territory is used as a meeting place for the parent returning from the sea, aiming to take over from the parent brooding or staying with the chick. For these two species, topographical clues help the meeting of birds. Song is used solely for checking the partner's identity.

The King penguin faces a more serious problem of IR. The species makes no nest, warming the egg, then the chick, between its feet. Moreover, it has no territory, but only a preferred area in the colony where the breeding adult wanders, called the 'attachment zone' [10]. There is no definite meeting place for the parents, making the problem of IR more difficult to solve than for the two preceding species.

Emperor penguins probably face the most complex situation. This species makes no nest and owns no territory. The breeding parent wanders about freely in the colony area. Topographical clues seem to be used scarcely [11] or not at all [9] for the meeting of parents.

It has been shown [4] that these four species rely on their song to meet, recognize or check the identity of their partner.

In this paper we try to assess:

– if an individual signature can be found in the temporal domain (emission rhythm of the song), independently of its frequency content;

– if an individual signature can be found in the frequency domain (spectral content) of the song, independently of the emission rhythm;

– if the sharpness of these signatures (frequency PIC and temporal PIC) relate to the increasing difficulty of finding the partner in the four species under study.

Material and methods

Data acquisition

Bird songs were recorded at close distance (about 1 m), using a Beyer Dynamic M69 microphone mounted on a perch and connected to a Nagra IV tape recorder (tape speed 19.5 cm/s). The number of songs recorded in the four species was as follows: King penguin 73 songs from

15 individuals; Adelie penguin 60 songs from 11 individuals; Emperor penguin 46 songs from 7 individuals; Macaroni penguin 72 songs from 12 individuals; total songs 251; total individuals 45. In King and Emperor penguins, where the songs of males and females were different, we have chosen recordings of females only.

The set of 251 songs was then digitized with a sampling frequency of 22 255 Hz. The analysis of the samples was then able to reveal their frequency content up to half this value, i.e., 11 127.5 Hz (Nyquist frequency). Signal dynamics were coded on 8-bit dynamics.

Data processing

Temporal analysis of signals

The energy profiles of songs were computed for 20 ms frames (*figure 1*). The choice of this duration was made taking into account what is known about the sensory abilities of birds. Electrophysiological analysis [12] revealed that most birds are able to distinguish between two sounds separated by only 2.5 ms. This discrimination was dependent on the frequency and amplitude of signals. Furthermore, the experiments of Jouventin et al. [3] on the Emperor penguin showed, without doubt, that the temporal resolution threshold was less than 15 ms. Nothing is known for the three other species. In order to avoid the risk of situating our study on the edge of the auditory abilities of penguins, we chose to use a temporal window lasting 20 ms.

In the first step, the energy content of the signal was computed for each consecutive 20-ms frame of the signal (445 consecutive values).

The energy content e_i for frame i is given by

$$e_i = \frac{\sum_{k=1}^{k=445} (x_{ik} - \bar{x})^2}{445}$$

where x_{ik} denotes the value found in the kth point of frame i and $\bar{x} = \dfrac{\sum_{k=1}^{k=445} x_{ik}}{445}$ denotes the mean value of the signal over frame i. For example, a 3-s song comprised 150 energy values.

Summing the energy content of each frame e_i ($i = 1...n$) gives the total energy E of the signal: $e_1 + e_2 + e_3...e_n = E$. Thus the series $e_1, e_2...e_n$ (referred to here as the energy profile) can be considered as a discrete approximation of the continuous energy density function of the signal [16]. Furthermore, any information related to the frequency content of the signal is lost during this evaluation, exactly as intended.

The second step aimed to devise a measure of proximity between any two energy profiles. Either between signals coming from the same individual (intra-individual comparison) or between signals coming from two different individuals (inter-individual comparison) of the same species.
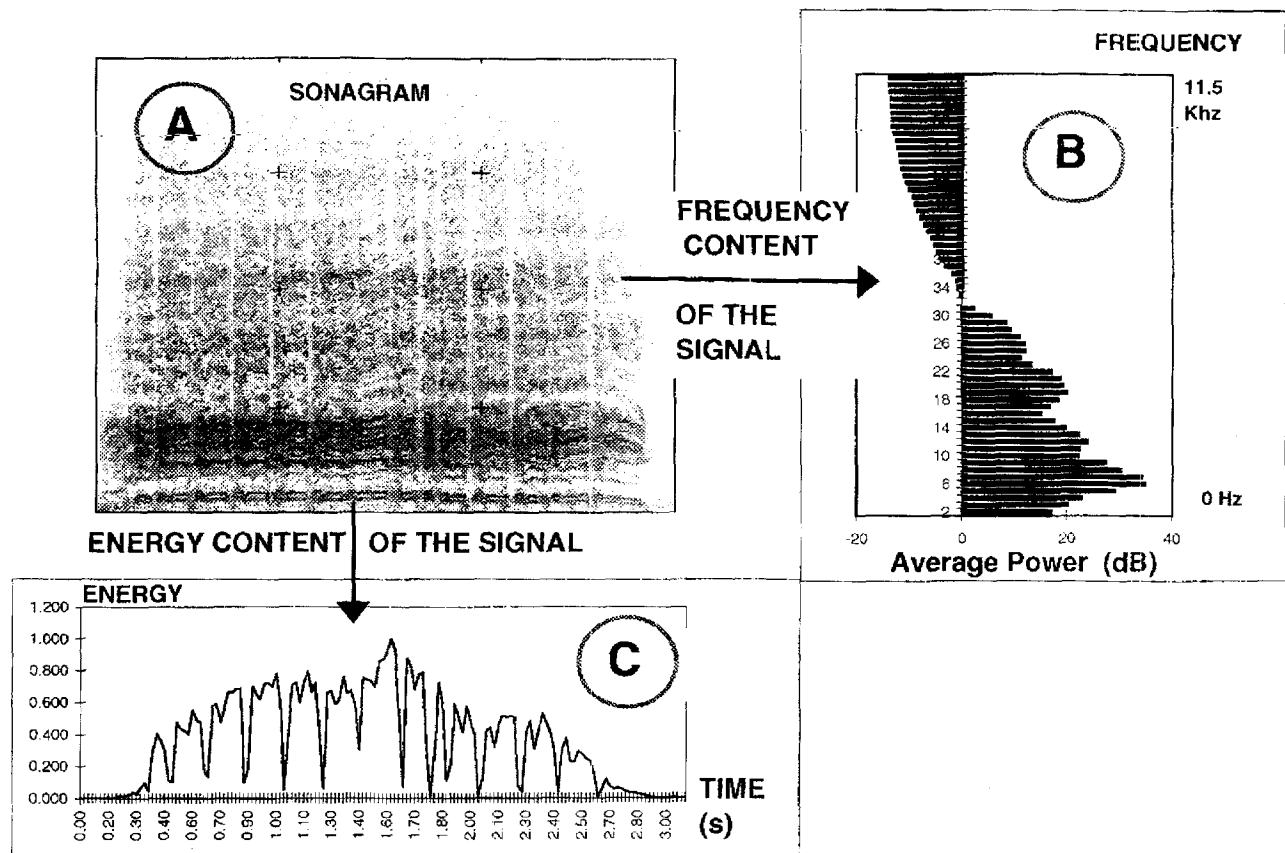
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Figure 1. The song of an Emperor penguin (sonagram in A) is analyzed separately in two domains.

B. The average power spectrum (expressed in dB), revealing the frequency content of the song with a 174-Hz bandwidth. **C.** The energy profile of the song computed on 20-ms frames. The rhythm of emission is clearly marked. Any temporal information has vanished from (B); while any frequency information has vanished from (C). Processing data sets (B) and (C) separately allows the study of individual recognition to be made in either of the two domains, independently of the other.

The hypothesis of an acoustic signature in the temporal domain assumes that the songs emitted by the same bird exhibit very similar energy profiles, whereas the songs emitted by two different birds exhibit much larger differences.

Since the total duration of song was never the same (except in the case of the Emperor penguin), whether for a given individual or two different individuals, the lengths of the energy profiles were never the same. Thus, to find a proximity measure between two songs of unequal length, a complete set of all the possible cross correlations between the two signals was first computed. The highest value was finally selected as the measure of proximity (table I). Spearman's non-parametric rank correlation coefficient was used to avoid any hypothesis related to linearity.

The proximity measures were then defined in both the songs of the same individual (intra-individual correlations) and the songs of different individuals (inter-individual correlations).

For example, for one individual of king penguin, seven songs were recorded. All the intra-individual proximity measures were computed, giving $N = 7 \times 6 \times 0.5 = 21$ values. Doing the same on the 15 individuals gave $N = 182$ intra-individual proximity measures for this species. The median value of these 182 measures was considered for subsequent tests. At the inter-individual level, within the same species, the number of comparisons between any possible pair of songs increased, yielding $N = 3052$ inter-individual proximity measures.

The distributions of the correlation coefficients were found in most cases to be largely skewed. For this reason only non-parametric tests of comparison were used (Mann-Whitney test), to avoid hypotheses related to normality or homoscedaticity.

Frequency analysis of the signals

This step consisted in computing the average spectrum of the signal. For the choice of the frequency bandwidth used in the analyses we took into account the frequency abilities of birds and the expected precision of calculation. According to Dooling [13], birds were able to detect a 20-Hz shift in a 2000-Hz signal but this depended on the energy profile of the sound tested [14]. The lack of

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Species	Median of intra-individual correlation coefficients (m1)	Median of inter-individual correlation coefficients (m2)	Difference and its significance (Mann-Whitney test)	Potential of individual coding in the time domain: m1/m2
King Penguin	0.91 (n = 182)	0.48 (n = 3052)	0.43 ***	1.9
Emperor Penguin	0.74 (n = 167)	0.44 (n = 2054)	0.30 ***	1.7
Adelie Penguin	0.57 (n = 148)	0.46 (n = 1883)	0.12 ***	1.2
Macaroni Penguin	0.63 (n = 262)	0.52 (n = 2655)	0.11 ***	1.2

The energy content of the signal always appears to be more strongly correlated within individuals than between ($P < 0.001$). The ratio of the two medians is used to estimate the PIC.

data on the frequency discrimination abilities of penguins suggested care was required. Thus, the analysis was made using 63 frequency bands, each 174 Hz wide. The signal was processed by i) extracting slices of 128 consecutive values, with a 64-point overlap on the preceding slice; ii) weighting the slice by a Hamming window; iii) computing a Fourier transform of the weighted slice (Welch's method [15, 16]). MATLAB software was used for spectral computations. On output the Fourier transform yielded 64 frequency bands each 174 Hz wide. The power spectrum was then computed by squaring the magnitude of each band. Averaging the power spectrum on all slices finally gave an efficient, non-biased estimation of the mean power spectrum of the signal. Since the overall variation of power in a single song spans several orders of magnitude, the values were log-transformed in decibels. The decibel (dB) measure of a power P is defined as: power density in decibels = 10 log10 P [28].

Upon termination, any information related to the temporal rhythm of the emission was lost, exactly as intended.

Among the four species, the energy of the signal concentrated at lower frequencies: 31 frequency bands only were used by Adelie penguins, 32 in Emperor penguins, 39 in Macaroni penguins, 40 in King penguins.

As expected the first frequency band (0–174 Hz) gathered mainly a blend of background and wind noises. This band was excluded from all subsequent analysis.

Instead of computing intra- and inter-individual correlations between the energy content of each frequency band, we took advantage of the fact that the number of frequency bands was always the same in all the power spectrums, thus allowing the use of multivariate analysis.

For each species in turn, the data were submitted to a stepwise discriminant analysis in order to assess the separability of individuals as well as the number of frequency bands required to achieve this differentiation. In the data matrix, rows were the songs, variables were the power of each frequency bands (in dB). Computations were carried out using PROC STEPDISC of SAS [17].

Results

Temporal analysis of signals

In all cases the median of intra-individual correlation coefficients between songs (m1) was found to be higher than for inter-individual correlation coefficients between songs (m2). The differences were always highly significant (Mann-Whitney test, $P < 0.001$).

It is possible to compute, species by species, the ratio of the two medians m1 and m2. This ratio brings out the discrepancy between intra-individual variation (as measured by m1) and the inter-individual variation (as measured by m2). Higher values were found in those species where the temporal emission rhythm of songs appeared both homogeneous for a given individual (large m1) and largely different from those of a conspecific (low m2). This ratio could be taken as a measure of the PIC in the temporal domain. Higher values (> = 1.7) were found in the emperor penguin and the king penguin. Lower values (< 1.3) were found in the Adelie penguin and the Macaroni penguin.

Frequency analysis of signals

Discriminant analysis performed on the mean power spectrum clearly separated all individuals in all four species. The error-rate in cross-classifying the data set was always zero.

These results suggest that in our data set, for the four species under study, each individual clearly possesses a unique and clear-cut spectral content in its song. In the frequency domain, the individual acoustic signature appeared non-ambiguous.

Nonetheless, species differed as to the number of frequency bands by which different individuals could be distinguished. Some species seemed to perform better than others.

Extreme values were found in the Emperor penguin, where the 20 lower frequency bands (out of 31 in the call spectrum) seemed to be sufficient for a complete separation of individuals and in the Adelie penguin where 29 frequency bands (out of 30 in the call spectrum) are required to do the same. The King penguin (34 frequency bands out of 39) and the Macaroni penguin (32 frequency bands out of 38) were in an intermediate position between the two extremes. In all species the lower frequency bands concentrate most of the discriminating power.

Out of the four species, the Emperor penguin seemed to make the most efficient use of its frequency domain. A rough index of its PIC can be measured by the ratio of the

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number of frequency bands in the complete power spectrum to the number of frequency bands needed for discriminating between individuals. Here PIC = 31/20 = 1.6. Values of PIC in the frequency domain for the three remaining species were found to be 1.2 (King penguin and Macaroni penguin) and 1 (Adelie penguin).

Discussion

Relationship between PIC and the difficulty of finding the partner

As stated in the *Introduction*, the problem posed by individual recognition differs from species to species.

PICs in the temporal domain *(figure 2)* were found to be high in the Emperor penguin and in the King penguin, species for which no topographical clues (nest or territory) could help the birds to find each other. In contrast, in the Macaroni penguin and the Adelie penguin, such topographical clues do occur, indicating meeting places. In these two species, PICs were lower than in the previous two. The highest PICs in the frequency domain were found in the Emperor penguins and the lowest in the Adelie penguins. PICs for King and Macaroni penguin were intermediate between the two extremes.

Previous studies [9, 18] on sound spectrograms of penguins have shown the same results. Thus, a direct relationship seems to exist between the PIC efficiency and the lack of visual clues available to orient the search for the partner.

It is impossible to distinguish the role of temporal and frequency coding among the birds from the existence of temporal or frequential PICs. However, since IR is present or effective only within species subject to strong selective pressures, it is generally considered as an adaptative process. Thus parameters such as the difficulty of change over, the distance between the nest or coloniality can explain the existence of PICs or the high degree of discrimination between partners or between parents and chicks. [9, 19–22].

Independent analysis of the frequency and temporal components of signals: advantages and limits

The method reported in this paper is new because it allows separate analysis of two different domains where the bird might code its individual signature: the temporal rhythm of emission (temporal coding) and the spectral content (frequency coding) of song. Computing these two decompositions separately allows large data sets, suited for further statistical analysis to be easily gathered. For example, a 3-s song of the emperor penguin was described by 150 values in the temporal domain and 31 values in the frequency domain. This method facilitates the comparison between species because data were computed in the same way regardless of the signals, the individual or the species. There is no observer selection except the frequency and temporal bandwidth used in calculation.

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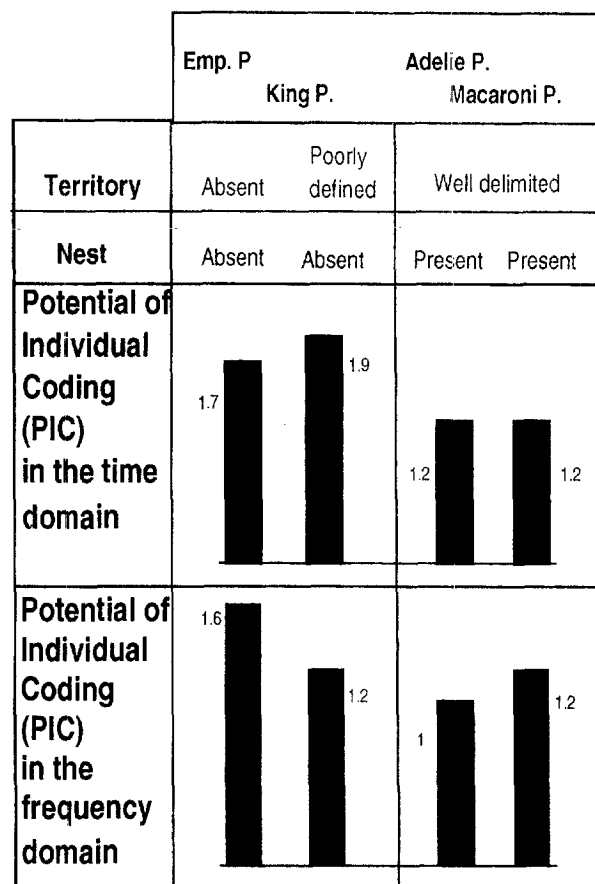| Emp. P King P.		Adelie P. Macaroni P.	
Territory	Absent	Poorly defined	Well delimited
Nest	Absent	Absent	Present Present
Potential of Individual Coding (PIC) in the time domain	1.7	1.9	1.2 1.2
Potential of Individual Coding (PIC) in the frequency domain	1.6	1.2	1 1.2

Figure 2. Relationship between the potential of individual coding (PIC) of penguins and the presence (or lack) of a territory and a nest.

Species lacking both (Emperor and King penguins) cannot rely on visual or topographical clues to meet the partner. Their PICs appear stronger than for the two remaining species (Adelie and Macaroni penguins) where a territory and a nest are present.

Nevertheless, such an analysis supposes the presence of an energy modulation in the time domain of the signal. A signal whose oscillogram does not reveal or reveals little energy modulation (alarm calls of numerous passerine birds) or a very short signal will not allow the distinction of different individuals in the temporal domain. In the frequency domain, energy modulation versus frequency is also necessary. A monochromatic signal would make the discrimination between individuals impossible. This type of method seems to be well adapted to the study of complex signals but less efficient to analyse the songs of some passerine birds.

On the other hand, methods generally used to describe the lack of variation of a song in the temporal and frequency domains used few parameters such as syllable and silent lengths, fundamental frequency, frequency with maximum level, highest frequency [4, 5, 9, 23, 24]. In these comparative studies, it is necessary to take into account the specificity of acoustic structure of each spe-

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cies, ie, to adapt the method of calculation of the PICs. For example, measures of syllable duration were different for King penguin (song without sharp amplitude declines) than for Emperor penguin (song with strong gap amplitude). The syllable duration was measured between minima of energy for the Emperor penguin and between maxima for the King penguins [9].

Potential of individual coding and systems of coding–decoding of information

A study of potential individual coding in the four species of penguins permits identification of species whose recognition signal structure is the most adapted to coding individual information.

This study suggests that a clear-cut separation between individuals could be observed in the frequency domain, some species performing better than others in this domain, and finally that the rhythm of emission differs greatly from one individual to the other in some species. Nevertheless, our results reveal only potentials, they do not prove that the birds effectively use both channels for recognizing each other.

The potential of coding in the temporal domain can correspond to different types of coding information based on modulation of energy in time. For example, some analyses have shown that syllable duration can code emotional state in the belted kingfisher [25] or individual information in the domestic pigeon Columba livia domestica [4]. The emission rhythm allows sex identification in the emperor penguin [3] or can have a role in species recognition in skylarks Alauda arvensis [26]. The information can also be based on energy modulation in the frequency domain. For example, the harmonic structure of the signal is used in the decoding of distress call in lapwing Vanellus vanellus [27] and in species recognition in the Bonelli's Warbler Phylloscopus bonelli [28].

The PICs are now identified in both the temporal and the spectral domain in the four species under study. The next step will be their experimental assessment.

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