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ORIGINAL PAPER

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Individual identity coding depends on call type in the South Polar skua *Catharacta maccormicki*

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Abstract In colonial birds, acoustic communication is essential for mate recognition. The South Polar skua (*Catharacta maccormicki*) lives in loose colonies and is highly territorial for feeding and breeding. We studied the potential of individual identity coding in the three main calls of the South Polar skua repertoire: the courtship, the contact and the alarm calls. We investigated parameters in both temporal and frequencial domains, i.e. amplitude modulation, frequency modulation and power spectrum density. For each parameter, the intra- and inter-individual variabilities were calculated. The ratio between these values represents the potential of individuality coding (PIC) of the considered feature. Low values of PICs for amplitude and frequency modulations show that both parameters may not be used for individual recognition. In contrast, high values of PIC for the power spectrum density indicate that the energy distribution among the frequency spectrum is likely to be an individual marker. PIC also varies according to the call type. Both courtship and contact calls have a higher potentiality of individual identity coding than the alarm call. The two former calls may allow individual recognition whereas the latter may not, and this last result can be extrapolated to many other species.

Introduction

In most seabirds, acoustic communication is essential during social relationships such as mating or parent-offspring interactions (Falls 1982). Individual recognition supported by acoustic signals has been shown in many species (Beer 1979; Jouventin1982; Lambrechts and Dhondt 1995) and is particularly developed in colonial birds which have to find their mate or chicks among numerous individuals. It is essential because it permits the collection of energetic profits during the feeding of the chicks: parents feed only their own chicks (Davies and Carrick 1962). During the breeding season, individual recognition assures that mates meet, especially for seabirds which are monogamous and often paired for several years. Individual recognition contributes to the increase of breeding success and fitness of the species (McArthur 1982).

The South Polar skua, *Catharacta maccormicki*, is a monogamous nesting seabird living on the Antarctic continent in isolated pairs or loose colonies (14 nests/ha), and showing strong territorial behaviour in breeding and land feeding. This species emits three types of calls: courtship, contact and alarm calls (Spellerberg 1971; Jouventin and Guillotin 1979; Pietz 1985). The courtship call may allow recognition between mates during the courtship period, and is often emitted in repeated sequences presenting up to 12 calls, when the pair meets on the territory used in the previous year, in order to reestablish the pair. The contact call is shorter and is emitted during fast meeting, for example, when a paired adult comes back to its nest. This call is directed to the mate or the chicks. The alarm call is used in a danger situation, e.g. when an intruder approaches the nest territory. It often elicits reaction in neighbouring birds. Alarm and contact calls are sometimes emitted in series. Considering the emission context of those three calls, we assume that the courtship and contact calls may provide more information about the identity of the sender than the alarm call.

The aim of this study is to investigate the acoustic parameters likely to carry information about individual identity, and to evaluate the relative ability of each of the three call types to support individual recognition process. In birds' signals, individual identity may beencoded by temporal and frequency acoustic

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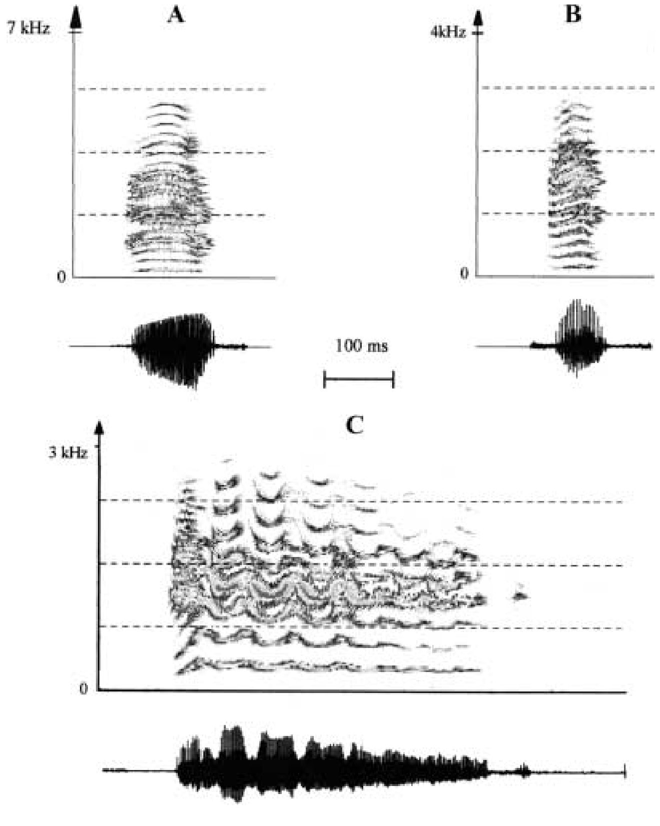


Fig. 1 Spectrograms and oscillograms of the three studied calls: **A** courtship call, **B** contact call, **C** alarm call (window size 1024). The three call types are different in their duration. The longest one is the alarm call (622 ms ± 172, measured from the oscillogram), then the courtship call (155 ms ± 25) and finally the contact call (88 ms ± 21).The courtship call is a short unit often repeated 1–12 times

parameters: these are amplitude and frequency modulations, frequency spectrum, call duration and syllable rhythm (Busnel 1977; Falls 1982). To be potentially involved in the coding of individual identity, a given parameter has to show an inter-individual variability greater than its intra-individual variability. For each parameter, we assess the intra-individual and inter-individual variabilities, and we calculate the ratio between them to define a Potential for Individual identity Coding (PIC) (Lengagne et al. 1998). We then compare the PICs among the three call types to evaluate their relative ability to carry information about individual identity.

Materials and methods

Signal acquisition

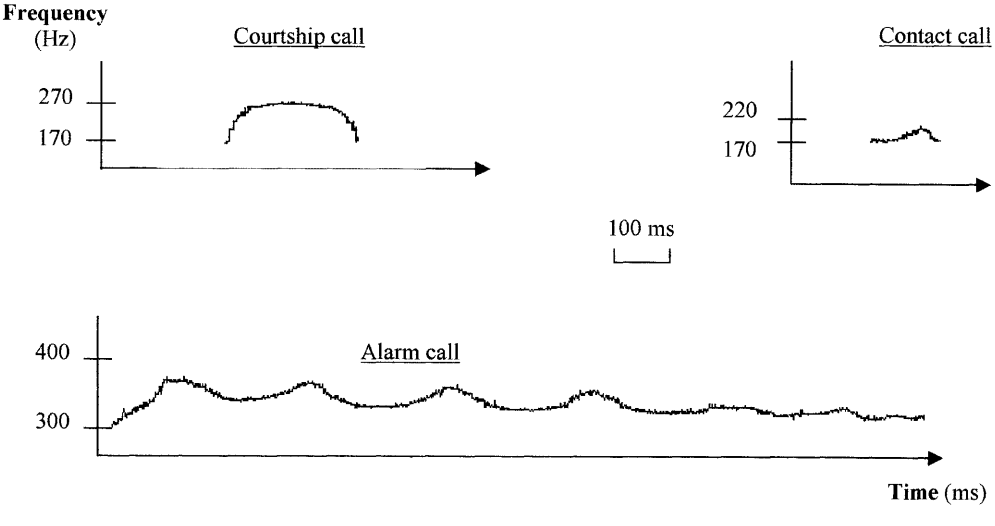
The South Polar skua calls used for our study were recorded at Terre Adélie (66°40′S, 140°01′E, Antarctica), using an omnidirectional Sennheiser MD 421 microphone (frequency range 150–15,000 Hz ± 1 dB) connected to a Nagra IV tape recorder (tape speed 19.5 cm/s; frequency range 30–20,000 Hz ± 1 dB). All the recordings were performed at a distance of 2–3 m from the caller using a 2-m boom. We obtained the courtship calls' recordings during the courtship behaviour. Recordings of the contact calls were made when a bird came back to its nest and met its partner and/or its chicks. The alarm calls were recorded when an intruder approached too close to a nest. The differences between the behaviours when the birds produced the different calls were so obvious that there could be no confusion between the three types of calls.

We analysed the three main calls cited above: the courtship, contact and alarm calls (Fig. 1). As a sample, we took 57 courtship calls from 5 individuals, 18 contact calls from 4 individuals, and 35 alarm calls from 7 individuals. As the structure of male and female calls were not different, we analysed both sexes' calls for each call type (Pietz 1985). Calls were digitised with a sampling frequency of 22,050 Hz (16 bit resolution), using a 120 dB/octave anti-aliasing filter.

Signal analysis

Signal analysis was performed with the customised analysis software, Syntana (Aubin 1994). We studied parameters in both temporal and frequency domains (Beeman 1998; Lengagne et al. 1998). In the temporal domain, we calculated amplitude envelopes using the analytical method (Mbu Nyamsi et al. 1993). To investigate the time periodicity and follow the frequency modulation of the fundamental frequency, we calculated the cepstrum (Fig. 2), defined as the power spectrum of the logarithm of the power spectrum (Noll 1967). The cepstrum has a strong peak, corresponding to the fundamental frequency of the signal being analysed.

Fig. 2 Frequency modulation of the fundamental frequency (cepstrum method; FFT window size 256; sliding step ten samples corresponding to 0.5 ms). The sliding corresponds to the number of points of displacement of the FFT window along the file. Each call type presents frequency modulations (*FM*). The average FM bandwidth of the fundamental frequency is different between calls: 50 Hz for the contact call (assessed graphically from the cepstrum), 100 Hz for the courtship call. In the alarm call, the FM bandwidth decreases with time from 80–90 Hz to 10 Hz



In the frequency domain, to assess the repartition of energy among the spectrum of the call, we calculated the spectrum of squared amplitude (Fig. 3), i.e. the power spectrum density (PSD, Randal and Tech 1987).

Assessment of the Potential of Individual identity Coding

The following analysis was performed independently for each call type.

For a given parameter, we obtained a set of data for each individual (e.g. a set of amplitude envelopes). Firstly, we calculated a set of intra-individual correlation coefficients using each individual data set of the studied parameter; e.g. each amplitude envelope belonging to a given individual was correlated with all the other amplitude envelopes of the same individual. Secondly, we calculated a set of inter-individual correlation coefficients using all the individual data sets; e.g. each amplitude envelope belonging to a given individual was correlated with all the other amplitude envelopes of all the individuals. To calculate the coefficient of correlation between two amplitude envelopes, we elaborated a program in the laboratory. As the durations of calls were different within and between individuals, the envelopes were correlated using the duration of the shortest call.

To avoid any hypothesis related to linearity, we used the Spearman's non-parametric rank correlation coefficient. As the distributions of correlation coefficients were skewed in most cases, we used a non-parametric test for the comparison of medians (Wilcoxon Mann-Whitney test) (Sherrer 1984).

The ratio between the medians (respectively, m1 and m2) of intra-individual correlation coefficients and inter-individual correlation coefficients was calculated to represent the PIC of the studied parameter. For a given parameter, a PIC value superior to 1 means that this parameter may be used for individual recognition since its intra-individual variability is less important than its inter-individual variability (Jouventin 1982; Robisson et al. 1993; Lengagne et al. 1998). PIC values are considered high when superior to 2 (Robisson et al. 1993).

Results

Power Spectrum Density

For each call type, the median of intra-individual correlation coefficients of the power spectrum density is significantly higher than the median of inter-individual correlation coefficients (Table 1). The contact call shows the highest PIC value (2.80), and the lowest PIC value (1.34) is obtained with the alarm call. The energy distribution among the spectrum is likely to support individual information in both courtship and contact calls. This parameter is less individualised in the alarm call.

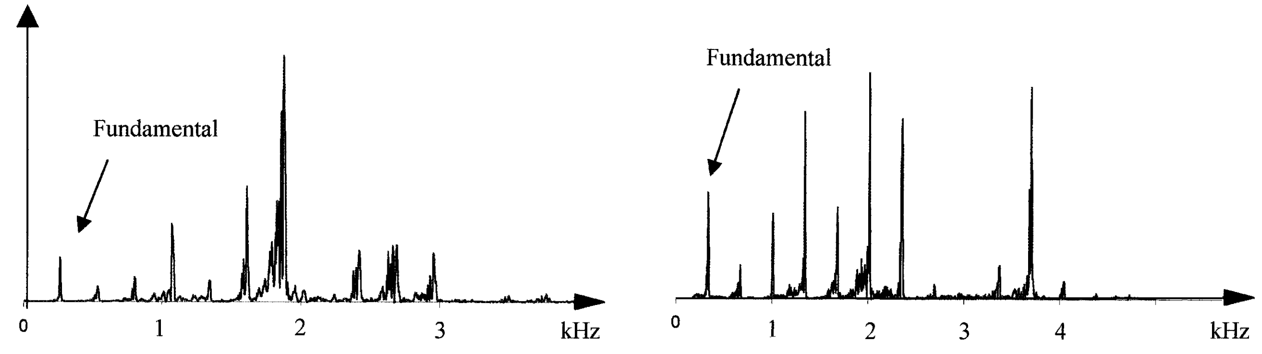


Fig. 3 Frequency spectra of courtship calls from two different birds. All calls are broadband calls. Each PSD spectrum is composed of a fundamental frequency and its related harmonics. The value of the fundamental frequency (270 and 330 Hz respectively in the two examples) and the repartition of energy among the harmonics are different between individuals (window size 4096 pt, 186 ms)

Frequency modulation

No significant differences are found between the medians of intra- and inter-individual correlation coefficients of the frequency modulation whatever the call type. For each call type, we obtained values near 1 for intra- and inter-individual correlation coefficients, leading to PIC values not significantly different from 1 (Table 2).

Potentiality of individuality coding by frequency modulation is weak in the three call types.

Amplitude envelope

No significant differences are found between the medians of intra- and inter-individual correlation coefficients whatever the call type. For each call type, the PIC is not significantly different from 1 (Table 3). Amplitude modulation may not support individual identity coding.

Discussion

Our analysis of the acoustic parameters suggests that the South Polar skua may not rely on temporal parameters such as amplitude modulations or frequency modulations for individual recognition. Indeed, frequency modulations may not be a good individual marker. For this parameter, the PIC is not significantly different from 1. This indicates that frequency modulations are stereotyped in each call type whatever the individual. Moreover, for amplitude modulations, all PICs values are near to 1. Amplitude modulations can not be used by the South Polar skua for individual recognition either. In fact, only the frequency spectrum is likely to be used for individual recognition, since for this parameter, PICs

Table 1 Potential for Individual identity Coding (*PIC*) for power spectrum density. High values for PICs show that this parameter could be an individual marker, especially in contact and courtship calls

Call type	Median of intra-individual correlation coefficients (m1)	Median of inter-individual correlation coefficients (m2)	Difference between m1 and m2	Ratio m1/m2 PIC
Courtship call ($n=5$ individuals)	0.14	0.06	0.08*	2.33
Contact call ($n=4$ individuals)	0.28	0.1	0.18*	2.8
Alarm call ($n=7$ individuals)	0.55	0.41	0.14*	1.34

*$P<0.01$ (Wilcoxon Mann-Whitney test)

Table 2 Potential for Individual identity Coding for frequency modulation. Values equal to 1 were found, so frequency modulations may not support individual recognition (*NS* non significant, Wilcoxon Mann-Whitney test)

Call type	Median of intra-individual correlation coefficients (m1)	Median of inter-individual correlation coefficients (m2)	Difference between m1 and m2	Ratio m1/m2 PIC
Courtship call ($n=5$ individuals)	0.998	0.998	0.0 NS	1
Contact call ($n=4$ individuals)	0.994	0.996	0.002 NS	0.998
Alarm call ($n=7$ individuals)	0.986	0.983	0.003 NS	1.003

Table 3 Potential for Individual identity Coding for amplitude envelopes. Low values for the three calls can be observed. The amplitude modulation does not appear to be more correlated within individuals than between and may therefore not support information about individual identity (*NS* non significant, Wilcoxon Mann-Whitney test)

Call type	Median of intra-individual correlation coefficients (m1)	Median of inter-individual correlation coefficients (m2)	Difference between m1 and m2	Ratio m1/m2 PIC
Courtship call (n = 5 individuals)	0.73	0.69	0.02 NS	1.06
Contact call ($n=4$ individuals)	0.75	0.68	0.04 NS	1.1
Alarm call ($n=7$ individuals)	0.78	0.76	0.07 NS	1.03

are higher than 1 whatever the call type. However, only courtship and contact calls present high values of PIC (superior to 2) for the frequency spectrum parameter. In previous studies on colonial birds, such as the king penguin (*Aptenodytes patagonicus*) (Aubin and Lengagne 1997), a non-nesting penguin, it has been shown that frequency modulations were essential for mate and chick recognitions. In contrast, for colonial species with nests such as the Adélie penguin (*Pygoscelis adeliae*) or the macaroni penguin (*Eudyptes chrysolophus*) (Lengagne et al. 1998), frequency modulations were less important for individual recognition. It was also shown that amplitude modulations are often not used for individual recognition by colonial birds (Aubin and Lengagne 1997; Jouventin et al. 1999). The individual recognition system of the South Polar skua appears to be like those of the nesting-penguins, which also pay attention to the spectral profile of the calls (Aubin and Jouventin, in press). These different species seem to converge to the frequency-based filter model where the output signal is correlated to the spectrum of the input signal and the gain of the filter (Hopkins 1983). The South Polar skua lives in loose colonies and is a territorial bird. As with nesting penguins, it has the opportunity to use visual cues in its environment, e.g. to locate its nest. These visual cues are complementary to the acoustic parameters, and could explain why the acoustic signature for individual coding is so simple.

The courtship and contact calls present a higher potential for individuality coding than the alarm call. This result is not surprising because both calls are involved in intra-specific social relationships where individual discrimination is important. In contrast, the potential of individuality coding contained in the alarm call is weak. The alarm call does not need to carry individual information because it contains a message of danger addressed to any bird. Previous studies on other species have shown that such calls often present an inter-specific value with a stereotyped structure found in several species of birds (Marler 1957; Aubin 1991). Aubin and Brémond (1989) demonstrated that the basic form of an alarm call is a carrier frequency with several harmonics, modulated slowly in frequency. This pattern is found in the South Polar skua alarm call.

The courtship call allows recognition between mates. This call is emitted when the pair meets on the territory used in the previous year, in order to re-establish the pair. Skuas are monogamous and pair for several years. Individual recognition between mates has to be unambiguous. This is a sine qua non condition for breeding success. Indeed, if there is no individual recognition between mates, breeding success is compromised (Jouventin and Guillotin 1979). The contact call is emitted during mate and parent-offspring recognition. With the courtship call, individual recognition has to be accurate to assure the fitness of the species. This difference between call types of the ability to carry individual identity information seems, then, adaptive to their functional role.

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