Cocktail-party effect in king penguin colonies

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The king penguin, *Aptenodytes patagonicus*, breeds without a nest in colonies of several thousands of birds. To be fed, the chick must recognize the parents in a particularly noisy environment using only vocal cues. The call an adult makes when seeking the chick is emitted at a high amplitude level. Nevertheless, it is transmitted in a colonial context involving the noise generated by the colony and the screening effect of the bodies, both factors reducing the signal-to-noise ratio. In addition, the adult call is masked by a background noise with similar amplitude and spectral and temporal characteristics, enhancing the difficulty for the chick in finding its parents. We calculate that the maximum distance from the caller at which its signal can be differentiated from the background noise (signal-to-noise ratio equal to 1) should not exceed 8–9 m in a feeding area. But our tests show that, in fact, chicks can discriminate between the parental call and calls from other adults at a greater distance, even when call intensity is well below that of the noise of simultaneous calls produced by other adults. This capacity to perceive and extract the call of the parent from the ambient noise and particularly from the calls of other adults, termed the 'cocktail-party effect' in speech intelligibility tests, enhances the chick's ability to find its parents.

Keywords: cocktail-party effect; penguins; vocal recognition

1. INTRODUCTION

All marine birds are monogamous for several reasons, including the continuous feeding trips necessary between sea and breeding grounds, and the fact that both sexes brood and rear the chicks (Lack 1968). Most species are colonial and the partner must be identified by its mate or its young. In the penguin family, individual recognition would seem to be particularly difficult because colonies often number several thousand individuals. Moreover, the identification occurs in a particularly noisy environment, with vocal but not visual or olfactory cues (Jouventin 1982). In the genus *Aptenodytes*, the difficulty is enhanced because there is no nest, the parents carrying the single egg or chick on their feet. Therefore, they have few, if any, landmarks to help in finding their partner and they constitute good models for the study of acoustic recognition.

The king penguin, *Aptenodytes patagonicus*, breeds in dense colonies numbering from a few hundred to 300 000 pairs, on the flat shorelines of subantarctic islands. This large bird, 0.9 m in height and 12 kg in body weight, incubates the single egg on its feet. When the chick hatches, it continues to be brooded by one of the parents until large enough to be left alone in the colony. At this stage of the breeding cycle, both parents are out at sea foraging up to 500 km away (Jouventin *et al.* 1994). The first detailed field study (Stonehouse 1960) demonstrated fidelity between mates and between parents and their chick during the breeding season. Jouventin (1982) analysed the display calls of different individuals and conducted experiments on individual recognition in natural conditions between adults. Robisson (1992) demonstrated that frequency parameters

were important for signal recognition in pairs. Parent–offspring recognition nevertheless remained poorly studied in this species, although the identification of parents by the chick has obvious survival value.

During the brooding period, which extends over nearly six months, chicks are pushed out of the area in which they hatched. In addition, there is continuous movement of adults incubating their eggs as a succession of new breeders arrive. Huddles or small groups of chicks appear in feeding areas on the edges of the breeding grounds and the parent has to locate its chick among several hundreds of other chicks (Barrat 1976). The adult, coming from the sea to feed its chick, makes its way to the area of the colony where the chick is usually located (the rendezvous site) and, walking, calls at regular intervals. The chick in the flock calls in reply, running towards its parent to beg for food (Stonehouse 1960; Jouventin 1982). Therefore the parental call has to be distinguished from among the calls of other parents and chicks, and from the display calls of mating pairs. This recognition process is made more difficult not only by these extraneous noises, but also by propagation problems due to the distance between parent and chick and to the mass screen of birds, which together impose a particularly difficult problem of acoustic communication in an extreme colonial environment. In physical terms, as the acoustic signals propagate, they are degraded to some extent by blurring of amplitude and frequency parameters induced by selective frequency-filtering reverberation and atmospheric turbulence and by attenuation produced by absorption, geometric attenuation and multiple scattering (Willey & Richards 1982; Michelsen & Larsen 1983). Consequently, the degree of degradation of the signal increases with the distance of propagation. In addition, the number of

bodies that the signal must cross also increases when the distance from emitter to receiver increases. The screening effect of the bodies, often neglected or underestimated in studies dealing with colonial seabirds, would presumably enhance degradation.

To study how the parent is recognized by its chick in natural conditions, i.e. in a high level of ambient noise, we have quantified some of the problems that the chick must deal with. First, we described the main characteristics of the call that the adults make when returning to the colony to feed the chick, which we term the parent call. Second, we measured the ambient noise of the colony in the feeding area. Third, we studied the propagation of adult calls in the feeding area to analyse the degradation of the signal at different distances, quantifying the effect of the mass body screen by comparison with propagation in an open area. Then, we conducted experiments with chicks to determine mean and maximal distances of detection of the parental call. Finally, we tested the ability of chicks to discriminate parental calls in a 'jamming' situation, i.e. among extraneous adult calls.

In humans, this phenomenon has been analysed and called the 'cocktail-party' effect (Cherry 1966). In animals, several authors have suggested its occurrence (Busnel 1977; Wiley & Richards 1982). Using the model of king penguins breeding in noisy colonies without nests, we have been able to investigate this process of acoustic recognition against a background noise.

2. MATERIALS AND METHODS

(a) *Subjects and study area*

The field study was conducted in the southern Indian Ocean, at Possession Island, Crozet archipelago (46°25′ S, 51°45′ E) from 11 December 1995 to 16 January 1996, in a 10 ha colony (1 ha $= 10^4$ m^2) containing about 40 000 pairs of adult king penguins and about 1500 chicks (equivalent to 1.6 birds m^2). By the size, the number and the density of birds, the studied colony is quite representative of other colonies existing in subantarctic islands. Tested chicks were banded on a flipper for identification.

(b) *Electroacoustic material*

Adult king penguins were recorded using an omnidirectional Sennheiser MD211 microphone mounted on a perch (2.5 m) and connected to a Sony TCD10 Pro II DAT recorder (sampling frequency $= 44.6$ kHz, frequency response flat within the range 20–20 000 Hz ± 1 dB).

For measurements of sound pressure level (SPL in dB), we used a Bruël & Kjaer Sound Level Meter type 2235 (linear scale, slow setting) equipped with a microphone type 4176.

To broadcast signals, we used a 4200 Uher tape-recorder (19 cm s^{-1}) connected to a 50 W Audix PH3 self-powered loudspeaker (frequency response 100–5600 Hz ± 2 dB). For propagation tests, the experimental signals were re-recorded by means of an omnidirectional Revox JB 10 microphone connected to a Nagra IV tape-recorder (frequency range 30–20 000 Hz $\pm$ 1 dB).

(c) *Sound synthesis and analysis*

Analogue signals were digitized through a 16-bit Oros Au21 acquisition card (with an anti-aliasing filter of 120 dB per octave) at a sampling frequency of 16 kHz. They were stored on the hard disk of a PC microcomputer and then examined and modified with the Syntana analytical package (Aubin 1994).

(d) *Experimental procedures*

(i) *Adult parental call analysis*

To measure the amplitude at which a parental call was produced, SPL measures (one reading per call) were taken during the calls of 11 birds. The beak-to-microphone distance was 1 m. Recordings of parental calls were analysed with the Syntana package, in order to reveal their main characteristics (spectral composition, temporal patterning of amplitude and frequency parameters).

(ii) *Ambient noise measurements*

To determine the mean level of the ambient noise of the colony, 20 SPL readings were taken at intervals of 15 s in a representative area of the colony: a feeding zone in the centre of the colony. The sound level meter was at a height of 0.9 m (i.e. the height of a penguin head).

The ambient noise was also recorded in the same place, for a period of 4 min. The record was then examined with the analytical package to determine the spectral composition of the ambient noise and the duration of periods of silence. To analyse the spectral composition over 4 min, 937 successive fast Fourier transforms (FFTs; window size $= 4096$ data points, $\Delta f = 4$ Hz) were calculated and averaged. The proportion of the energy (in per cent) in different frequency bands was analysed by means of the Welch calculation. The duration of silences was measured on the amplitude function (envelope) of the 4-min period. This function, expressed in dB, was calculated by means of the Hilbert transform (Mbu-Nyamsi *et al.* 1994). Each period with a level more than 30 dB below the mean level of the ambient noise calculated previously was considered as a period of silence.

All measurements and recordings were taken between 11.00 and 12.00 during calm weather, with a wind speed less than 10 km h^{-1}, a relative humidity of 83%, and a temperature of 6–8 °C.

(iii) *Tests on propagation of parental call*

To estimate the maximum distance at which a parental call can be differentiated from the background noise, a parental call was broadcast repetitively through the colony of penguins, in the centre of the feeding area. These experiments were done at same time of day as the measurements of ambient noise. A loudspeaker and microphone were mounted on a tripod at a height of 0.9 m (i.e. the height of a king penguin head) and were positioned at distances of 1 m (reference), 7 m and 14 m. These relative positions of speaker and microphone were chosen to simulate some typical acoustic adult–chick search situations inside the feeding area of a colony (Jouventin 1982). To quantify the screening effect of the bodies of birds, the recordings were compared with propagation records made at the same microphone and loudspeaker height and the same distances, but without any penguins present. The SPL of the broadcast signals was *ca.* 95 dB at 1 m from the loudspeaker. The series of recorded calls was then examined in the amplitude-versus-frequency and the amplitude-versus-time domains. Only recorded calls with no overlapping foreign calls were retained for the analysis ($n = 10$ in each case).

For the spectrum analysis, we calculated an FFT (window size $= 512$ data points, $\Delta f = 31$ Hz) at the middle of the first syllable (see vertical line on spectrogram of figure 1*a*) for each selected call of the series. The spectral content of this part of the

syllable had been judged to be representative of the spectral content of a penguin call. To minimize the influence of accidental and non-representative events occurring in the environment, spectra corresponding to each situation of propagation were averaged. Each average spectrum was compared with the other by Pearson product–moment correlation.

We used an envelope calculation for the analysis of the amplitude function of the whole call. The envelope was then digitally filtered using FFTs (window size = 4096 data points, overlapping 50%, bandpass = 0–20 Hz) as we wanted to focus only on the main amplitude modulations of the call. As for spectral analysis, and for the same reason, envelopes of selected files of the series were averaged. Pearson correlations were used to compare each average envelope (63 600 data points) with the other. To measure the attenuation of amplitude during propagation, we compared the amplitude values of the signals recorded at 7 m and 14 m with the corresponding amplitude value of a reference signal (here the recording at 1 m) for each point of the envelope curves. The calculation was done using the formula $20 \log A_p/A_0$, where A_p represents the amplitude value of the propagated signal and A_0 the amplitude value of the reference signal (Lienard 1978). Thus, we obtained a curve of the instantaneous attenuation in dB of the call for two distances of propagation: 6 m (7 m − 1 m) and 13 m (14 m − 1 m). Without reference to the recording taken at 1 m, the degree of attenuation of the signal at a given distance would be underestimated, as both the signal and the background noise contributed to the result.

(iv) *Tests of detection of the parental call by the chick*

Parental calls were recorded opportunistically from adults on their return to the colony. Each bird was then followed until it achieved a rendezvous with its chick several minutes and calls later. The chicks were tested with the experimental signals two or three days later, during the absence of their parents. Each signal tested was repeated twice at an interval of 5 s. The SPL of the broadcast signals was *ca.* 95 dB at 1 m from the loudspeaker.

Birds responses to experimental signals

In natural conditions, the recognition process of the parental call was determined by an obvious behavioural change in the chick's attitude: it turned its head in the direction of the signal source, called in reply, and then approached (often running) directly towards the loudspeaker. The other chicks in the vicinity, resting or preening themselves, did not react to the extraneous call (i.e. no change of behaviour was observed). The intensity of response of tested chicks to playback signals was evaluated by a five-point scale ranked as follows: class 0 (none) = no reaction; class 1 (weak) = head turned; class 2 (medium) = calls after the second broadcast; class 3 (strong) = calls after the first broadcast; class 4 (very strong) = calls after the first broadcast, approaches in the direction of the loudspeaker and stops in the vicinity (less than 2 m). This behavioural scale is similar to those used in previous studies dealing with the king penguin (see Jouventin 1982; Robisson 1990).

Test of detection in relation to distance

Two identical parental display calls, separated by an interval of 5 s, were broadcast to the corresponding chick at different distances, in a feeding area with a normal density of birds between the chick and the loudspeaker. The loudspeaker was mounted on a tripod at a height of 0.9 m. The experiment

started at a distance from the chick to the loudspeaker of 20 m. The series of two signals was played back and the behaviour of the chick observed. Then, the chick-to-loudspeaker distance was reduced by 1 m by moving the loudspeaker closer. During the manipulation of the loudspeaker, some birds situated between the chick and the source moved away. To give the birds time to return to the vicinity of the loudspeaker, a pause of 6 min was observed. Then, the series was played back again, approaching by steps of 1 m, until a detection process was observed (response from class 1 to class 4). The test with this chick was then definitively stopped. Thirty chicks situated in the centre of the colony were tested. For each distance tested, we noted the number of birds between the chick and the loudspeaker. A problem with a playback design where presentation occurs at successively closer distances to the chick until it responds is that there is a possibility of progressive sensitization to the stimulus; a playback design with randomized distances for each test could therefore appear more suitable. However, a randomized presentation was not suited to the actual field conditions. The problem of the randomized presentation was that, once the process of recognition occurred, the chick tried to localize the parent and moved continuously in the colony. So the experiment with that particular chick would have to be paused and the remaining distances of recognition would have needed to be tested with the same chick on another day, when environmental circumstances and the chick's motivational state may be different.

Tests of detection in relation to jamming

To estimate the minimal discrimination threshold of the parental call in a jamming situation, a series of mixed signals was broadcast to the chick. Six adult calls were superimposed (mixed) using a simple amplitude addition. One corresponded to the parental call (PC) that was known to the chick to be tested, whereas the other five were extraneous adult calls (ECs). This jamming mimics a situation frequently observed in a feeding zone. The five ECs had the same average acoustic level and the duration of each of them was always greater than the duration of each PC tested. The superimposition results in a mixed signal with a total lack of silences. In addition, the spectral characteristics of the EC chosen were very close to those of the PC tested (the difference not exceeding *ca.* 15 Hz for the fundamental frequencies). The strong frequency modulations of syllables generate, after addition, numerous overlapping of frequencies. In these conditions, it can be considered that the PC is almost entirely masked by the EC both in temporal and frequency domains.

To measure the threshold of detection of the PC by the chick, we tested signals with different PC/EC intensity level ratios. These ratios were defined as $E = 20 \log(A_{PC}/A_{EC})$, where E represents the emergence level of the PC in dB, A_{EC} the absolute amplitude of the mixed EC and A_{PC} the absolute amplitude of the PC.

Fifteen chicks were tested with each of five E values: −9, −6, −3, 0 and +3 dB. For the same reasons as previously for distances, the emergence levels were not presented in a randomized order but in an increasing one, with a pause of 5 min between successive values. The distance between the loudspeaker and the bird was *ca.* 7 m.

3. RESULTS

(a) *Parental calls*

The measurements of the SPL of parental calls recorded at 1 m give a mean value ± s.d. of 95.4 ± 0.4 dB

(*a*)

syllables

1 s

(*b*)

wind + flipper flaps
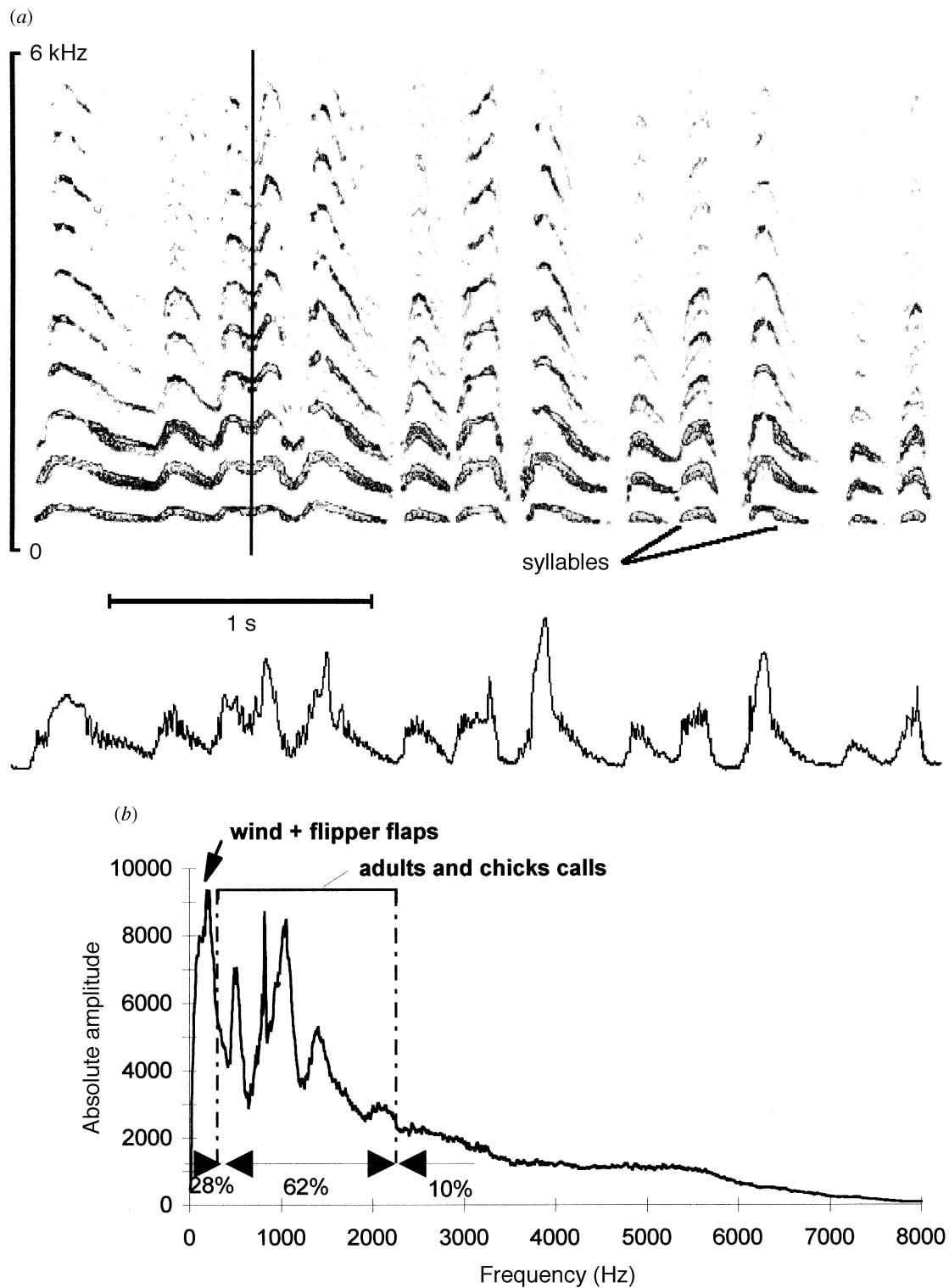
adults and chicks calls

28% 62% 10%

Figure 1. (*a*) Spectrogram and envelope of a parental call of an adult king penguin. (*b*) Spectra of a 4-min recording of the background noise of the colony (average of 937 FFTs, window size = 4096 data points, $\Delta f = 4$ Hz, Hamming window). Values expressed in percentages represent distribution of energy.

($n=11$). The call is composed of a series of sound components separated by pronounced amplitude declines that coincide with falls in frequency (figure 1*a*). The sound's components between two frequency and amplitude minima have been termed 'syllables' by Jouventin (1982) and Robisson (1992). The call duration varied from 3 to 6 s (mean 4.45 ± 1.16 s, $n=66$) and the first syllable is generally the longest. The spectral composition of a syllable is characterized by two frequency bands (two-voices phenomenon) with their respective harmonics. For each harmonic series, most of the energy is concentrated between 500 and 2500 Hz, for the fundamental (fo) and the three first overtones, with a maximum level corresponding most often to the harmonic 2fo.

(b) *Ambient noise*

The average value of the SPL of the ambient noise measured at a distance of 2 m from the edge of the colony was 74.1 ± 3.4 dB ($n = 20$).

The analysis of silences during the 4-min record gives the following results: 57 silences were noted, with a minimum duration of 0.03 s, a maximum duration of 3.60 s and a mean duration of 0.64 s (s.d. = 0.69). The sum of periods of silences during the 4-min recording period was 36.46 s, i.e. only 15% of the period of observation.

The ambient noise has a broad spectrum ranging from 100–150 Hz to 5000–6000 Hz, with distinct main peaks (figure 1*b*). Above 6000 Hz, the noise of the colony is at least 30 dB less than the main peaks and can be considered as negligible. The wind (weak during the experimentation) and, in particular, the sound of flipper flaps generate a marked peak at 200 Hz. The other main peaks ranging from 500 to 1800 Hz correspond to the frequencies of different adult calls. The least marked and highest-pitched peak (2200 Hz) corresponds mainly to the frequency of the chicks' calls (Jouventin 1982).

(c) *Parental call propagation*

In 'open-field' conditions, i.e. no birds between the microphone and the loudspeaker, frequency peaks corresponding to the parental call attenuate as the distance increases, and peaks that are the result of non-biologically significant signals (wind, flipper flaps) keep the same levels (figure 2). When there are birds between the emitter and receiver, frequencies above 1000 Hz are more severely attenuated, compared with the previous situation. This is particularly so at a distance of 14 m, when attenuation of the peaks of the parental call is so strong that these peaks tend to disappear into the background noise of the colony. With birds between the emitter and the receiver, the background noise may approach or surpass in amplitude the signal at a relatively short distance. Thus, correlation between the recorded signal at 1 m and other propagated signals decreases as distance and obstacles due to bird bodies increase (table 1).

If we consider now the amplitude function (envelope) of the whole call, modification of the propagated signal, compared with the recording at 1 m, is weak only for the signal recorded at 7 m, in an open field condition (table 1). Modifications are stronger for the signal recorded at the same distance but with birds between the emitter and the receiver. It is the same for both the recordings taken at 14 m. For the recording at 14 m with birds, modification is so high that correlation with the recording at 1 m is almost zero. At this distance, with bodies as obstacles, attenuation of the call is so high that the amplitude gaps that separate syllables tend to disappear. On figure 3, it appears that attenuation is regularly increasing as the distance and the number of intervening bodies increase. If we consider the mean attenuation of the calls recorded at 7 and 14 m compared with the call recorded at 1 m, we obtain 15.6 ± 4.9 dB for a propagation of 6 m, and 23.3 ± 6.7 dB for a propagation of 13 m. Both these results concern measures made without penguins between the emitter and the receiver. When penguins are present, mean attenuation is distinctly higher, being 17.1 ± 5.8 dB for a distance of 6 m (with five penguins

directly in the speaker–microphone axis) and 26.2 ± 7.1 dB for a distance of 13 m (with 14 intervening bodies).

(d) *Detection of the parental call by the chick, in relation to distance*

Our experiments reveal that the chicks detect, recognize and localize the parental call without ambiguity (response class 4) at a relatively short distance (about 11 m, with a mean number of ten intervening birds) (table 2). However, head orientation towards the loudspeaker (response class 1) is observed at a greater distance (about 14 m, with a maximum observed at 18 m, and with a mean number of 15 intervening birds).

(e) *Detection of the parental call by the chick in regard to jamming*

Our experiments indicate that the chick detects its parental call in an extreme jamming situation (table 3). The recognition process still occurs with an emergence level of the parental call (compared with the extraneous calls) of -6 dB, i.e. well below the level of the noise (here derived from five mixed calls). This proves that chicks are able to recognize their parents in spite of a strong temporal and frequential masking effect. This process fails to operate only with an emergence level of -9 dB. The value of -6 dB corresponds to a propagation of 7 m and the performance should be less at a greater distance.

4. DISCUSSION

The distance at which a signal is detectable is linked to the emergence of the signal. Detectability can be examined from the point of view of both amplitude and frequency.

(a) *Detectability of the parental call in relation to amplitude emergence*

The display call is emitted by the adult with an SPL of 95 dB, a relatively high but not exceptional value, as similar SPLs are mentioned for some oscine (Dabelsteen 1981; Seibt & Wickler 1977) and non-oscine birds (Robisson 1991). As SPL diminishes with distance according to the inverse square law (6 dB per doubling of distance), the calculated SPL of the parental call at 1 km would be 35 dB, still loud enough to be heard, but not in the noisy environment of a penguin colony. The call is produced and transmitted in a colonial context involving the background noise and propagation among bodies, both reducing the broadcast distance.

The mean background noise level measured is 74 dB. This is very close to the 70 dB measured by Robisson (1991) in a colony of emperor penguins, *Aptenodytes forsteri*. Assuming that the adult call of the king penguin is emitted with an amplitude of 95 dB, the emergence level of the adult call would be $95 - 74 = 21$ dB. If we consider that the distance of detectability of a signal corresponds to the distance from the source over which the amplitude of the signal is equal to the amplitude of the background noise (signal-to-noise ratio = 1), the maximum range of transmission of the call, deduced from the inverse square law, would be about 11 m. In our propagation tests done in open field conditions, the measured attenuations fit well with the amplitude decrease that would be expected
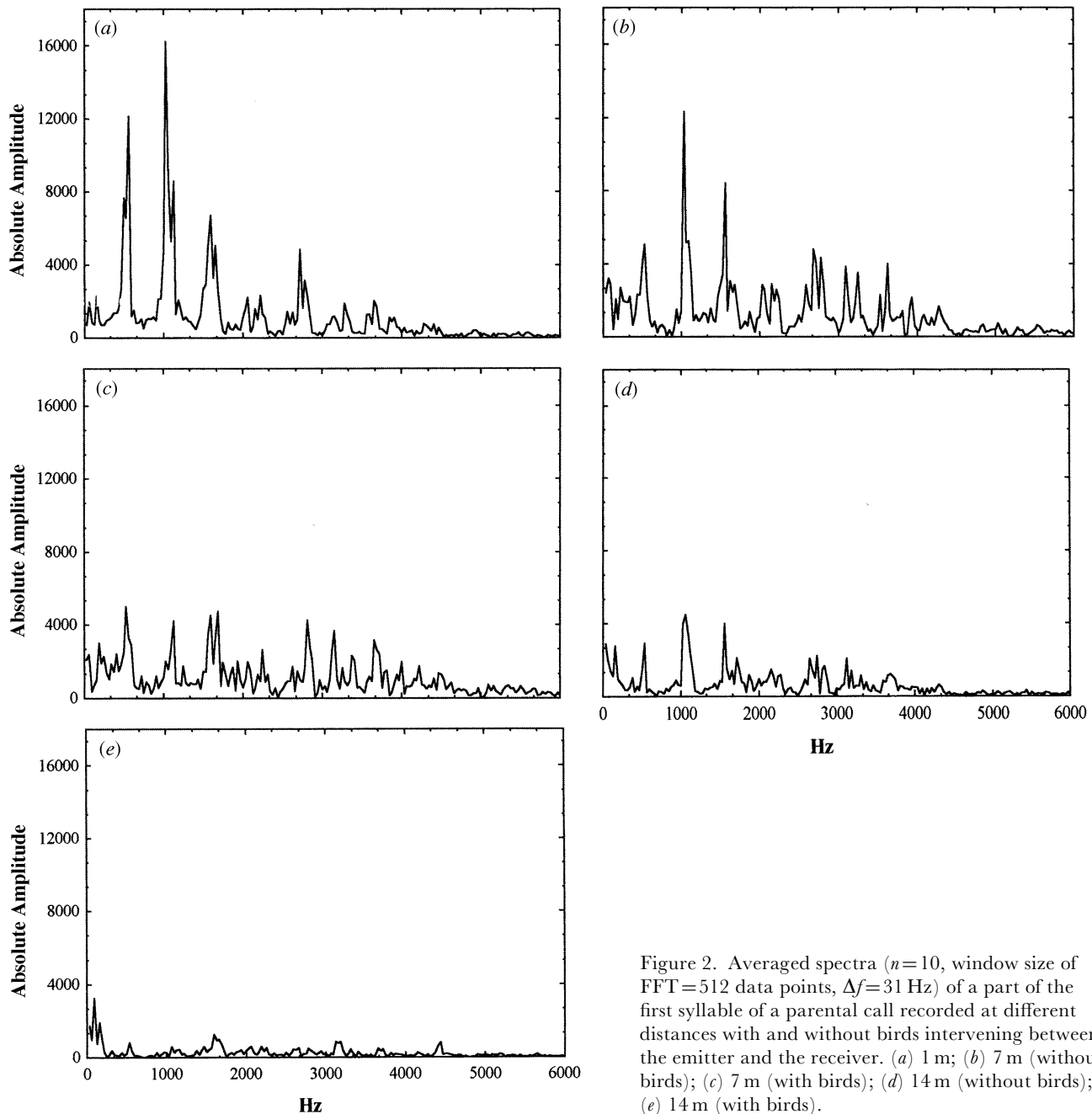
Figure 2. Averaged spectra ($n=10$, window size of FFT$=512$ data points, $\Delta f=31$ Hz) of a part of the first syllable of a parental call recorded at different distances with and without birds intervening between the emitter and the receiver. (*a*) 1 m; (*b*) 7 m (without birds); (*c*) 7 m (with birds); (*d*) 14 m (without birds); (*e*) 14 m (with birds).

according to the inverse square law, which describes the case of spherical spreading. Thus we found an attenuation of 15.6 dB for a propagation of 6 m, and 23.3 dB for a propagation of 13 m, close to the expected (calculated) values of 15.6 and 22.3 dB, respectively. When measurements were performed with penguins between the emitter and the receiver, there is an excess attenuation (EA) of 1.5 dB at a distance of 6 m, and 3 dB at a distance of 13 m. EA occurs because porous volumes, such as penguin bodies, absorb sounds (Wiley & Richards 1978; Dabelsteen 1981). The greater the distance, and the greater the number of bodies crossed, the more the SPL decreases (for example, in this case: 1.5 dB for five birds at 6 m; 3 dB for 14 birds at 13 m). With EA, the maximum expected range of transmission of an adult call should not exceed 8–9 m in a feeding area, which is a particularly short distance. On the other hand, our tests with birds prove that chicks recognize their parent's call at a greater

distance (mean distance 14.43 m for a class 1 response and 10.58 m for a class 4 response). One possible explanation is that chicks are able to detect the parent's call even if the signal-to-noise ratio is less than 1. The second experiment with chicks confirms this fact, as the process of recognition occurs even if the level of the parent call is 6 dB below the level of the background noise (here the mixed calls of five adults).

Thus, with the king penguin species, the distance of recognition of the parent call by the chick is greater than the distance at which the signal cannot be differentiated in amplitude from the background noise.

(b) *Detectability of the parental call in relation to frequency emergence*

The parental call is a complex sound based on harmonics series from 400 Hz to over 5000 Hz, with 80% of the energy being concentrated in a frequency band of

Table 1. *Pearson product–moment correlation for averaged spectra* (*n*=10, *FFT*=512 data points) *and averaged envelopes* (*n*=10, 63 600 data points) *of the parental call recorded at different distances, with and without other birds intervening between the emitter and the receiver*

(Significance levels: [***], $p < 0.001$; [**], $p < 0.01$; [*], $p < 0.05$.)

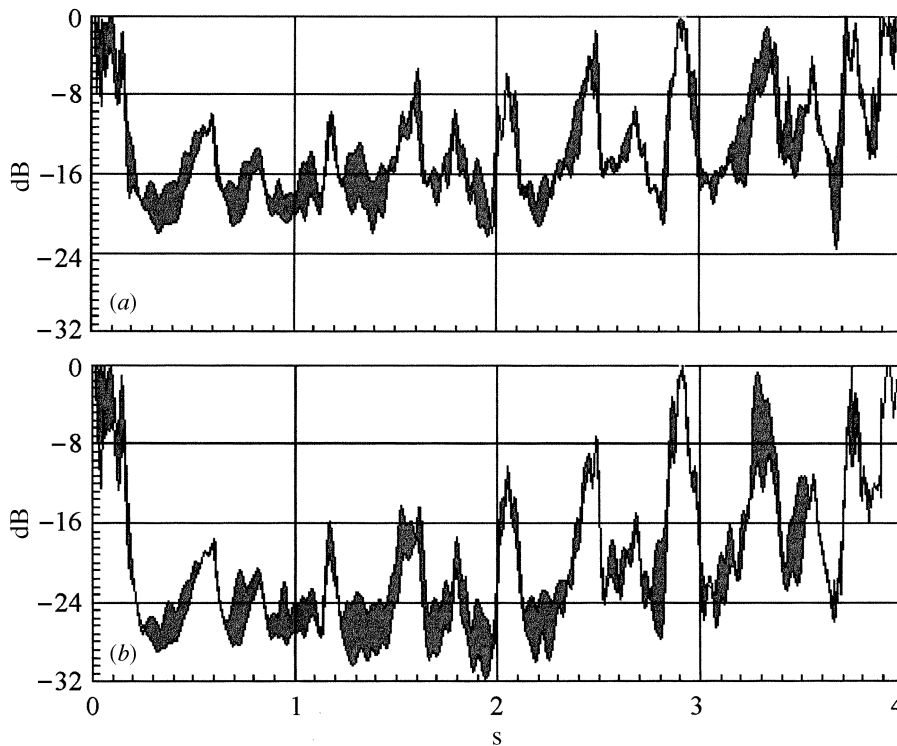| variables (intervening birds)	1 m	7 m (absent)	14 m (absent)	7 m (present)	14 m (present)
averaged spectra					
1 m	1.00	0.72[***]	0.64[***]	0.47[***]	0.27[*]
7 m (absent)	—	1.00	0.75[***]	0.44[***]	0.37[***]
14 m (absent)	—	—	1.00	0.55[***]	0.53[***]
7 m (present)	—	—	—	1.00	0.42[***]
14 m (present)	—	—	—	—	1.00
averaged envelopes					
1 m	1.00	0.77[***]	0.28[**]	0.54[***]	0.05[*]
7 m (absent)	—	1.00	0.20[**]	0.37[***]	0.05[*]
14 m (absent)	—	—	1.00	0.23[**]	0.09[*]
7 m (present)	—	—	—	1.00	0.26[**]
14 m (present)	—	—	—	—	1.00

Figure 3. Instantaneous attenuation functions of propagated calls compared with the recorded call (reference) at 1 m. (*a*) Attenuation at 6 m, without (above) and with (below) birds; (*b*) attenuation at 13 m, without (above) and with (below) birds. Grey area represents the difference (in dB) between the curves.

400–2000 Hz (Robisson 1992). During propagation at short distance (less than 15 m) in an open field, the intensity level of each peak is lowered, but the relative levels of each peak are maintained. Effectively, at a short distance and at a height of 1 m, ground and atmospheric absorption effects are insufficient to attenuate low and high frequencies; thus, frequencies outside the 1–3 kHz frequency band, termed the 'sound or acoustic window' (Morton 1975; Martin 1981; Willey & Richards 1982), are also preserved. So, when the call propagates in an open field, at a height of 1 m on a smooth ground surface over a short range, the overall shape of the spectrum is maintained. Spectra of signals at 1, 7 and 14 m are strongly correlated. This is not the case when bodies of penguins intervene, as some of the most energetic peaks (including that at 1000 Hz) are more severely attenuated than others. The shape of the spectrum is strongly modified compared with the recording taken at 1 m, whereas at 14 m, the peaks tend to disappear in the background noise. All our spectral analyses correspond to quiet periods, i.e. with birds in the immediate vicinity remaining silent. Presumably, in more normal situations this tendency will be stronger. Effectively, the spectral analysis shows that the ambient noise consists of the sum of biological and non-biological noises that do not overlap in frequency. The only noises that cover the same frequency band as that of an adult call, and which would thus theoretically lead to a masking effect (Scharf 1970),

Table 2. *Tests of detection of the parental call by the chick with respect to distance and number of bird bodies crossed*

intensity of responses	distance (m) of detection mean ±pm: s.d. (min–max)	number of intervening penguins mean±s.d.	tested chicks *n*
1	14.43±2.94 (9–18)	14.57±3.20	7
2	13.71±1.98 (10–17)	13.14±2.79	7
3	12.75±2.06 (10–15)	13.75±3.86	4
4	10.58±2.11 (8–16)	10.17±2.90	12

Table 3. *Tests of detection of the parent call by the chick with respect to a jamming situation (parental call masked by five extraneous calls)*

(Values correspond to the number of birds responding for each intensity class of responses and each emergence level. There is a significant difference between the five emergence situations of the series. This difference is mainly due (44.16%) to the signal at -9 dB, which was either unrecognized or poorly recognized by the chicks.)

intensity of responses (n=15)	-9 dB	-6 dB	-3 dB	0 dB	$+3$ dB
0	11	2	0	0	0
1	2	3	1	0	0
2	2	3	0	1	0
3	0	5	11	3	2
4	0	2	3	11	13
percentage contribution to χ^2	44.16	9.46	18.72	10.22	17.44

Kruskal–Wallis test $H=51.01$, d.f.$=4$, $p<0.001$

are the calls produced by other adults. In a feeding zone, the emission rate of these calls is high and periods of silence are infrequent. For a bird singing or hearing, only 15% of the time can be used and pauses are short (mean duration 20 ms) and unpredictable. Penguins, and particularly the king penguin, are large animals able to call loudly, an ability that is probably useful in overcoming the sound of the sea and of the wind, but which cannot prevail against the calls of their equally loud neighbours. In these conditions the masking effect is important, from a temporal and a frequency point of view, and it increases the difficulty for the chick of extracting the information provided by its parent's call, even at a relatively short distance. Nevertheless, the chick does succeed, as shown by the jamming experiment. Direct tests of the chick with the parental call, in the presence of masking by five other calls, showed that the penguin chicks have an exceptional capacity to discriminate the correct call from extraneous calls.

(c) *Cocktail-party effect*

In numerous studies, detectability of a signal refers to the maximum distance from the emitter at which its signal can be differentiated from the background noise. This was termed propagation distance by Morton (1975,

1986), active space by Marten & Marler (1977) and Brenowitz (1982), and effective range by Heuwickel (1990). A signal may be detectable but not discriminable. In most studies concerning propagation of animal sounds, it is stated that the discrimination (or communication) range is less than the detection range (Brenowitz 1982; Wiley & Richards 1982; Gerhardt & Klump 1988; Dabelsteen *et al.* 1993). With the king penguin chick, the opposite situation applies because discrimination is possible even when the signal of interest is apparently obscured by the background noise. Some results of behavioural studies in the laboratory suggest that a signal-to-noise ratio of -4 to -5 dB may be sufficient for birds to detect signals (Dooling & Searcy 1981; Hienz & Sachs 1987). These values are similar to those found in our study, but they were obtained in laboratory conditions using operant conditioning techniques, and thus the motivational state of the birds is not the same. In addition, pure tones were masked with continuous broadband noise. In these conditions, the acoustic properties of the masker and those of the signal are different, and therefore the extraction of the information must be facilitated. In addition, in our experimental procedure the mixed calls are emitted from a common source. This mode of emission enhances the difficulty for the chick to discriminate the parental call. It is well known that when a signal of interest and masking noises originate from spatially separated sources, birds make use of directional cues to improve the sensitivity to the signal (Dooling 1982).

To our knowledge, only two field studies have studied experimentally how a bird's signal is detected amid background noise in a natural environment. Brenowitz (1982), studying the red-winged blackbird, *Agelaius phoeniceus*, added a broadband noise to the playback of a natural song. The bird did not respond when the signal-to-noise ratio was 0 dB, but recognition was achieved at a signal-to-noise ratio of 3 dB. Brémond (1978, unpublished data), studying the wren *Troglodytes troglodytes*, added either a wide-band noise or the songs of heterospecific birds to the territorial song of the wren. Recognition occurred in more than 75% of cases when the signal-to-noise ratio was 0 dB. Again, these findings concern signals masked by sounds with different spectral and temporal characteristics.

Communication is fully hampered by an ambient noise when the signal and the noise have similar amplitude, temporal and spectral properties. Our results demonstrate that the noise in the colony has a high SPL, that it is almost continuous and that several birds occupy the spectrum at a time. The overlap in these conditions would appear to be strong temporally and in terms of frequency and of amplitude. There is an almost total masking effect, increasing the difficulty the chick has in detecting its parent. Nevertheless, the chick can compensate for this masking effect as it is able to detect an information-carrying signal whose intensity is below that of a background noise with similar temporal and spectral characteristics.

Faced with the problem of finding its parents in a seabird colony among several thousand congeners, the adult call is inadequate to ensure the communication alone. Identification of the parent call is not only a passive problem of sound attenuation during propagation,

but also an active problem of parasitic noises. With the king penguin chick, we have observed a twin strategy particularly adapted to increase the efficiency of the communication. The ability of the chick to perform parent identification in such a constraining environment results not only in its capacity to reduce the distance of communication within a rendezvous site, but also in its exceptional sensorial capacity to discriminate in spite of the masking effect of the colonial life. This process of perception against a background noise (i.e. the 'cocktail-party effect') is presumably linked to an acoustic communication system that is closely adapted to these behavioural and environmental constraints.

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