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Acoustic communication in a king penguin colony: importance of bird location within the colony and of the body position of the listener

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Abstract This study focuses on the propagation of the display call used for individual recognition between penguin partners. Transmission of acoustic information in a noisy environment such as a king penguin colony is very difficult. Conditions of propagation were examined for two areas of the colony (hatching and courtship areas) and reception at three heights from the ground (10, 45 and 90 cm). Signal modification was assessed in terms of attenuation of signal, amplitude modulation and spectral content. The acoustic recognition of the mate, which is decisive for breeding success, took place in the hatching area where signal degradation was less great for all parameters studied. When the receiver was located 10 cm above the ground, degradation of the signal was much more pronounced than when it was located 45 or 90 cm above ground. The characteristic incubating attitude of the king penguin (i.e. standing with the head at 45 cm above the ground) enables it to receive the main part of the signal in spite of the noisy environment.

Introduction

The progressive degradation of acoustic signals during atmospheric propagation from sender to receiver was examined extensively about 20 years ago (Morton 1975; Marten et al. 1977; Wiley and Richards 1978) and has more recently received attention in the context of colonial seabirds (Aubin and Jouventin 1998). Transmission of sounds in natural habitats differs markedly from that expected in homogeneous non-scattering media. Numerous studies have revealed characteristics of propagation in different habitats: forests with different types of foliage, fields with different densities of plants, pasture consisting of tall grasses or marsh where water forms a reflective surface (Aylor 1971; Morton 1975; Marten and Marler 1977; Brenowitz 1982; Cosens and Falls 1984; Waas 1988; Mathevon et al. 1996; Naguib 1996). In these different habitats, the signal can be extensively modified more or less by various processes such as atmospheric absorption or scattering effects. These modifications can impair or even prevent communication between individuals. Communication can also be disturbed by background noise, which is often generated by conspecifics. This constraining situation, observed in crowded nesting colonies of seabirds, has to date been studied in a few situations (Robisson 1991). Colonial living results in a continuous background noise of calls with similar temporal and spectral properties. Moreover, after propagation in such environments, key signal parameters such as spectral composition, amplitude and frequency modulations may be strongly modified.

The king penguin (*Aptenodytes patagonicus*) breeds without a nest, carrying the egg on the feet, in large colonies of thousands of birds on the shores of subantarctic islands. Incubating and rearing are undertaken alternately by the two members of a pair (Weimerskirch et al. 1992). At the changeover, when a parent returns from foraging, it searches for its mate among hundreds of other birds of the attachment zone (Barrat 1976). The returning bird calls several times at different distances, with a call termed the display call (Derenne et al. 1979; Jouventin 1982; Robisson 1990). After hearing the response of its mate, the returning bird searches for it. Once together, the two birds proceed to exchange the egg or the young chick. Thus, the final step of the re-

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search of the mate, in the attachment zone, depends in the first instance on the display call of the mate (Derenne et al. 1979; Jouventin et al., in press). This display call must be distinguished among the calls of all the other birds. Individual acoustic recognition is made more difficult, not only by the jamming effect of other calls, but also by propagation problems arising from the male-female distance and by the massive screen of birds, which together impose a particularly difficult problem for the transmission of information.

Fundamental to understanding the communication system of this species and the constraints upon it is the knowledge of the broadcast distances in different natural emitter-receiver situations. Ignoring moulting birds which stay near the river and always remain silent, the colony studied comprised two main areas where the density of birds differ: the hatching area (HA) and the courtship area (CA) (Barrat 1976). Another natural experimental situation occurs during the vocal recognition between mates: the head of the receiving (incubating) bird could be at different heights from the ground. Among these situations, the screening effects of the bodies, the signal to noise ratio and the ground effect could differ and could consequently induce differences in how the call is propagated.

The aim of this study was to investigate the broadcast distance for the different conditions of propagation in the colony by analysing song degradation in terms of attenuation of the call, and changes in amplitude modulation and spectral composition. In a first test we studied the importance of the two areas of the colony with respect to communication. In a second test we studied the importance of three positions of the receiver on signal reception.

Materials and methods

Location

The recordings and experiments were carried out at La Baie du Marin, Possession Island, Crozet Archipelago (46°25′S, 51°45′E) during December 1995, the beginning of the 1996 breeding season for the king penguin. Because of the desynchronized breeding cycle, different stages of birds can be observed in the same colony during this period: non-breeders, immature birds, adults moulting, mating or laying and also moulting chicks. The colony numbered about 40,000 pairs of breeding birds (Guinet, C. unpublished data).

Characteristics of the king penguin call

The display call used for individual recognition consists of a series of harmonically related frequency bands (Fig. 1). Most of the energy is concentrated between 450 and 2500 Hz (Robisson 1992a). The call corresponds to a series of sound components separated by strong amplitude declines which have been termed syllables by Jouventin (1982) and Robisson (1992b). The SPL (Sound Pressure Level) of the display call measured 1 m in front of the beak of the bird is about 90–95 dB (Robisson 1993a).

Playback and analysis

For sound pressure level measurements (SPL in decibels, defined as 20 log (P/P_0) where P is the measured sound pressure and P_0 the reference level of 2×10^{-5} N/m^2), we used a Bruel and Kjäer Sound Level Meter type 2235 (linear scale, slow setting). Recorded display calls were broadcast with a Uher 4000c tape recorder (19 cm/s) connected to a Nagra-Kudelski self-powered amplifier (7 W) and an Audax loudspeaker. The frequency response variability of the loudspeaker was less than ±4 dB in the range 1–9 kHz. The signal was played back at a level equivalent to that uttered in natural conditions. Propagated signals were recorded with a Nagra III B tape recorder (19 cm/s) and a Beyer Dynamic M 69 microphone (±2 dB for frequency range 150–15,000 Hz). Recorded tapes were digitized with a 16 bit Oros Au21 acquisition card equipped with an anti-aliasing filter (low pass filter, fc = 6.4 kHz; −120 dB/octave) at 16 kHz sampling rate. Records were examined in time and frequency domains using analytic software written in our laboratory (Aubin 1994).

Ambient noise measurements

We measured the mean level of the ambient noise in the two areas of the colony, HA and CA. The sound level meter was at a height of 1 m, and at a distance of 2 m from the edge of the two areas. Instantaneous measures of the SPL were taken at 15-s intervals for 5 min (N = 20 measures). For each area, we computed mean and SEM of the SPL values. To compare levels of the ambient noise, we used a non-parametric test (Mann-Whitney U test).

Experimental conditions

Broadcast experiments

For these experiments, we chose a representative call of king penguin. The frequency and temporal values of this call corresponded to the mean values measured in previous studies for this species (Jouventin 1982; Robisson 1992b). The king penguin call propagated was repeated five times at intervals of 5 s. The propagation distances, i.e. the distances between the loudspeaker and the microphone, chosen on the basis of previous observations of Robisson (1993b), were the same in both experiments: 1 m (reference signal), 7 m (average distance between two birds when the incoming one started the acoustic search of the partner) and 14 m (maximum distance of recognition observed). Experiments were conducted between 1400 and 1700 hours under clear, dry weather conditions, with a wind speed of less than 3 m/s.

Test 1 (effect of the two areas of the colony). The first studied area was the HA. We found here adults with an egg. The density of birds was on average 2.2 pairs/m^2 (personal observation 2.1–2.3 pairs/m^2, and Barrat 1976, 2.2 pairs/m^2). The second area studied was the CA where there were chicks of the previous year, juveniles and adults searching for a partner for mating. In this area, the density of birds averaged 4 birds/m^2 (personal observation). In both areas, playback experiments were conducted with loudspeaker and microphone placed at 90 cm above the ground.

Test 2 (effect of the height of receiver). The position of the calling bird was always the same: it raised its beak slowly to a vertical position, stretched its neck to its fullest extent and gave vent to the call (Jouventin 1982). By contrast, the receiver (the incubating bird) could take different positions, rising to its feet or crouching in the characteristic incubating attitude with back bowed and head lowered between the shoulders. Finally, during hot weather, birds could be observed lying on the ground. For these three positions, height of the ear was 90, 45 and 10 cm respectively. To imitate the

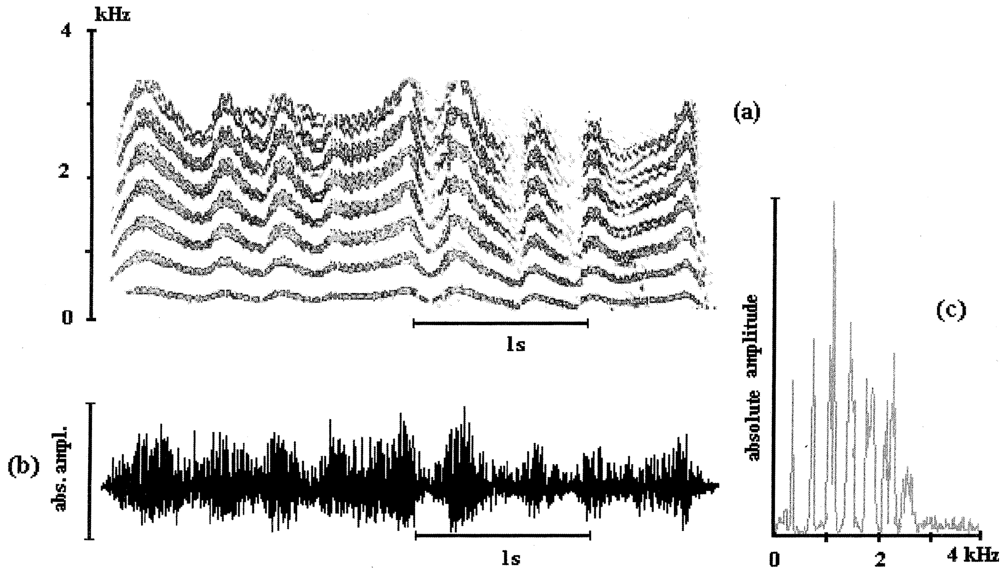

Fig. 1 King penguin call. Spectrogram (**a**), oscillogram (**b**) and spectrum analysis (**c**)

natural positions of the emitter and of the receiver, the loudspeaker was placed at 90 cm above the ground and the microphone recording the signal broadcast at 90, 45 and 10 cm respectively. As the incubating attitude (ear at 45 cm) was not observed in the CA, experiments on the effect of the height of receiver were conducted only in the HA.

Analysis of the broadcast signal

In both tests, we analysed the attenuation of call, the amplitude modulation and the spectral content of propagated signals.

Attenuation of call. The aim was to measure amplitude attenuation during propagation. The amplitude envelope of each propagated call was calculated using the analytic signal calculation described by Mbu Nyamsi et al. (1994). Each envelope (N = 24,628 points) was digitally filtered using a short-term overlapping (50%) fast Fourier transform (FFT) (window size 2048, bandpass 0–50 Hz) so as to conserve only the slow amplitude modulation of the call. The call attenuation for each situation was defined as:

$$CA = 20\log(As/Ais)$$

with CA = attenuation in decibels, As = amplitude value of the propagated call, and Ais = amplitude value of the reference signal. We compared the amplitude values of the signals recorded at 7 m and 14 m to the corresponding amplitude value of the reference signal recorded at 1 m. Thus for each situation of propagation (two areas, three heights), we obtained an attenuation in decibels of the call for two distances of propagation: 6 m (7–1 m) and 13 m (14–1 m). This method allows us to compensate for the contribution of background noise to the amplitude values. To compare attenuation of the calls we used a non-parametric test (Mann-Whitney U test). When the same marginal distribution was used for several comparisons, the Bonferroni-corrected P values were calculated to assess the final significance of the test.

Amplitude modulation. The aim was to compare the amplitude modulation of the signal before and after propagation through the colony. To minimize the influence of accidental events occurring in the environment, the five envelopes corresponding to each test condition and distance of propagation were averaged. To assess the degree of similarity, a Bravais-Pearson correlation coefficient between each of the 38,448 points of the averaged envelope of the propagated signal and corresponding points of the control signal was computed.

Spectral content. The aim was to analyse the modification of the spectral content of the call during propagation. We computed an FFT (window size 512, Δf = 31 Hz) in the middle of the fourth syllable, the part of the call considered representative of the spectral content of the whole signal (see Fig. 1). To minimize the influence of accidental events occurring in the environment, the five spectra of the five propagated calls corresponding to each test situation were averaged. A Bravais-Pearson correlation coefficient was then computed for each frequency point between the averaged experimental spectrum of the call and that of the control signal.

Table 1 Attenuation of the call for different situations of propagation (mean ± SE). Effects of area and height of reception

		Attenuation after 6 m propagation (dB)	Attenuation after 13 m propagation (dB)
Effect of area	Courtship	19.4 ± 0.89	26.4 ± 1.58
	Hatching	17.4 ± 0.69	27.3 ± 1.69
Effect of height (cm)	10	21.3 ± 0.49	32.7 ± 1.47
	45	19 ± 1.05	27.7 ± 1.83
	90	17.4 ± 0.41	26.9 ± 0.58

Results

Propagation in the two areas of the colony

Ambient noise measurements

The ambient noise in the colony was found to differ between the two areas. We obtained a mean ±SE of 69.25 ± 0.27 dB SPL in the HA and 74.1 ± 0.76 dB in the CA. The levels of ambient noise measured in the two areas were statistically different ($P < 0.001$).

Attenuation of the call

Results are presented in Table 1. The call attenuation showed a significant increase as the distance of propagation increased from 6 to 13 m (7 dB in the CA, 9.9 dB in the HA; $P < 0.01$ for the effect of distance propagation in the two areas).

Attenuation obtained after 6 m propagation differed by 2 dB between the HA and the CA and there was 1 dB of difference after 13 m propagation but these differences between the two areas were not significant.

Modification of amplitude modulation

In the two areas, the correlations between the 38,448 points of averaged envelopes of propagated calls and corresponding points of the envelope of the reference signal were found to be significant after 6 m of propagation (CA, $r = 0.54$, $P < 0.01$; HA, $r = 0.65$, $P < 0.01$). A strong decrease of the correlation was observed for 13 m of propagation; only the correlation obtained in the HA was found significant (CA, $r = 0.01$, NS; HA, $r = 0.21$, $P < 0.01$). The relative decrease in the correlation of the amplitude modulation between 6 and 13 m was stronger in the CA than in the HA.

Modification of the spectral content of the propagated calls

Correlation of averaged spectrum between the propagated signals and the reference signal showed a decrease as the distance of propagation increased (CA, $r = 0.42$, $P < 0.01$ after 6 m and $r = 0.11$, NS, after 13 m of propagation; HA, $r = 0.60$, $P < 0.01$ and $r = 0.28$, $P < 0.01$ respectively). Correlations obtained in the HA were greater than those obtained in the CA. Except for 13 m of propagation in the CA, all the correlations were found significant at $P < 0.01$. The original spectral contents of the call are represented in Fig. 1; Fig. 2a emphasizes the modifications of the spectral content during propagation. For the 7 m propagation, the main frequency peaks of the signal remain in both areas. The attenuation was weaker in the HA than in the CA. For the 14 m propagation in the CA, the spectral content of the signal was strongly modified and disappeared in the noise. The propagation in the HA was more favourable, particularly for the fundamental frequency and the first two harmonics.

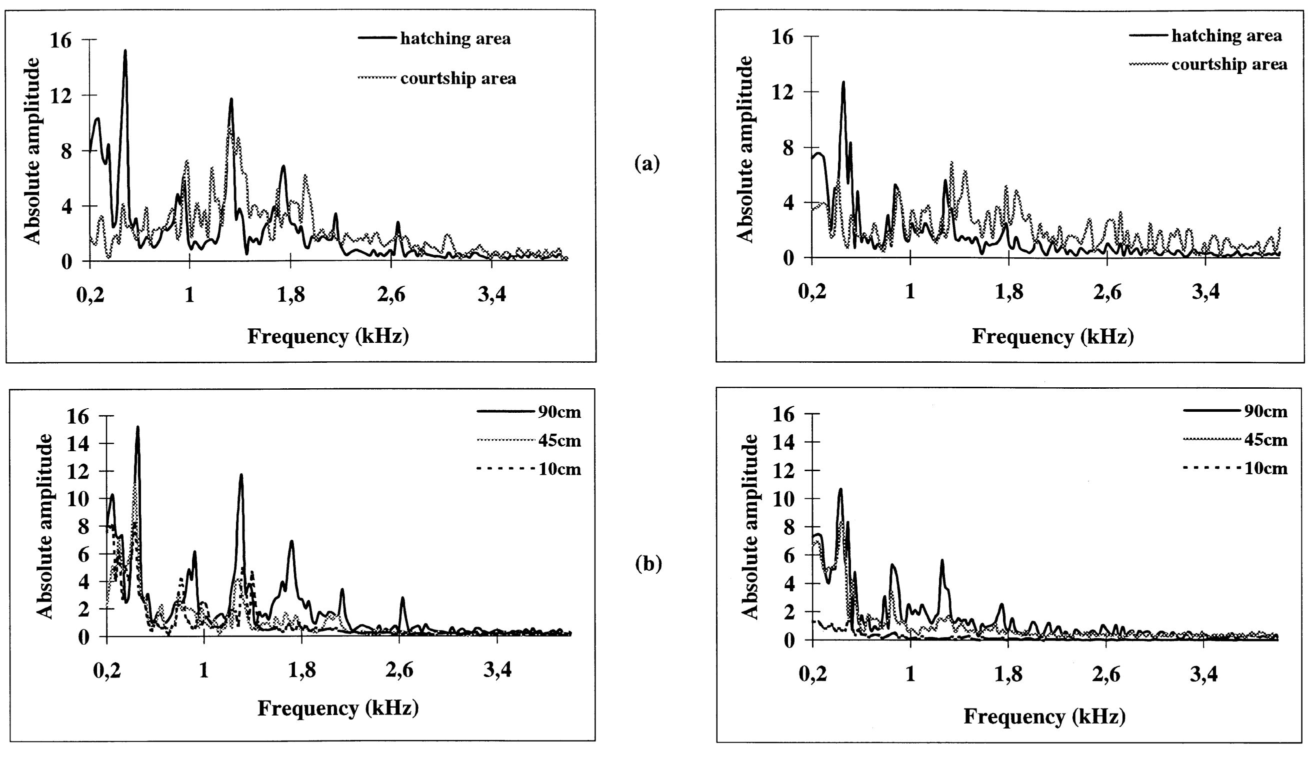

Fig. 2 Alteration of spectral contents after 7 m of propagation (*two figures on the left*) or 14 m of propagation (*two figures on the right*). **a** Effect of area of colony. **b** Effect of height of reception

Propagation at different heights from the ground

Attenuation of the call

Results are presented in Table 1. The attenuation of calls showed a significant increase as the distance of propagation increased from 6 to 13 m (11.4 dB, 8.7 dB and 9.4 dB for the heights above the ground, respectively, of 10, 45 and 90 cm; $P < 0.01$ for the three heights). The greatest differences were obtained between the situations 10 and 90 cm above the ground (3.9 dB for the 6 m propagation, $P < 0.01$ and 5.8 dB for 13 m propagation, $P < 0.05$). The situation at 45 cm above the ground was close to the 90 cm situation (no significant differences for these two heights for 6 m, as well as 13 m, propagation).

Modification of the amplitude modulation (Table 2)

Compared to the 1-m signal, the modification of the averaged amplitude envelope of propagated signals was extensive. Whether the distance of propagation was 6 or 13 m, the 10-cm and 45-cm recording situations show very weak, almost zero, correlations with the reference signal. In contrast, for the 90-cm situation, the correlation was still significant after 6 and 13 m propagation. Nevertheless, after 14 m propagation, the correlation had dropped considerably.

Modification of the spectral content of the propagated calls

Spectral correlations between the averaged spectrum of the signal recorded at 1 m and propagated signals were all significant. Correlations decreased as the distance of propagation increased from 6 to 13 m. The correlations were particularly weak for the recording situations near the ground (Table 2). The original spectral contents of the call were represented in Fig. 1, and Fig. 2b emphasizes the modifications of the spectral content of the propagated call. For the 7-m propagation, at 10 and 45 cm above the ground, peaks of the signal corresponding to low frequencies (< 1500 Hz) still appeared, whereas high frequencies were largely attenuated. In contrast, at 90-cm height, the spectral content of the signal was conserved. For the 14-m propagation, the signal received at 10 cm above the ground was totally degraded. At 45 cm above the ground, only the fundamental and the first harmonic frequencies emerged from the background noise. Compared to the 90-cm situation, all frequencies above 1000 Hz were strongly attenuated.

Discussion

Communication in the two areas of the colony

The three measures of degradation of the signal used in our study (attenuation of call, amplitude modulation and spectral content) showed strong degradation with increasing broadcast distance in both areas. However, there are clearly differences between the courtship area and the hatching area in the extent to which calls are degraded and these reflect differences in the prevalent patterns of social behaviour in the two areas.

During propagation, attenuation of the signal seems to be greater in the CA than in the HA, even if the difference was not significant. This can be explained by a higher density of penguins in the CA (twofold birds/m^2 in the CA). The screening effect of penguin bodies causes absorption and multiple scattering effects and, with the greater density of penguins in the CA, the screening effect is enhanced. Associated with an increase in the background noise level (+4.85 dB), it causes a reduction of the signal to noise ratio here. The alteration of the amplitude envelope was so high in the CA that the amplitude gaps that separate syllables tended to disappear after 14 m of propagation (weak correlations between envelopes of propagated calls and reference signal). Thus, concerning the amplitude parameters, communication appears more difficult in the CA than in the HA. From the frequency point of view, propagation was more constrained in the CA than in the HA. In both areas, the main frequency peaks of the signal were still present after 7 m of propagation. But, after 14 m of propagation in the HA, most of the peaks disappear and

Table 2 Pearson product-moment correlation (*r*) for averaged envelopes and averaged spectrum. Envelopes and spectrum of control and propagated signals were compared for different heights and distances of propagation

Distances of propagation (m)	Heights (cm)	Correlation for averaged envelopes	Correlation for averaged spectra
7	10	0.06	0.34**
	45	0.08	0.44**
	90	0.58**	0.55**
14	10	0.006	0.16*
	45	0.04	0.27**
	90	0.15**	0.32**

*$P < 0.05$;**$P < 0.01$

all of them were found embedded in the background noise in the CA. Vocal communication does not have the same importance in the two areas. Acoustic recognition is a decisive process for the breeding success of seabirds (Brooke 1978; Guillotin and Jouventin 1980). The incoming bird arriving from the sea has to find its mate in the hatching area after a few calls. If it does not succeed, the incoming bird returns to the sea, and the pair fails to reproduce. As the detection and the discrimination of the display call appear easier in this area (less degradation of the signal during propagation), less time might be required for location of a particular individual in the crowded community (incubating bird moves during incubation). This allows birds to limit the time they spend inside the colony and so, to limit the high aggressiveness and the vigorous territorial defence of the breeders (2500 pecks given per individual per 24 h, Le Maho et al. 1993). By contrast, communication in the CA is between solitary birds searching for a future mate. In this area, calls serve to announce the arrival of a bird ready for breeding and are, in fact, addressed to the whole colony. The detection of the display call is more difficult in the CA. But king penguins do repeat the information, i.e., the call is emitted many times during the few days or weeks before mating (Stonehouse 1960). Contrary to what happens in the HA, birds are not aggressive within the CA. Even if the CA is the more constraining part of the colony for acoustic communication, there are more opportunities to establish communication between prospective mates. Moreover, it seems to be easier for a bird coming back to land to breed to find a suitable mate in the CA among several hundred birds than to find its own partner in the HA.

Communication at different heights

Near the ground, the amplitude modulation of the signal was strongly modified. The call emitted at 95 dB (Aubin and Jouventin 1998) showed strong attenuation (32.7 dB). In addition, the level of background noise (69–74 dB) makes the detection of the signal very difficult even if birds can detect the display call when its intensity is well below that of the ambient noise (Aubin and Jouventin 1998). The 90- and 45-cm heights, being less attenuated, appear to be the best heights for communication. From the frequency point of view, while the spectral content was already modified after 7 m at 10 and 45 cm above the ground, the strongest differences were observed at 14 m. At this distance, frequencies in the call are attenuated to such an extent at 10 cm above the ground that the whole spectral content disappears in the background noise. However, low frequency peaks were conserved at 45- and 90-cm height (with more modifications at 45 than at 90 cm). At ground level, frequencies are strongly attenuated by the ground effect (Marten and Marler 1977; Marten et al. 1977). This effect could explain some of the attenuation observed for the 10-cm situation. The multiple scattering effects and the frequency-dependent absorption due to bodies of penguins may also induce important differences. Thus, communication at 10 cm above the ground was more constraining than at 90-cm height.

The chance of hearing the call of the mate as it arrives from the sea is low for a bird that is lying on the ground but in the HA, where birds of a pair have to communicate for nest relief, this position was seldom observed. However, in the CA, some birds were observed lying on the ground, especially during warm summer days. Birds in this position are generally found to be sleeping, so the acoustic communication would seem to be of no importance to them. The characteristic incubating attitude of king penguins, standing up, head at 45 cm high and with the egg on the feet, enables them to receive the main part of the signal in spite of the noisy environment. The 45-cm situation can be considered as intermediate for the reception of information in a colonial context. It should be noted that penguins adhere to a synchronized exchange of partners: the bird on the nest does not have to be alert all the time. The 90-cm situation was the most favourable. At the beginning of the change-over, when the incubating bird hears the call of its mate for the first time, it leaves its incubating attitude, rises to its feet and assumes what we have demonstrated to be the best position for signal reception.

Communication in a seabird colony

Communication in a seabird colony appears poorly adapted to transmission of individual information over a long range (Falls 1982). In order to be effective for the king penguin, communication involving the individual recognition of mates is performed at short or moderate ranges. In spite of the extreme environment of the colony, the king penguin must send a precise message of individuality. In previous studies, it has been demonstrated that coding/decoding processes are often based on those sound features that best survive transmission losses across natural habitats (Brémond and Aubin 1990). Thus, broadcast distance can be analysed according to the relevant characteristics of the signal that are not degraded by the environment. Amplitude modulation is used for individual recognition in the emperor penguin (Jouventin 1972), but this parameter shows rapid degradation in king penguin colonies and thus would probably not serve to identify an individual of the latter species over large distances. The same could be said for the degradation of higher frequencies in the king penguin spectrum. Other parameters, such as the low frequency modulation observed in the king penguin's syllables, however, may better serve as individual acoustic features (Jouventin et al., in press). Indeed, low frequency modulation, only slightly degraded during propagation, seems to ensure accurate transmission of information (Wiley and Richards 1978). We have shown that the attenuation of the call is great after 14 m of propagation. By decreasing the signal to noise ratio, this phenomenon increases the difficulty for the receiver of extracting relevant information from the emitter's call. It should be noted, however, that some specific perceptual processes of signal detection and recognition enable the receiver to detect a signal embedded in noise (Brémond 1978; Brenowitz 1982; Brémond and Kreutzer 1986, Jouventin et al., in press). The ability of an adult to find its partner may relate not only to its body position and location in the colony but also to the use of a communication system adapted to this noisy environment. The next step will be an experimental assessment of the acoustic search of the mate in the colony.

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