Acoustic convergence between two nocturnal burrowing seabirds: experiments with a penguin *Eudyptula minor* and a shearwater *Puffinus tenuirostris*

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The evolution of acoustic signals is influenced by environmental constraints. We studied two sympatric but unrelated seabirds: the Little Penguin *Eudyptula minor* and Short-tailed Shearwater *Puffinus tenuirostris*, to examine the degree to which similarities in their ecology had led to convergence in their calls. Both species nest in burrows in Southern Australia and, at night, are highly vocal and territorial. First, we analysed the physical characteristics of the territorial call. Secondly, we studied the transmission of calls through burrows and varying distances through vegetation. Thirdly, we used playback experiments of natural signals to demonstrate that the response disappears between 4–8 m, and of modified signals to understand the coding–decoding process linked to the territorial function of the call. The structure of the territorial calls of the two species clearly differs, but both species produce a succession of gaps in amplitude and frequency, and a high degree of redundancy. Our experiments show that, to decode the territorial message, birds pay attention only to parameters that are less degraded during propagation and ignore fine details of structure that are quickly degraded, even at relatively short distances (< 8 m). In both species, territorial information is mainly conveyed by the rhythmic succession of two sounds (syllables or subsyllables), birds paying attention to the FM structure of these successive sounds but not to the AM. This convergent coding is adaptive in that it reduces the possibility that the meaning may be distorted by interference from noise and acoustic screening.

The physical characteristics of animal sounds and the situations in which they are used are subject to natural selection and reflect the ecological relationships of the species. We might therefore expect sounds used socially to be optimized according to the selection pressures acting on the caller at the time the sound is produced. Interest has recently grown in how the evolution of acoustic signals has been influenced by environmental constraints (Wiley & Richards 1982). Marler (1955) first pointed out the structural convergence between the signals of different species. Chappuis (1971) and Morton (1975) proposed correlation models between acoustic signals and acoustic properties of habitats, after finding that bird species of tropical forests used lower-pitched songs with narrower frequency ranges than their open-country counterparts. The physical structure of signals is linked to their biological function (Marler 1957, 1959). Some signals, such as territorial or mate attraction songs and distress calls, have presumably evolved under selection pressures to maximize transmission distances (Marten & Marler 1977, Marten et al. 1977, Wiley & Richards 1978, 1982, Brenowitz 1982, Brémont & Aubin 1989).

We studied the calls of two seabirds belonging to different orders but both breeding in burrows and using vocalizations to communicate at night. The fact that these birds are nocturnal and live in burrows (a constraining environment for sound) means that this is a good model for the study of a possible convergence in the acoustic communication systems of two species which are phylogenetically distant.

The Little Penguin *Eudyptula minor* and the Short-tailed Shearwater *Puffinus tenuirostris* both breed on the shore in Southern Australia. They are similarly sized (less than 1 kg for the penguin, the smallest of its family, and 650 g for the shearwater according to

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Marchant & Higgins 1990) and have similar habits. During the day, they fish at sea and come ashore just after dusk, to relieve their mate or to feed the chick, staying at the nest over night. During the austral summer, these two species breed and compete for the same burrows under grasses, bushes or trees (burrows being 60–80 cm long for the penguin and usually more for the shearwater). At times they share a complex burrow with a common entrance, or the same burrow may have an alternating pattern of residence from one year to another (Stahel & Gales 1987). Both species are strongly territorial and colonial. In Penguin colonies, nests are often separated by several metres whereas Shearwater nests are typically only 1 m apart. Rookeries of both species are extremely noisy at night and completely silent by day, with brooding birds sleeping in burrows when mates are fishing. Both species are more vocal and active at night.

For both species, aggressive interactions between owners and intruders are common around the nest. These interactions consist mainly of a vocal exchange between an individual within a burrow and another near the entrance. For both species, the acoustic response consists of a sequence of, on average, 10–12 calls. In this study, we only focus on the territorial function of the calls, well known in penguins (Jouventin 1982) and in petrels (Warham 1988). The other functions of these complex calls, which advertise both sex and identity, are outside the scope of this study (see Aubin & Jouventin 1998 and Jouventin et al. 1999 for the acoustic system of individual recognition in penguins; Jouventin 1982 and Waas 1991 for the Little Penguin; Brooke 1978 for the Manx Shearwater Puffinus puffinus; James & Robertson 1985, Brooke 1986 and Bretagnolle 1996 for the petrel family).

These two unrelated species live in the same environment and share many habits. Do divergences or convergences exist in the physical features and codes of these calls, constrained by the same physical and biological pressures? To address this question, we first analyse the physical characteristics of the territorial calls of the two species. Second we study their modification during propagation at a distance within the coastal environment, and thirdly we investigate the coding–decoding processes of these territorial calls, using playback experiments.

**METHODS**

**Study area and data collection**

Research was conducted from December to January during the 1996/97 penguin and shearwater breeding season at the Penguin Reserve on Phillip Island, Australia (38°31' S, 145°08' E). All work was conducted between 22:00 and 01:00 h when both species were judged to be at the peak of their social activity on the breeding colony.

As shearwater calls (and responses induced) differ between sexes (Brooke 1978), the calls of 43 male Little Penguins (hereafter Penguins) and 34 male Short-tailed Shearwaters (hereafter Shearwaters), sexed using bill measurements, were recorded opportunistically near the burrow entrance, with a microphone mounted on a 2.5-m pole, about 50 cm in front of the calling birds. Playback tests were carried out on different males in their nesting burrows.

**Recording and playback material**

Calls were recorded using an omnidirectional Sennheiser MD211N microphone (frequency response: 150–15 000 Hz ± 2 dB) connected to a Sony TCD10 Pro II digital audiotape recorder (sampling frequency: 48 kHz; frequency response flat within the range 20–20 000 Hz). For playback experiments, the tape recorder was connected to a PSP-2 E.A.A. pre-amplifier and a 20-W self-powered amplifier built in the laboratory, equipped with an Audax loudspeaker (frequency response 100–5600 Hz ± 2 dB).

**Sonographic methods**

Signals were digitized through a 16-bit SoundBlaster AWE 32 acquisition card at a sampling frequency of 11 025 Hz for the Penguin and 22 050 Hz for the Shearwater. They were subsequently examined with the Syntana analytic package (Aubin 1994).

Acoustic characteristics of calls were measured in the time domain on envelopes and in the frequency domain on fast Fourier transform (FFT) spectra (window size: 4096 for the Penguin and 8192 for the Shearwater; Δf = 2.7 Hz). Energy distribution was calculated on spectra, using Welch’s method (Oppenheim & Schafer 1989).

**Acoustic features of the call**

Acoustic features of 321 calls from 26 male Penguins (mean number of calls analysed per individual: 12.3 ± 4.6 sd calls) and of 125 calls from 16 Shearwaters (mean per individual: 7.8 ± 2.4 calls) were analysed.

For Penguin calls we measured: (1) in the temporal domain, the durations (in s) of the exhalant (EX)
syllable (Te) and inhalant (IN) syllable (Ti); (2) in the frequency domain, the frequencies (Hz) of maximum amplitude in the EX syllable (Fmaxe) and IN syllable (Fmaxi). We also measured the frequency bandwidth within which 80% of the energy of the EX syllable was concentrated (F80%).

For the Shearwater, we analysed: (1) in the temporal domain, the durations (calculated from envelope analysis) of the EX syllable (Te), subsyllable a (Ta), subsyllable b (Tb) and the IN syllable (Ti); (2) in the frequency domain, the values of frequencies of maximum amplitude in subsyllables a and b (Fmaxa, Fmaxb) and the frequency bandwidth within which 80% of the energy of the EX syllable was concentrated (F80%). Coefficients of variation for mean values of each acoustic feature were calculated for each individual (mean CV). An inter-individual coefficient of variation (CVi) was calculated using mean characteristics of the calls from each of the individuals analysed. CVi and CV were calculated from the formula: CV = 100 × (1 + 1/4 n) × sd/x (Sherrr 1984). Ratios (CVi/mean CV) were calculated for both species. One-way ANOVA was also used to compare the significance of the between- and within-individual variation (Miller 1978, Sokal & Rohlf 1981).

Propagation tests
To assess the modification of signals during propagation through the natural habitat, calls of both species were broadcast and recorded at different distances. Propagation tests were conducted during clear and dry weather, with a wind speed less than 10 m/s. To simulate natural situations, the microphone was fixed 15-20 cm above the ground (approximately head height for a bird) either inside (30 cm) the burrow or outside at the entrance. Located among bushes, thinly grassed and gentle slopes, burrows are about one metre long and 20 cm wide, but broader at the entrance. The loudspeaker was positioned 15-20 cm above the ground, at different distances: 1 (reference), 2, 4 and 8 m. For each species, we broadcast a representative call, i.e. a signal whose frequency and temporal values follow the mean values previously measured for each species (see Figs 1 & 2 and Table 1). Two series (one for each species) of ten identical calls repeated were broadcast. Thus, the sounds of the test tape were recorded under a 4 × 2 × 2 factorial design, i.e. four distances, two microphone positions and two call types. The test tape was then examined in the amplitude versus frequency domain using Syntana software.

To analyse the spectral composition of the signals, successive overlapping (50%) FFTs (window size: 4096 for the Penguin and 8192 for the Shearwater; Δf = 2.7 Hz) were calculated for both species, and in each situation of propagation. The number of successive overlapping FFTs was calculated so as to cover the entire Penguin call and the EX syllable of the Shearwater in the time domain. Successive FFTs were averaged, providing a mean spectrum of the signals studied. Finally, to minimize the influence of accidental and unrepresentative events occurring in the environment, the ten averaged spectra corresponding to the ten identical calls repeated for each situation of propagation were themselves averaged.

Playback experiments
Series of natural and modified signals were played back to Penguins (P series) and to Shearwaters (S series) and two kinds of experiments were conducted.

The first was to test the effect of emitter-receiver distance on intensity of territorial response. A natural territorial call was broadcast to the corresponding species at different distances from the burrow. The birds tested (seven Penguins and five Shearwaters) were inside the burrow. As for the propagation experiments, the distances chosen were 1, 2, 4 and 8 m. Each bird was then tested with four distances, with the order of presentation of the signal at different distances randomized between birds. Calls were played at a natural sound pressure level (SPL). The SPL was on average 90.2 ± 1.9 dB for the Penguins and 85.4 ± 2.2 dB for the Shearwaters, measured at 1 m from the loudspeaker with a Bruel and Kjaer Sound Level Meter type 2235 (linear scale, slow setting) equipped with a 1-inch condenser microphone type 4176.

The second was to study the main acoustic features conveying territorial information. We played back series of modified signals to Penguins (P series) and Shearwaters (S series). Signals were played back 1 m outside the burrow entrance, at the same SPL as above with the tested birds inside their burrows. Each bird was tested with a sequence of modified signals associated with a sequence of natural (control) signals. A sequence consisted of 12 successive signals separated by a 1 s of silence. Such a temporal presentation follows the mean values encountered for both species during natural territorial interactions (see also responses to control signals in Table 1). The paired sequences of signals (modified–natural) were separated by 1 min of silence. After a 15-min pause, a new paired sequence of signals was played back. The 15-min pause
was designed to allow birds to recover their natural activity. The presentation of paired signals (both natural and modified) was randomized. To prevent habituation, no bird experienced more than one playback session (two paired sequences) per night. In addition, no playback sessions were played to a particular adult more than twice, and never on consecutive nights. In our experiments, on average, per individual, 2.4 paired sequences were tested for the Penguin and 3.2 paired sequences for the Shearwater.

**Natural calls**

Natural calls of a species were played back either to the same species (as a control signal CS) or to the other species (as an extraneous signal ES). In a preliminary experiment, each bird was tested with a series of natural calls of its own species (four for the Shearwaters and six for the Penguins). A 15-min pause period was applied between each natural call of the series. The series of natural Shearwater and Penguin calls were played back respectively to ten Shearwaters and ten Penguins. For each species, the responses to the different natural calls were quite similar. On the basis of these results and of the previous call analysis, we selected one representative call for each species. As all the modified signals used in our playback experiments were produced from these two natural calls, a problem of pseudoreplication might occur (McGregor et al. 1992).

Nevertheless, in our playback experiments, the presentation of signals was paired: a natural call (CS) and a reconstructed one. For each reconstruction, the natural call was modified according to only one dimension: a frequency or a temporal parameter. When using a simple dimension as an independent variable, the levels of the variable can be under direct control of the experimenters, and therefore are less likely to be affected by external variables (Hopp & Morton 1998). The use of artificially modified or constructed stimuli allows us to control the differences between our stimuli, minimizing greatly the problem of pseudoreplication (McGregor et al. 1992).

**Frequency modified signals**

Signals were modified either in the frequency domain or in the time domain. The frequency bands of the calls were modified in two ways. First, natural calls were filtered by band-pass digital filters. This was done by applying FFT filtration (window size: 4096 for the Penguin and 8192 for the Shearwater). As reported previously, the frequency band of the Penguin call can be divided into two parts: below and above 2800 Hz.

Thus, we defined the corresponding band-pass signals P1 and P2. Shearwaters use three main frequency bands (below 1700, between 1700 and 4500, above 4500 Hz). Thus corresponding band-pass signals S0, S1, S2 were constructed. Secondly, natural calls were shifted up or down in frequency by applying short-term overlapping (50%) FFT followed by a linear shift (+ or −) of each spectrum and by short-term FFT−1 (Randall & Tech 1987). As previously, the window size was 4096 for the Penguin and 8192 for the Shearwater (ΔF = 2.7 Hz). Values of the linear shifts of the spectra were: +200, +100, −100, −200, −300 Hz. The corresponding signals for both the species were signals P3 and S3 (+300 Hz) to signals P8 and S8 (−300 Hz).

**Temporally modified signals**

Temporal parameters of the calls were modified in two ways. First, they were modified by removing frequency or amplitude modulations (FM and AM). Signals P9 and S9 correspond to a carrier frequency without any FM. The carrier frequency was a harmonic series and the value of the fundamental frequency of the natural call. To this carrier frequency we applied the AM (the envelope) that was extracted from the natural calls, using the Hilbert transform calculation (Brémond & Aubin 1992, Mbu-Nyamsi et al. 1994). Thus, due to the application of the envelope, the temporal succession of syllables of the original call was kept while FM was lacking. Further from this, signals P10 and S10 correspond to signals on which the AM of a natural call was removed without modification of the natural FM and the natural carrier frequency. This was made possible by applying the analytic signal analysis concept (Mbu-Nyamsi et al. 1994).

The result was signals with natural FM but without any AM. Secondly, they were modified by alteration of the temporal succession of syllables. To test if the alteration of IN and EX syllables played a role in recognition, two kinds of signals were constructed: P11 and S11 corresponded to signals with only EX syllables and P12 and S12 to signals with only IN syllables (the corresponding IN or EX ‘complementary’ syllable being removed and replaced by a silence of equivalent duration). Finally, due to the structure of the Shearwater call, two additional tests were made for this species. Signals S13 and S14 corresponded to calls with either only EXa subsyllables respectively or only EXb subsyllables respectively (the corresponding...
EX subsyllables and the IN syllables being removed and replaced by silences of equivalent durations).

**Interpretation of responses**

It is a common observation that Little Penguins and shearwaters, which are highly territorial, respond (vocally) to calls of their own species emitted near their burrow (e.g. Jouventin 1982 for the Little Penguin, Brooke 1978 for the shearwater). To evaluate the intensity of response of tested birds to playback signals, several behavioural responses were observed (approach, call, latency to response, etc.). These often occur at the same time and are correlated but we selected the number of calls emitted (during the playback and during the 1-min period immediately after the playback) as the most objective measure of response for analysis.

For playback experiments with modified signals, a paired analysis was performed by comparing the response to the experimental signal with the response to the control one (natural signal). As data were paired and not normally distributed, we used the sign test with \( \alpha = 0.05 \) (Sherrer 1984).

**RESULTS**

**Temporal and frequency characteristics**

The calls of territorial Penguins and Shearwaters (Figs 1 & 2) are structured with distinct sound sequences repeated, each of them being composed of two successive parts: an inhalant (IN) syllable and an exhalant (EX) one. In the Little Penguin call, the EX syllable corresponds to an harmonic series exhibiting rapid modulation in frequency and amplitude, while the IN syllable corresponds to an harmonic series slowly modulated in frequency and amplitude. The energy is mainly centred on the 300–2000 Hz and the 3000–5000 Hz frequency bands. In the Shearwater call, the EX syllable is composed of two successive subsyllables, the first (EXa) being a harmonic series with some fast frequency sweeps up and down and gaps of amplitude, and the second (EXb) an harmonic series slowly modulated in frequency and amplitude. The IN syllable is noisy and without a particularly well-defined structure of frequency and amplitude modulations. The energy is mainly centred on three frequency bands: 0–1500 Hz, 2000–4500 Hz and 4800–5500 Hz.

Mean acoustic values for temporal and frequency parameters have been calculated for the calls of the two species (Table 1). The within-individual variation was less than that between individuals for all the parameters. This suggests that differences between individuals have a physical basis.

**Propagation through the environment**

Figures 3 and 4 show that higher frequencies tend to disappear as distance increases. This is due mainly to atmospheric absorption and to multiple reflection, diffraction and refraction of sound by vegetation (Wiley & Richards 1982). Lower frequency peaks were

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*Figure 1. Sonagram of the territorial call of a male Little Penguin Eudyptula minor (window size of the FFT 1024; \( \Delta f = 21 \) Hz; spectral resolution: 100 Hz; overlap 80%) and acoustic features taken into account in the analysis. \( T_e \), exhalant syllable; \( T_i \), inhalant syllable; \( F^\text{max} \), maximum amplitude in the exhalant syllable; \( F^\text{max} \), maximum amplitude in the inhalant syllable; \( F_{80}\text{max} \), frequency bandwidth within which 80% of the energy is concentrated.*
higher when calls were recorded inside burrows. This is probably the consequence of a resonance phenomenon linked to the size and the shape of the burrow. In this constraining environment, main peaks clearly diminish after a short distance either inside (2 m) or outside (4 m) the burrows.

**Playback experiments**

Our experiment indicates a significant effect of distance of emitter on vocal response of receiver \((P < 0.01, \text{Friedman two-way ANOVA, df} = 3; \chi^2 = 13.90, n = 7, \text{for the Penguin}; \chi^2 = 11.50, n = 5 \text{for the Shearwater}). The mean number of calls emitted by the birds tested in response to a territorial call emitted at a distance of 4 m was low, particularly for the Penguins, and neither species responded to a conspecific signal emitted at 8 m (Fig. 5).

For acoustic features supporting territorial information, the responses to the second series of playback

![Table 1](image.png)

**Table 1.** Variation of selected temporal and frequency parameters within each individual and between individuals in Little Penguin (analysis of 321 calls from 26 individuals) and Short-tailed Shearwater (analysis of 125 calls from 16 individuals).

<table>
<thead>
<tr>
<th>Variables</th>
<th>Within-individual variation</th>
<th>Between-individual variation</th>
<th>ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Range of means</td>
<td>Mean CV,</td>
<td>Mean ± sd</td>
</tr>
<tr>
<td>Penguin</td>
<td>T, (s)</td>
<td>0.458–1.799</td>
<td>14.622</td>
</tr>
<tr>
<td></td>
<td>T, (s)</td>
<td>0.301–0.745</td>
<td>14.177</td>
</tr>
<tr>
<td></td>
<td>F_a max (Hz)</td>
<td>308–1319</td>
<td>12.950</td>
</tr>
<tr>
<td></td>
<td>F_b max (Hz)</td>
<td>928–1810</td>
<td>11.299</td>
</tr>
<tr>
<td></td>
<td>T_0 (s)</td>
<td>323–940</td>
<td>39.879</td>
</tr>
<tr>
<td>Shearwater</td>
<td>T, (s)</td>
<td>0.577–0.927</td>
<td>14.608</td>
</tr>
<tr>
<td></td>
<td>T, (s)</td>
<td>0.254–0.599</td>
<td>14.257</td>
</tr>
<tr>
<td></td>
<td>T, (s)</td>
<td>0.062–0.132</td>
<td>26.820</td>
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<tr>
<td></td>
<td>T, (s)</td>
<td>0.056–0.106</td>
<td>24.010</td>
</tr>
<tr>
<td></td>
<td>F_max (Hz)</td>
<td>1396–3953</td>
<td>20.018</td>
</tr>
<tr>
<td></td>
<td>F_max (Hz)</td>
<td>373–1499</td>
<td>60.843</td>
</tr>
<tr>
<td></td>
<td>R^0.5 (Hz)</td>
<td>182–2750</td>
<td>59.836</td>
</tr>
</tbody>
</table>

**P < 0.001; *P < 0.01; *P = 0.40.**
experiments are given in Tables 2 and 3.

**Frequency domain**

For filtered signals, significant differences from the control signal (CS) were found only for the high-pass signals (P2 and S2 for the Penguin and Shearwater, respectively). In the frequency shifts series, significant differences between some signals and the CS appear (± 300 Hz, P3 and P8 signals, for Penguins; + 300 Hz, S3 signal, for Shearwaters). Nevertheless, for both species, the other signals of the series elicit responses that do not differ significantly from those observed for the CS.

**Temporal domain**

Signals with a natural AM and without FM (P9 and S9) triggered weak territorial responses. Highly significant
differences were found between these signals and the CS. In contrast, signals with a natural FM and without AM (P10 and S10) triggered stronger territorial responses and did not differ significantly from the CS. For calls whose sequence syllable was manipulated, it appeared that broadcasting of only one syllable (EX or IN) was insufficient to elicit responses in Penguins (P11 and P12 signals). For Shearwaters, birds still responded when only the EX syllable was broadcast (S11 signal): there was no significant difference from the CS. In contrast, there were almost no responses when the IN syllable alone was broadcast (S12). Finally, when only a subsyllable (EX\textsubscript{ex}, signal S13 or EX\textsubscript{ex}, signal S14) was broadcast, the intensity of responses was weak: the differences from the CS were highly significant.

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Acoustic convergence between two burrowing seabirds

As we saw in playback experiments at different distances from the burrow, birds replied only to calls emitted near the entrance or in the immediate vicinity of the burrow. In both species, the coding of the territorial information is simple, highly redundant and consequently adapted to transmit an unambiguous territorial message at a short range in a particularly absorbent environment. To decode the territorial message, birds pay attention only to parameters that are less degraded during propagation and ignore fine details of structure that are quickly degraded, even at relatively short distance (< 8 m).

**DISCUSSION**

**Common environmental constraints**

The clustered vegetation of breeding sites constitutes a constraining environment for the transmission of calls. Sounds attenuate rapidly during transmission, particularly those of higher frequency. After 8 m, spectra of both species are reduced to a narrow frequency band. The feature that appears to be relatively consistent between the two species is the pattern of syllables or subsyllables in successive rhythmic gaps of amplitude and frequency. Such structures are well known to be adapted for transmission at long range (Morton 1975, Wiley & Richards 1982). Nevertheless, when the receiver is in its burrow, attenuation of the signal

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**Table 2. Response of Little Penguin to experimental signals (each signal is compared to a control signal).**

<table>
<thead>
<tr>
<th>Signal</th>
<th>Modification</th>
<th>n</th>
<th>Mean number of calls ± sd</th>
<th>Sign test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Frequency domain</td>
<td>Signal</td>
<td>Control</td>
<td>P value</td>
<td></td>
</tr>
<tr>
<td>P1</td>
<td>BP &lt; 2800 Hz</td>
<td>9</td>
<td>7.00 ± 4.69</td>
<td>10.89 ± 6.51</td>
</tr>
<tr>
<td>P2</td>
<td>BP &gt; 2800 Hz</td>
<td>8</td>
<td>0.25 ± 0.71</td>
<td>8.13 ± 4.39</td>
</tr>
<tr>
<td>P3</td>
<td>Shift + 300</td>
<td>13</td>
<td>4.15 ± 5.44</td>
<td>12.08 ± 5.99</td>
</tr>
<tr>
<td>P4</td>
<td>Shift + 200</td>
<td>15</td>
<td>12.07 ± 6.18</td>
<td>14.00 ± 6.77</td>
</tr>
<tr>
<td>P5</td>
<td>Shift + 100</td>
<td>14</td>
<td>14.93 ± 11.91</td>
<td>13.50 ± 9.44</td>
</tr>
<tr>
<td>P6</td>
<td>Shift - 100</td>
<td>14</td>
<td>16.43 ± 12.09</td>
<td>11.14 ± 5.93</td>
</tr>
<tr>
<td>P7</td>
<td>Shift - 200</td>
<td>13</td>
<td>21.31 ± 20.35</td>
<td>11.92 ± 8.29</td>
</tr>
<tr>
<td>P8</td>
<td>Shift - 300</td>
<td>12</td>
<td>5.67 ± 5.65</td>
<td>14.00 ± 9.65</td>
</tr>
<tr>
<td>Temporal domain</td>
<td>Signal</td>
<td>Control</td>
<td>P value</td>
<td></td>
</tr>
<tr>
<td>P9</td>
<td>Lack of FM</td>
<td>17</td>
<td>5.00 ± 5.02</td>
<td>14.71 ± 6.48</td>
</tr>
<tr>
<td>P10</td>
<td>Lack of AM</td>
<td>15</td>
<td>14.00 ± 5.85</td>
<td>14.13 ± 7.92</td>
</tr>
<tr>
<td>P11</td>
<td>EX syllable</td>
<td>14</td>
<td>5.50 ± 4.52</td>
<td>10.36 ± 5.21</td>
</tr>
<tr>
<td>P12</td>
<td>IN syllable</td>
<td>12</td>
<td>4.17 ± 5.46</td>
<td>11.25 ± 4.14</td>
</tr>
<tr>
<td>Exogenous signal</td>
<td>Signal</td>
<td>Control</td>
<td>P value</td>
<td></td>
</tr>
<tr>
<td>ES</td>
<td>Shearwater call</td>
<td>8</td>
<td>0.88 ± 1.81</td>
<td>10.75 ± 5.12</td>
</tr>
</tbody>
</table>

One-tailed sign test: ns, not significant; **P < 0.01; *P < 0.05.
emitted at 8 m is so high that the whole signal disappears into the background noise, as demonstrated by the playback experiments. Thus, the Penguin and Shearwater calls appear to be able to carry over long distances, but conditions of transmission and reception are often so constraining (through wind, vegetation, burrow conditions) that both species should only expect to establish communication at short range.

### Convergent coding

When we compared the structure of territorial calls between the two species, we found little similarity in call characteristics. The differences are obvious and probably due in part to the anatomy of species. However beyond these structural differences, a basic general similarity appears. The original calls of both species show an alternation of two sounds (that we have termed syllable or subsyllable) with a gap in frequency and amplitude. Is this similarity due to a convergence? This is of course difficult to answer. On the one hand, these species are unrelated. On the other, there are many examples of other penguin genera (Jouventin 1982) and petrels (Bretagnolle 1996), where congeneric species (two for *Eudyptula* and 15 for *Puffinus*) coexist but produce completely different calls. This relationship between calls of different species within the same genus makes pseudoreplication (McGregor et al. 1992) unlikely. These two species, living in a constraining acoustic environment, share the same vocal code, despite distinct ancestry, because the selection pressures acting on them have been similar. This has led to convergent evolution.

#### Role played by these different acoustic features in the coding process

Playback experiments indicated that neither species is tuned to a precise frequency analysis since entire calls that have been shifted strongly (200 Hz) up or down still elicit territorial responses. In fact, it appears that both species pay attention to the lower spectra, the presence of high frequencies being unnecessary to elicit territorial responses. In fact, it appears that both the original calls of both species are resistant to degradation (low frequencies, slow FM, gap of frequency and of amplitude).

The common structure of the calls and the

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**Table 3. Response of Short-tailed Shearwater to experimental signals (each signal is compared to a control signal).**

<table>
<thead>
<tr>
<th>Signal</th>
<th>Modification</th>
<th>n</th>
<th>Mean number of calls ± sd</th>
<th>Sign test P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Frequency domain</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S0</td>
<td>BP &lt; 1700 Hz</td>
<td>11</td>
<td>11.55 ± 1.86</td>
<td>0.945 ns</td>
</tr>
<tr>
<td>S1</td>
<td>1700 &lt; BP &lt; 4500</td>
<td>11</td>
<td>7.64 ± 2.69</td>
<td>0.055 ns</td>
</tr>
<tr>
<td>S2</td>
<td>BP &gt; 4500 Hz</td>
<td>10</td>
<td>1.10 ± 2.33</td>
<td>0.001 **</td>
</tr>
<tr>
<td>S3</td>
<td>Shift + 300</td>
<td>11</td>
<td>6.91 ± 4.55</td>
<td>0.020 **</td>
</tr>
<tr>
<td>S4</td>
<td>Shift + 200</td>
<td>11</td>
<td>6.36 ± 4.50</td>
<td>0.145 ns</td>
</tr>
<tr>
<td>S5</td>
<td>Shift + 100</td>
<td>18</td>
<td>11.22 ± 2.34</td>
<td>0.941 ns</td>
</tr>
<tr>
<td>S6</td>
<td>Shift - 100</td>
<td>18</td>
<td>9.39 ± 3.79</td>
<td>0.315 ns</td>
</tr>
<tr>
<td>S7</td>
<td>Shift - 200</td>
<td>11</td>
<td>7.91 ± 4.35</td>
<td>0.363 ns</td>
</tr>
<tr>
<td>S8</td>
<td>Shift - 300</td>
<td>11</td>
<td>7.73 ± 6.00</td>
<td>0.055 ns</td>
</tr>
<tr>
<td>Temporal domain</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S9</td>
<td>Lack of FM</td>
<td>10</td>
<td>1.10 ± 2.42</td>
<td>0.001 **</td>
</tr>
<tr>
<td>S10</td>
<td>Lack of AM</td>
<td>12</td>
<td>12.75 ± 1.76</td>
<td>0.887 ns</td>
</tr>
<tr>
<td>S11</td>
<td>EX syllable</td>
<td>10</td>
<td>9.00 ± 3.50</td>
<td>0.055 ns</td>
</tr>
<tr>
<td>S12</td>
<td>IN syllable</td>
<td>11</td>
<td>0.82 ± 2.71</td>
<td>0.001 **</td>
</tr>
<tr>
<td>S13</td>
<td>EXa syllable</td>
<td>10</td>
<td>5.90 ± 2.73</td>
<td>0.001 **</td>
</tr>
<tr>
<td>S14</td>
<td>EXb syllable</td>
<td>10</td>
<td>4.10 ± 3.11</td>
<td>0.001 **</td>
</tr>
<tr>
<td>Extraneous signal</td>
<td>Penguin call</td>
<td>9</td>
<td>0.33 ± 1.00</td>
<td>0.002 **</td>
</tr>
</tbody>
</table>

One-tailed sign test: ns, not significant; **P < 0.01.
similarity of coding of territorial information does not imply that confusion between these two species occurs, as we have shown: Shearwaters usually do not reply to Penguins and vice versa. This is probably due to differences in rhythm, duration and FM structure of syllables and subsyllables, however a common feature is used to communicate the territorial message.

Information represented by the patterned arrangement in two 'binary' units of sounds is highly redundant (Brackenbury 1978), being based on the repetition of identical units of information at two levels. Nevertheless, it is enough for a territorial function where the breeder has only to know that a conspecific is approaching and merely has to reply: 'keep out, this burrow is occupied'.

A multi-level communication system

In complex signals such as the calls of seabirds, there is often a segregation of information among the different parts of the call (Emlen 1972). Some components may convey species information for territorial defence, while others convey individual information for the recognition of mates, the location or the motivational state of the caller etc. Details of the Penguin and Shearwater calls may serve other functions, such as individual recognition or indicating motivation through 'grading' of the signal (Marler 1976). The fine structure of these calls can only be heard at short range, by the owner in the burrow or at the entrance where an arriving bird provides precise information. For example, sex differences and individual vocal recognition has been shown in the Manx Shearwater (Brooke 1978). The individuality of the call has been shown in the Little Penguin by analysing acoustic parameters (Jouventin 1982). Fine details of structure may also provide information on the location of the calling bird. It is well known that sounds propagating in dense vegetation acquire irregular amplitude fluctuations and reverberations masking rapid AM (Richards & Wiley 1980, Wiley & Richards 1982). The analysis of these modifications allows the receiver to estimate the distance of the caller, a process termed 'ranging' (Morton 1982, McGregor & Krebs 1984, Naguib 1995, 1998, Holland et al. 1998, Hillmann et al. 1998). It is also well known that the analysis of the frequency band of a harmonic series allows the receiver to appreciate the spatial (angular) location of the caller. Birds can locate wide spectrum signals better than narrow spectrum ones (Knudsen 1980, Morton 1982, Park & Dooling 1991). The Penguin and Shearwater vocalizations both have obvious AM features and broad spectra. These characteristics would be particularly helpful to the burrowing bird to estimate the distance and direction of an intruder, and to the flying Shearwater or to the prospecting Penguin to find an unoccupied burrow.

Thus, the same complex call of these two seabirds serves several functions according to the range and the context. This multi-level communication system associates sophisticated and rough features and can be used at different ranges according to the robustness of each component of the signal to resist degradation. For the territorial use of the call (from several metres), the general pattern of succession of two sound units in these nocturnal burrowing seabirds seems a simple, efficient and convergent solution to solve a problem of transmission in a constraining environment.

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ENDNOTE

1Sounds were mathematically and physically defined either in the time domain (amplitude versus time) or in the frequency domain (amplitude versus frequency). Time structure can be measured on envelopes [which represent the temporal evolution of maxima of positive amplitudes] and frequency structure on spectra (which are obtained, on digitized signals, using the fast Fourier transform calculation).

REFERENCES

Brooke, M. de L. 1978. Sexual differences in the voice and individ-

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