Bioacoustics
The International Journal of Animal Sound and its Recording, 2000, Vol. 10, pp. 259–285
0952-4622/00 $10
© 2000 AB Academic Publishers

BIOACOUSTICS OF SOUTHERN ELEPHANT SEALS. I. ACOUSTIC STRUCTURE OF MALE AGGRESSIVE VOCALISATIONS

SIMONA SANVITO[1*] AND FILIPPO GALIMBERTI[2]

[1]*Dipartimento di Scienze Ambientali e del Territorio, Università degli Studi di Milano, Via Emanueli 15, 20126 Milano, Italy*
[2]*Elephant Seals Research Group, Sea Lion Island, Falkland Islands*

ABSTRACT

Southern elephant seal *Mirounga leonina* males have a complex and stereotyped system of access to breeding females. The single most important component of male behaviour is vocal signalling, which is used to settle agonistic encounters in most cases. Most aspects of the breeding biology of the species have been studied in depth, but detailed information about the structure of vocalisations is not readily available. Here, we present data about the acoustic structure of aggressive male vocalisations collected in the Falkland Islands and we compare these data to published data on the northern elephant seals. Our main goal is to describe the structure of sounds as a preliminary and indispensable step towards analysis of their functional significance.

Male vocalisations are low-pitched sounds, made up of pulse trains, with little frequency modulation. Low frequency and high sound pressure level are typical of male vocalisations in Pinnipedia, but they were particularly evident in southern elephant seals, probably due to the unusually large body size. The comparison with published data on northern elephant seals was not very easy, due to differences in acoustic terminology and methodology, but it revealed many similarities between the species.

We also carried out a detailed analysis of variability of different acoustic variables. We discovered that frequency and intensity measures have lower variability than temporal ones and should hence be the most effective way to convey information about the individual who emits the vocalisation.

Keywords: Southern elephant seal, *Mirounga leonina*, vocalisations, bioacoustics, spectral analysis, agonistic behaviour, Falkland Islands.

---

[*]current address for correspondence: Biology Department, Memorial University of Newfoundland, St. John's, Newfoundland, A1B 3X9, Canada.

INTRODUCTION

The genus *Mirounga* comprises two species, the northern elephant seal *Mirounga angustirostris* and the southern elephant seal *M. leonina*. Both species have been widely studied, especially with respect to their breeding biology (Le Boeuf and Laws 1994). The bioacoustics of the northern species has also been studied in detail (Bartholomew and Collias 1962, Shipley et al. 1981, Shipley et al. 1986). The bioacoustics of the southern species, however, has not: the only published data concerns a preliminary comparison of male vocalisations between the two species and is based on quite scanty data for the southern one (Le Boeuf and Petrinovich 1974a).

In 1995 we started a long-term research project on elephant seals of the Falkland Islands and we recorded sounds of individuals of different sex and age classes. In this paper, the first of a series on southern elephant seals bioacoustics, we present a detailed account of the acoustic structure of aggressive vocalisations produced by males. We chose these vocalisations as the first part of our study of southern elephant seals communication because the stereotypy of these sound emissions simplifies their analysis and because of their functional significance in relation to the mating system (Galimberti 1995).

Elephant seals very frequently use acoustic signals during the two land phases of their yearly cycle, the moulting and the breeding season (Le Boeuf and Laws 1994), while they probably do not do so while in the water (Fletcher et al. 1996). Airborne acoustic communication is particularly intense during the breeding phase. The mating behaviour of southern elephant seals is very competitive; females form large and clumped groups and males compete heavily to get control of these groups (McCann 1981). Breeding success is related to male competition in both elephant seals species (Le Boeuf and Reiter 1988) and in various southern elephant seals populations (Campagna et al. 1993, Galimberti 1995, Modig 1996). As in most land breeding pinnipeds (Schusterman 1978, Miller 1991), competition between males is often mediated through aggressive vocalisations (McCann 1981), which are used to settle the majority of agonistic encounters and also play an important role in all-out fights (Fabiani 1996). Hence acoustic signals may have a significant effect on mating success (Sanvito 1997) and should be a primary target of the action of sexual selection.

The accurate study of the structure of a signal is fundamental to the understanding of its functional significance and the process of adaptation of the signal to the physical and social environment (Miller 1991). This structural approach has a primary relevance for acoustic signals, due to their intrinsic complexity (Miller and Murray 1995). Hence our goal is to describe in detail the acoustic structure of male aggressive vocalisations and to compare our data with information available for the northern species.

MATERIALS AND METHODS

General information

Fieldwork was carried out during two consecutive breeding seasons (September-November, 1995 and 1996) at Sea Lion Island (Falkland Islands; SLI hereafter). SLI is the main breeding site of the small elephant seals population of the Falklands and it shelters a small and localised population (about 560 breeding females; Galimberti and Boitani 1999). All breeding males were individually marked by putting plastic cattle tags (Jumbo Rototag, Dalton Supplies Ltd.) in the interdigital membrane of the hind flippers and by painting an identification code on their flanks with hair dye (Galimberti and Boitani 1999).

Sound recording

Recordings of male sounds were accomplished in two different situations: standard solicitation and agonistic encounters. In the first situation, each male was recorded by direct stimulation of the animal by the person in charge of the recording or by a co-worker. When closely approached by humans, elephant seal males in breeding condition react with the same stereotyped aggression pattern that they use during regular encounters with other males (Galimberti 1995): the first phase of this pattern is the emission of aggressive vocalisations (McCann 1981). Advantages of this recording protocol were: i) systematic coverage of all breeding males, ii) optimal environmental conditions for recordings (short distance and thus high signal-to-noise ratio), and iii) standardisation of the stimulus, which facilitated comparisons between males. Vocalisations during agonistic contests were recorded opportunistically during the whole length of each breeding season. A preliminary comparison of sounds emitted in natural and artificial stimulation conditions revealed no differences from both a behavioural and an acoustical point of view. Hence direct stimulation was an effective way to record male elephant seals vocalisations (Sanvito 1997).

Recordings were made with portable digital recorders (Sony Digital Audio Tape recorder TCD-D7) and two different microphones, a supercardioid electric condenser interference transducer microphone (Sennheiser ME88), with a frequency response 50-15,000 Hz, and a dynamic cardioid microphone (Sennheiser MD 441), with a frequency response of 30-20,000 Hz. The dynamic microphone reduced the risk of saturation caused by the very high sound pressure levels in the elephant seal vocalisations.

In order to analyse balanced samples, we randomly selected 5 recordings per male from samples ranging between 5 and 67 recordings per male. Younger individuals were slightly under-represented in our sample: they stayed on the land for shorter periods during the breeding season and hence were much more difficult to record. We recorded males during the whole breeding season, but we concentrated recording activities during peak haul out of females.

Acoustic measurements used in the final analysis were extracted from 26 hours of recordings (11 hours with 1,046 vocalisations in 1995 and 15 hours with 1,414 vocalisations in 1996). In this paper we consider just individuals almost or fully mature and with totally developed vocalisations. We analysed vocalisations emitted by 57 males (adults and large subadults): 31 individuals during the 1995 breeding season (18 adults and 13 large subadults with 150 vocalisations) and 26 during the 1996 breeding season (20 adults and 6 large subadults with 127 vocalisations). Except where specified, we used these samples in the analysis.

Sound pressure level

Measurements of sound pressure level (SPL) of vocalisations of wild animals are intrinsically difficult to obtain. In order to have absolute values of SPL, it is crucial to know the distance between the sound source and the microphone. This is not easy to measure in the field, even with elephant seals.

To gather measurements of SPL of male elephant seals, we used the same protocol of standard solicitation described above and a sound level meter (model 1400, Quest Technologies) fitted with a metric reference (a short pole of known length attached to the instrument). We moved close (about 1 m) to the target animal and pointed the sound level meter towards the mouth, keeping the point of the pole between the lower canines. We used the HOLD function of the sound level meter, resetting it at every bout and we tried to measure maximum SPL of each bout of the vocalisation. This was not always possible: in 18% of 290 vocalisations we were not able to measure every bout. The sound level meter was set to "C" weighting and "FAST" response and we fitted it with a windscreen to reduce wind noise. This should not produce any acoustic attenuation in the frequency range in which elephant seals have their maximum energy emission (Instructions for models 1400 and 2400 sound level meters, Quest Technologies). We measured SPL at 55 cm distance and we normalised these measurements to SPL at 1 m (Serway 1986). All the values were in dB and were referred to 20 μPa. We collected SPL measurements from 216 vocalisations for a total of 374 bouts from 24 adult and large subadult males.

Spectral analysis

Parameters used for spectral analysis (Charif et al. 1995) were: Hamming window function with frame length of 21.33 ms (1,024 points) and corresponding filter bandwidth of 190.31 Hz; frames overlap of 50% with a time grid resolution of 10.67 ms; frequency grid resolution of 11.72 Hz (FFT = 4,096 points).

The spectral resolution was carefully chosen to resolve the pulse train structure of the elephant seals vocalisations (every pulse lasts about 20 ms) and to maintain a good frequency resolution. The calculation of the fundamental frequency (F0) was easier and also more precise when the pulse rate was obtained from the waveform, rather than from the spectrogram. With this method, it was not necessary to do the analysis with a very narrow filter bandwidth to discern the formants (whose frequency range is undoubtedly higher than the F0), allowing a better evaluation of the time characteristics of the sound.

Along with waveforms and spectrograms we analysed also amplitude spectra (with amplitude calculated as $20 \log_{10} p/p_0$, where p is the actual sound pressure and p_0 is the standard reference pressure in air, equal to 20 μPa).

Sound measurement

Recordings were transferred in digital format, with 48 kHz sampling frequency and 16 bit resolution of the original recording, to a Macintosh Quadra 650 computer fitted with an Audiomedia II digital audio card and Sound Designer II 2.8 software (Digidesign Inc.). The sound measurements and spectral analysis were carried out using Canary 1.2 software (Cornell Laboratory of Ornithology). We used the Igor Pro 3.03 software (Wave Metric Inc.) for high resolution plotting of waveforms, spectrograms and spectra.

Male elephant seals aggressive vocalisations are made up of a series of sound emissions called "bouts". Each bout was further subdivided into "syllables" and "syllable parts". We defined a *syllable* as a single acoustic event, with a continuous spectrographic trace with respect to the time axis (Kroodsma 1977, Pavan 1992) and a *syllable part* as a portion of a syllable characterised by constant pulse rate; the fundamental frequency was constant in each syllable part. A complete and accurate description of animal vocalisations should analyse all the aspects of the acoustic structure. Therefore we considered four classes of variables: temporal, frequency, sound amplitude and internal structure of bouts.

Vocalisation was the basic unit of analysis, because it is the fundamental component of acoustic communication of elephant seals. The high repeatability of measures obtained at vocalisation level justified the choice (Sanvito and Galimberti 2000). Unless specified, we used average vocalisation values to describe the global acoustic structure of signals. There was no risk of pseudoreplication involved in doing so, because the number of vocalisations per male was balanced (5 vocalisations per male) and hence all males had an equal contribution in the statistical calculations.

We measured many different parameters from each vocalisation and bout. The full list of parameters with their description is presented below.

Temporal parameters

The following temporal parameters were measured from the waveform of vocalisations (Figure 1).

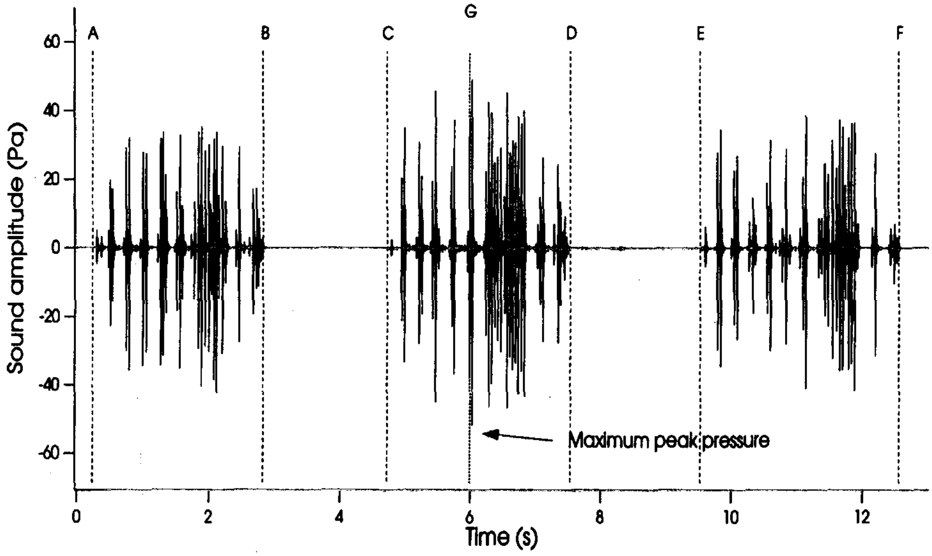

Figure 1. Adult male vocalisation, with temporal parameters (this was a vocalisation composed of three bouts). Temporal parameters were: vocalisation length (A-F); bout lengths (A-B, C-D, E-F); intervals between bout lengths (B-C, D-E); ratio signal length/total length or Q_BOUT ([A-B +C-D + E-F]/A-F). In the second bout we also indicate maximum peak pressure (G) and relative peak time (C-G/C-D).

- number of bouts per vocalisation (= number of bouts emitted during the vocalisation)
- bout length (= time interval in seconds between the beginning and the end of a single bout)
- interval between bouts (= time interval in seconds between the end of a bout and the beginning of the following one)
- vocalisation length (= time interval in seconds between the beginning of the first bout and the end of the last bout of a vocalisation)
- ratio signal length/total length, Q_BOUT (= ratio between the total duration of all the bouts of a vocalisation and the total duration of the vocalisation, i.e. the proportion of vocalisation with signal)
- relative peak time (= ratio between absolute peak time, i.e. the time from the beginning of the bout at which the highest amplitude in the bout occurs, and the bout length)
- syllable part with maximum peak pressure length, DELTA_T (= length of syllable part in which the maximum peak pressure occurs). The fundamental frequency was calculated from this part.

Intensity parameters

Intensity parameters were measured from average power spectra of bouts, spectrograms and waveforms for the 1996 data only. All the measures in dB are referred to 20 μPa. We recorded complete vocalisations from different distances, hence we considered only relative measures of sound intensity. The only exception was the measurement of the absolute sound pressure level obtained with sound level meter.

The following intensity parameters were measured.

- instantaneous relative peak intensity (= ratio between instantaneous peak intensity per Hertz, i.e. the maximum intensity/Hz in the bout, calculated from the spectrogram, and peak pressure, i.e. the pressure in the selected bout that has the maximum absolute value, calculated from waveform). This variable measures the instantaneous effect of the frequency band with maximum energy on the whole energy emitted on all frequency bands.
- total relative peak intensity (= same as the previous parameter, but calculated over the entire bout: ratio between total peak intensity per Hertz, i.e. the maximum intensity/Hz in the whole bout, calculated from the spectra as the amplitude of the maximum peak, and average intensity, i.e. the average intensity in the selected bout equivalent to average sound pressure level of the whole bout, calculated from the spectrogram). This variable measures the effect of the frequency band with maximum energy on the whole energy emitted on all frequency bands, averaged over the whole bout.

- absolute sound pressure level, SPL (= maximum sound pressure level in dB, normalised at 1 m, measured with the sound level meter).

Frequency parameters

The following frequency parameters were measured from average power spectra of bouts and from waveforms for the 1996 data only (Figure 2).

- dominant frequency (= the frequency in Hertz at which, on average, the highest amplitude in a bout occurs, calculated from the average amplitude spectrum of a bout as the frequency at which the highest amplitude peak occurs)
- fundamental formant (= minimum frequency in Hertz at which a considerable part of energy occurs during the whole bout, hence calculated from the average amplitude spectrum of a bout as the minimum frequency at which a considerable and evident amplitude peak occurs); often equal to dominant frequency. This is the main formant. Formants are parts of the frequency spectrum that are reinforced by resonant properties of the vocal tract (Miller and Murray 1995). In some cases we found a secondary peak, at lower frequency, with reduced intensity and close to the main peak: this peak was ignored for fundamental formant calculations.
- fundamental frequency, F0 (= for sounds with pulse train structure, such as elephant seals vocalisations, the F0 (Hz) is equal to the pulse rate; we calculated it from the waveform in the "part" of the bout in which there is the maximum peak amplitude, as the pulse rate in that part of the bout, i.e. the ratio between the length of that part (DELTA_T) and the number of pulses contained in it: Zuberbuhler et al. 1997, Watkins 1967).
- peak frequency (= the frequency in Hertz at which the highest amplitude in a bout occurs, at instantaneous level, calculated from the spectrogram of a bout as the frequency at which the highest amplitude peak occurs)
- 6 dB bandwidth (= width in Hertz of the frequency band around the dominant frequency where the signal in the amplitude spectrum attenuates by 6 dB). This was calculated on the average spectrum of a bout by finding two frequencies F1 and F2 around the dominant frequency (F1 < dominant frequency < F2) where the spectrum level is 6 dB below the peak value; the 6 dB bandwidth is defined as the difference F2-F1.
- minimum frequency at -6 dB (= F1 in Hertz of the previous definition)

For some frequency parameters we calculated two different ranges: the primary range (= difference between maximum and minimum average

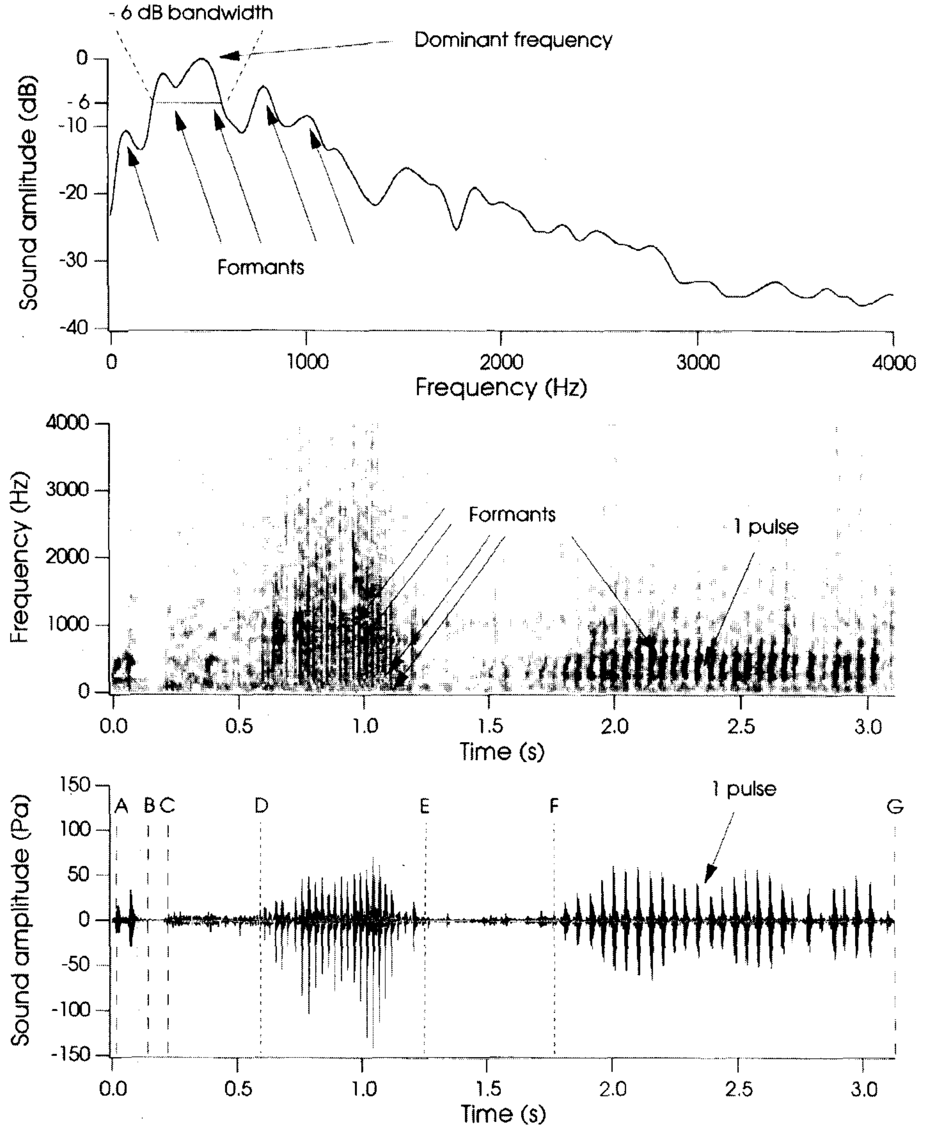

Figure 2. Structure of one bout. From the top: amplitude spectrum, spectrogram and wave form of a bout composed of two syllables (A-B and C-G in the waveform), the latter composed of four parts (C-D, D-E, E-F and F-G in the waveform); A-G represents bout length. In the amplitude spectrum, we indicated the main formant frequencies, the dominant frequency and 6 dB bandwidth. In the spectrogram, we indicate the same formant frequencies indicated in the spectrum and one pulse.

value that the variable assumes among all the vocalisations); the secondary range (= difference between the average of maximum values assumed by the variable in each vocalisation and the average of minimum ones).

Internal structure of a bout

Structural parameters were measured from waveforms and spectrograms for 1996 data only as follows (Figure 2).

- number of syllables per bout (= number of syllables, equal or not, forming each bout)
- syllable rate (= number of syllables per second, calculated as the ratio between the number of syllables per bout and the length of that bout)
- number of types of syllable per bout (= number of different syllables in one bout)
- Shannon index (= Shannon index of evenness calculated for the syllable composition of the bout). To obtain a concise measure of the structural complexity of bouts, we calculated an evenness measure based on the frequency of different kinds of syllable in the bout, using the Shannon index divided by the maximum possible index to obtain a measure independent from the number of syllables (Krebs 1989).

Statistics

Calculations of derived variables and manipulations of spectra were made with programs written in HyperTalk (Apple Computer Inc.) and Mathematica (Wolfram Research Inc).

Statistics were calculated as means plus standard deviations, or as medians plus median absolute deviations (MAD; Rousseeuw and Croux 1993) for asymmetric non-normal variables. The shape of distribution of variables was characterised by the index of skewness (g_1; Sokal and Rohlf 1981). In scatterplots we presented a LOWESS (Trexler and Travis 1993) line to help the visualisation of trends. We verified homogeneity between the two breeding seasons for each measured variable using the Mann-Whitney test. All statistics and tests were calculated using StatView software (Abacus Concepts Inc.).

RESULTS

Aggressive vocalisations of male southern elephant seals, corresponding to *V2* of McCann (1981) and with *VO2* of Sandegren for the northern species (1976), were low-pitched sounds, made up of pulse trains, with little frequency modulation and very high power. Vocalisations, the higher level unit of communication in this species, were made up from one or more bouts (Figure 1). The animal exhales during the bout emission and inhales during the interval between bouts. The number of bouts emitted per vocalisation during agonistic interactions was related to the male "personality" and to the specific context of emission. Each bout was made up from a pulse train, with enough delay between pulses that bouts sounded atonal to the observer.

Each bout comprised an internal structure of syllables and syllable parts. We recognised formants as dark bands in spectrograms, rather linear with respect to the time axis. These bands indicate frequencies of concentration of high energy and were only slightly frequency modulated in each bout (Figure 2).

TABLE 1

Descriptive statistics for all parameters for aggressive vocalisations of males in the Sea Lion Island population. Values were calculated at vocalisation level (except for sound pressure level, calculated at individual male level). The first five temporal parameters (above the thick line) were averaged for 1995 and 1996 breeding seasons, while other values refer to 1996 only.

Variables	n	Mean	SD	Min	Max	CV
N° of bouts	277	2.1	1.7	1	13	0.811
Vocalisation length (s)	277	8.97	8.46	1.07	56.79	0.944
Bout length (s)	277	3.39	1.26	1.07	11.41	0.372
Interval length (s)	277	1.82	0.63	0.51	3.75	0.346
Signal length/total length	137	0.74	0.08	0.57	0.93	0.105
Part with max peak pressure (s)	127	0.78	0.51	0.16	3.09	0.644
Relative peak time	127	0.64	0.22	0.015	0.963	0.336
Inst. rel. peak intensity	127	0.74	0.027	0.65	0.81	0.037
Total rel. peak intensity	127	0.76	0.025	0.69	0.81	0.032
Sound pressure level (dB)	24	109.0	3.1	103.8	114.1	0.029
Dominant frequency (Hz)	127	364	171	202	961	0.471
Fundamental formant (Hz)	127	264	47	202	527	0.178
Fundamental frequency (Hz)	127	25	6	15	44	0.245
Peak frequency (Hz)	127	414	218	178	1617	0.525
6 dB bandwidth (Hz)	127	516	355	88	1869	0.688
-6 dB min. frequency (Hz)	127	181	73	0	481	0.403
N° of syllable per bout	127	4.8	3.5	1	18	0.742
Syllable rate (syll./s)	127	1.44	1.17	0.23	4.58	0.813
Forms of syllable per bout	127	2.3	0.7	1	4	0.298
Shannon index	116	0.88	0.17	0.37	1	0.198

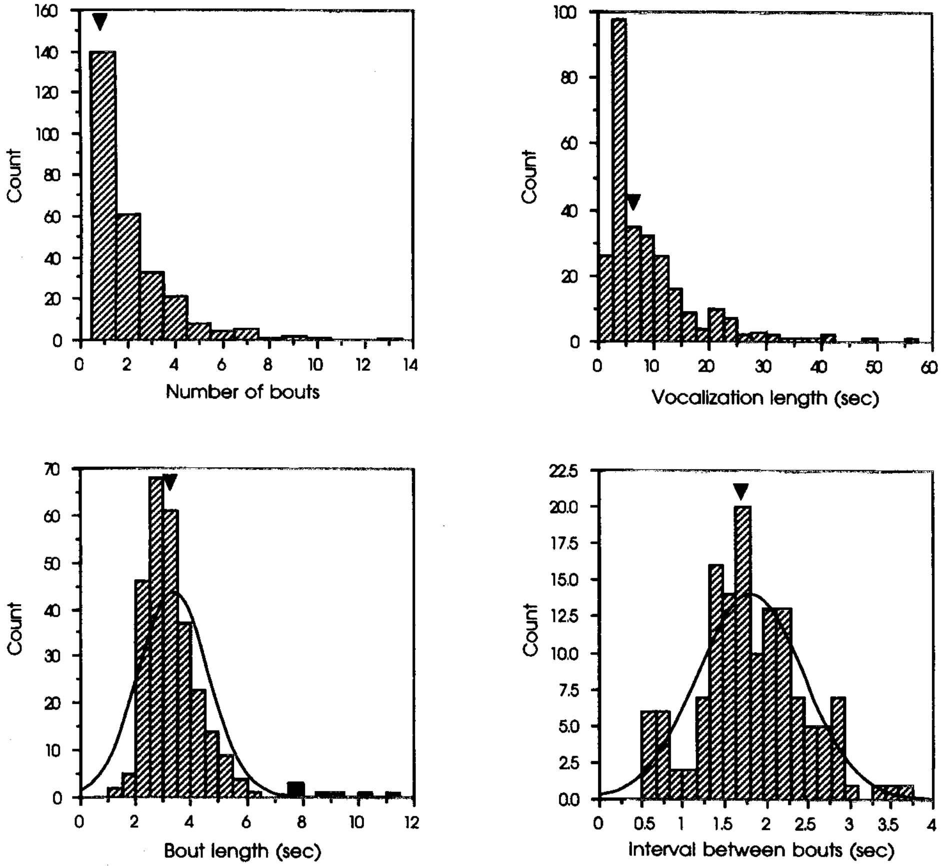

Figure 3. Frequency distribution of temporal variables. Arrows indicates the median values. On bottom graphs, line indicates the normal curve fitted to data. The slight deviation from normality of bout length was due to some outliers, indicated with filled bars in the graph (bottom left).

Temporal variables (Table 1; Figure 3)

The frequency distribution of number of bouts per vocalisation was highly skewed ($g_1 = 2.465$) with the median equal to 1 and MAD equal to 0. Most of the vocalisations were composed of 1 or 2 bouts (ranging from 1 to 7 in 1995 and from 1 to 13 for 1996) and about the 90% of the vocalisations had no more than 4 bouts. The frequency distribution of vocalisation length reflected the number of bouts distribution; it was very skewed ($g_1 = 2.267$) and the greatest number of occurrences were in the lowest portion of the distribution range. Median value was 5.968 s (MAD = 3.107). The frequency distribution of bout length was normal, but with evident outliers (Figure 3). Median value was equal to 3.067 s (MAD = 0.552). The mean 'interval between bouts length' was 1.823 ± 0.631 s (n = 137). The mean ratio of signal length on total length (Q_BOUT; see definition of variables) was 0739 ± 0.077; therefore more than 75% of the vocalisation was occupied by signal. Relative peak time had a rather skewed distribution in 1996 (g_1 = 2.235), with median equal to 0.670 s (MAD = 0.136). Hence, the peak of amplitude usually was in the last part of the bout. Finally, length of the part with the maximum peak pressure (DELTA_T; see definition of measured variables) had a skewed distribution in 1996 with median value of 0.669 s (MAD = 0.252).

Intensity variables (Table 1; Figure 7)

Instantaneous relative peak intensity and total relative peak intensity had similar normal distributions and mean values respectively equal to 0.744 ± 0.027 and 0.764 ± 0.025.

We calculated the maximum sound pressure level for each bout of the vocalisation and then we calculated from these values the mean for each vocalisation. Samples were not balanced for different males; so, to avoid pseudoreplication, we used males as our analysis unit. Notwithstanding the small sample size, the distribution was clearly bimodal. The mean value was 109.0 ± 3.1 dB, ranging from 103.8 to 114.1 dB (n = 24). The two most frequent classes were 106 dB (4 males) and 111 dB (4 males). The shape of the distribution was probably due to differences in SPL between adult and large subadult males. The mean value for the former was 109.7 ± 3.1 dB (n = 18), while for the latter it was 106.9 ± 2.3 dB (n = 6).

Frequency variables (Table 1)

The dominant frequency median value was 281 (MAD = 55) Hz with a skewed distribution (g_1 = 1.415; Figure 7). The primary range was rather wide (759 Hz, from 202 to 961 Hz) while the secondary one was considerably narrower (53 Hz, from 337 to 390). Most of the values were grouped around the median value: in fact 64% (81 of 127 vocalisations) of values were included in the range between 200 and 330 Hz. Peak frequency had also a skewed distribution (g_1 = 2.102; Figure 7) with primary range rather wide and secondary one considerably narrower (respectively 106 and 1438 Hz). The median value was 328 (MAD = 94) Hz.

Fundamental formant was normally distributed (Figure 4), with some outliers in the right hand side of the distribution: hence the primary range was rather wide (326 Hz) compared with the secondary one (11 Hz). Nevertheless, the dispersion of this variable was small with a mean value of 264 ± 47 Hz. Fundamental frequency was low and the mean value was 25 ± 6 Hz (range = 15 - 44 Hz; Figure 4). 6 dB bandwidth was rather asymmetrically distributed (g_1 = 1.110; Figure 7) with median value equal to 498 Hz (MAD = 223) and the minimum frequency of this range had a median value equal to 188 Hz (MAD = 33; Figure 4).

Internal structure of bouts (Table 1; Figure 5)

Vocalisations were built up from sequences of bouts, each one with exactly the same internal structure as the others. Hence, although the functional unit of communication is the vocalisation (males emitted complete vocalisations during social communication), the structural unit is the bout and we analysed in detail its syllables composition.

The number of kinds of syllable per bout ranged from 1 to 4 with mean value equal to 2.26 ± 0.67 and a normal distribution. On the other hand, frequency distributions of syllable number per bout and syllable rate were clearly bimodal.

The frequency classes most represented for syllable number were the ones centred on value 2 with 50 occurrences and on value 9 with 18 occurrences (n = 127). Syllable rate had two modal classes with central values equal to 0.75 syllable/s (59 occurrences) and 3.25 syllable/s (15 occurrences). Also the Shannon index calculated on syllable frequency was bimodally distributed: most occurrences were equal to 1 (total homogeneity) and the other modal class was equal to 0.625 (11 occurrences).

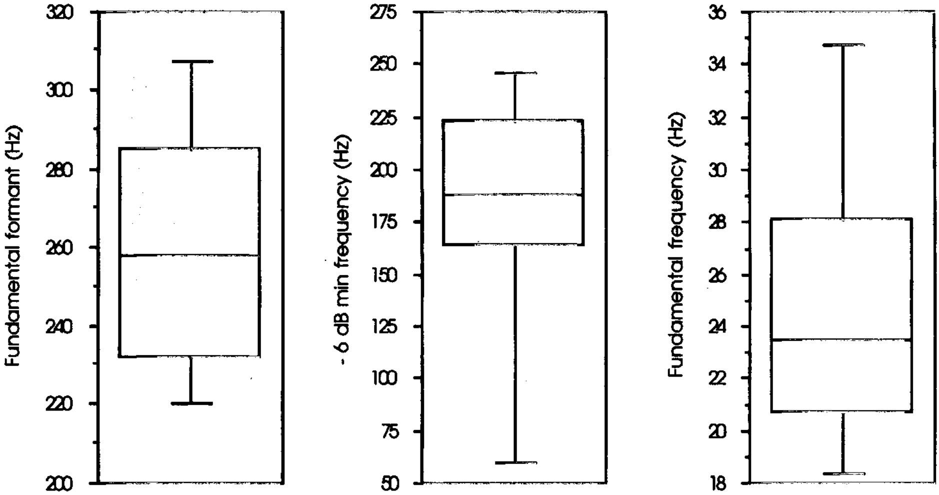

Figure 4. Boxplots of three frequency variables: fundamental formant, minimum frequency at -6 db, and fundamental frequency. Boxes indicates points included between 25 and 75 percentiles, horizontal line in boxes indicates the median and the external lines indicates 10 and 90 percentiles.

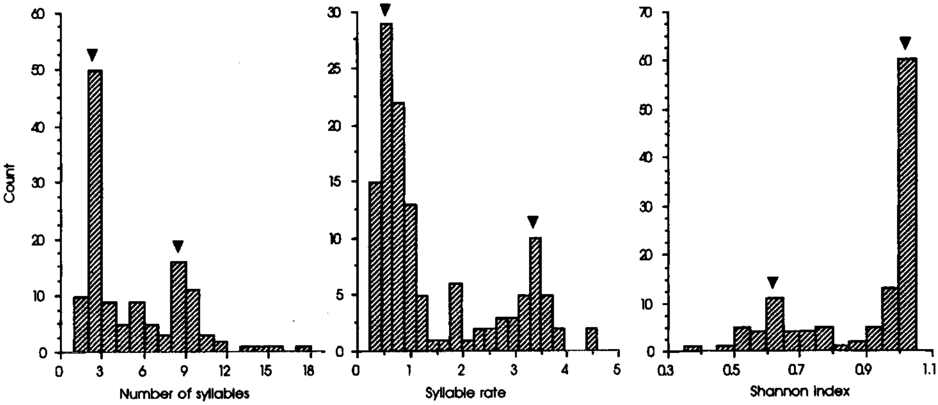

Figure 5. Frequency distributions of bout structure variables. All distributions were bimodal and arrows indicate the modal classes.

Correlations between variables

To preserve homogeneity with the rest of the description of sound structure, we calculated correlations between variables using average vocalisation values (Tables 2 and 3). The risk of pseudoreplication involved in this method, instead using of using values calculated at the individual level, should be limited, for several reasons: the focus is on description and exploration instead of on strict inference; the number of vocalisations is balanced between males and hence each individual gives an equal contribution to estimated statistics; and we found small probability values in most correlation tests.

Temporal and bout structure (Table 2)

Correlations between temporal and structural variables were calculated on a sample of 75 vocalisations.

The correlation coefficient between number of bouts per vocalisation and vocalisation length was, as expected, very high ($r = 0.912$, $p < 0.0001$), while bout length and vocalisation length were not strongly correlated ($r = 0.332$, $p = 0.0035$): the duration of vocalisation depends more on the number of bouts than on the duration of those bouts. We found another high correlation between bout length and interval between bouts length ($r = 0.697$, $p < 0.0001$). During bout emission males exhale, while during the interval between bouts they inhale. Hence, the longer the bout, the longer should be the following interval. Ratio between signal length and total length (Q_BOUT) was significantly correlated with both number of bouts per vocalisation and vocalisation length (respectively, $r = -0.547$, $p < 0.0001$ and $r = -0.427$, $p = 0.0001$), which were themselves highly

TABLE 2

Correlation matrix (Pearson's r in the upper middle and p values in the lower) between acoustic parameters describing temporal domain and macrostructure (n = 75). P values in bold represent table wise significance at 0.05 level (sequential Hochberg test).

	1	2	3	4	5	6	7	8	9	10	11	12
N° of bouts (1)		**0.912**	-0.026	-0.019	**-0.547**	0.071	0.128	0.085	0.071	0.090	0.027	-0.086
Voc. Length (2)	**<0.0001**		0.332	0.248	**-0.427**	0.343	0.149	0.168	-0.006	-0.092	-0.079	0.072
Bout length (3)	0.8221	0.0035		**0.581**	0.345	**0.759**	0.073	0.190	-0.123	**-0.441**	-0.261	**0.399**
Interval length (4)	0.8736	0.0320	**<0.0001**		-0.336	**0.393**	-0.061	0.135	-0.061	-0.247	-0.078	0.240
Signal/total length (5)	**<0.0001**	**0.0001**	0.0022	0.0030		0.221	-0.021	-0.050	-0.134	-0.249	-0.112	0.199
Abs. rel. peak time (6)	0.5477	0.0024	**<0.0001**	**0.0004**	0.0565		**0.693**	0.199	-0.135	-0.343	-0.183	0.306
Inst. rel. peak time (7)	0.2748	0.2024	0.5335	0.6024	0.8592	**<0.0001**		0.088	-0.073	-0.055	-0.048	0.041
Part max peak press. (8)	0.4689	0.1490	0.1018	0.2475	0.6702	0.0862	0.4538		**-0.461**	**-0.471**	**-0.378**	**0.462**
N° of syllable (9)	0.5468	0.9569	0.2923	0.6033	0.2522	0.2508	0.5348	**<0.0001**		**0.936**	**0.560**	**-0.883**
Syllable rate (10)	0.4424	0.4317	**<0.0001**	0.0324	0.0309	0.0024	0.6418	**<0.0001**	**<0.0001**		**0.575**	**-0.941**
Forms of syllables (11)	0.8167	0.5009	0.0235	0.5068	0.3384	0.1156	0.6818	**0.0007**	**<0.0001**	**<0.0001**		**-0.405**
Shannon index (12)	0.4634	0.5403	**0.0003**	0.0377	0.0874	0.0073	0.7279	**<0.0001**	**<0.0001**	**<0.0001**	**0.0003**	

correlated. These relationships were expected because the increase in length of the vocalisations depended on an increase in the number of bouts, which in turn determined a more than proportional increase in number of parts without signal. We found an important correlation between absolute peak time (used to calculate the relative peak time) and bout length ($r = 0.759$, $p < 0.0001$). In fact, relative peak time being equal, the longer bouts will have a greater absolute peak time. As expected also absolute and relative peak time were strongly correlated ($r = 0.693$, $p < 0.0001$).

Finally, we calculated correlations between variables of the bout syllable structure and we found significant values between all of them (Table 2; Figure 6). In particular, we found a strong correlation between number of syllables per bout and syllable rate ($r = 0.936$, $p < 0.0001$). Conversely, number of syllables per bout and bout length were not related; hence, if the number of syllables varies independently from bout length, then also the number of syllables per time unit will vary. We found significant correlations between the length of the part with maximum peak pressure (DELTA_T) and all the parameters of the internal structure of the bouts. Two measures concerning the internal structure of bout (syllable rate and Shannon index) were also positively correlated with bout length.

Frequency and intensity (Table 3)

Correlations between frequency and intensity variables were calculated on a sample of 127 vocalisations.

We calculated correlations between frequency and intensity parameters both at instantaneous and bout level, in order to verify if instantaneous measures were able to characterise the structure of the whole bout. We calculated correlations between two measures of intensity, absolute relative peak intensity (whole bout measure) and instantaneous peak intensity and we found a high correlation ($r = 0.822$, $p < 0.0001$; Figure 7 bottom right); we then calculated correlations between two measures of frequency, dominant frequency (whole bout measure) and peak frequency, finding again a high correlation ($r = 0.909$, $p < 0.0001$; Figure 7 bottom left). This high correlation between instantaneous and whole bout measures suggests that the bout structure is defined by that part in which the maximum energy is released and that the energy distribution in the different frequency bandwidths is homogeneous during the whole bout length. Hence the dominant frequency and also the other formants were rather stable, with small modulation.

We found significant negative correlations between frequency measures (peak frequency, dominant frequency and fundamental formant) and relative peak intensity measures (instantaneous and total). We also found strong and significant positive correlations between 6 dB bandwidth and the same frequency measures (Table 3;

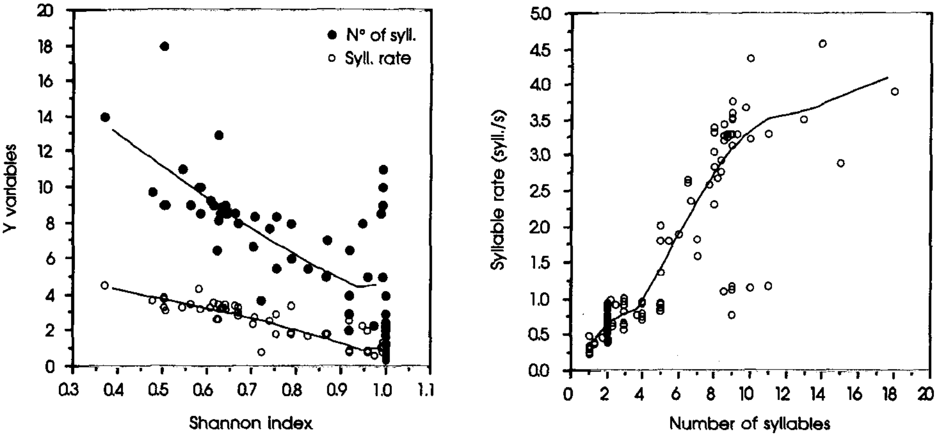

Figure 6. Scatterplots of number of syllables and syllable rate vs. Shannon index (left) and of number of syllables vs. syllable rate (right). Lines indicate LOWESS fitted to data with tension equal to 0.66.

Figure 7 top right: correlation between 6 dB bandwidth and dominant frequency). Hence, lower frequency vocalisations had more concentrated energy at peak and dominant frequency than higher frequency vocalisations.

We found strong and significant positive correlations also between relative peak intensities (instantaneous and total) and 6 dB bandwidth (Table 3; Figure 7 top left: correlation between 6 dB bandwidth and total relative peak intensity). Both these parameters describe how much energy was concentrated around the dominant frequency. Finally, the 6 dB bandwidth was, as expected, negatively correlated with its minimum frequency: the larger the bandwidth the lower the minimum initial frequency.

We explored the correlation structure between the frequency domain set and temporal domain set of variables, but we did not find any significant correlation.

Multivariate correlation structure

To better elucidate the correlation structure of the whole set of variables, we first examined whole correlation matrices of the three main groups of variables using the Bartlett test of sphericity. We found significant correlations in the temporal variables matrix (Bartlett statistic = 184.3, df = 15, $p < 0.0001$), in the frequency variables matrix (Bartlett statistic = 191.0, df = 15, $p < 0.0001$) and in the structure variables matrix (Bartlett statistic = 446.0, df = 6, $p < 0.0001$). Structure variables were globally more correlated than temporal and frequency ones.

TABLE 3

Correlation matrix (Pearson's r in the upper middle and p values in the lower) between frequency and intensity (n = 127). P values in bold represent table wise significance at 0.05 level (sequential Hochberg test).

	1	2	3	4	5	6	7	8
Inst. rel. peak intensity (1)		**0.809**	**-0.398**	**-0.332**	-0.180	-0.217	**0.309**	**-0.647**
Abs. rel. peak intensity (2)	**<0.0001**		**-0.504**	**-0.453**	**-0.264**	0.056	**0.309**	**-0.793**
Peak frequency (3)	**<0.0001**	**<0.0001**		**0.648**	0.092	-0.185	-0.080	**0.582**
Dominant frequency (4)	**0.0001**	**<0.0001**	**<0.0001**		0.199	-0.064	0.119	**0.532**
Fundamental formant (5)	0.0430	**0.0026**	0.3038	0.0248		0.022	0.262	**0.280**
Fundamental frequency (6)	0.0142	0.5325	0.0376	0.4777	0.8069		-0.032	-0.047
Min. frequency at -6 dB (7)	**0.0004**	**0.0004**	0.3704	0.1828	0.0028	0.7176		**-0.300**
6 dB bandwidth (8)	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**0.0014**	0.6031	**0.0006**	

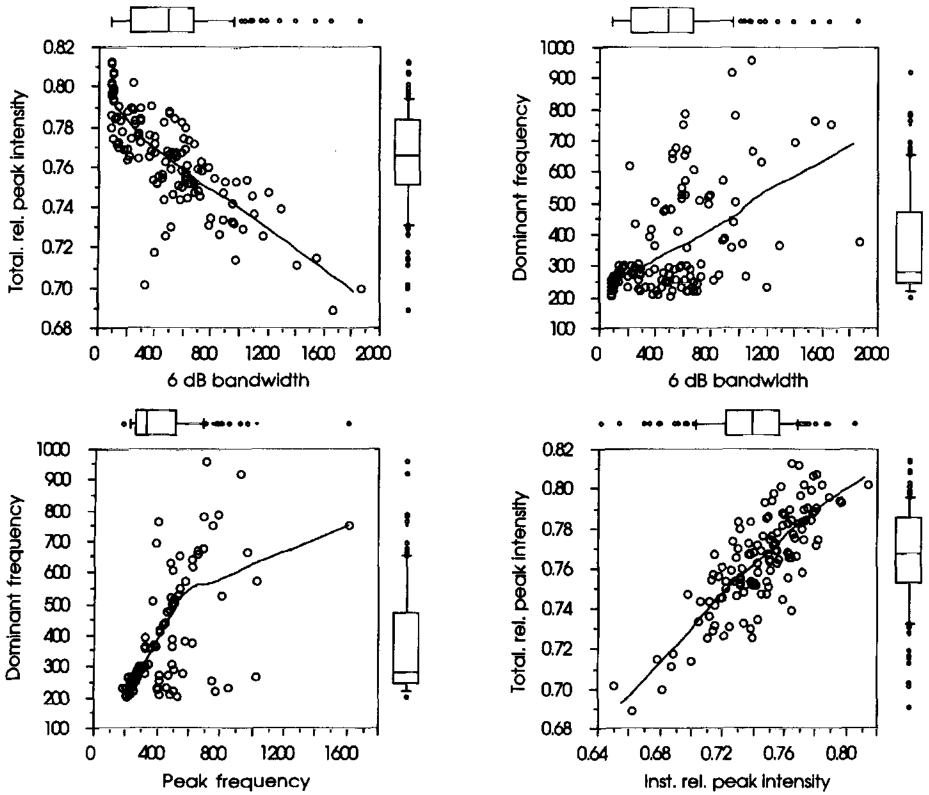

Figure 7. Top left: relationship between 6 dB bandwidth and total relative peak intensity; top right: relationship between 6 dB bandwidth and dominant frequency; bottom left: relationship between peak frequency and dominant frequency; bottom right: relationship between total relative peak intensity and instantaneous relative peak intensity. A couple of boxplots is fitted on the margins of each scatterplot to represent the distributions of the corresponding variables. Lines indicate LOWESS fitted to data with tension equal to 0.66.

We then applied principal components analysis to the full variables set (18 variables). Notwithstanding the large univariate correlations between some variables, PCA was not able to effectively reduce the number of variables needed to fully describe the multidimensional structure of our data. The first component explained only 25% of the variance of the initial matrix and 7 components were needed to explain 80% of the variance. We employed a jackknife delete one test on components and we found that the first 5 components were significant at 0.05 level and have to be retained. We then repeated PCA for matrices of subsets of variables (temporal, frequency, bout structure), to evaluate the multidimensional correlation structure inside each group. For the frequency variables matrix (6 variables) we found that the first component explained 38% of variance (4 components needed to explain 80% of variance); for the temporal variables matrix (6 variables), the first component explained 32% of variance (4 components needed to explain 80% of variance); and for the structure variables matrix (4 variables) the first two components explained 94% of the original variance. In all, principal component analysis revealed a complex multivariate structure of the matrix of measured variables, which was not effectively reducible to a small set of components. Only structure variables were sufficiently correlated to be reduced to a single linear combination of original variables.

Between vocalisations variability of parameters

We calculated mean values of CV between vocalisations for temporal, frequency and intensity parameters (1996 data, n = 127). We considered the following temporal parameters: vocalisation length, bout length, interval between bouts length, Q_BOUT, relative peak time, part with maximum intensity length; the frequency parameters of peak frequency, dominant frequency, dominant formant and fundamental frequency; and the intensity parameters of instantaneous and total relative peak intensity (Table 3; Figure 8). The analysis revealed a larger variability among temporal measures than among frequency and intensity ones (respectively 0.456 ± 0.263; 0.355 ± 0.169 and 0.035 ± 0.102). A similar relationship for temporal and frequency measures is known for Weddel seal vocalisations (Miller 1991).

DISCUSSION

Elephant seals aggressive vocalisations

Male elephant seal aggressive vocalisations were low-pitched sounds, made up of pulse trains, with limited spectral frequency modulation and very high power. These characteristics should in part be moulded by the reduction in directionality of sound perception due to the loss of the external ear (Mohl 1968) and by the high level of background noise of the elephant seals' breeding habitat and social system, as in other land breeding pinnipeds (Peterson and Bartholomew 1969, Schusterman 1978). In fact, all of these features result in highly directional vocalisations optimised for detection in an environment characterised by strong wind and surf (Wiley and Richards 1978). Similar directional qualities were also found in the northern species, which exhibits a gross vocalisation structure comparable to the southern species and which breeds in rookeries even more crowded and noisier than southern ones (Bartholomew and Collias 1962).

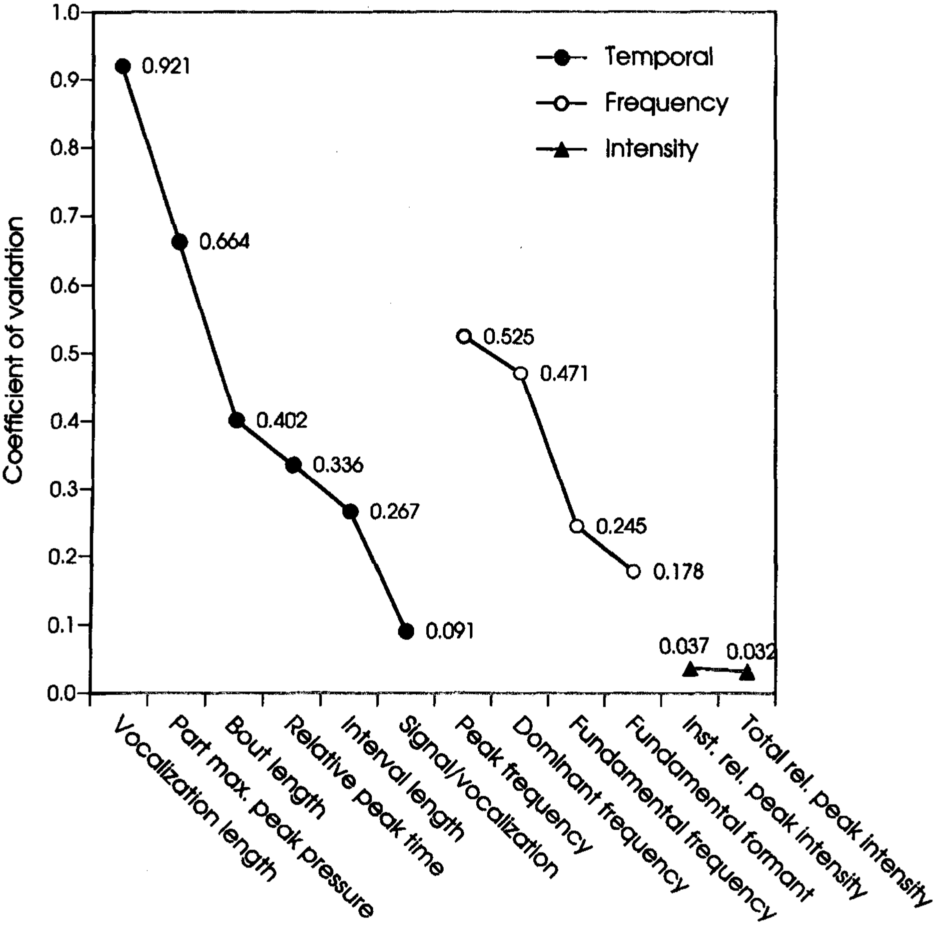

Figure 8. CV profiles (Miller 1991) of temporal, frequency and intensity parameters.

In many other pinniped species, male aggressive vocalisations are pulse sounds (*M. angustirostris*: Shipley et al. 1981, *Monacus schauinslandi*: Miller and Job 1992, *Eumetopias jubata*: Gentry 1970, *Arctocephalus spp.*: Stirling and Warneke 1971, *Odobenus rosmarus*: Stirling et al. 1987). Low frequency and limited frequency modulation are common characteristics of most aggressive vocalisations in different mammals and birds (Marler 1956, Tembrock 1968).

The internal anatomy of this species is not very well known (Murphy 1914), hence the mechanism of production of sound is unclear. Pulse-like male aggressive vocalisations of *Mirounga* seems to be produced by the air exhaled through the mouth and hence through the vocal cords (Sandegren 1976), rather than through the proboscis, as asserted by some authors (Bartholomew and Collias 1962). In fact among other pinniped species, males emit pulsing vocalisations (New Zealand fur seals, Hawaiian monk seals, Antarctic fur seals, Steller Sea Lions and walruses), but none of these has a proboscis (Miller 1974, Miller and Job 1992, Gentry 1970, Stirling et al. 1971, Stirling et al.1987). Moreover, female and young male elephant seals, lacking the proboscis, are able to emit pulsing vocalisations. So the role of proboscis in sound production seems to be marginal, at least for aggressive vocalisations, while it seems to have a role in production of "snort" sounds. Notwithstanding this, the proboscis is directly linked to the vocal tract, is expanded during vocalisations, probably has a role in sound amplification and could be responsible for resonance phenomena.

Acoustic structure of vocalisations

Southern elephant seals male aggressive vocalisations were composed of a basic unit, the bout, repeated a variable number of times; hence, the total duration varied from a few seconds, to almost a minute. During natural contests the vocalisation length was greatly influenced by rival behaviour and by the specific history of the contest. During standard recordings the level of stimulation for different males was the same. Therefore the variation in length of vocalisations between males, which was high, should reflect their different capabilities and propensities to vocalise.

Data on temporal parameters for the northern species and for other populations of the southern species were scarce and comparisons were hampered by differences in terminology and methodology. Bout length for Californian species is 6.05 ± 1.89 s (n = 107 males during a 5 year period; Le Boeuf and Petrinovich 1974a), more or less twice the length for southern males of Sea Lion Island (3.39 s). Vocalisation length of southern elephant seal males of the Valdés Peninsula was estimated at 19.1 ± 8.3 s (Le Boeuf and Petrinovich 1974a), but due to difference in recording methods, this estimate is not directly comparable with ours.

All frequency values were low; in particular the pulse structure of these sounds resulted in a very low F0, equal to the pulse rate. Frequency features of acoustic signals were linked to the large size of male elephant seals: the bigger the emission apparatus, the lower the frequency of the emitted sounds. No other pinnipeds are as large as elephant seals and in fact no other pinniped species emits such low vocalisations. Comparable F0 and fundamental formant values were found only in the northern species (Bartholomew and Collias 1962, Le Boeuf and Petrinovich 1974a, Le Boeuf and Petrinovich 1974b), but the differences in terminology make a comparison quite difficult. In fact, it was rather clear from the observation of published spectrograms and wave forms that the parameter normally cited as F0 for *M. angustirostris* does not correspond to our F0 (equal to pulse rate), but our fundamental formant, while what we call F0 is the parameter called *claps rate* or *pulsation rate* (Bartholomew and Collias 1962). So the F0 in the two species was not so different: 15/25 pulses per second (Hz) for the northern one (Bartholomew and Collias 1962) and 25 ± 6 Hz for the southern one (this study). Comparable data for other southern populations was missing.

Regarding the fundamental formant, Le Boeuf and Petrinovich (1974a) found a value of 202 ± 54 Hz (n = 19) for the Año Nuevo Island northern population and 233 ± 90 Hz for the southern species of Punta Norte, Argentina. For the northern species Le Boeuf and Peterson (1969) reported values ranging from 250 to 750 Hz, while Le Boeuf and Petrinovich (1974b) reported an average of 212 Hz in a 5 year period. In the Sea Lion Island population, the fundamental formant had a mean value of 264 Hz; differences between southern and northern species for this parameter were therefore small.

Finally, we did not find in the literature any reference to the dominant frequency, but, from visual inspection of spectrograms for the northern species, the energy seems almost entirely below 2,500 Hz and concentrated around 250-500 Hz (Bartholomew and Collias 1962, “fig. 8. Clap-threat of adult male”). This was in accordance with the available evidence from Sea Lion Island. We found that 70% of the total energy emitted is concentrated around the peak frequency, measured both at instantaneous level and averaged on the whole bout. No comparable data is available for the northern species.

Absolute sound pressure levels were very large. A comparison with other pinnipeds was not easy because this parameter was rarely measured and cited, in particular in wild animals. It was measured only for some captive male California sea lions (Schusterman 1978), with maximum values ranging from 95 to 103 dB at about 2 m (equivalent to 101-109 dB at 1 m), while in our study we found an average of 109 dB with maximum equal to 117 dB at 1 m. From the scarce data available we may conclude that pinnipeds tend to have very powerful vocalisations and that elephant seals emit unusually powerful sounds that may be perceived at great distance, a valuable feature due to their use in agonistic encounters.

Both the univariate and multivariate analysis of the correlation structure between variables revealed a very low redundancy. The full set of variables is required to fully describe structure of sounds and this is a strong indication of the fundamental complexity of signals. Internal bout structure is quite easy to summarise in one or few linear combinations of variables, but temporal and frequency domain variables are not. This result has a significant theoretical and practical impact on the functional study of elephant seals acoustic communication.

ACKNOWLEDGEMENTS

We wish to thank Roberto Sanvito for his advice on many different technical problems of the research and Maria Luisa Sanvito for her enthusiastic support; Carla and Alberto Galimberti for their long-lasting and strenuous support of our researches on seals and sea lions; Anna Fabiani, Ilaria Marzetti and Alice Camplani for the dedication demonstrated while in the field; prof. Gianni Pavan of the Centro Interdisciplinare di Bioacustica (Pavia) for his very kind advice on all aspects of bioacoustics; prof. Luigi Boitani of the Università degli Studi "La Sapienza" (Roma) for his assistance during every phase of our research on elephant seals; the Falkland Islands Government for permission to carry out our research in the Falklands; the Falkland Islands Development Corporation, Mr. Normand and Mr. Gray for letting us to do the field work on Sea Lion Island; Mr. King of the Secretariat for his help with research permits; Mr. Gurr of the Secretariat for his enthusiastic support of our research; two anonymous referees for their comments on the first draft. Special thanks go to David and Patricia Gray for their kind and constant help during our stay on Sea Lion Island.

REFERENCES

Bartholomew, G. A. & Collias, N. E. (1962). The role of vocalisation in the social behaviour of the Northern Elephant Seal. *Anim. Behav.*, **10**, 7-14.

Campagna, C., Lewis, M. & Baldi, R. (1993). Breeding biology of southern elephant seals in Patagonia. *Mar. Mammal Sci.*, **9**, 34-47.

Charif, R. A., Mitchell, S. & Clark, C. W. (1995). *Canary 1.2 User's manual.* Cornell Laboratory of Ornithology; Ithaca, NY.

Fabiani, A. (1996). Aspetti strutturali e funzionali del comportamento agonistico maschile nell' elefante marino del sud (*Mirounga leonina*). Degree Thesis. Università degli Studi di Roma "La Sapienza", Roma.

Fletcher, S., Le Boeuf, B. J. & Costa, D. P. (1996). On board acoustic recording from diving northern elephant seals. *J. Acoust. Soc. Am.*, **100**, 2531-2539.

Galimberti, F. (1995). Competizione tra i maschi e selezione sessuale nell' elefante marino del sud (*Mirounga leonina*) della Penisola di Valdés. PhD Thesis. Università degli Studi di Roma "La Sapienza", Roma.

Galimberti, F. & Boitani, L. (1999). Demography and breeding biology of a small, localised population of southern elephant seals (*Mirounga leonina*). *Mar. Mammal Sci.*, **15**, 159-178.

Gentry, R. L. (1970). *Social behavior of the Steller sea lion.* PhD.Thesis. University of California, Santa Cruz, California.

Krebs, C. J. (1989). *Ecological methodology.* Harper and Row Publishers; New York.

Kroodsma, D. E. (1977). A re-evaluation of song development in the song sparrow. *Anim. Behav.*, **25**, 390-399.

Laws, R. M. (1994). History and present status of southern elephant seal. In *Elephant seals. Population ecology, behavior and physiology,* (B. J. Le Boeuf and R. H. Laws, eds). University of California Press; Los Angeles (CA).

Le Boeuf, B. J. & Peterson, R. S. (1969). Dialects in elephant seals. *Science*, **166**, 1654-1656.

Le Boeuf, B. J. & Petrinovich, L. F. (1974a). Elephant seals: interspecific comparisons of vocal and reproductive behavior. *Mammalia*, **38**, 16-32.

Le Boeuf, B. J. & Petrinovich, L. F. (1974b). Dialects of northern elephant seals, *Mirounga angustirostris*: origin and reliability. *Anim. Behav.*, **22**, 565-663.

Le Boeuf, B. J. & Reiter, J. (1988). Lifetime reproductive success in northern elephant seals. In *Reproductive success* (T. H. Clutton-Brock, ed.). University of Chicago Press; Chicago and London, pp. 344-362.

Le Boeuf, B. J. & Laws, R. H. (1994). *Elephant seals. Population ecology, behavior and physiology.* Univ. California Press, Los Angeles (CA).

Marler, P. (1956). The voice of the chaffinch and its function as a language. *Ibis*, **98**, 231-261.

McCann, T. S. (1981). Aggression and sexual activity of male southern elephant seals, *Mirounga leonina. J. Zool. Lond.*, **195**, 295-310.

Miller, E. H. (1974). Social behaviour between adult male and female New Zealand fur seals, *Arctocephalus forsteri* (Lesson) during the breeding season. *Aust. J. Zool.*, **22**, 155-173.

Miller, E. H. (1991). Communication in pinnipeds, with special reference to non-acoustic signalling. In *The behaviour of the Pinnipeds.* (D. Renouf, ed.). Chapman and Hall; London, pp. 128-235.

Miller, E. H. & Job, D. A. (1992). Airborne communication in the Hawaiian monk seal, *Monachus schauinslandi.* In *Marine Mammal Sensory Systems,* eds (J. A. Thomas, R. A. Kastelein and A. Y. Supin.). Plenum Press; NewYork, pp. 485-531.

Miller, E. H. & Murray, A. V. (1995). Structure, complexity, and organization of vocalisations in harp seals (*Phoca groenlandica*). In *Sensory systems of aquatic mammals,* eds (R. A. Kastelein, J. A. Thomas and P. E. Nachtigall, eds). De Spil Publishers; Woerden, The Netherlands, pp. 237-264.

Modig, A. O. (1996). Effects of body size and harem size on male reproductive behaviour in the southern elephant seal. *Animal Behaviour*, **51**, 1295-1306.

Murphy, R. C. (1914). Notes on the sea elephant, *Mirounga leonina* (Linneus). *Bull. Am. Mus. Nat. Hist.*, **33**, 63-79.

Pavan, G. (1992). Bioacustica. In *Dizionario di etologia.* (D. Mainardi, ed.) Einaudi; Torino, p. 97.

Peterson, R. S. & Bartholomew, G. A. (1969). Airborne vocal communication in the California sea lion (*Zalophus californianus*). *Anim.Behav.*, **17**, 17-24.

Rousseeuw, P. J. & Croux, C. (1993). Alternatives to the median absolute deviation. *J. Am. Stat. Ass.*, **88**, 1273-1283.

Sandegren, F. E. (1976). Agonistic behavior in the male Northern Elephant seal. *Behaviour*, **57**, 136-158.

Sanvito, S. (1997). Struttura, ontogenesi e funzione dei vocalizzi maschili nell' elefante marino del sud (*Mirounga leonina*). Degree Thesis. Università degli Studi di Milano, Milano.

Sanvito, S. & Galimberti, F. (2000). Bioacoustics of southern elephant seals. II. Individual and geographical variation in male aggressive vocalisations. *Bioacoustics* **10**, 287-307.

Schusterman, R. J. (1978). Vocal communications in pinnipeds. In *Behavior of captive wild animals,* eds (H. Markowitz and V. J. Stevens). Nelson-Hall; Chicago, pp. 247-308.

Serway, R. A. (1986). *Physics for scientists and engineers,* 2 ed. Saunders College Publishing; Philadelphia.

Shipley, C., Hines, M. & Buchwald, J. S. (1981). Individual differences in threat calls of northern elephant seal bulls. *Anim. Behav.*, **29**, 12-19.

Shipley, C., Hines, M. & Buchwald, J. S. (1986). Vocalisation of Northern Elephant Seal bulls: development of adult call characteristics during puberty. *J. Mammal.*,

67, 526-536.

Sokal, R. R. & Rohlf, F. J. (1981). *Biometry.* 2nd edition. Freeman; San Francisco.

Stirling, I. & Warneke, R.M. (1971). Implications of a comparison of the airborne vocalisations and some aspects of the behaviour of the two Australian fur seal *Arctocephalus spp.* on the evolution and present taxonomy of the genus. *Aust. J. Zool.,* **19**, 227-241.

Stirling, I., Calvert, W. & Spencer, C. (1987). Evidence of stereotyped underwater vocalisations of male Atlantic walruses (*Odobenus rosmarus rosmarus*). *Can. J. Zool.,* **65**, 2311-2321.

Tembrock, G. (1968). Land mammals. In *Animal communication.* (T. Sebeok, ed.) Indiana University Press; Bloomington.

Trexler, J. C. & Travis, J. (1993). Nontraditional regression analysis. *Ecology,* **74**, 1629-1637.

Watkins, W. A. (1967). The harmonic interval: fact or artifact in spectral analysis of pulse trains. In *Marine bio-acoustics.* (W. N. Tavolga, ed.) Pergamon Press; Oxford.

Wiley, R. H. & Richards, D. G. (1978). Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behav. Ecol. Sociobiol.,* **3**, 69-94.

Zuberbuhler, K., Noé, R. & Seyfarth, R. M. (1997). Diana monkey long-distance calls: messages for conspecifics and predators. *Anim. Behav.,* **53**, 589-604.

Received 20 September 1998, revised 26 February 1999 and accepted 15 March 1999.