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BIOACOUSTICS OF SOUTHERN ELEPHANT SEALS. II. INDIVIDUAL AND GEOGRAPHICAL VARIATION IN MALE AGGRESSIVE VOCALISATIONS

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ABSTRACT

In traditional studies of animal communication, individual variability was sometimes considered less relevant than species specific aspects, mostly because the goal was the classifications of sounds in repertories. However, individual variability seems to have a significant role in signal function and evolution. In this paper, we analyse individual variation in the structure of aggressive vocalisations of male southern elephant seals and we compare sounds from our main study population, Sea Lion Island (Falkland Islands), with sounds recorded in the nearby population of the Valdés Peninsula (Patagonia, Argentina).

We firstly analysed the repeatability of acoustic parameters at vocalisation and male level. Repeatability of bouts of the same vocalisation was extremely high and this confirmed that vocalisation is the fundamental level of organisation of male acoustic communication in this species. Also repeatability of vocalisations of individual males was very high and hence sounds may effectively convey information about identity of the individual who emits the sound.

Male aggressive vocalisations were categorised into a small number of types and each male emitted always the same type of vocalisation. We compared the typology of sounds emitted by Sea Lion Island males with vocalisations by Valdés Peninsula males and we found striking differences. The two populations shared none of the sound types and, although similar in fundamental acoustics, sounds from the two populations had a different macrostructure. We conclude that these two populations show dialects in male acoustic communication, although the scarcity of recordings from other populations limits the scope of this conclusion.

Keywords: Southern elephant seal, *Mirounga leonina,* vocalisations, bioacoustics, individual variation, geographic variation, dialects, Falkland Islands, Valdés Peninsula.

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INTRODUCTION

In a previous paper (Sanvito and Galimberti 2000) we described the acoustic structure of male southern elephant seal aggressive vocalisations. We found that males emit vocalisations composed of a series of "bouts", each one with a distinct pattern of "syllables" and "syllable parts" and characterised by low frequency and high sound pressure level. We also found preliminary indications of a large variability between individuals. Individual variation in signal structure is not usually the core interest in bioacoustic analysis; traditional studies of animal communication were more concerned with the classification of repertories at the species level (Clark 1982). Notwithstanding this, individual variability may have an important effect on signal function and has a fundamental role in theoretical modelling of signal evolution (Johnstone 1997). Individual variation among individuals in vocal signals could be a cue for individual recognition. Inter-individual variation in male vocalisation has been found in other pinnipeds (*Arctocephalus forsteri*: Stirling 1971; *Mirounga angustirostris*: Shipley et al. 1981; *Odobenus rosmarus*: Stirling et al. 1987) and this variation has a clear social function (e.g. in male-male competition).

Another important component of variability in acoustic communication is geographic variation. Consistent differences in the predominant song or call of adults from different populations of the same species are usually labelled dialects (Marler and Tamura 1962). In most bird species, acoustic signal structure shows some variation between different populations (Marler and Tamura 1962, Pavan 1992). This phenomenon also has been identified in some mammals (*Macaca fuscata*: Green 1975), in particular in marine mammals (*Orcinus orca*: Deecke et al. 1998; *Physeter macrocephalus*: Weilgart and Whitehead 1997) and in some Pinnipedia species (*Leptonychotes weddelli*: Thomas and Stirling 1983; *Arctocephalus* spp.: Stirling and Warneke 1971).

Often dialects are based on differences in vocal repertoire in the same geographic region (e.g. Weddel seal), while sometimes they are based on differences in a particular element of the repertoire. Dialects were identified in male aggressive vocalisations of northern elephant seals *Mirounga angustirostris* (Le Boeuf and Peterson 1969, Le Boeuf and Petrinovich 1974). This species suffered a dramatic decrease in number and breeding range at the beginning of the century. During the 1960s, a phase of population increase, part of the original breeding range was re-colonised and this resulted in a scattered distribution with limited gene flow between different colonies. This in turn produced variations in aggressive vocalisations of males that, under spectrographic analysis, revealed that differences between colonies were sufficient to be classified as proper dialects. The successive expansions of the population increased the movements of young individuals between the original colonies and some of the new ones and this led to a reduction in differences in male vocal communications between these new colonies and the original ones.

In this paper we analyse variation in structure of aggressive vocalisations in southern elephant seals *Mirounga leonina.* We first examine individual variation in the population of Sea Lion Island (Falkland Islands) and then we analyse geographic variation by comparison with vocalisations recorded in the Valdés Peninsula (Patagonia, Argentina). The populations of Sea Lion Island and Valdés Peninsula are almost isolated during the breeding season (Lewis et al. 1996; Galimberti and Boitani 1999) so that gene flow between the two should be very limited.

MATERIALS AND METHODS

General information

Field work was carried out during one breeding season (mid August–mid September 1994) at Punta Delgada (Valdés Peninsula, Argentina – PD hereafter) and during two consecutive seasons (September–November, 1995 and 1996) at Sea Lion Island (Falkland Islands – SLI hereafter; Figure 1). The PD population of elephant seals is a part of the large Peninsula Valdés population (about 13,000 breeding females; Lewis et al. 1998). Movements of breeding males between the PD study area and adjacent areas were quite common (unpublished data). On the other hand, SLI (the main breeding site of the elephant seals population of the Falklands) shelters a small and localised population (about 560 females) with almost no movements of breeding males outside the island (Galimberti and Boitani 1999).

Details of data collection and sound recording protocols for the SLI population, together with details on sound measurement, are given elsewhere (Sanvito and Galimberti 2000). At PD we recorded a total of 4 hours of vocalisations (334 complete ones); we analysed the temporal and macrostructure of 126 vocalisations emitted by 27 males (17 adults and 10 large subadults) using the same protocol employed for SLI. Except where specified, we refer to these samples in the analysis.

Statistics

In many cases, data from different breeding seasons were pooled after a preliminary test of homogeneity (Mann-Whitney test). Statistics were calculated as mean plus standard deviation, or as median plus

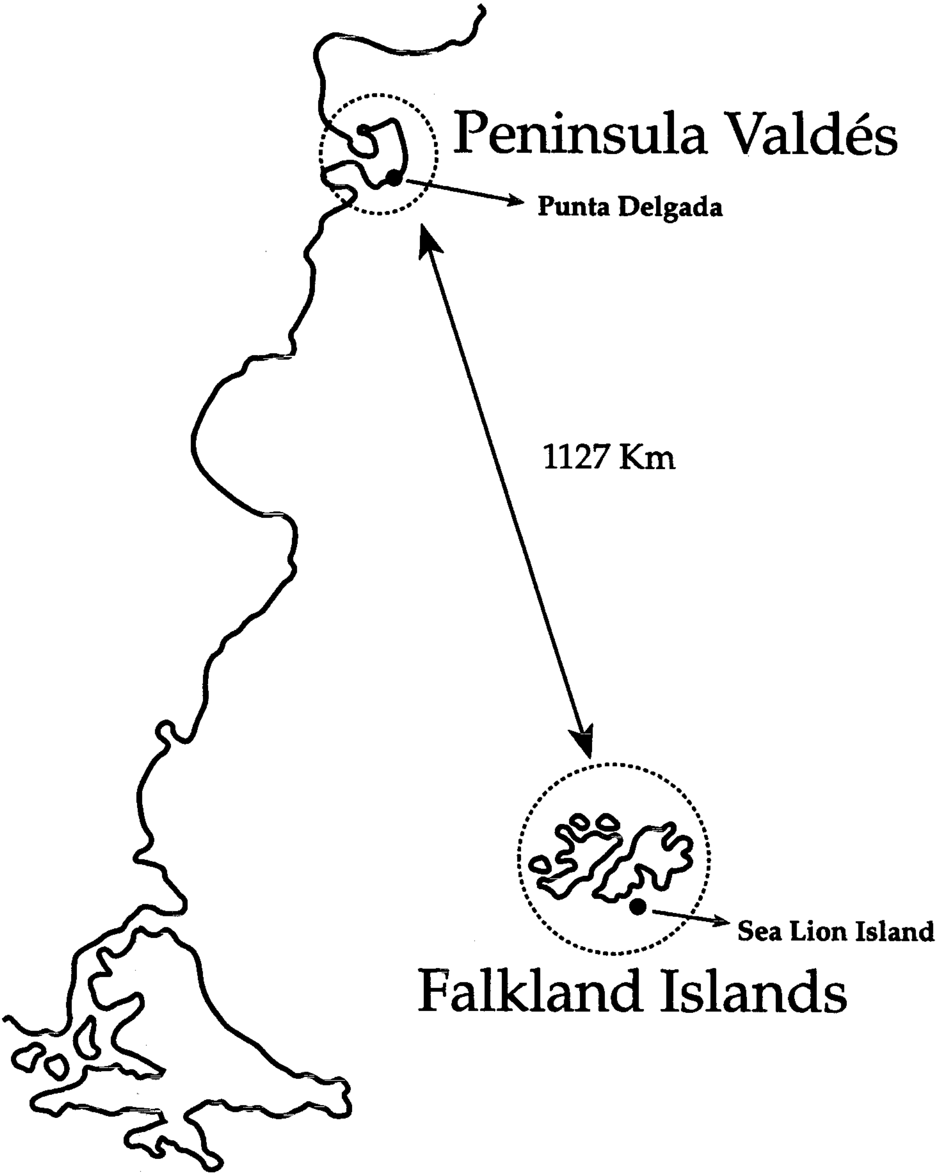

Figure 1. Geographic location of Sea Lion Island (52° 26' S, 59° 05' W) and Punta Delgada (42° 46' S, 63° 38'W). We present the geodesic distance, calculated from geographic co-ordinates using IERS-92 ellipsoid.

median absolute deviation (MAD: Rousseeuw and Croux 1993) for skewed non-normal variables.

To evaluate the constancy of bout structure per vocalisation and of vocalisations per male, we calculated repeatability indices from variance components (Lessells and Boag 1987). Repeatability is equivalent to the intraclass correlation coefficient (Sokal and Rohlf 1981) and measures the proportion of variance between hierarchical levels of classification (in our case bouts, vocalisations, males). We tested significance of repeatability indices by randomisation ANOVA (Manly 1996).

We categorised sounds into a small number of classes by visual inspection of waveforms and spectrograms. To verify accuracy of this classification we set up a blind test with a random selection of ten vocalisations: we presented each vocalisation three times in random order. Each vocalisation was classified correctly during each trial. To verify precision of this visual classification we applied a discriminant analysis (Kanwal et al. 1994, Boughman and Wilkinson 1998) to the full set of log transformed variables (macrostructure, time domain and frequency domain). We ran a preliminary MANOVA test using randomisation (Manly 1991) to verify applicability of discriminant analysis before calculating discriminant functions.

Basic statistics and tests were calculated using StatView software (Abacus Concepts Inc.), discriminant analysis was carried out by SYSTAT (SYSTAT Inc.) and randomisation tests were carried out by RT software (Manly 1996), with 10,000 randomisations in each test.

RESULTS

Repeatability of measures

In this species, the vocalisation is the basic functional structure of male communication and each male seems to have peculiar vocal features (Sanvito 1997). To analyse variability at different levels of the hierarchical organisation of signals, we calculated a simple standardised measure of relative variability, the coefficient of variation. We then compared CVs calculated for all bouts, for bouts in each vocalisation and for bouts from each male. For all variables we found that relative variability was higher for the first series of CVs, calculated for all bouts, than for CVs calculated for bouts per vocalisation or for bouts per male (Figure 2). We also discovered that variability was lower at vocalisation level than at male level (Figure 2), with the only exception of relative peak time, which showed almost the same variability at male and vocalisation level.

We then calculated repeatability values (Table 1) for all variables at vocalisation level between bouts ($n = 272$) and at male level between vocalisations ($n = 127$). On average, repeatability values were high, both at vocalisation level (0.70 ± 0.21, 60% of values higher than 0.70) and at male level (0.56 ± 0.20, 50% of values higher than 0.50).

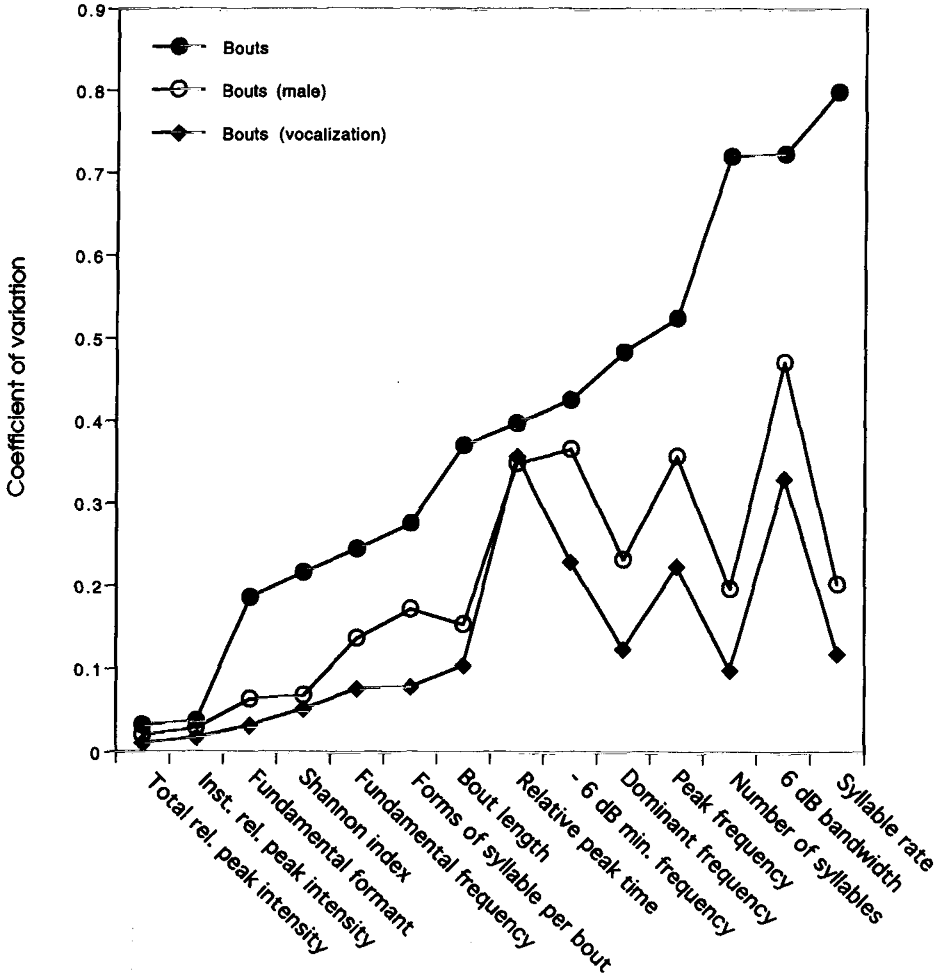

Figure 2. Coefficient of variation profiles of bouts at different levels of the hierachical organisation of acoustic signals. For each acoustic variable we calculated CVs on all bouts, on bouts of each vocalisation, and on bouts of each male.

Temporal variables calculated for whole vocalisations (such as number of bouts and vocalisation length) had low repeatability, while temporal variables calculated for bouts (bout length and interval between bouts) had very high values of repeatability; hence, the temporal structure of vocalisations depended mostly on the structure of the single bouts. Sound intensity variables had high repeatability values: the absolute sound pressure level had the maximum repeatability. Both sound intensity and frequency variables showed higher repeatability levels for each parameter calculated on the whole bout, rather than for the instantaneous ones (hence, we considered the

TABLE 1

Repeatabilities of acoustic parameters calculated at vocalisation level between bouts and at male level between vocalisations.

Variables	Vocalisation	Male
N° of bouts		0.454
Vocalisation length		0.366
Signal length/total length		0.361
Bout length	0.808	0.768
Interval between bouts length	0.467	0.700
Relative peak time	0.229	0.391
Inst. relative peak intensity	0.650	0.431
Total relative peak intensity	0.834	0.605
Sound pressure level	0.814	0.742
Peak frequency	0.385	0.354
Dominant frequency	0.753	0.405
Fundamental formant	0.921	0.635
6 dB bandwidth	0.586	0.604
–6 dB minimum frequency	0.625	0.192
Fundamental frequency		0.619
Part with max peak pressure		0.440
Number of syllables per bout	0.918	0.820
Syllable rate	0.970	0.880
Kinds of syllable per bout	0.744	0.497
Shannon index	0.719	0.879
Average repeatability	0.695 ± 0.209	0.557 ± 0.197

former as the most meaningful measures of the bout structure). Frequency measures with very high repeatability were the fundamental formant and the fundamental frequency. Finally, parameters describing syllable composition of bouts were also highly repeatable. In all, we found a high level of constancy and repeatability of acoustic structure of vocalisations.

Macrostructure of aggressive vocalisations and typology classification

We identified vocalisation types distinctive to each population using the internal structure of the bout (ordering, "part" composition and length of syllables that compose each bout). These types were recognisable both in recordings under artificial stimulation and in recordings under natural conditions, and each male emitted the same type of vocalisations in all situations.

We recognised four vocalisation types: drumming (D) and continuous (C) vocalisations had a homogeneous and well defined structure and were shared by different males (Figure 3); atypical (A)

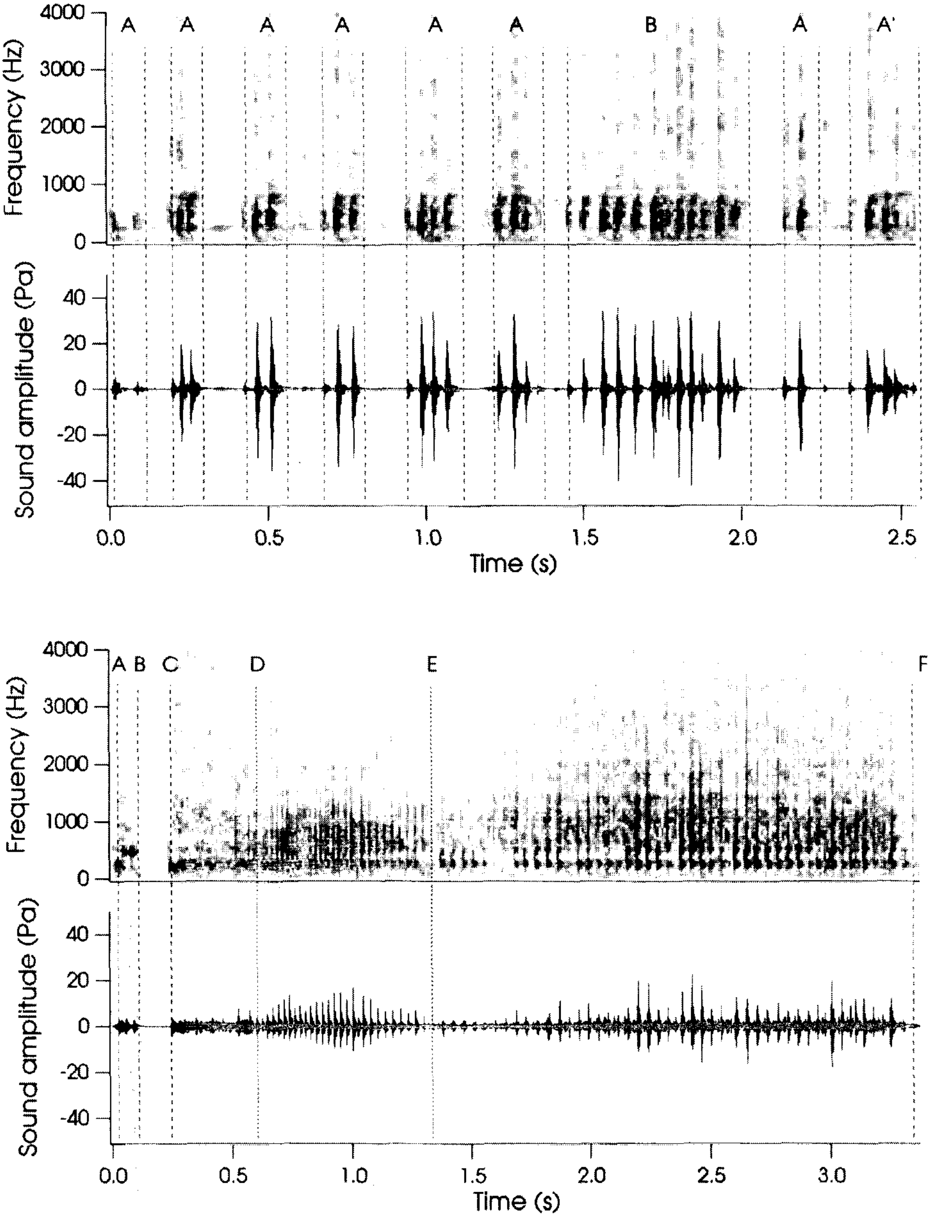

Figure 3. Bout of a "drumming" (top) and a "continuous" (bottom) vocalisation. The drumming bout was composed of many equal syllables (A), by a longer syllable (B) near the end of the bout, and by the last syllable (A′) similar to A, slightly longer and with closer pulses. The continuous bout was composed of just two syllables (A-B and C-F), the latter still composed of three parts (C-D, D-E and E-F).

TABLE 2

Vocalisation types distinctive to Sea Lion Island and Punta Delgada populations.

Type	SLI	PD	Syllable pattern	Notes
D	X		AAAAAABAA	Each syllable made up by one part
C	X		ABC	The 2nd (or 2nd and 3rd) syllable made up by 3-5 parts
G		X	AB/ABA	1 or 2 gargling parts (or syllables), plus 1 with high power
E		X	AB/ABA	Like G, but with some explosive pulses in the gargling parts

vocalisations also had a defined structure but were typical of just one male; non-structured (NS) vocalisations had a much less regular structure (Table 2). Each male always emitted just one type of vocalisation. The only two exceptions were two large subadult males that during 1995 breeding season varied their vocalisations, emitting both C and NS types (one of them came back in 1996, adopted a C vocalisation and kept it in 1997).

In the sample of 57 males, 35.1% emitted D vocalisations, 31.6% C, 21.1% A, and 8.8% NS. The majority (89.5%) of mature males emitted well-structured vocalisations (C, D and A) and 76.5% of them emitted one of the two main types (C or D): hence, the variation of sound macrostructure between males was limited. Individual males emitted the same vocalisation type throughout the whole breeding season. Hence, vocalisation type was a stable component of phenotype in mature males.

Bouts of drumming vocalisations (Figure 3) were made up of more syllables (ranging from 5 to 12); syllables were of two or three different kinds and they were repeated in the bout following in a regular pattern (AAAAAABAA'). A and A' were similar in length but slightly different in pulse rate. Syllable B was more or less twice as long as A, but had similar pulse rate. All syllable types were composed of one "part" (the pulse rate in the syllable was constant).

Bouts of continuous vocalisations (Figure 3) were composed of two or three different syllables. The first one was always made up of 1-3 pulses (generally 1), while the other two syllables were sometimes connected (bouts formed of 2 syllables) and sometimes not (bouts formed of 3 syllables). The second syllables were composed of more syllable "parts", characterised by a different pulse rate (2-5 parts, but typically 4).

To verify applicability of our classification by visual inspection, we carried out a discriminant analysis between C and D vocalisations, using the main set of acoustic variables (18 variables, see Sanvito and

Galimberti 2000). We ran a preliminary MANOVA with randomisation test (10,000 randomizations) and we found a very significant difference between C and D vocalisations (Wilk's $\lambda = 0.03206$, $p = 0.0001$). We then calculated a discriminant function (Figure 4) and compared the classification obtained by this function with our visual classification. We found a 100% concordance in the classification of 58 vocalisations (32 C and 26 D, excluding vocalisations missing in some variables). With just one exception, vocalisations of the two groups were concentrated around respective centroids (Figure 4, left). The variables that had a greater effect on the discriminant function were: number of syllables (standardised canonical coefficient: 4.3453), number of types of syllable per bout (-2.6616), bout length (-2.1652), Shannon index (1.7760), ratio signal length/total length (1.6185), vocalisation length (1.2360) and syllable rate (-1.0627). All these variables are structure or time domain variables and most of them belong to the first group. To explore the effect of different groups of variables on the classification by discriminant function, we ran a separate analysis on structure, time domain and frequency domain matrices. Using the structure variables matrix 1.1% of vocalisations was misclassified; the corresponding figures were 6.6% when analysing the time domain matrix, and 30% when analysing the frequency domain matrix. In all, both macrostructure and time variables were sufficiently different between vocalisations of the two types to guarantee a good classification. Also the joint analysis of time and frequency domain guaranteed a good classification (1 error in classification of 60 vocalisations), without contribution of structure variables.

Structural differences between C and D vocalisations

To analyse in detail differences in acoustic structure between C and D vocalisations as classified by visual inspection only, we carried out univariate tests on structure, time domain and frequency domain variables (Table 3; Figure 5). We detected statistically meaningful differences in bout length between C and D vocalisations, the first ones longer than the second ones (t-test with randomisation: mean difference = 0.67 s; $p = 0.0001$). C vocalisations had also longer intervals than the D ones (t-test with randomisation: mean difference = 0.40 s; $p = 0.0002$). The difference in the syllable part with maximum peak pressure length (DELAT_T) between C and D vocalisations was large, with longer parts for the continuous ones (t-test with randomisation: mean difference = 0.57 s; $p = 0.0001$).

Considering frequency parameters, we found differences between C and D vocalisations with respect to the peak frequency (t-test with randomisation: mean difference = 115 Hz; $p = 0.0126$). Also differences in fundamental formant between C and D vocalisations

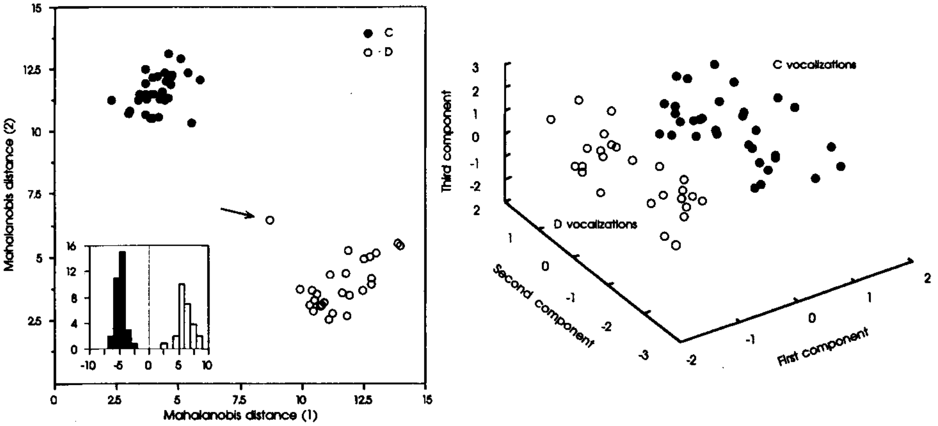

Figure 4. Left. Scatterplot of Mahalanobis multivariate distances of vocalisations of C (filled circles) and D (open circles) type from centroids of respective groups. The only outlier (arrow) is a vocalisation of a male that had a vocalisation somewhat different from the typical C vocalisations: notwithstanding this, both visual inspection and discriminant function attributed this vocalisation to C type. The inset in the left corner is a histogram of discriminant coefficients for C (filled bars) and D (open bars) vocalisations.
Right. Scatterplot of C and D vocalisations in the space defined by the first three principal components of a PCA analysis carried out using the same variable set of the discriminant analysis (as in Sanvito and Galimberti 2000).

were significant (t-test with randomisation: mean difference = -31 Hz; p = 0.0008). On the other hand, differences between the -6 dB minimum frequency values were only marginally significant, while differences for the 6 dB bandwidth were not significant, even though the mean values were rather different. Finally, there were no meaningful differences in fundamental frequency and dominant frequency between C and D vocalisations.

Intensity parameters showed a small difference between C and D vocalisations. Instantaneous relative peak intensity and total relative peak intensity had statistically meaningful differences between the two types (t-test with randomisation: mean difference = -0.0120; p = 0.0248 and mean difference = -0.0216; p = 0.0001), but with very small magnitude and differences in SPL were small (about 1 dB) and not significant.

Finally, as expected, we found large differences between C and D vocalisations in variables that describe the internal structure of the bout. The bimodal distribution of structure variables (Sanvito and Galimberti 2000) reflects these differences. We found significant differences between types in all parameters, except for the number of types of syllable per bout (Table 3). The ranges of variables were clearly non-overlapping between types.

TABLE 3

Differences between C and D vocalisations in acoustic parameters. Sample size is 55 vocalisations for C and 40 for D types except for interval length and signal length/total length ($n_C = 33$, $n_D = 28$) and for the Shannon index ($n_C = 53$, $n_D = 34$). Mean values were presented ± standard deviation. Probabilities of tests on mean difference (MD) and variance ratio (F) were calculated by randomisation (10000 samples); values in bold were significant at 0.05 or less.

Variables	$Mean_C$	$Mean_D$	MD	$p(MD)_{10000}$	F	$p(F)_{10000}$
Vocalisation length (s)	12.8 ± 11.7	11.5 ± 11.8	1.3	0.5988	0.9762	0.9717
Bout length (s)	3.5 ± 0.8	2.9 ± 0.6	0.7	**0.0001**	2.0741	**0.0079**
Interval length (s)	2.2 ± 0.4	1.7 ± 0.3	0.4	**0.0002**	1.9250	0.0577
Signal length/total length	0.711 ± 0.058	0.706 ± 0.065	0.0054	0.7198	0.8171	0.5725
Relative peak time	0.700 ± 0.234	0.661 ± 0.137	0.0394	0.3493	2.9418	**0.0007**
Part with max peak pressure (s)	1.06 ± 0.51	1.7 ± 0.3	0.58	**0.0001**	5.3387	**0.0001**
Inst. rel. peak intensity	0.741 ± 0.028	0.753 ± 0.021	-0.012	**0.0248**	1.8326	0.0597
Total rel. peak intensity	0.756 ± 0.022	0.778 ± 0.021	-0.022	**0.0001**	1.0177	0.9560
Peak frequency (Hz)	496 ± 264	382 ± 157	115	**0.0126**	2.8381	0.0557
Dominant frequency (Hz)	410 ± 201	351 ± 142	58	0.1255	2.0088	**0.0451**
Fundamental formant (Hz)	251 ± 39	282 ± 50	-31	**0.0008**	0.5979	0.6431
Fundamental frequency (Hz)	23 ± 5	25 ± 7	-2	0.1283	0.4904	0.9573
-6 dB min. frequency (Hz)	169 ± 72	218 ± 49	25	0.0749	1.2881	0.5295
6 dB bandwidth (Hz)	618 ± 365	369 ± 249	-3	0.9727	1.2893	0.5161
N° of syllables per bout	2.2 ± 0.5	2.4 ± 0.7	-5.6	**0.0001**	0.0233	**0.0001**
Syllable rate (syll./s)	2.2 ± 0.5	7.8 ± 3.5	-2.1	**0.0001**	0.0274	**0.0001**
Forms of syllable per bout	0.65 ± 0.19	2.78 ± 1.14	-0.22	0.0952	0.5615	0.0700
Shannon index	0.99 ± 0.004	0.64 ± 0.13	0.36	**0.0001**	0.0009	**0.0001**

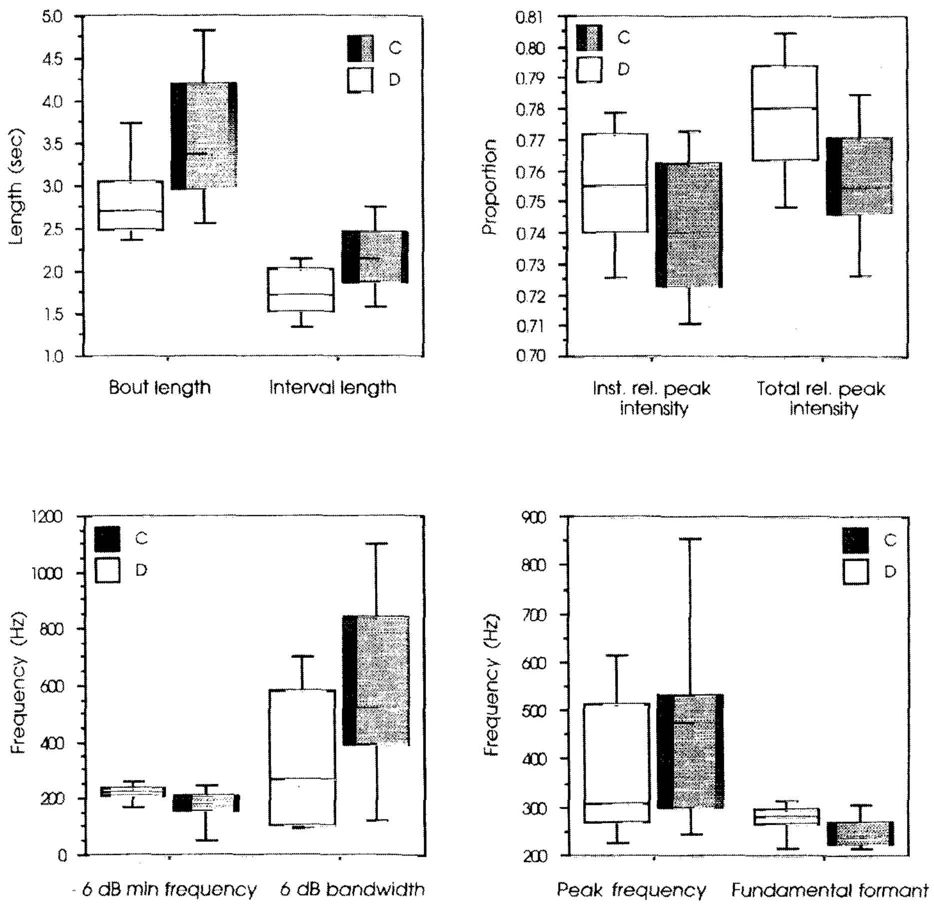

Figure 5. Boxplots of some acoustic variables of C and D vocalisations. Boxes indicate points included between 25 and 75 percentiles, horizontal lines in boxes indicates the median and the external lines indicate 10 and 90 percentiles.

Correlations found between the length of the part with maximum peak pressure (DELTA_T) and measures of the internal structure of the bouts (Sanvito and Galimberti 2000) were mostly due to differences between C and D vocalisations in the length of the part containing the peak of pressure.

We compared variability of C and D vocalisations using randomisation tests on variance ratio of variables. We found significant differences in all structure variables and in some temporal and frequency variables (Table 3). The most interesting aspect of the differences in variance between C and D vocalisation is that variance in structural variables is lower for C vocalisations, while variance in time and frequency domain variables is lower for D ones. In other words, C vocalisations had a more stereotyped bout structure but D vocalisations had a more stereotyped time and frequency domain structure.

Comparison between populations

Sound structure at Punta Delgada

The peculiar feature of the vocalisations of PD males was the presence of a long portion of pulsing signal (sometimes forming whole syllables) with very low sound intensity, resulting in a "gargling" sound (Figure 6, top). This effect is in part produced by the vibration of the proboscis caused by air exhalation. Another peculiar feature was the intermixing of gargling parts with 2 or 3 "explosive" pulses (Figure 6, bottom). These pulses were well spaced and loud, similar to the sound of a tam-tam gong.

We identified three kinds of vocalisations, the two main ones, gargling (G) and explosive (E) and a secondary one (A), made by some males with a structured vocalisation distinctive to each male (Table 2).

In the G vocalisations (Figure 6) each bout had one high intensity part and one or two "gargling" parts, while in the E vocalisations (Figure 6) the gargling parts contain 2 or 3 explosive pulses. G and E types were similar: basic structure was the same and the only difference was the presence/absence of the explosive pulses.

In all, 66% of the males emitted vocalisations with at least one explosive or gargling component in the bout, which were typical of PD population. The share of A males of PD population (34%) was bigger than the one of SLI (25%): this was possibly due to the larger size and the higher male mobility of the Valdés Peninsula population.

The number of bouts per vocalisation had a median value equal to 2 bouts (MAD = 1) in a very asymmetric distribution ($g_1 = 1.199$) and 60% of vocalisations were composed of 1 or 2 bouts, ranging from 1 to 9 (Table 4).

Vocalisation length had an asymmetric distribution ($g_1 = 1.208$) with median value equal to 8.607 s (MAD = 5.741) and the largest number of occurrences in the lowest portion of the distribution range. The bouts length median was 2.848 s (MAD = 0.914), while the mean interval between bouts length was 2.289 ± 1.284 s (n = 76: the vocalisations composed of more than 2 bouts): 88% of vocalisations had intervals between bouts not longer than 3 s. The share of vocalisation effectively occupied by signal (Q_BOUT), had a mean value of 0.670 ± 0.123 (n = 76); that is, more than ¾ of the vocalisation.

Relative peak time had a symmetric distribution and the mean value was 0.443 ± 0.217: hence the amplitude peak was usually in the central part of the bout.

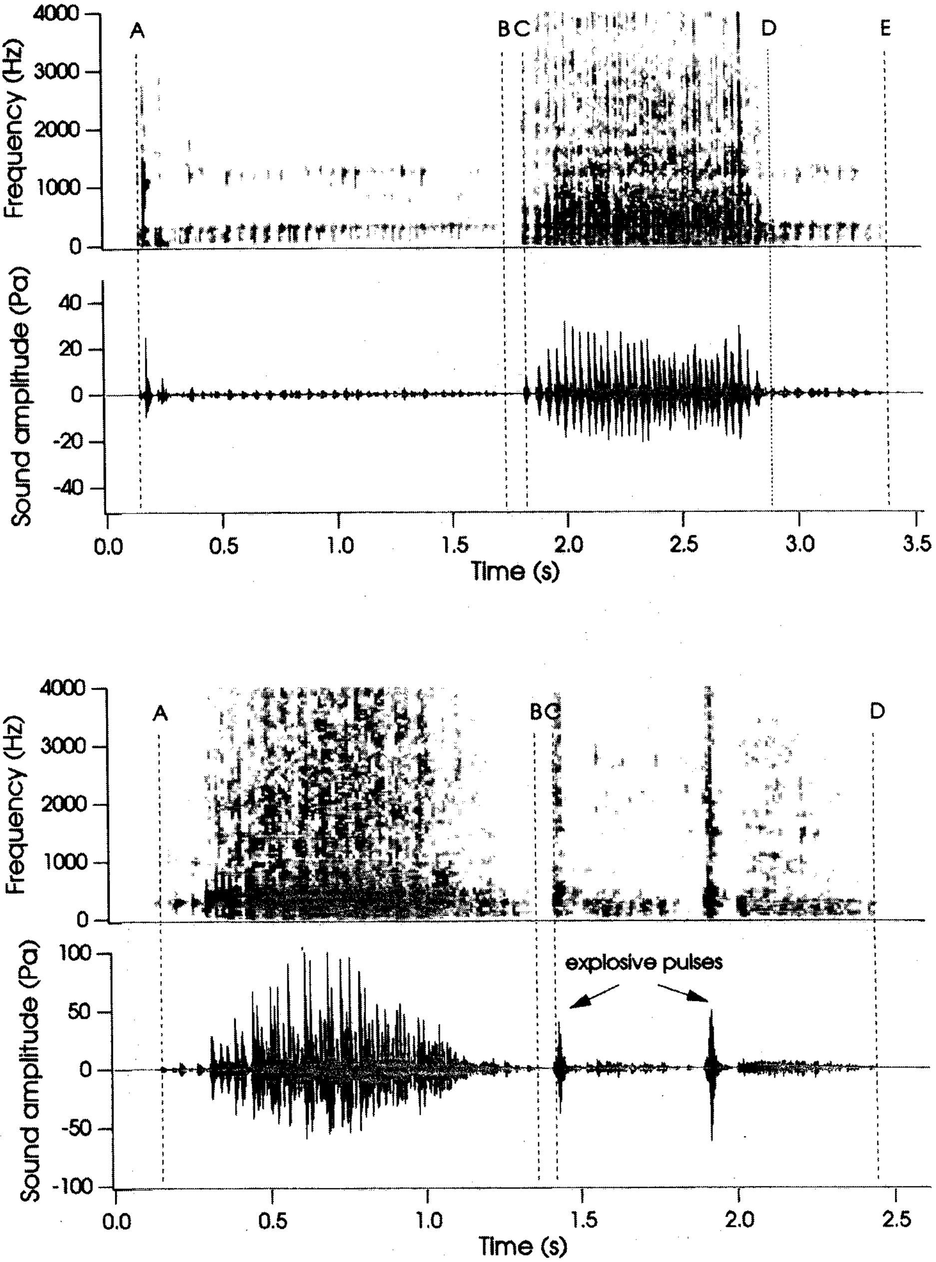

Figure 6. Bout of a "gargling" (top) and an "explosive" (bottom) vocalisation. The gargling bout was composed of two syllables (A-B and C-E); the former was composed of just one gargling part, while the latter was composed of two parts (C-D with high energy and D-E that is a gargling one). The explosive bout was composed of two syllables (A-B and C-D), each one composed of just one part.

TABLE 4

Descriptive statistics of temporal parameters for Punta Delgada population. Values were calculated at the vocalisation level.

Variables	n	Mean	SD	Min	Max	CV
N° of bouts	126	2.595	1.855	1.000	9.000	0.715
Vocalisation length (s)	126	11.567	9.534	1.035	49.601	0.824
Bout length (s)	126	3.336	1.588	1.035	8.960	0.476
Interval length (s)	76	2.289	1.284	0.510	8.963	0.561
Q_BOUT	76	0.670	0.123	0.403	0.954	0.184
Relative peak time	126	0.443	0.217	0.024	0.956	0.491

Similarities and differences between PD and SLI

Both at PD and SLI elephant seals vocalisations were low frequency sounds, whether regarding the dominant frequency, the F0, the fundamental formant and the main other formants. The sounds were very characteristic due to the pulse train structure. The temporal structure was rather constant at individual level, at least for mature males, whose vocalisations were very stereotyped. Sound intensity level reached very high values and internal bout composition was typical of different individuals and populations.

The main differences between the two populations were in the bout structure and reflected the different vocalisation types distinctive to each population: PD vocalisations were categorised into completely different types from SLI ones. In particular syllables with a gargling or explosive structure were present in the vocalisations of males of PD population while they were almost absent in the ones of SLI. The presence of such a vocal structure was the most evident difference between the two populations (independently from the other bout structure features). Only one Falklands male had a vocalisation very similar to the gargling type of PD and none coming from Valdés had a vocalisation identifiable in the continuous or drumming types, distinctive of the other population. G and E vocalisations contained less energy than the ones typical of SLI. In fact a big part of the bout was occupied by a very soft signal (the gargling or explosive parts). This feature was the main difference between the populations, but the syllable composition and the macrostructure of vocalisations were also very different (Figure 6). Moreover, in both populations there were some males classified as A type, with a structured vocalisation, but with variable features not referable to any other distinctive type of SLI or PD. Finally, in both the populations, younger males usually emitted non-structured vocalisations (Sanvito 1997).

For the temporal structure, all the parameters considered had different values in the two populations. The main difference was in the relative peak time (t-test with randomisation: mean difference = -0.1702; p = 0.0001). This difference was related to the different internal structure of bouts: at PD, the amplitude peak occupied an earlier position in the vocalisation than at SLI, because the remaining parts of the sound were usually occupied by gargling without peaks of intensity; at SLI, peak intensity was more spread along the bout and it was usually located in the last third both in C and D sounds.

Other important differences were found in two strongly correlated parameters, the interval between bouts and the Q_BOUT. At PD, the inspiration pauses were longer than at SLI (t-test with randomisation: mean difference = -0.4524; p = 0.0003) and hence the share of vocalisation occupied by signal was lower (t-test with randomisation: mean difference = 0.0612; p = 0.0009).

In order to compare the multivariate time structure of sound between populations, we log-transformed the variables to improve the symmetry and the homoscedasity (excluding number of bouts due to high correlation with vocalisation length) and we ran a multivariate analysis of variance with randomisation test. The two populations showed a clear difference in time structure (Wilks' λ = 0.7551; p = 0.0001). Hence, although the general structure of sound emission (pulse train) was similar between the two populations, we found important and distinctive differences that could be ascribed to different local dialects.

DISCUSSION

Individual variability of vocalisations

The main advantage of the analysis of acoustic properties of sounds at individual level is the assessment of the relative importance of intra- and inter-individual variability. The most common assumptions in theories of signal evolution are the constancy of signal structure emitted by the same individual in the same context and the variability between individuals (Johnstone 1997). We found both qualities in southern elephant seals vocalisations. Variation of the acoustic structure of different bouts and vocalisations emitted by the same male was small, while variation between individuals was large. Repeatability analysis supports the hypothesis that vocalisations are an important and homogeneous structure of male communication and that males have well-defined individual vocal features. Repeatability was large for all the variables of macrostructure, for most frequency variables, for all temporal variables with the exception of the ones measured on the whole vocalisation and for the most important measures of relative sound intensity. On the other hand, variability between males was large for all the considered variables. Thus, acoustic signals may in principle carry valuable information about identity of the individual who produced them (Shipley et al. 1986).

Types of vocalisations

The composition of syllables and syllable parts of southern elephant seal sounds was regular and stereotyped. The constancy of the macrostructure of vocalisations was so high that it was possible to classify male vocalisations into a small set of sound types and the attribution of each male to a specific type was very repeatable. The most interesting aspect of this regularity is that it permitted the reduction of the complex array of sounds emitted by different males of different populations to a simple typology and this also facilitates comparisons between local populations. Classification based on visual inspection of waveforms and classification based on statistical analysis of sound measurements gave concordant results, confirming that the sound classes have very different acoustic structure. Basic aspects of macrostructure are, as expected, very different between sound classes but time and frequency domain variables were also different. At Sea Lion Island, C vocalisations had longer bouts and intervals between bouts than the D ones. The resulting bout "rhythm" was very different, being more rapid and regular in D vocalisations. This type was more rhythmic due to both the internal bout structure (with a lot of similar syllables, emitted with an higher rate and resulting in a smaller Shannon index) and the bout spacing (shorter and closer bouts). Moreover, frequency and relative intensity measures suggest that in D vocalisations the share of sound energy carried by dominant frequency was larger than in the C ones, while there were opposite trends in peak frequency and fundamental formant.

Dialects

In northern elephant seals, syllable rate (called pulse rate by some authors, as the rate at which whole syllables occur in the bout; Bartholomew and Collias 1962) and syllable length allowed the recognition of dialects among different populations or among colonies breeding in different islands (Le Boeuf and Petrinovich 1974). In this species, bouts have a simpler and more fixed structure than in *M. leonina*. They are mostly composed of syllables that are all the same, each one including a variable, but constant for each male, number of pulses recurring at regular intervals in the bout (Bartholomew and Collias 1962, Shipley et al. 1981, Shipley et al. 1986). This structure could be compared with the Sea Lion Island drumming sound, even though in the latter sound syllables were not all the same because there was always a longer syllable, sometimes with different pulse rate. Syllables in northern elephant seal vocalisations are all either composed of just one pulse (clap threat) or all composed of 3-7 pulses (burst threat), or some are composed of one and others by more pulses (patterned clap threat) (Bartholomew and Collias 1962, Shipley et al. 1986). With a such simple structure it is rather easy to recognise different dialects based on few very significant parameters.

Despite the higher complexity of sound macrostructure of the southern species, the comparison between Sea Lion Island and the Valdés Peninsula revealed a general similarity in the gross structure of sounds but significant differences between fine structure and sound typology. This difference is an indication of the presence of a dialects system similar to the one found in the northern species (Le Boeuf and Peterson 1969, Le Boeuf and Petrinovich 1974). The Falklands and the Valdés Peninsula are both populations of the South Georgia stock, but they are almost isolated during the breeding season. Resighting in the Falklands of elephant seals tagged in the Valdés Peninsula is quite common during the moulting season but not during the breeding season (Lewis et al. 1996, Galimberti and Boitani 1999). On Sea Lion Island during the breeding season we never saw tagged individuals from other populations. Gene flow between the populations should therefore be very limited.

The main differences between Punta Delgada and Sea Lion Island was in the bout structure of sounds and reflected the different vocalisation types found in each population: Punta Delgada vocalisations were classifiable in types completely different from Sea Lion Island ones. Typical vocalisations from Punta Delgada contained less energy than the ones typical of Sea Lion Island. In fact a big part of the bout was a very soft signal (the gargling or explosive parts). This feature was the main difference between the populations, but syllable composition and temporal structure of vocalisations were also different. In both populations we found some males with a structured vocalisation but with variable features not referable to any other distinctive type. These vocalisations were not comparable between populations.

Unfortunately, recordings from other populations of southern elephant seals are not readily available. Hence the evidence for the presence of dialects is limited only to the Valdés Peninsula and the Falklands.

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