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SOURCE LEVEL OF MALE VOCALISATIONS IN THE GENUS *MIROUNGA*: REPEATABILITY AND CORRELATES

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ABSTRACT

Male vocalisations have an important role in mating tactics, breeding strategies and sexual selection. Most studies of vocalisations are concentrated on the time and frequency domains, while the intensity of sound, an important acoustic parameter that should be related to body size, is almost completely ignored as a possible honest signal of resource holding potential (RHP) and cue for mate choice. In this paper, we analyse the repeatability, the correlations with age and size, and the relationship with breeding status of source level (SL) of male vocalisations in the two species of elephant seals (*Mirounga leonina* and *M. angustirostris*). We found a high repeatability of SL, equal or higher than the repeatability of frequency domain parameters estimated in a previous study. Southern elephant seal males were significantly larger and produce significantly more powerful vocalisations than northern males. Moreover, in each species SL was related to age, body size, and breeding status of males, but relationships were weak and accounted for just a small proportion of SL variance. We conclude that, although SL may be an honest signal of gross differences of RHP, it is not, by itself, a good candidate for the transmission of high-resolution information on individual phenotype. A combination of SL and frequency components could be, on the contrary, an effective way to communicate RHP.

Keywords: male vocalisations, source level, honest signals, elephant seals, *Mirounga*

INTRODUCTION

There is an increasing interest in the evolution and function of animal acoustic communication (Simmons et al. 2002). Male vocalisations have an important role in various aspects of mating tactics, evolution and sexual selection, including individual recognition of neighbour males (Fernández-Juricic et al. 1999), male competition for mates (Clutton-Brock & Albon 1979; McElligot et al. 1999) and female choice (McComb 1991). Most studies on the structural and functional

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correlates of male vocalisations have been focused on time and frequency domains (Simmons et al. 2002). There is very limited information regarding another important aspect of vocalisations, the absolute intensity of sound, usually measured as the source level (SL), i.e., the sound pressure level (SPL = the logarithm of the ratio between the sound pressure emitted and a standard reference pressure, 20 μPa in air: Charif et al. 1995) measured on the acoustic axis at 1 m distance from the source.

There is very little information on SL of animal species and SL has very rarely been measured in wild-living mammal species in the air, although measurements are available for vocalisations emitted by marine mammals in the water (Rasmussen et al. 2002). SL was measured in the air in only one Pinnipedia species, the California sea lion *Zalophus californianus* (Schusterman 1978). The lack of information on absolute SL in free-ranging individuals is probably related to the practical problems involved in getting calibrated measurements of animal vocalisations, in particular in the field (Nelson 2000). The measurement of SL requires a standardisation of the distance from the source, a task that is not easily accomplished in field work settings.

In humans, SL depends on the lungs' size that is, in turn, related to body size, although the relationship is not exact, and many other factors are involved (Titze 1994). This relationship can be expected to hold also in other mammals that have a similar sound production mechanism. Therefore, SL may convey information about the phenotype of the male and can be an "honest" signal of its resource holding potential (Kotiaho et al. 1999; Fitch & Hauser 2002). Notwithstanding this, to our best knowledge the relationship between SL and body size has never been tested in any mammalian species (e.g., a standard textbook on animal communication, Bradbury & Vehrencamp (1998), omits any reference to this relationship).

Male vocalisations are a very important component of competition for access to females in the species of the genus *Mirounga* (Bartholomew & Collias 1962; Sanvito & Galimberti 2000a). Male elephant seals interact at short distance (0-50 m) by facing one another and using a mixture of conventional display and direct fight, in which the audio component plays a main role (in one of the study populations more than 70% of agonistic interactions includes a vocal display; Fabiani (1996)). In this study, we present data on field measurements of SL in free ranging males of southern (*M. leonina*; hereinafter SES) and northern elephant seals (*M. angustirostris*; hereinafter NES). We calculate individual repeatability of SL, compare SL among the two species and analyse the structural and functional correlates of SL, focusing on age class, body length and breeding status.

METHODS

Field work was carried out on southern elephant seals during four breeding seasons (1996-1998 and 2000) at Sea Lion Island (Falkland Islands; hereinafter SLI), and on northern elephant seals during one breeding season (2001) at San Benitos Islands (Baja California, Mexico; hereinafter SBI). In both cases, the local population was rather small, with 40-70 breeding males per season. Males were marked using commercial hair dye. At SLI, they were also tagged (Jumbo Rototags, Dalton Supplies Ltd.) to permit recognition between seasons. Additional information on the marking protocol is presented elsewhere (Galimberti & Boitani 1999).

SL (in dB) was measured with a digital sound level meter (Model 1400, Quest Technologies), in standard condition of solicitation of males (Sanvito & Galimberti 2000a). Elephant seals react to a human approach with the same stereotyped aggression pattern that they use during interactions with other males, starting with the emission of aggressive vocalisations. The sound level meter was fitted with a 1-meter long reference pole and the tip of the pole was kept between the lower canines of the male during measurement. To avoid the transmission of vibration the pole was not in contact both with the animal and the microphone of the sound level meter. We measured the maximum SL of each bout in a vocalisation (using the peak hold function of the instrument), and then averaged the bout measurements to obtain an average vocalisation SL (see Sanvito & Galimberti 2000a). Sound level meter was set to "C" weighing and "FAST" response, and fitted with a windscreen to reduce wind noise.

At SLI, we measured SL of 1342 vocalisations made by 162 males (mean = 7.1 to 9.6 vocalisations per male; details in Table 1). From these measurements, we calculated the mean SL of each male and we used these mean values (= "individual SL") to analyse correlates of SL. Twenty-five males (18.4%) were present for 2-4 seasons (61 seasonal values, mean = 2.4 ± 0.65 per male), while 111 more were measured in one season only. Although we were aware of the risk of pseudo-replication (Bart et al. 1998), we considered independent the seasonal values of males that were measured in more than one season. Repeated values represented only 37.6% of the data set and the number of repetitions per male was low, with just 2 males (1.5%) with four seasons and 7 (5.1%) with three. Moreover, male elephant seals present a significant growth spur after puberty (McLaren 1993) and, therefore, they experience a so large variation in structural and behavioural phenotype (Clinton 1994), that consecutive yearly values may be considered biologically independent. To examine the effect of non-independence of individual data points across years, we replicated some of the analysis by selecting a single breeding season at random for males present in more than one season. We obtained qualitatively similar results to the full analysis, although the power of each statistical test was lower due to the smaller sample size. Hence, we are presenting the results of the full analysis only. At SBI we measured SL of 245 vocalisations made by 17 males (mean = 14.4 ± 7.3 vocalisations per male) during one breeding season only.

Males were classified in increasing age categories by two independent observers both at SLI and SBI, using a standard nomenclature in use for both NES and SES species (SAM1 = sub-adult male class 1, SAM2 = sub-adult male class 2, SAM3 = sub-adult male class 3, SAM4 = sub-adult male class 4, AD = adult male; e.g., Deutsch et al. (1994)). Classes were based on male morphology, in particular scarring of the chest and development of the proboscis, and not on body size. Classification was found to be reliable at SLI (Galimberti & Boitani 1999). To test reliability of the SBI classification, we ordered categories and converted them to ranks. Correlation among the independent classification of the two observers was very high (Spearman rank correlation, with randomisation test: rho = 0.955, n = 57 males, $P < 0.0001$).

We determined male size by visually comparing them in the field and by using a photogrammetric method (Haley et al. 1991). Each observer produced an ordering of males by repeatedly comparing size among dyads of resting males. The ordering of each observer was then converted to ranks, and ranks were compared among observers. Agreement was very high (three breeding seasons, Spearman rank correlation, with randomisation test: rho ranging from 0.972 to 0.985, P always < 0.0001). A consensus rank (mean between ranks attributed by observers) was then used in the analysis. Nose to tail body length was calculated from pictures of males resting on packed sand taken from the side, with a calibrated surveying pole in the frame. Repeatability of body length of SES males, as measured using the photogrammetric method, was high both in 1996 (90 measurements for 24 males, 3.8 ± 1.9 per male; $R = 0.839$, $P = 0.0000$, 95% confidence interval = 0.736-0.942) and 1997 (76 measurements for 26 males, 2.9 ± 1.3 per male; $R = 0.869$, $P = 0.0000$, 95% confidence interval = 0.783-0.954). For NES males, repeatability was also high, although the sample size was much smaller (28 measurements for 10 males, 2.8 ± 1.1 per male, $R = 0.942$, $P = 0.0000$, 95% confidence interval = 0.876-1.000).

Statistics are presented as mean ± standard deviation. Repeatability was calculated using variance components (Lessels & Boag 1987) and was tested for significance using randomisation, to avoid bias due to the uneven number of replicates per male. Being a ratio between variance components, repeatability is a relative measure that can be used to compare variables measured on different scales, and with different accuracy and precision (e.g., Becker 1984). Calculations and tests were run in StatView 5 (SPSS Inc.) and Stata 7 (Stata Corp.).

TABLE 1

Samples, SL repeatability, and individual SL statistics. Statistics of vocalisations per male are presented as mean ± standard deviation, with range in parentheses. R = repeatability; P = probability of the randomisation test on R, 10000 replicates; 95% CI = 95% asymptotic confidence interval for R. SD = standard deviation; CV = coefficient of variation.

Pop.	Year	No voc.	No males	Voc. per male	R	P	95% CI	Mean	SD	Min	Max	CV
SLI	1996	288	34	8.5 ± 4.7 (2-22)	0.769	0.0000	0.664-0.874	110.5	3.34	102.9	116.0	0.030
	1997	460	48	9.6 ± 5.5 (3-27)	0.715	0.0000	0.613-0.817	110.1	3.22	102.9	116.1	0.029
	1998	268	34	7.9 ± 4.5 (3-22)	0.760	0.0000	0.653-0.870	110.7	3.16	104.9	118.3	0.029
	2000	326	46	7.1 ± 4.4 (2-20)	0.627	0.0000	0.502-0.756	111.0	2.65	105.9	119.7	0.024
	All							110.6	3.07	102.9	119.7	0.028
SBI	2001	245	17	14.4 ± 7.3 (3-28)	0.740	0.0000	0.589-0.897	104.2	3.51	98.5	111.2	0.034

RESULTS

Source level

Yearly statistics for individual SL are presented in Table 1. The repeatability of SL was high both at SLI and SBI (Table 1). Intra-individual variation of SL was low, with a coefficient of variation in the range 0.001-0.047 (mean = 0.014). Individual SL had a normal distribution both at SLI (Shapiro-Wilk test: W = 0.95-098, P > 0.14 in all years) and SBI (W = 0.98, P = 0.94) and it was homogeneous among years at SLI ($F_{3,158} = 0.728$, P = 0.54).

Differences among the species

SES males were larger than NES males (380.4 ± 27.8 cm, n = 50 vs 308.6 ± 29.0, n = 10; mean difference = -71.8 cm; Unpaired samples t-test: t 58 = -7.412, P < 0.0001). SL was much higher in the southern elephant seal than in the northern (mean difference = 6.4 dB; Unpaired samples t-test: $t_{177} = 8.070$, P < 0.0001), while variance was homogeneous (F test: $F_{16,161} = 1.301$, P = 0.48). The difference was significant also when comparing the northern species with each year of the southern (Figure 1).

Correlations with male phenotype

At SLI, although there was an increase in SL with age (mean difference between SAM1 and AD = 2.2 dB), intermediate sub-adult classes had similar SLs and there was a large overlap of confidence limits (Figure 2). As a whole, the difference between age classes was not significant (ANOVA: $F_{4,148} = 1.633$, P = 0.1689). Only adult males had an higher SL than other males (mean difference = 1.103 dB; $t_{151} = 2.134$, P = 0.0345). At SBI, due the small sample, we were only able to compare SAM4 and AD. Adults had an higher SL (mean difference = 3.564 dB; Unpaired samples t-test: $t_{13} = 2.084$, P = 0.0575).

At SLI, the dataset included 27 to 34 males per year for which both individual SL and size rank were available. There was a negative (i.e., increase of SL with increase in size), but non significant, correlation between SL and size rank in all four years of study (Spearman rank correlation: rho = -0.259 to -0.308, P = 0.10 to 0.11). A similar result was found in NES at San Benitos (rho = -0.396, n = 17, P = 0.11). A photogrammetric estimate of body length was available for two breeding seasons at SLI, 1996 (n = 18 males with measured SL) and 1997 (n = 17 males). Yearly sample size was small, and individual measures were homogeneous both for SL (mean

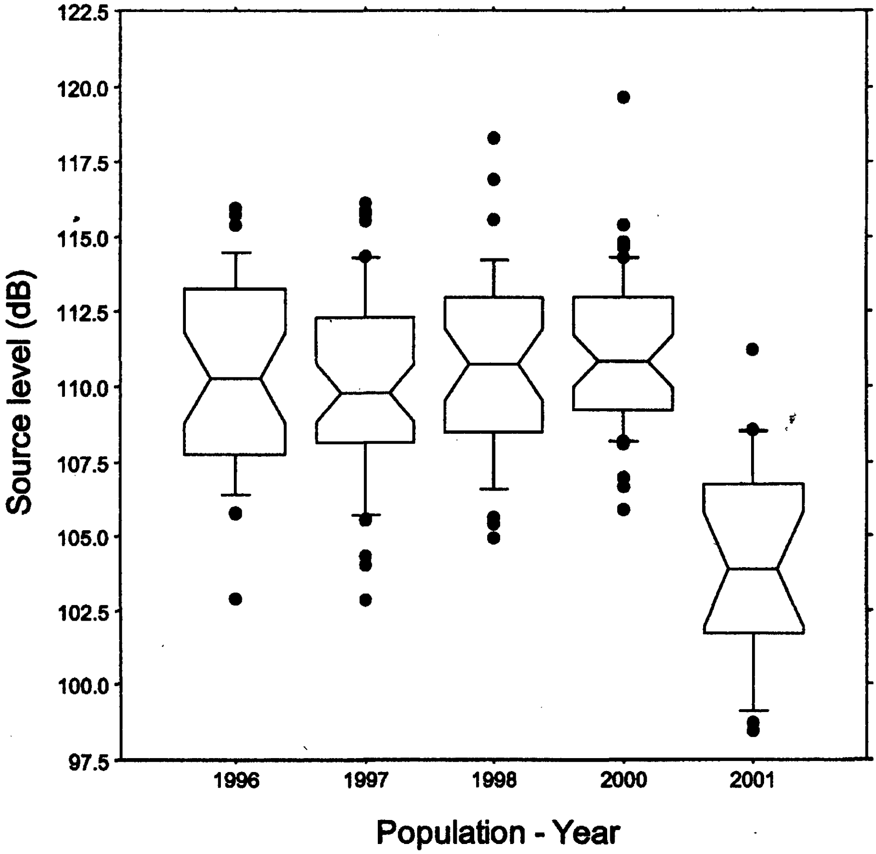

Figure 1. Boxplots of SL split by population and year. Notches in the boxes represent 95% confidence intervals around the median (each box is notched at the median and returns to full width at the lower and upper confidence limits; McGill et al. 1978), so a visual comparison of the notched boxes is a non-parametric test of differences between years and populations. 1996-1998 and 2000 southern elephant seals of SLI; 2001 northern elephant seals of SBI.

difference = 0.333 dB; Unpaired samples t-test: $t_{33} = 0.310$, $P = 0.76$) and body length (mean difference = 6.2 cm; Unpaired samples t-test: t 33 = 0.744, P = 0.46), so we pooled the data. SL significantly increased with body length (Linear regression: n = 35 males, b = 0.061, se(b) = 0.019, t = 3.15, P = 0.0034), but there was a large dispersion of points (Figure 3), the proportion of SL variance explained by body length variance was low ($R^2 = 0.232$), and the 95% confidence interval of the regression coefficient was rather large (0.022-0.101).

Harem holders had a higher SL than non-holders both at SLI (mean difference = 1.209 dB; Unpaired samples t-test: $t_{160} = 2.204$, P = 0.0289) and SBI, although in the latter case the difference was non significant (but note the high effect size and low power: mean

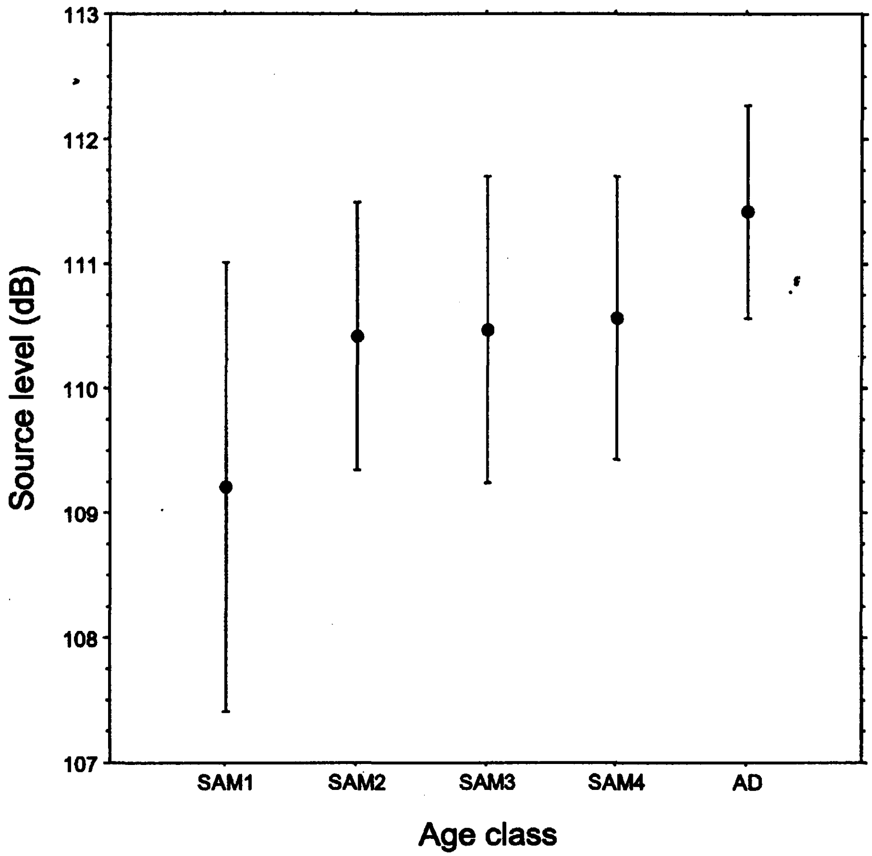

Figure 2. Mean and 95% confidence interval of SL of southern elephant seal age classes.

difference = 3.065 dB; $t_{15} = 1.741$, $P = 0.1022$; effect size $d = 0.87$, post-hoc power = 0.47).

DISCUSSION

To be a reliable signal of resource holding potential, source level should be a good individual trait, being stable within and variable between individuals. Moreover, it should be correlated with one or more structural trait of the individual phenotype that may affect the outcome of agonistic contests. In elephant seals, fighting success and dominance rank are related to age and body size, and determine mating success (Haley et al. 1994; McCann 1981).

Our study demonstrates that SL has a high repeatability both in southern and northern elephant seals. In a previous article (Sanvito &

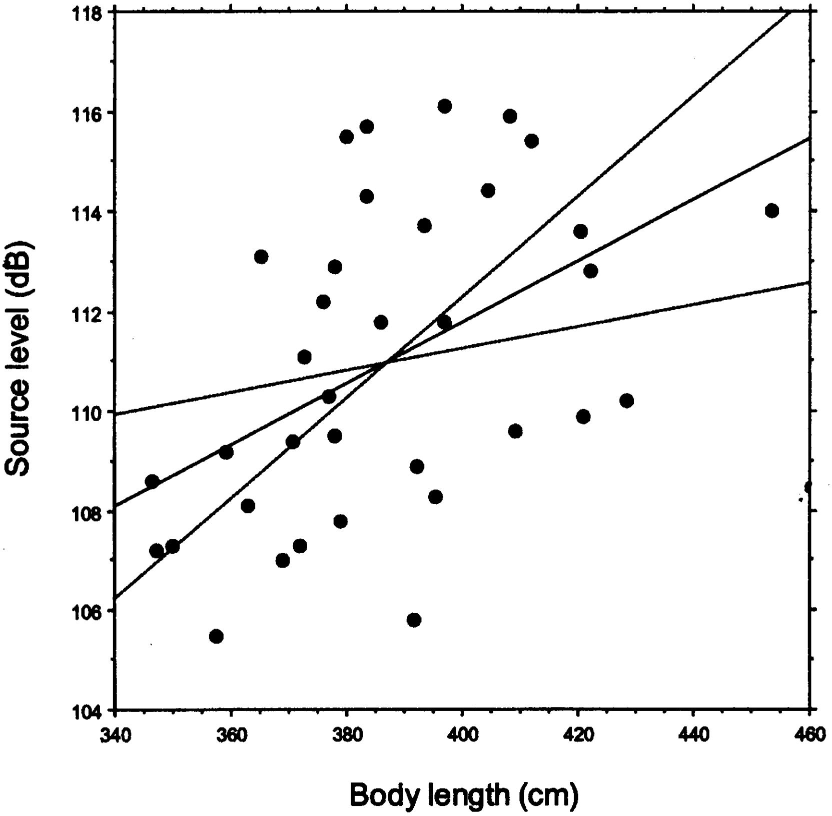

Figure 3. Scatterplot of SL versus nose-tail length as estimated by the photogrammetric method in southern elephant seals. The solid line is linear regression, dashed lines are 95% confidence limits for the regression slope.

Galimberti 2000b) we showed that various time and frequency domain aspects of elephant seal vocalisations are repeatable. SL is very repeatable at the individual level, even more than frequency characteristics of vocalisations that are usually considered a good indicator of individual size. For example, in our sample of SES males, SL is more repeatable than fundamental frequency, which is related to vocal folds size (Titze 1994) and which in frogs and toads is a reliable index of body size (Ryan (1980); but contrasting results were found in some vertebrate species (Fitch 1997)). SL is also more repeatable than formant frequencies which, in primates and humans, are a good index of body size, being directly correlated with vocal tract size (Fitch 1997; Riede & Fitch 1999). In our study SL is sufficiently stable within individuals to be considered a good individual trait and a potential cue of body size.

Information about the mechanism of vocalisation production in elephant seals are almost completely lacking. The same holds in general for SL regulation in mammal vocalisations. In humans and primates, SL depends on lung size and pressure, size and shape of the sound source and the sound resonator (respectively the vocal folds and vocal tract), pressure developed in the rest of the vocal tract, and musculature (Titze 1994; Åkerlund & Gramming 1994). Since lung size and body size are correlated in vertebrates, any acoustic measure related to lung size is also related to body size (Fitch & Hauser 2002). Elephant seals should have a similar SL regulation system, but further studies on the mechanism of vocalisation production are needed. In elephant seals, SL is related to age class and size of the male, but the relationship is not very strong and it is quite variable. Only the extreme age classes show a significant difference, and only a small proportion of the variance in SL is explained by the variance in body size. On the other hand, when comparing the two species of the genus *Mirounga*, which may be considered to possess the extremes of the body size range of the genus, the difference in SL is very large and significant. This seems to be in agreement with the results obtained in humans. Due to the complexity of the mechanism of SL regulation, large adult males are able to emit more powerful sounds than smaller and younger ones, but there is a lot of variation in this trend, because many factors other than size are involved (Titze 1994). Moreover, age may reflect "training" and "experience", two important factors in sound production. In humans, training in voice production affects SL performance (Åkerlund & Gramming 1994). This may explain the increase of SL with age in elephant seals, which may adjust vocalisations to maximise SL during development. This is not surprising, since there is a clear development in the individual capability of vocal production in both species of the genus *Mirounga* (Sanvito 1997; Shipley et al. 1986).

A specific problem of the use of amplitude cues in the transmission of information is that the perception of these cues, contrary to time and frequency domain cues, can be strongly affected by the orientation and distance of the emitter. The effect of orientation should be of minor importance in the *Mirounga* genus, because males interact by facing one each other at short distance. There is no published information about the capability of elephant seals to evaluate distances. Being a predator species, however, and also because the mean interaction distance is short, its range is limited (0-50 m in vast majority of cases) and the breeding habitat is fully open, they should be able to estimate the actual distance of opponents.

SL of male vocalisations may convey information on gross differences between phenotype classes (i.e., adults versus non adults, big versus small) but is not sufficiently correlated with the structural phenotype to be a good candidate for the transmission of high resolution information on resource holding potential of individuals. In humans, SL and fundamental frequency are closely related (Titze 1994); if lung pressure is kept constant, SL increases with increased fundamental frequency, which explains why children and adult males may reach similar absolute SL, but at different frequencies. This probably holds for other mammals as well. A small oscillator can produce low frequency oscillations, but its capability to convert their energy to emitted acoustic energy is physically constrained (Hauser & Fitch 2002). Therefore, there is a structural trade-off between low frequency and high power of sound emission, a trade-off that bigger animals are better suited to overcome than smaller ones. Older elephant seal males are, in fact, able to emit lower pitched vocalisations than younger ones, while maintaining high SL (Sanvito 1997). Therefore, absolute SL alone may give only a rough indication of size, but the combination of frequency domain structure (fundamental frequency and formant frequencies in particular) and SL may be a much better index of it.

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