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# Vocal signalling of male southern elephant seals is honest but imprecise

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In the most common models of communication, it is assumed that animals provide reliable information about phenotype, and hence can settle competitive contests without physical interactions like fights. This assumption has rarely been tested for wild mammals. Recent studies of mammals have revealed relationships of vocal attributes to age and body size. Here, we analyse relationships of frequency attributes of agonistic vocalizations to phenotype (age, body size, proboscis size and agonistic behaviour) in males of the southern elephant seal, *Mirounga leonina*, a species with intense male competition for access to females, and in which vocalizations are used frequently to settle male–male contests. We analysed formant structure and vocal tract size, and found that nasal and oral components of the vocal tract contribute separately to vocal formants; hence, the male's proboscis serves to elongate the vocal tract. We also found that formants in the upper part of the frequency spectrum (fourth and fifth in particular) and formant dispersion convey significant information about age, size and resource holding potential at large, and, therefore, can be honest signals of a vocalizer's phenotype. Explained variance was statistically significant in our study and in similar studies but was not high, so formant structure cannot serve as the sole basis of acoustic assessment. Other possible sources of information exchanged in elephant seal contests are nonvocal acoustic signals (e.g. vibrations) and optical displays.

*Keywords*: animal communication; bioacoustics; elephant seal; *Mirounga leonina*; *Phocidae*; sexual selection; vocalization

Vocal communication is an important component of sexual competition in many animal species, often playing a crucial role in determining the outcome of agonistic contests (Andersson 1994). It has been suggested frequently that acoustic signals may convey honest information about attributes of a vocalizer's phenotype such as body size or maturity (Morton 1977; Clutton-Brock & Albon 1979; Harper 1991; Fitch & Hauser 2002; Kitchen et al. 2003; Reby & McComb 2003). Elephant seals, *Mirounga*, are an excellent model to study honesty of acoustic signals, because of the intense competition among adult males for access to females and the widespread use of vocalizations in male–male agonistic behaviour (Sanvito & Galimberti 2000a). Males sometimes fight, but most contests are settled by vocalizations only, and the majority of male–male interactions include vocalizations (Sanvito et al., in press a). The importance of vocalizations in male elephant seal behaviour has been long recognized (Laws 1956; Bartholomew & Collias 1962), but detailed information on acoustic structure of vocalizations has become available only recently (Sanvito & Galimberti 2000b). Furthermore, most research has been conducted on the northern elephant seal, *M. angustirostris*, which is smaller and less sexually size-dimorphic than its southern hemisphere sister species *M. leonina* (Le Boeuf & Peterson 1969; Le Boeuf & Petrinovich 1974; Sandegren 1976; Shipley et al. 1981, 1986). Although the literature contains various anecdotal statements about the role of male vocal behaviour in elephant seal reproduction (Sandegren 1976; McCann 1981), there has been almost no attempt to test specific hypotheses about the function of vocalizations.

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The source level of male vocalizations in *M. leonina* is only a rough indicator of a vocalizer's size or age (Sanvito & Galimberti 2003), and simple temporal and other structural acoustic features are unrelated to size or age, and are probably produced by an imitative learning process, possibly favouring individual recognition (S. Sanvito, F. Galimberti & E. H. Miller, unpublished data). The source-filter theory of human vocal production (Fant 1960) has been applied recently to nonhuman mammalian vocalizations, providing new opportunities to investigate honest signalling by investigating relationships between spectral properties of vocalization and phenotype at the individual level (Fitch 1994, 2000). In this model, the air stream produced by the lungs provides the energy to cause the laryngeal vocal folds (the sound 'source') to vibrate and produce sound. This sound then travels through the supralaryngeal vocal tract where its spectrum is altered ('filtered') because of resonances of the vocal tract, which are affected by the size and shape of supralaryngeal cavities and by the individual's tongue position before being uttered through the nostrils or mouth. Vocal tract resonances act as a band-pass filter applied to the original sound, selectively amplifying some frequencies and damping others, and producing what are known as formant frequencies or formants (i.e. frequencies that are reinforced supralaryngeally; Fry 1979; Fitch 1994; Miller & Murray 1995). A vocalization's fundamental frequency (F0) is the rate of vibration of the vocal folds and is unrelated to formant frequencies, which can vary independently from F0 during vocal production (Fry 1979; Fitch 2000). In theory, therefore, acoustic features may reflect both source and filter-related attributes, and hence could provide two independent kinds of information about a vocalizing individual's phenotype, such as size or shape of vocal tract components.

F0 depends directly on mass, length and tension of the vocal folds. An increase in the mass or length of the vocal folds produces a decrease in F0, and an increase in tension produces an increase in F0. All three factors can be modified considerably by the action of laryngeal muscles; thus, the same individual can readily change the fundamental frequency of the sounds produced within the limits of morphological constraints (Fry 1979; Rendall et al. 2005). The weak relationship of vocal-fold attributes to body size results in F0 being a poor indicator of body size in mammals (Fry 1979; McComb 1991; Reby & McComb 2003). In contrast, formants are constrained by vocal tract length. Formants and their spacing (formant dispersion) are known to decrease with an increase in vocal tract length across individuals in several mammalian species (Fry 1979; Fitch 1997). The mammalian vocal tract can be modelled as a uniform tube closed at one end (glottis) and open at the other (mouth) (Fitch 1997, 2000; Reby & McComb 2003; Fischer et al. 2004). In this model, formants and vocal tract length are linked, so one can estimate the formants that should be produced by a certain vocal tract length and vice versa. Since the vocal tract is bounded by the bones of the skull, which size is in turn closely related to body size, formants could convey reliable information about the vocalizer's body size (Fitch 2000) and are good candidates as an honest signalling system in mammalian vocal communication (Fitch & Hauser 2002).

The source-filter model is attractive because of its simplicity, but many variations of the uniform-tube model exist in real sound-production systems. In all models, F0 depends on the source, and the spectrum of the vocal signal produced depends on supralaryngeal resonances, but spectral details vary across models. For example, the tube could simply vary in cross-sectional size, which would cause formants to be unequally spaced (Fischer et al. 2004). The situation becomes more complex when more than one resonator is present. In humans and other mammals, the nasal cavities can contribute to vocalization depending on the position of the velum: when it is lowered, air can pass through the nasal cavity, which then becomes part of the sound-emission tract and contributes to filtering effects (Fry 1979; Fitch 1994). Multiple resonators may interfere with one another and produce anti-resonances, or may be in phase and reinforce one another (Fry 1979). Inference of specific anatomical–physiological effects from sound structure therefore must be done with caution (Chen 1996).

Anatomy of the elephant seal larynx has been well described (Schneider 1964; Dong et al. 1993), but whole vocal tract anatomy is poorly known (Murphy 1914). Moreover, male elephant seals have a prominent proboscis that changes in size and conformation with age (Laws 1953; Sanvito et al., in press b). This structure, which females lack, is a classic secondary sexual characteristic (Darwin 1871), but its role in vocalization is uncertain, if not often neglected on the basis of anecdotal data (Sandegren 1976). However, it seems reasonable to assume that the proboscis plays a role in vocalization because the nostrils are open and air passes through them during vocalization (S. Sanvito & F. Galimberti, unpublished data). In different mammalian species that have been studied using cineradiographic methods (dogs, goats, pigs and cottontop tamarins: Fitch 2000), loud calls seem to be characterized by velar closure, hence closing off the nasal passages, but in some cases (dog whines and pig grunts: Fitch 2000), the vocalizations appear to be nasally produced. Adult male *M. leonina* are very large and correspondingly have a large proboscis, averaging 74 cm (maximum 94 cm) in dorsal outline length in lateral aspect (Sanvito et al., in press b). Because the proboscis increases vocal tract length, it may affect sound properties that exaggerate the perceived size of the calling seal (Fitch & Hauser 2002). Finally, the presence of two resonators could enable more varied combinations of formants than would a single resonator (Chen 1996). The nasal tract is longer than the oral tract but is smaller in diameter and, owing to energy absorption in nasal side branches and turbinates, some weak low-frequency formants, not explained by the oral tract resonances, should be expected (Fry 1979; Fitch 2000).

We investigated relationships of formant structure with the individual characteristics of males for a large sample of southern elephant seals of the Falkland Islands. We considered single phenotypic traits (size and age in particular) as well as broader measures of resource holding potential. We evaluated whether vocalizations convey reliable information about the vocalizer, and if so, which acoustic features are best at doing so. Following the source-filter theory of vocal production, we expected formants (upper ones in particular) to be related to body size, and hence to be good candidates as honest signals of resource holding potential. In contrast, we expected fundamental frequency to be a poor signal of body size. Finally, we propose a preliminary model of sound production for the species.

## METHODS

Data were collected during 10 breeding seasons (September–November 1995–2004) at Sea Lion Island, SLI (Falkland Islands; 52°26′S, 59°05′W), which shelters a small and localized population of southern elephant seals (Galimberti & Sanvito 2001), comprising approximately 550 females and 60 breeding males. All males were tagged for individual identification (≥two tags per individual; Jumbo Rototag, Dalton ID Systems Ltd, Henley-on-Thames, U.K.) during previous breeding seasons; some were tagged as pups and others were tagged upon their arrival on land in their first breeding season. All breeding males also were individually marked with hair dye for distant identification (Galimberti & Boitani 1999).

### Recording Protocol and Acoustic Analysis

All audio recordings of male agonistic vocalizations were obtained by standardized stimulation, in which a person approached a subject animal, eliciting a stereotyped vocal response that males give in natural encounters with other males. Vocalizations produced under standard stimulation are identical to those given in natural encounters, from a behavioural and acoustical point of view (Sanvito & Galimberti 2000a). We recorded vocalizations throughout each breeding season and obtained recordings for 251 individual males. Some males were recorded for more than one breeding season (range 1–6, mean ± SD = 1.7 ± 1.1), so the number of males × number of years (=male-years) that included a recording for each male was 418. We used portable digital recorders (Sony DAT TCD-D100) and dynamic cardioid microphones (Sennheiser MD 441, frequency response, 30–20 000 Hz; sensitivity at 1 kHz, 1.8 mV/Pa ± 2 dB). Sounds were recorded at a sampling frequency of 48 kHz with 16-bit resolution. Sound measurement and spectral analysis were carried out with Canary (v. 1.2; Macaulay Library, Cornell Laboratory of Ornithology, Ithaca, New York, U.S.A.), and with programs written in Igor Pro 4.0.9 (WaveMetrics Inc., Lake Oswego, Oregon, U.S.A.) and in Revolution 2.0 scripting language (Runtime Revolution Ltd, Edinburgh, U.K.). We used the following settings for spectral analysis (Charif et al. 1995): Hamming window function with frame length of 21.33 ms (1024 points) and corresponding filter bandwidth of 190.31 Hz; frame overlap of 50% with a time-grid resolution of 10.67 ms and a frequency-grid resolution of 11.72 Hz (fast Fourier transform, FFT = 4096 points).

Aggressive vocalizations of southern elephant seal males are composed of a series of different numbers of sound emissions (‘bouts’), which are further subdivided into ‘syllables’ and ‘syllable parts’ (Sanvito & Galimberti 2000a). A syllable is a single acoustic event, with a continuous spectrographic trace over time. A syllable part is a portion of a syllable characterized by constant pulse rate. Hence, F0 is constant in each syllable part. We measured the following eight frequency variables.

(1) Fundamental frequency (F0; in Hz) was calculated on waveforms as the pulse rate (Zuberbühler et al. 1997) of the predominant (=longer/more intense) syllable part of a bout.

(2–6) The first five formant frequencies (F1–F5; in Hz) were measured on the bout average power spectrum as the first five evident frequency peaks (Fig. 1).

(7) Formant dispersion (in Hz), which has been proposed as an indicator of vocal tract length and body size (Fitch 1997; Reby & McComb 2003), was calculated as the average spacing between consecutive formants: (F5 − F1)/4.

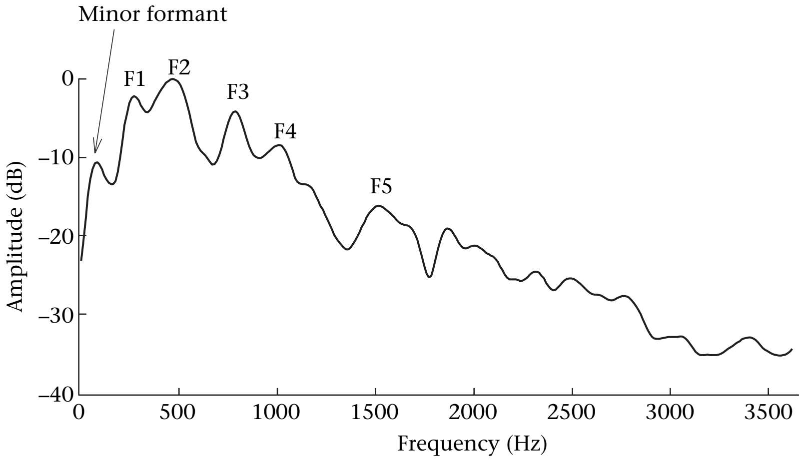

**Figure 1.** Measurement of formant frequencies. Spectral peaks F1–F5 are the formant frequencies. Formant dispersion was calculated as (F5 − F1)/4. Minor formant is the frequency of the very first spectral peak (usually below 100 Hz), which was not always detectable.

(8) Minor formant (in Hz) was measured as the first peak in the power spectrum, at lower frequency (often < 100 Hz) and reduced intensity with respect to F1 and just preceding it (Fig. 1).

We calculated year-specific mean values for each male for each acoustic variable. Additional details on recording and acoustic analysis are given in Sanvito & Galimberti (2000a).

## Age Estimation

Age was known for males tagged as pups and estimated to ±1 year for other males on the basis of external morphology (Clinton 1994; Galimberti & Boitani 1999). Mean intraobserver reliability in age classification using morphology was 0.95, and interobserver reliability ranged from 0.93 to 0.99 for two to four observers. Congruence of the whole classification was checked using lifetime records of males present for more than two breeding seasons and by comparing assigned age categories with actual age for males tagged at birth. Overall, we knew the age of 188 individual males (355 male-years) and had full information on all acoustic variables as well as age, body size and behavioural measures for 91 individuals (126 male-years).

## Body Size Estimation

We estimated body length of undisturbed animals using photogrammetry (Haley et al. 1991; Bell et al. 1997). We photographed animals from the side, while they were lying on level flat substrates, using a telescopic 4-m-long surveying pole with 1-cm increments (Model 406 BIS/D, Salmoiraghi Strumenti Spa, Milano, Italy) held horizontally over the animal's long-body axis. Images were measured using Object Image software (http://simon.bio.uva.nl/object-image.html), with the pole as scale.

## Proboscis Traits

We used a similar photogrammetric method to measure proboscis size. One observer elicited a head-up posture by approaching an animal and held a 2-m segment of the surveying pole in front of and aligned with the long-body axis of the animal. A second observer photographed the animal's head from the side at a distance of 2–3 m, adjusting the position of the camera as the animal moved, in order to achieve the best alignment. During each display, we took several photographs using a motor drive, and we selected the picture with the best alignment and maximal proboscis expansion. Images were measured with Object Image software.

We chose three variables to measure proboscis size (Fig. 2): proboscis length, measured as the maximal linear length of proboscis (trunk length hereafter), and outline lengths, measured as the total curvilinear length of the first and second bumps of the proboscis. We chose these specific variables because, of the ones having high repeatabilities, they were the ones that better summarized our own visual impression of overall proboscis size. We collected data on proboscis size of 66 males in the 1996 and 2002 breeding seasons. We calculated measurement error using variance components estimated from a model II ANOVA (Lessells & Boag 1987). Repeatabilities were high (trunk length: $R = 0.891$; outline of first bump: $R = 0.900$; outline of second bump: $R = 0.800$).

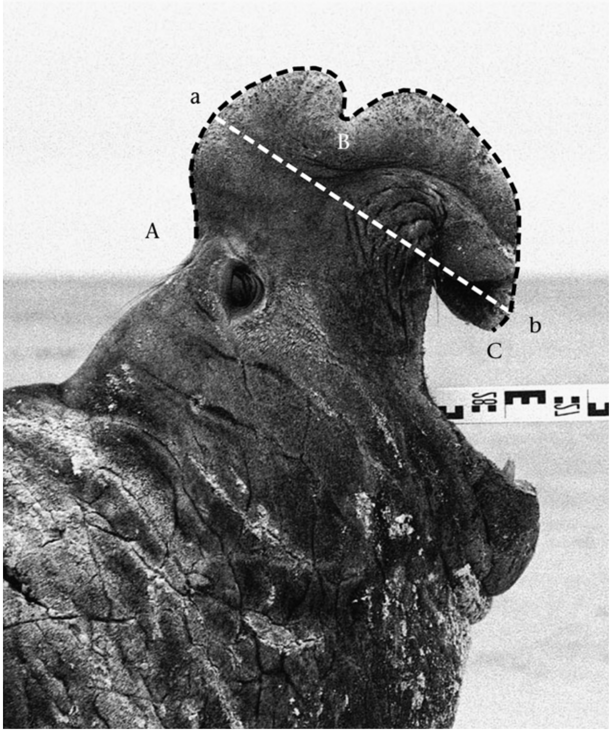

**Figure 2.** Proboscis measurements. Trunk length = linear length between points a and b; outline lengths of first bump = curvilinear length between points A and B; outline lengths of second bump = curvilinear length between points B and C.

## Behavioural Traits

We observed agonistic interactions for 2-h periods using an all-occurrences sampling norm and a continuous recording norm (Altmann 1974) and noted the identity of interactants, and of the initiators and winners (Galimberti et al. 2003). In total, we observed 25 671 agonistic interactions between males in 7852 h of observation spanning the length of each breeding season. Observation periods were randomly distributed across hours of the day, tidal phases, breeding beaches and harems. We carried out observations only during the day, because a pilot study showed no difference in activity level between night and day (see also Baldi et al. 1996). For each male we calculated an agonistic activity index (AAI) as the mean number of agonistic interactions initiated by the male per observation period; only males observed for at least 20 periods (i.e. ≥40 h) were included.

Resource holding potential (RHP) is the ability of an individual to compete for a resource (Maynard Smith & Parker 1976). It depends on numerous and diverse structural and behavioural traits of an individual (Haley 1994; Galimberti 1995; Braschi 2004). Some of these can be readily measured (e.g. age and size), but others are more difficult or impossible to measure in the field (e.g. motivation and personality). Moreover, an individual's RHP is a relative measure that depends on the distribution of phenotypic traits of other individuals. Therefore, we used success in competition, as measured from David's dominance score (DDS; Gammell et al. 2003), as a proxy for the suite of latent, often not measurable, traits that globally constitute RHP. In our study population, dominance hierarchies were linear, circularities were rare, and the dominance rank of each male was stable during each breeding season (Galimberti et al. 2003), so estimation of dominance was easy and a single seasonal dominance score could be used. Yearly scores were calculated from dyadic agonistic interaction matrices, and then converted to relative scores ranging from 0 (minimum DDS) to 1 (maximum DDS) to permit comparison among years. We estimated DDS for 191 males. As another, more conventional, measure of RHP, we ran a principal component analysis using the variables body length, age and AAI. The first component explained 80% of the variance of the three original variables. We used the first principal component score (PCAS) for each male as a summary measure of RHP.

Hereafter we refer to age, body size, proboscis size, AAI, DDS and PCAS together as 'phenotypic' (i.e. nonacoustic) traits.

## Estimation of Vocal Tract Size

We first estimated expected size of oral and nasal components of the vocal tract from formant structure, and then estimated them directly from photogrammetric measurements of males, for comparison. To estimate vocal tract length from formant frequencies, we treated the vocal tract as a uniform tube, closed at the glottal end and open at the other end (mouth or nostrils) using the relationship $\mathrm{VTL} = ((2i-1)c)/(4F_i)$, where $F_i$ are formant frequencies, $c$ is sound velocity in air (350 m/s), and VTL is vocal tract length (Reby & McComb 2003). We calculated expected oral tract length from F5, because upper formants, which are not affected by the shape of the upper vocal tract (e.g. mouth, tongue), are the best indicators of vocal tract length. In contrast, we calculated expected nasal tract length from the minor formant. We expected resonances due to the nasal tract to be less intense and lower in frequency than oral tract resonances, because the nasal tract is longer and narrower. Hence, the upper nasal formants will be masked by more intense oral formants, becoming immeasurable in power spectra. Therefore, the very first peak (minor formant) observed in the power spectrum was the only suitable nasal resonance for estimating nasal tract length.

There is no published information on the position of the larynx in the vocal tract, or on the length or shape of the vocal tract for pinnipeds. In any event, measurements on anatomical specimens probably are not representative of vocal tract size during vocalization (Fitch 2000), and the larynx and the vocal tract in general are dynamic structures in the vocalization process (Nishimura et al. 2003). Southern elephant seal vocalizations are composed of rhythmically uttered pulse trains, and frequently one can observe a protrusion of the male's chest that moves rhythmically during vocalization (Fig. 3); we interpret these as movements of the larynx, as in the red deer, *Cervus elaphus* (Fitch & Reby 2001). We used position of the protuberance to estimate vocal tract length for 16 adult males. Measurements were made using photogrammetry, as described above. We estimated the path of air emission

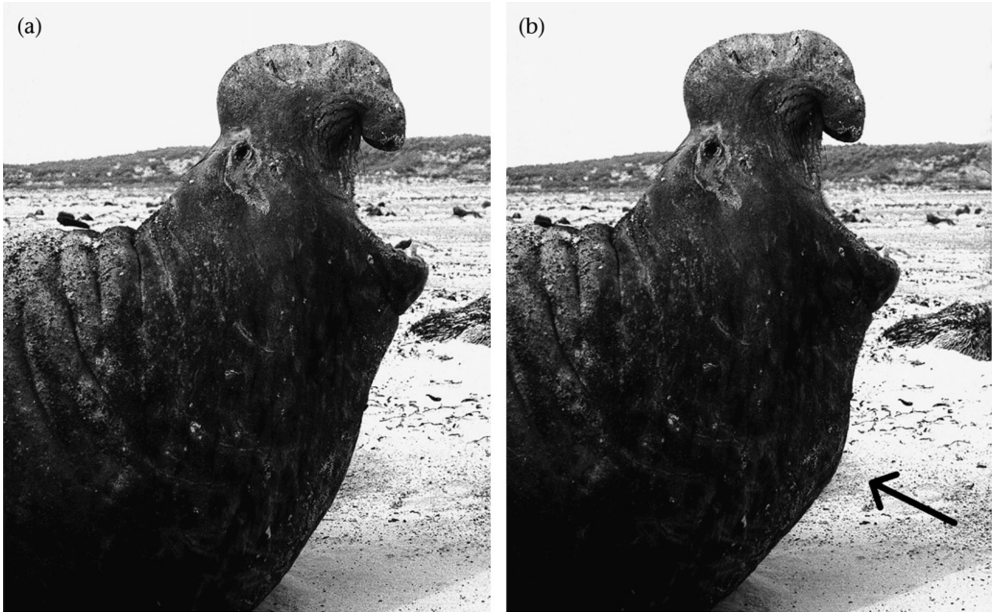

**Figure 3.** Adult male southern elephant seal, *Mirounga leonina*, during vocalization. (a) Immediately before starting to vocalize. (b) During vocalization. Arrow indicates likely position of larynx (the bump moves rhythmically during vocalization).

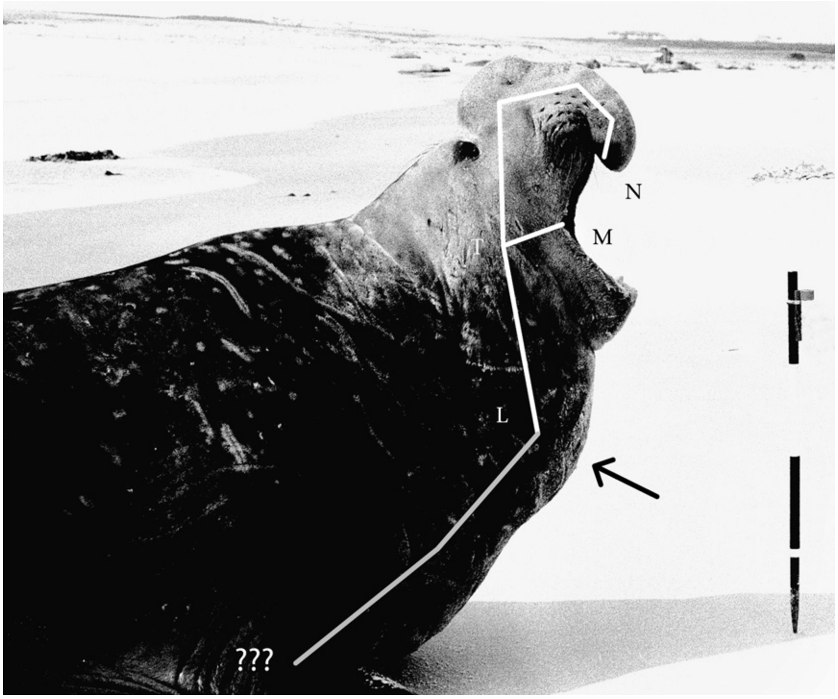

**Figure 4.** Measurements made on vocal tract components of vocalizing male southern elephant seals, *Mirounga leonina*. L = larynx; T = throat; M = mouth; N = nostrils. Oral tract path, L—T—M: nasal tract path, L—T—N. Arrow indicates likely position of larynx (see Fig. 3b). Grey line indicates hypothetical vocal tract (assuming uniform-tube model), estimated from minor formant in vocalization and assuming that the minor formant is produced only by the oral tract.

during vocalizations through the mouth (oral tract, from larynx to throat and lips) and through the nostrils (nasal tract, from larynx through throat and nasal passages and out of the nostrils; Fig. 4). These estimates are approximate, but they should give a realistic range of variation of the vocal tract length in elephant seals and can be compared with the estimates derived from formants.

## Statistics

Descriptive statistics are presented as arithmetic mean ± SD. To explore bivariate relationships of frequency features of vocalization and phenotype, we made scatterplots with LOWESS smoothers (Trexler & Travis 1993) of each phenotypic trait versus each formant feature and ran univariate ordinary least squares (OLS) regressions of each phenotypic trait versus each frequency feature (Bruckert et al. 2006). Scatterplots showed no sign of nonlinear relationships between phenotype and frequency features in most cases; therefore, we used only linear models in the following analyses. We calculated the coefficient of determination (i.e. the proportion of the phenotypic trait variance explained by the linear relationship with the frequency feature) as a summary measure of the capability of frequency features to convey information about phenotype. To assess the importance of different acoustic variables, we computed stepwise multiple regressions of each phenotypic trait versus the whole set of acoustic features. We then ran mixed-effect regressions with the acoustic variables retained by the stepwise procedure to cope with the longitudinal structure of our data set (i.e. multiple measures on the same males across years). A Lagrange multiplier test was used to assess significance of the random effect. However, plain (i.e. nonmixed-effect) regression was used for analyses involving proboscis traits

**Table 1.** Covariance and correlation matrix between acoustic variables

| Acoustic trait | F0 | Minor formant | F1 | F2 | F3 | F4 | F5 | Formant dispersion |
|---|---|---|---|---|---|---|---|---|
| F0 | (73) | 13 | 123 | 257 | 549 | 576 | 652 | 132 |
| Minor formant | *0.066* | (572) | *0.300* | *0.183* | *0.263* | *0.264* | *0.275* | 440 |
| F1 | *0.306* | 339 | (2224) | 3607 | 5124 | 6314 | 6536 | 1077 |
| F2 | *0.225* | 587 | *0.571* | (17 959) | 20 351 | 23 214 | 25 217 | 5402 |
| F3 | *0.309* | 1310 | *0.521* | *0.728* | (43 501) | 48 891 | 52 086 | 11 740 |
| F4 | *0.250* | 1711 | *0.495* | *0.640* | *0.866* | (73 295) | 77 795 | 17 869 |
| F5 | *0.239* | 2101 | *0.433* | *0.588* | *0.780* | *0.898* | (102 378) | 23 961 |
| Formant dispersion | *0.205* | *0.243* | *0.302* | *0.533* | *0.744* | *0.873* | *0.990* | (5722) |

Estimates of covariance are above the diagonal and those of Pearson's *r* are below (in italic); variances (in parentheses) are on the main diagonal. All correlations were significant ($P < 0.01$ after sequential Bonferroni correction), except that between minor formant and F0.

**Table 2.** Covariance and correlation matrix between phenotypic traits

| Phenotypic trait | Age | Body length | Trunk length | AAI* | DDS† |
|---|---|---|---|---|---|
| Age | (4.3) | 48.0 | 3.9 | 1.5 | 233.8 |
| Body length | *0.824* | (839) | 64.4 | 28.9 | 3425.9 |
| Trunk length | *0.544* | *0.595* | (18.1) | 3.5 | 365.1 |
| AAI* | *0.591* | *0.635* | *0.559* | (1.7) | 151.1 |
| DDS† | *0.767* | *0.758* | *0.676* | *0.698* | (25 762) |

Estimates of covariance are above the diagonal and those of Pearson's *r* are below (in italic); variances (in parentheses) are on the main diagonal. All correlations were significant ($P < 0.01$ after sequential Bonferroni correction).
*Agonistic activity index.
†David's dominance score.

because in this case the data set was not longitudinal. We calculated the standard error of regression coefficients using a jackknife delete-one procedure and tested the significance of their differences from 0 using a randomization test with 10 000 resamplings (Manly 1991). We compared regressors of multivariate models using standardized coefficients (betas; Rawlings 1988). We checked for multicollinearity of regressors with the variance inflation factor, VIF $= 1/(1 - r_j^2)$, where $r_j^2$ is the coefficient of determination of the linear regression of regressor *j* on other regressors in the model; VIF $> 10$ suggests a multicollinearity problem (Rawlings 1988). We checked normality (Shapiro–Wilk test) and homoscedasticity (White test) of each regression model's residuals. Statistical analyses were performed with Stata v. 9 (Stata Corporation Inc., College Station, Texas, U.S.A.).

## RESULTS

### Correlations among Acoustic Traits and among Phenotypic Traits

We expected high correlations among F1–F5, because they are all products of the same mechanism (i.e. the filtering of the oral tract), and we expected low correlations with the minor formant, which we assumed to be the product of nasal tract filtering, and with F0, produced by the sound source. All correlations between acoustic variables were significant except between F0 and the minor formant (Table 1). Many correlations were high, especially between upper formants and formant dispersion, while others were moderate to weak, especially for F0 and the minor formant. The Bartlett test of sphericity was significant ($\chi^2_{28} = 5723.4$, $P < 0.0001$).

All correlations between phenotypic variables were strong and significant (Table 2). The strongest correlations were found between age and body length, and between

**Table 3.** Summary of simple linear regression analyses of phenotypic versus acoustic variables

| Response and predictor variables | *N* | $r^2$ | *b*±SE | $p_{10k}$ | *p* |
|---|---|---|---|---|---|
| Response variable: age | | | | | |
| F0 | 148 | 0.05 | −0.020±0.020 | 0.11 | <**0.001** |
| Minor formant | 126 | 0.10 | −0.013±0.006 | **0.006** | <**0.001** |
| F1 | 148 | 0.04 | −0.010±0.005 | **0.030** | <**0.001** |
| F2 | 148 | 0.11 | −0.003±0.001 | **0.002** | <**0.001** |
| F3 | 148 | 0.22 | −0.005±0.001 | <**0.001** | <**0.001** |
| F4 | 148 | 0.23 | −0.004±0.001 | <**0.001** | <**0.001** |
| F5 | 148 | 0.29 | −0.004±0.001 | <**0.001** | <**0.001** |
| Formant dispersion | 148 | 0.28 | −0.015±0.001 | <**0.001** | <**0.001** |
| Response variable: body length | | | | | |
| F0 | 148 | 0.03 | −0.044±0.337 | 0.38 | <**0.001** |
| Minor formant | 126 | 0.10 | −0.264±0.118 | **0.003** | **0.017** |
| F1 | 148 | 0.10 | −0.260±0.080 | <**0.001** | <**0.001** |
| F2 | 148 | 0.16 | −0.073±0.022 | <**0.001** | <**0.001** |
| F3 | 148 | 0.32 | −0.096±0.010 | <**0.001** | <**0.001** |
| F4 | 148 | 0.35 | −0.074±0.008 | <**0.001** | <**0.001** |
| F5 | 148 | 0.37 | −0.070±0.007 | <**0.001** | <**0.001** |
| Formant dispersion | 148 | 0.35 | −0.280±0.028 | <**0.001** | <**0.001** |
| Response variable: AAI* | | | | | |
| F0 | 146 | 0.06 | −0.047±0.011 | **0.005** | 0.41 |
| Minor formant | 124 | 0.07 | −0.016±0.005 | **0.004** | 0.80 |
| F1 | 146 | 0.05 | −0.010±0.002 | **0.008** | 0.62 |
| F2 | 146 | 0.09 | −0.004±0.001 | <**0.001** | 0.89 |
| F3 | 146 | 0.15 | −0.003±0.001 | <**0.001** | 0.77 |
| F4 | 146 | 0.12 | −0.002±0.000 | <**0.001** | 0.81 |
| F5 | 146 | 0.13 | −0.002±0.000 | <**0.001** | 0.74 |
| Formant dispersion | 146 | 0.13 | −0.008±0.002 | <**0.001** | 0.78 |

Models were fitted with male identity as a random effect. *P* estimates less than 0.05 (after sequential Bonferroni correction) are shown in bold. $N$ = number of males; $r^2$ = coefficient of determination; $b$ = regression coefficient; $p_{10k}$ = significance of *b*; $p$ = probability of Breush–Pagan test on significance of random effect.
*Agonistic activity index.

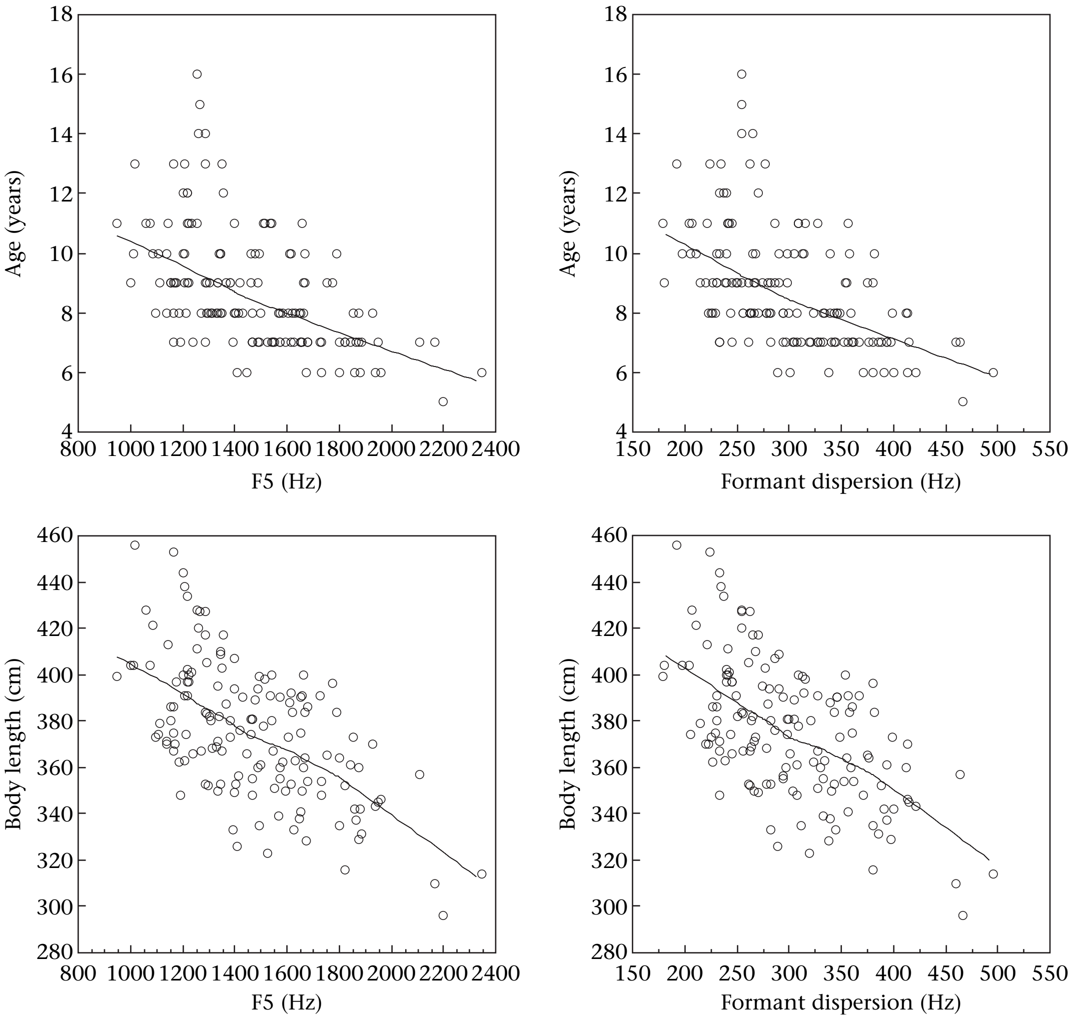

**Figure 5.** Relationships of body length and age to F5 and formant dispersion in male southern elephant seals, *Mirounga leonina*. Data points are for different males in each year of study; some individual males are shown for several years. Fitted lines are LOWESS smoothers.

the DDS dominance index and all other traits. The Bartlett test of sphericity was significant ($\chi^2_{10} = 192.5$, $P < 0.0001$).

## Relationships between Acoustic Features and Phenotypic Traits

### *Age*

We found significant negative relationships between age and each formant (Table 3, Fig. 5), but the proportions of variance in age explained by the relationships with formants were rather low ($r^2$ varied from 0.04 to 0.29) because of high dispersion of the data. The strength of the relationship was high for upper formants (F4 and F5) and formant dispersion, then decreased for lower formants. Formant dispersion was almost as good as F5 in predicting age. There was no significant relationship between age and the fundamental frequency.

Stepwise multiple regression analysis using age versus all acoustic variables retained only F5 and the minor formant, which were, therefore, the best predictors of the age of the vocalizer. The variance in age explained by this model was just slightly higher than the OSL regression with F5 or formant dispersion alone ($R^2 = 0.30$ versus 0.29 and 0.28, respectively). Comparison of betas between the two retained variables showed that F5 was the most important regressor ($\beta = -0.47$ versus $-0.017$). The variance component due to within-individual effects (i.e. male identity) was significant for univariate models except for F0, F1 and the minor formant (Lagrange multiplier test; Table 2), and for the final multiple regression model. This means that the power of most formants to predict vocalizer age shows small but significant variation between individuals.

### *Body length*

There was an inverse, significant ($P < 0.05$) relationship between body length and formants, but no relationship between body length and fundamental frequency (Table 3). The fifth formant and formant dispersion explained between 35% and 37% of the variance in body length (Fig. 5), and the percentage decreased for lower formants, with a minimum of 10% for F1 and the minor formant.

Stepwise multiple regression of body length versus all the frequency variables retained only F5, F2 and the minor formant. These variables together explained a rather large percentage (40%) of the variance in body length. F5 had the strongest relationship ($\beta = -0.47$), and the minor formant and F2 had a smaller and similar effect ($\beta = -0.18$; $F2 = -0.17$, respectively). Variance components due to male identity were significant for all univariate tests except for F1 and the minor formant (Table 2) and for the multivariate test.

### *Agonistic activity*

AAI was negatively related to frequency variables, but $r^2$ was small (maximum15%; Table 4). Only fundamental frequency and F5 were retained in the stepwise multiple regression ($r^2 = 0.17$). F5 had the strongest effect ($\beta = -0.33$). Variance component due to male identity was not significant in univariate or multivariate analyses.

### *RHP*

There was a significant inverse relationship between DDS and each frequency variable (Table 4). Variance of DDS explained by F3, F4, F5 and formant dispersion was moderate ($r^2 = 18{-}23\%$), and was very low (3–9%) for the other frequency variables (Table 4; Fig. 6). F5 explained the highest percentage of variance in DDS, and visual inspection of LOWESS on the scattergram revealed a bending in the relationship, with a reduction in slope, around 1700 Hz (Fig. 6). Stepwise multiple regression of DDS versus all acoustic variables retained only F5 in the model.

The other measure of resource holding potential, PCAS, decreased linearly and significantly with an increase in all the frequency features, and the strength of the relationship increased from the lower to the upper formants ($r^2$ from 0.08 to 0.33; Table 4, Fig. 6). The relationship with the fundamental frequency was also significant, but $r^2$ was very low. F0, F5 and the minor formant were retained in stepwise multiple regression analysis, which explained 38% of the variance in PCAS. In this model, F5 had the greatest effect (βs: $F5 = -0.48$; minor formant $= -0.19$; $F0 = -0.15$). Variance components due to male identity were significant for all univariate tests except for the minor formant, but were not significant for the multivariate test.

## A Model for the Elephant Seal Vocal Tract

The minor formant is characterized by very low frequency and intensity, so it is a good candidate for nasal resonance. To determine which frequency feature of the vocalization could be affected by the size of the proboscis, we ran a preliminary multiple regression of trunk length with all the frequency features. The only variable that was significantly related to trunk length was the minor formant ($\beta = -0.3151$; $P_{10k} = 0.0322$; all other variables: $P_{10k} > 0.34$). To determine which characteristics of a male phenotype more strongly affected the emission of this particular formant, we ran a multiple regression of the minor formant with different structural traits. We considered age, body length and three measures of proboscis size (linear length, and outlines of the first and second bumps). These variables were strongly correlated (Table 5), but not so much as to produce a significant problem of multicollinearity (maximum VIF was 5.14). The regression model explained 28% of variance in the minor formant; the only variable that significantly affected change in the minor formant was trunk length (Fig. 7).

**Table 4.** Summary of simple linear regression analyses of resource holding potential indexes (DDS and PCAS) versus acoustic variables

| Response and predictor variables | $N$ | $r^2$ | $b\pm$SE | $p_{10k}$ | $p$ |
|---|---|---|---|---|---|
| Response variable: DDS* | | | | | |
| F0 | 297 | 0.03 | −0.006±0.002 | **0.002** | <**0.001** |
| Minor formant | 264 | 0.04 | −0.002±0.001 | **0.002** | <**0.001** |
| F1 | 298 | 0.05 | −0.001±0.000 | <**0.001** | <**0.001** |
| F2 | 298 | 0.09 | −0.001±0.000 | <**0.001** | <**0.001** |
| F3 | 297 | 0.18 | −0.001±0.000 | <**0.001** | <**0.001** |
| F4 | 298 | 0.20 | −0.000±0.000 | <**0.001** | <**0.001** |
| F5 | 298 | 0.23 | −0.000±0.000 | <**0.001** | <**0.001** |
| Formant dispersion | 298 | 0.21 | −0.002±0.000 | <**0.001** | <**0.001** |
| Response variable: PCAS† | | | | | |
| F0 | 146 | 0.06 | −0.028±0.007 | **0.005** | <**0.001** |
| Minor formant | 124 | 0.12 | −0.011±0.004 | <**0.001** | 0.05 |
| F1 | 146 | 0.08 | −0.00767±0.002 | **0.002** | <**0.001** |
| F2 | 146 | 0.14 | −0.003±0.001 | <**0.001** | <**0.001** |
| F3 | 146 | 0.28 | −0.003±0.000 | <**0.001** | <**0.001** |
| F4 | 146 | 0.28 | −0.002±0.000 | <**0.001** | <**0.001** |
| F5 | 146 | 0.33 | −0.002±0.000 | <**0.001** | <**0.001** |
| Formant dispersion | 146 | 0.32 | −0.008±0.001 | <**0.001** | <**0.001** |

Models were fitted with male identity as a random effect. $P$ estimates less than 0.05 (after sequential Bonferroni correction) are shown in bold. $N$ = number of males; $r^2$ = coefficient of determination; $b$ = regression coefficient; $p_{10k}$ = significance of $b$; $p$ = probability of Breush–Pagan test on significance of random effect.

*David's dominance score.

†First principal component score.

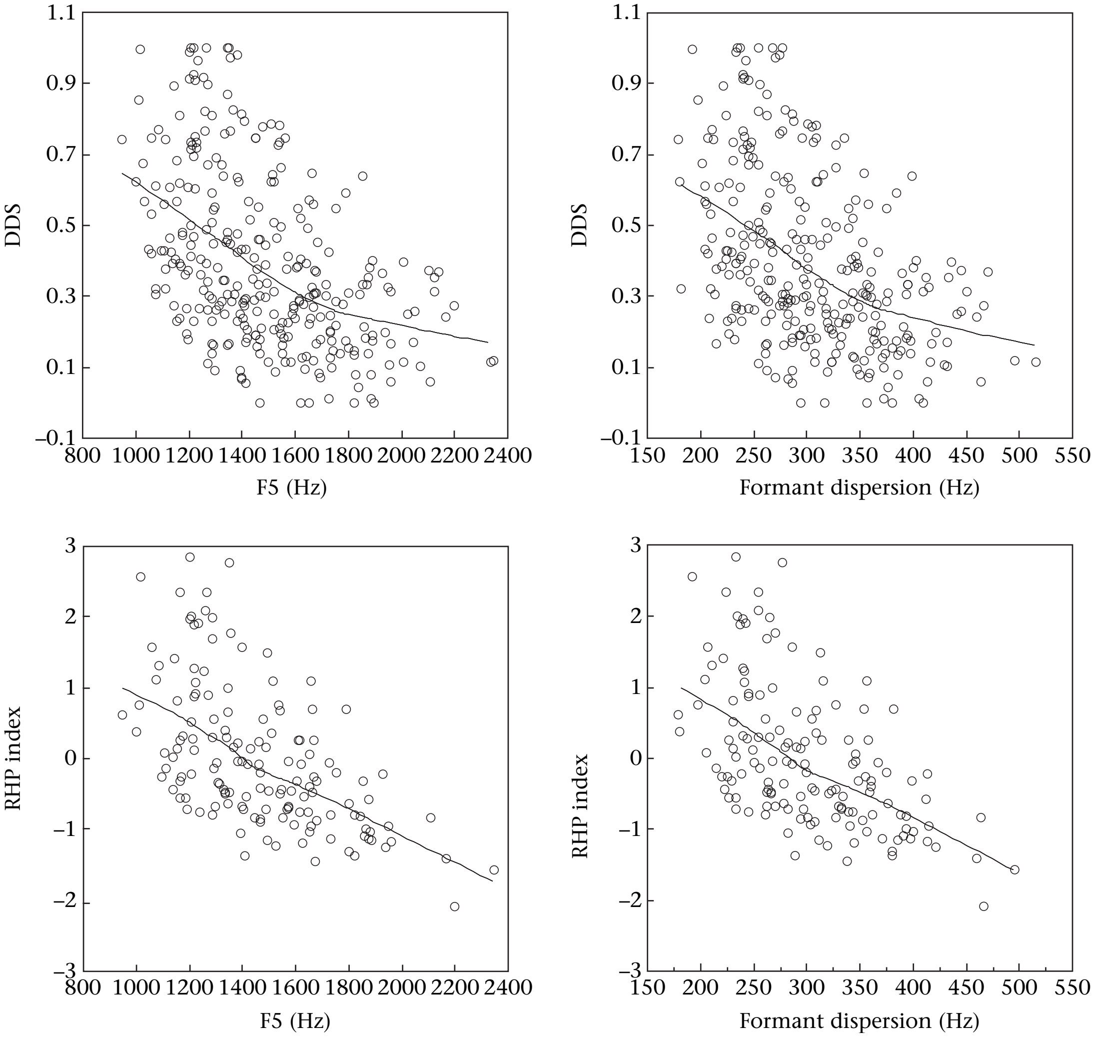

**Figure 6.** Relationships of measures of resource holding potential (RHP) to F5 and formant dispersion in male southern elephant seals, *Mirounga leonina*. DDS = David's dominance score; PCAS = first principal component score. Data points are for different males in each year of study; some individual males are shown for several years. Fitted lines are LOWESS smoothers.

Theoretically, upper formants are the best indicators of vocal tract length because they are not affected by the shape of the upper vocal tract (Fry 1979) and are the best index of body size (see above). Therefore we used F5 (assumed to be produced orally) for our first estimate of vocal tract length and we used the minor formant (assumed to be the first formant produced by the nasal tract) for the second estimate (Table 5). Mean F5 for adult males in our sample was 1326 Hz, corresponding to a mean oral tract length of 59 cm. The mean minor formant was 76 Hz, corresponding to a nasal tract length of 115 cm. From photogrammetry, mean oral tract length was 58 cm and nasal tract length was 114 cm ($N = 32$ photographs of 16 males; Table 6).

**Table 5.** Summary of stepwise multiple regression results for minor formant with phenotypic traits ($N = 47$, $r^2 = 0.28$)

| Response variables | $b$ | $\beta$ | $p_{10k}$ | VIF |
|---|---|---|---|---|
| Age | −1.706 | −1.774 | 0.34 | 3.55 |
| Body length | 0.096 | 0.107 | 0.44 | 4.64 |
| Trunk length | −2.758 | 0.965 | **0.005** | 5.14 |
| First bump outline length | 0.557 | 0.312 | 0.16 | 2.10 |
| Second bump outline length | 0.668 | 0.424 | 0.08 | 2.43 |

$N$ = number of males; $r^2$ = coefficient of determination; $b$ = partial regression coefficient; $\beta$ = standardized $b$; $p_{10k}$ = significance of $b$; VIF = variance inflation factor. Significant $p$ in bold.

## DISCUSSION

Our results indicate that aggressive vocalizations of male southern elephant seals convey reliable information about the vocalizer's phenotype. Frequency of formants (especially upper formants) explained a significant proportion of the variance in male age, size and resource holding potential. Therefore, formants and formant structure of vocalizations could be used to settle agonistic contests without close-range or physical interactions, including fights. In contrast, fundamental frequency was weakly

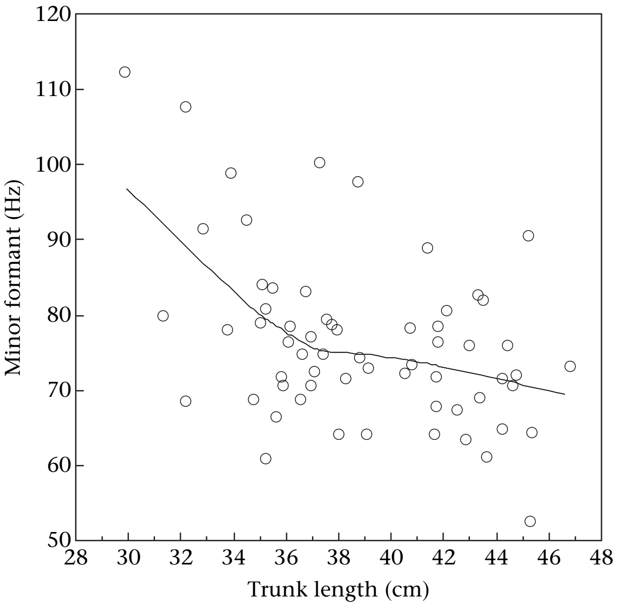

**Figure 7.** Relationship of proboscis (=trunk) length to the minor formant in vocalizations of male southern elephant seals, *Mirounga leonina*. The fitted line is LOWESS smoother. Data points are for different males.

related to phenotype, as for other mammalian species including humans (Fitch 1997; Reby & McComb 2003; Rendall et al. 2005). This pattern differs from that of nonmammalian species (Morton 1977; Davies & Halliday 1978; Ryan 1980), because mammalian vocal folds are not constrained by the neighbouring bony structures, so their size and shape can be changed easily during vocalization (Fry 1979; Fitch 1997; Fitch & Hauser 2002). Moreover, at least in humans and some other primates, development of vocal folds is partially dissociated from general body growth (Rendall et al. 2005).

In elephant seal vocalizations, F5 and the minor formant conveyed the most information about phenotype. Formant dispersion, proposed as a good summary measure of resonant properties of the vocal tract (Fitch 1997), was also a fair index of phenotype, but not as good as F5. Lower formants carried gradually less information going from F4 to F1, as in red deer (Reby & McComb 2003); however, correlations among formants complicates the interpretation of direct single-formant effects. The greater information content of upper formants is not surprising, because the frequency of lower formants depends on the shape of the supralaryngeal vocal tract, which can be modified during sound emission (Fant 1960; Fry 1979; Reby & McComb 2003). In humans, F1 is affected greatly by opening of the mouth, F2 and F3 are affected mostly by tongue position, and formants in the upper part of the frequency spectrum are related more to length of the vocal tract (Fry 1979). Nonhuman mammals were long thought to differ from humans in being unable to modify formant structure, because of the absence of a descended larynx and the weak ability to change the supralaryngeal vocal tract; however, increasing evidence suggests that these assumptions are not true (Hauser et al. 1993; Hauser & Schön-Ybarra 1994; Fitch 2000; Fitch & Reby 2001).

**Table 6.** Estimated and observed vocal tract lengths (VTL) for adult male elephant seals

| Variable | Mean (95% CI) | *N* (no. of males) |
|---|---|---|
| F5 (Hz) | 1326 (1286–1366) | 79 |
| F5 VTL (cm) | 59 (58–61) | 79 |
| Minor formant (Hz) | 76 (72–80) | 70 |
| Minor formant VTL (cm) | 115 (109–122) | 70 |
| Oral tract length (cm) | 58 (55–61) | 16 |
| Nasal tract length (cm) | 114 (109–119) | 16 |

F5 VTL: length of hypothetical vocal tract assuming that F5 is the fifth formant produced by its resonances; minor formant VTL: length of hypothetical vocal tract assuming that the minor formant is the first formant produced by its resonances (see text).

Elephant seals usually vocalize with an open mouth, but they can change posture while vocalizing. In addition, individuals differ in the postures they assume when they vocalize (S. Sanvito & F. Galimberti, unpublished data). Tongue position also varies: some males vocalize with the tongue at the back of the mouth and others have the tongue close to the teeth. For these reasons, it is not surprising that upper formants are better predictors of structural phenotype than lower formants. For instance, F1 of adult males averaged 258 Hz, and predicted F1 for a uniform tube is F5/9, or 147 Hz in our study: by opening the mouth, elephant seals roughly double the diameter of the vocal tract compared with the uniform-tube model, thereby greatly increasing F1.

In elephant seals, the presence of the proboscis, acting as a secondary resonator, complicates the interpretation of the frequency structure of vocalizations. Our multivariate analysis revealed that the minor formant is the second most informative vocal trait of a vocalizer's phenotype. The minor formant is related most strongly to trunk length and, therefore, could be the result of resonance in the nasal passage. An oral tract source of the minor formant is extremely unlikely, as length of this hypothetical vocal tract would be 115 cm long, which would place the larynx unrealistically low (Fig. 4). In contrast, for a nasal tract source, estimated tract length was in good agreement with measures obtained through photogrammetry. This model of vocal production, with the sound originating in the larynx and being expressed both from the nostrils and lips, also is in accordance with an oral tract length of approximately 60 cm, calculated from an observed value for F5. Attributes of the minor formant and its apparent source in the nasal tract support the idea that the nasal tract is an important extension of the vocal tract in southern elephant seals, and probably, also in northern elephant seals (cf. Sandegren 1976; McCann 1981). Vocal tract elongation is widespread in birds (tracheal elongation) and is known for some mammals, and may exaggerate the size information provided by acoustic signals (Fitch & Hauser 2002).

Strong correlations between formant traits and phenotype have been obtained for humans and other mammals on the basis of pooled data (Fitch 1997; Rendall et al. 2005). Much lower correlations (rarely with $r^2 > 0.40$)

have been found in studies on mature animals of one sex, as in our study (Reby & McComb 2003; Rendall et al. 2005). Our results confirm that formant attributes convey reliable information about a vocalizer's phenotype and can be honest signals (Fitch & Hauser 2002), but they also confirm that the variance of phenotypic traits explained by formant structure is moderate, and that many other factors may convey information about an individual's RHP. Most authors interpret statistically significant correlations between formant traits and phenotype as evidence for honest vocal signalling, but we suggest that the moderate levels of explained variance warrant a more cautious interpretation. The percentage of variance in phenotypic traits not explained by variance in formants was in most cases more than 50%. Therefore, the effectiveness of an assessment system based only on formants is, at least, dubious. Many factors can reduce the capability of formants to convey information about the phenotype. First, the elephant seal's vocal system is complicated by the presence of two interacting resonators, and this may reduce the strength of the relationships and increase the measurement error of formant frequencies. Moreover, cranial development is complex, with different elements growing at different rates, and does not parallel growth in or mirror general adult body size (King 1972; Johnson 1991; Hirakawa et al. 1992; Rendall et al. 2005). The relationship between body size and formants is, therefore, not expected to be as strict as usually assumed.

Vocalizations occur in most agonistic interactions between male elephant seals, and the use of vocalizations alone permits many contests to be settled. However, vocalizations are most effective when interacting males differ greatly in RHP, for example, when males are from different age classes (Braschi 2004). Even a moderate correlation between formant traits and phenotype may permit reliable assessment in such situations. Similarly, the source level of adult male vocalizations is a good index of age and size differences in this species but it is only approximate, and it is ineffective for discriminating among males of the same age (Sanvito & Galimberti 2003).

Vocalizations are only a part of the elephant seal display system, which includes optical cues, and probably nonvocal acoustic signals (e.g. vibrations; Shipley et al. 1992). A full evaluation of the assessment system should also include these signals (Miller 1991), a task that we are currently tackling.

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