Having a big nose: structure, ontogeny, and function of the elephant seal proboscis

Simona Sanvito, Filippo Galimberti, and Edward H. Miller

Abstract: The proboscis of male elephant seals (*Mirounga* Gray, 1827) has been suggested as an example of a secondary sexual trait since Darwin. There has been much speculation about its social function (e.g., optical signal of breeding status, amplification of vocalizations, cue for female choice). However, it has never been studied in detail, probably because its fleshy nature makes measurement difficult. In this paper, we employ photogrammetry to measure the proboscis and facial morphology of a large sample of wild, unrestrained, displaying male southern elephant seals (*Mirounga leonina* (L., 1758)). We describe ontogeny and allometry of the proboscis and analyze current phenotypic selection pressures on proboscis traits. We discuss the potential role of the proboscis in optical and acoustic signaling of male resource-holding potential and status. We demonstrate that proboscis size is positively correlated with age and body size independently, and that it is currently under a positive sexual selection pressure when the effect of selection on body size is removed. We suggest that selection on proboscis size is functionally related to the emission of agonistic vocalizations.

Résumé : À la suite de Darwin, on considère le proboscis des éléphants de mer (*Mirounga* Gray, 1827) comme un exemple de caractère sexuel secondaire. On a beaucoup spéculé sur la fonction sociale de cet organe (par exemple, comme signal optique du statut reproductif, amplificateur des vocalises, signal pour le choix des femelles). On ne l'a cependant jamais étudié en détail, probablement parce que sa nature charnue rend les mesures difficiles. Dans notre étude, nous utilisons la photogrammétrie pour mesurer le proboscis et la morphologie faciale chez un grand échantillon d'éléphants de mer du Sud (*Mirounga leonina* (L., 1758)) mâles, sauvages et libres au moment de leurs parades reproductives. Nous décrivons l'ontogénie et l'allométrie du proboscis et nous analysons les pressions phénotypes actuelles de sélection sur les caractères du proboscis. Nous discutons du rôle potentiel du proboscis dans la signalisation optique et acoustique du statut du mâle et de son potentiel de possession de ressources. Nous démontrons l'existence d'une corrélation positive indépendante entre la taille du proboscis, d'une part, et l'âge et la taille corporelle, d'autre part; la taille du proboscis est l'objet d'une sélection sexuelle positive, une fois retiré l'effet de la sélection sur la taille corporelle. Nous croyons que la sélection de la taille du proboscis est reliée fonctionnellement à l'émission de vocalises agonistes.

[Traduit par la Rédaction]

Introduction

Secondary sexual traits, i.e., traits involved in mate acquisition but not having a direct morphological or physiological function in reproduction, are a striking aspect of organic evolution (Darwin 1859, 1871). Elephant seals (*Mirounga* Gray, 1827) are an extreme example of sexual dimorphism in body size (Andersson 1994), with males being much larger than females (Le Boeuf and Laws 1994). Male elephant seals also have several secondary sexual traits such as the proboscis, which is an expansion of the nose that can be erected by muscular action (Laws 1953). The proboscis has been interpreted as a secondary sexual trait since Darwin (Darwin 1871): "The nose of the male sea-elephant … becomes greatly elongated during the breeding-season, and can then be erected. In this state it is sometimes a foot in length. The female is not thus provided at any period of life. The male makes a wild, hoarse, gurgling noise, which is audible at a great distance and is believed to be strengthened by the proboscis; the voice of the female being different. Lesson compares the erection of the proboscis, with the swelling of the wattles of male gallinaceous birds whilst courting the females". Darwin noted that the proboscis was largest during the breeding season, and suggested that it played a role in vocalization. The proboscis is present in both species of elephant seals but differs in shape and is larger in the smaller northern species (Laws 1953; Le Boeuf 1974; Briggs and Morejohn 1976; Le Boeuf and Laws 1994).

Sexual differences in facial morphology are widespread in pinnipeds (e.g., the "hood" of hooded seals, *Cystophora cristata* (Erxleben, 1777); Tyack and Miller 2001), presumably for optical signaling (Miller and Boness 1979; Miller 1991, 2002). Elephant seals appear to be unique among pinnipeds in exhibiting seasonal variation in facial morphology,

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with the proboscis being the largest during the breeding season even when relaxed (McCann 1981). The proboscis is expanded when males utter aggressive vocalizations, so (as Darwin suggested) may be involved in sound production (however, this interpretation has not been universally accepted; see Discussion below and Laws 1953). The proboscis may have evolved in relation to mate choice by females, although female mate choice is probably limited (Cox and Le Boeuf 1977) or absent (Galimberti et al. 2000) in elephant seals. The proboscis also could be an indicator of male age or body size, because it increases in size during physical maturation (Laws 1953; Sandegren 1976); however, some authors have suggested that individual variability in proboscis growth is so high that proboscis size cannot be used to estimate age accurately (McCann 1981), but none of them actually did any proboscis measurements.

Previous suggestions about functions of the elephant seal proboscis have been based on anecdotal information and indirect evidence. We used a photogrammetric method to measure the proboscis and facial area of a large sample of wild, unrestrained, male southern elephant seals (*Mirounga leonina* (L. 1758)) on the Falkland Islands. The proboscis is a fleshy trait, so it is difficult to measure, especially when it is enlarged during vocalization and agonistic displays at large; yet this is when measurements are likely to be most informative about behavioral function. Therefore, we made our measurements on vocalizing or displaying males. In this paper, we describe the structure of the proboscis, measurement repeatability, and individual variation. We then test two general hypotheses about the function of the erected proboscis during the breeding season: (1) the proboscis increases in size with age, so it can be used as an honest signal of age, and (2) the proboscis is positively allometric in relation to body size, so it can convey reliable information about body size of the bearer. Lastly, we carry out a phenotypic selection analysis to test the hypothesis that the proboscis is currently under direct, positive intrasexual selection.

Biology of the southern elephant seal

Elephant seals spend most of their life solitarily at sea, and most of their time at sea diving; they return to land twice each year to breed and molt (Laws 1994). Elephant seals are large and adults differ greatly in size: adult male and female southern elephant seals weigh around 2000–3000 (maximum 3700) kg and 300–600 (maximum 800 kg), respectively. Breeding males usually come to land well before the first females, and stay on land without eating for up to 3 months or more. During the breeding season, females gather in groups (“harems”) of variable size (2 to >300). Usually one adult male associates with each harem, keeps other males away, and engages in most of the copulations (each female enters a brief period of estrus about 3 weeks after giving birth). The combination of fasting and breeding effort results in significant energetic demands and loss of body mass. Growth of males is a two-phase process, with a postpubertal growth spurt (after ~5 years of age). Males mature physiologically years before they are large, strong, and experienced enough to get control of a harem at ~7 years of age (most harem holders are older). Males compete among themselves through vocalizations, optical threats, and fights, and establish a near-linear dominance hierarchy between males in which rank determines breeding success.

Materials and methods

General

Data were collected during two breeding seasons (September–November 1996 and 2002) at Sea Lion Island, Falkland Islands (SLI hereinafter), which has a small (~60 breeding males and ~550 breeding females) population of southern elephant seals (Galimberti et al. 2001). All males were individually marked with numbered cattle tags (jumbo Rototags; Dalton ID Systems Ltd., Henley-on-Thames, Oxon, England), some at birth and the remainder during their first haul out at SLI during the breeding season. In each breeding season, all breeding males also were uniquely marked with hair dye upon haul out for rapid identification. Further details on marking are described in Galimberti and Boitani (1999).

Estimation of age

Age was known for males tagged as pups and was estimated (to ±1 year) for other males, based on external features (Clinton 1994; Galimberti and Boitani 1999). We checked estimated ages using three criteria: (1) intra- and (2) inter-observer reliability and (3) correspondence with known age. Reliability was calculated using Kendall’s coefficient of concordance (Siegel and Castellan 1988), on the age attributed to marked males in a random sample of 10 daily censuses carried out during the 3-week period around the peak of the breeding season. Intraobserver reliability averaged 0.95 and interobserver reliability was 0.93–0.99. The validity of age estimation was checked using lifetime records of males that were present for three or more breeding seasons and by comparing the estimated age with known age for males tagged at birth. We carried out all analyses twice, on the full data set and on data only for males of known age. Results of the analyses were similar and our interpretations were identical, so we report below only on the full data set, because the sample size was larger and the sample included more older males.

Estimation of body length

Body length was estimated using a photogrammetric method (Haley et al. 1991; Bell et al. 1997), whereby animals lay on a flat surface with good alignment of body parts. Pictures were taken opportunistically when animals were on a level substrate. One person approached the seal from behind and held over its body a telescopic 4 m long surveying pole (scale with 1 cm increments) that was aligned with the seal’s long body axis. A second observer checked the alignment of the pole from in front of the seal’s head, using the midline of the proboscis as a reference, and then took photographs from the side at a distance of 10–20 m and with the camera 50–100 cm above the ground. Measurements from photographs after an animal substantially changed position or alignment were considered to be independent. We used a Canon EOS1 SLR camera with a 35–70 mm lens and Agfa 100 ASA black-and-white film, or a Canon PowerShot D20 digital camera at the highest resolution (3.1 megapixels). Black-and-white images were

Fig. 1. The photogrammetric method being used on a southern elephant seal, *Mirounga leonina*.

scanned as TIFF files. Pictures were measured using Object-Image version 2.20 (Vischer 2005), using the pole in the picture as a reference scale.

Measurement of the proboscis

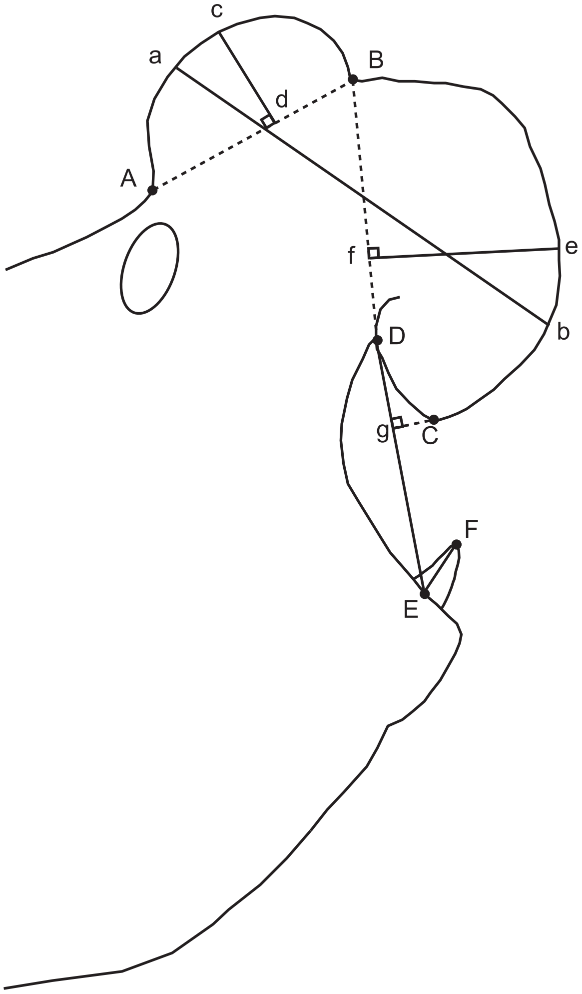
We used a similar photogrammetric method to measure the proboscis. One observer elicited a head-up posture and held a 2 m segment of the surveying pole parallel with the seal's long body axis, positioning the tip of the pole inside its mouth (between the lower canine teeth) (Fig. 1). A second observer took photographs from the side at 2–3 m distance. During each display, we took several photographs using a motor drive, and selected pictures with good alignment and maximal proboscis expansion. Photographs were taken using a Canon EOS1 SLR camera and 35–135 mm or 70–210 mm lens with black-and-white film. Negatives were scanned at high resolution, saved as grayscale TIFF files, and processed in Photoshop® (version 7; Adobe Inc., San Jose, California) to increase contrast and sharpness. Pictures were measured using Object-Image.

Proboscis measurements are shown in Fig. 2 and are defined in Table 1. Additional variables were calculated from the measured ones. In particular, because of correlations among proboscis traits (see Results), we ran principal component analysis (PCA) both on whole-proboscis traits (trunk_L, bump1_L, bump2_L, bump1_H, bump2_H, bump1_O, bump2_O) and on traits of the two bumps (respectively, bump1_L, bump1_H, and bump1_O; bump2_L, bump2_H, and bump2_O) separately. From these analyses, we retained the first principal components (PCs) as new variables (see Results). PCs were extracted from the covariance matrix with varimax rotation and scores calculated by linear regression.

Measurement error and repeatability

We calculated measurement error using variance components estimated from a model II ANOVA (Bailey and Byrnes 1990). Percent measurement error was calculated as the percentage of within picture or measurement variance on the total variance (i.e., within picture or measurement variance + among picture or measurement variance). We randomly selected 20 males, then randomly selected 1 picture for each male. Each of these pictures was measured three times to calculate error.

Fig. 2. Diagram of the measured traits of southern elephant seals; see Table 1 for definitions.



For each trait, we calculated repeatability (R, or the intraclass correlation coefficient), which is the proportion of among-individual variance on total variance (i.e., among-individual variance + within-individual variance). We estimated R using variance components from a model II ANOVA (Lessells and Boag 1987). We calculated confidence limits of repeatability using a jackknife delete-one procedure (Manly 1991), and tested its difference from zero using randomization (10 000 resamplings). Only males with three or more independent measures were included in the analysis (Bailey and Byrnes 1990).

Modelling proboscis growth

To study proboscis growth, we fitted three models: exponential model, simple linear regression, and piece-wise linear regression. Exponential curves derived from the Richards generalized curve are a standard method to fit growth data (Fitzhugh 1975; McLaren 1993). We fitted the following logistic curve: $\text{trait} = A/(1 + b\mathrm{e}^{-k\text{Age}})$, where A is the asymptotic length and $-k$ is the reduction in growth rate as age increases (b is a scaling factor not relevant here).

Recently, there has been a growing interest in multiphasic

Table 1. Definition of morphological variables considered in this study of southern elephant seals, *Mirounga leonina* (all units in centimetres, except for proportions and PC scores, which are unitless).

Variable name	Acronym	Definition	Reference to Fig. 2
Measured variables			
Canine length	canine_L	Total length of lower canine	EF
Trunk length	trunk_L	Maximal length of trunk	ab
Mouth length	mouth_L	Maximal opening of mouth, from where it joins trunk to base of lower canine	DE
Trunk fall	trunk_fall	Extent to which trunk falls over mouth, covering its opening	Dg
Free mouth	free_mouth	Extent of opening of mouth not covered by trunk	gE
1st bump length	bump1_L	Total width of 1st bump of trunk, measured as linear length of its base	Linear AB
2nd bump length	bump2_L	Total width of 2nd bump of trunk, measured as linear length of its base	Linear BD
1st bump outline	bump1_O	Total curvilinear length of 1st bump of trunk	Curvilinear AB
2nd bump outline	bump2_O	Total curvilinear length of 2nd bump of trunk	Curvilinear BC
1st bump height	bump1_H	Maximal height of 1st bump of trunk, perpendicular to AB	cd
2nd bump height	bump2_H	Maximal height of 2nd bump of trunk, perpendicular to BD	ef
Calculated variables			
Trunk size	trunk_size	Sum of curvilinear lengths of two bumps (AB + BC)	
Proportion 1st bump	p_bump1	First bump as proportion of total trunk (bump1_O/trunk_size)	
Inflation 1st bump	inflation1	Measurement of 1st bump expansion (bump1_O/bump1_L)	
Inflation 2nd bump	inflation2	Measurement of 2nd bump expansion (bump2_O/bump2_L)	
Trunk inflation	inflation	Measurement of total expansion of the trunk (inflation1 × p_bump1 + inflation2 × p_bump2)	
1st bump size	size_bump_1	Score of first principal component of first bump traits	
2nd bump size	size_bump_2	Score of first principal component of second bump traits	
Trunk 1st PC	trunk_PC1	Score of first principal component of whole trunk traits	
Trunk 2nd PC	trunk_PC2	Score of second principal component of whole trunk traits	

growth models (Koops 1986; Clinton 1994). A visual inspection of scatterplots of proboscis traits vs. age with fitted LOWESS smoother (Trexler and Travis 1993) showed a clear bending point in some cases. Therefore, we fitted the following piece-wise model with unknown bending point (Muggeo 2003): $\text{trait} = a_0 + b_1\text{Age} + b_d(\text{Age} - \text{BP})(\text{Age} - \text{BP})$, where BP is the bending point, a_0 is the intercept of the regression line before the bending point, b_1 is the slope of the regression line before the bending point, b_d is the difference in the slope between the regression line before and after the bending point, and Age > BP is a logic condition that returns 0 for ages ≤BP and 1 for ages >BP. Therefore, the slope of the regression line after the bending point (b_2) is equal to $b_d + b_1$. We tested the difference between steepness before and after the bending point by testing the null hypothesis H_0: $b_d = 0$ (for which b_1 and b_2 are the same). Logistic and piece-wise models were fitted with SYSTAT® version 11 (Systat Software Inc. 2004). Models were compared using Akaike's information criterion corrected for small sample sizes (AIC$_c$); a difference in AIC$_c$ ≥ 2 gives moderate evidence that the model with the lower AIC$_c$ should be preferred, whereas a difference of ≥7 gives strong evidence that this is the case (Burnham and Anderson 1998).

Allometry

We carried out univariate allometric analyses of facial traits (proboscis, mouth, and canines) using log-transformed data. There is no universal agreement on the best regression model to use in allometric analysis (McArdle 1988; La Barbera 1989). We used standard major axis regression (SMA) because (*i*) our variables were log-transformed; (*ii*) body size and facial traits were measured in the same unit (centimetres); and (*iii*) body size plus facial traits were measured using the same photogrammetric method, resulting in similar error variances. The application of SMA for the estimation of allometric coefficients requires a significant correlation between trait size and body size (Legendre and Legendre 1998), therefore, we calculated Pearson's *r* and tested its difference from 0 by permutation.

We analyzed multivariate allometry of the proboscis following Jolicoeur (1963), carrying out a PCA of the covariance matrix of log-transformed traits of the proboscis, then SMA regression of the first PC on log-transformed body-size data. We calculated standard errors and confidence intervals for the univariate and multivariate allometric coefficients by a jackknife delete-one procedure (Manly 1991).

Phenotypic selection

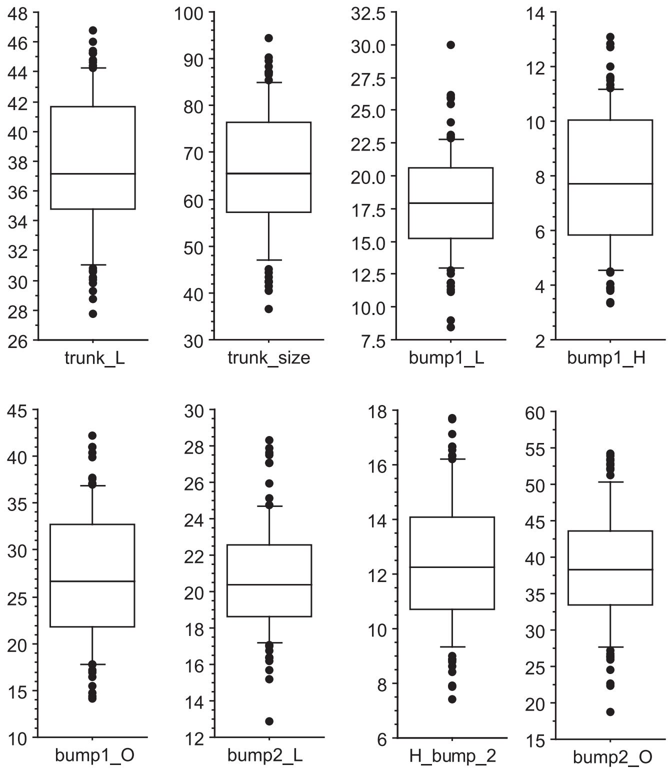
We carried out phenotypic selection analysis following Arnold and Wade (1984*a*, 1984*b*) and Conner (1996). We calculated three measures of individual fitness: female days (FF/DAYS, i.e., the sum of the number of females held by a male over each day of presence on land; Clutton-Brock et al. 1982); mating success (MS$_{100}$, i.e., the number of copulations with intromission ≥60 s observed per 100 h of observation; Campagna and Le Boeuf 1988); and the estimated number of females inseminated (ENFI, i.e., the proportion of observed copulations achieved by a male in a harem multiplied by the total number of females that bred in that harem, summed over all harems in which the male was

Table 2. Descriptive statistics for morphological traits of southern elephant seal proboscis.

					Normality		Homogeneity of means		Homogeneity of variances	
Trait	Mean ±SD (range)	CV (%)	Percent measurement error	Repeatability (*R*) and 95% CI	*W*	*P*	*t*	*P*	*F*	*P*
trunk_L	37.6±4.63 (27.8–46.8)	0.12	0.13	0.891 (0.849–0.934)	0.976	0.0895	–1.77	0.0805	0.0005	0.9825
bump1_L	18.0±4.02 (8.5–30.0)	0.22	3.00	0.833 (0.772–0.895)	0.993	0.9194	–1.43	0.1557	0.2912	0.5908
bump1_H	7.88±2.492 (3.35–13.09)	0.32	4.46	0.908 (0.872–0.945)	0.975	0.0737	–0.64	0.5269	0.0257	0.8730
bump1_O	27.0±7.15 (14.2–42.3)	0.27	4.33	0.900 (0.860–0.939)	0.977	0.1032	–0.88	0.3814	0.0479	0.8272
p_bump1	0.41±0.054 (0.28–0.52)	0.14		0.794 (0.721–0.867)	0.982	0.2222	0.18	0.8539	0.1560	0.6938
bump2_L	20.7±3.03 (12.9–28.3)	0.15	9.56	0.765 (0.683–0.846)	0.980	0.1578	–3.23	0.0017	0.2247	0.6366
bump2_H	12.4±2.42 (7.4–17.7)	0.20	0.33	0.835 (0.775–0.897)	0.979	0.1317	–2.66	0.0094	0.0113	0.9156
bump2_O	38.3±8.21 (18.8–54.3)	0.21	2.16	0.800 (0.729–0.872)	0.986	0.4559	–1.34	0.1822	0.1337	0.7155
trunk_size	65.3±13.55 (36.5–94.4)	0.21		0.87964 (0.833–0.926)	0.985	0.3601	–1.28	0.2039	0.0613	0.8050
inflation1	1.51±0.238 (1.11–2.17)	0.16		0.835 (0.773–0.896)	0.969	0.0254	0.77	0.4432	0.8819	0.3502
inflation2	1.85±0.278 (1.29–2.61)	0.15		0.699 (0.602–0.796)	0.981	0.2249	0.99	0.3254	1.5779	0.2123
inflation	1.71±0.242 (1.23–2.32)	0.14		0.757 (0.673–0.841)	0.989	0.6534	0.91	0.3663	1.3830	0.2427
trunk_fall	4.97±2.713 (0.12–10.61)	0.55	0.77	0.746 (0.660–0.833)	0.972	0.0471	–1.66	0.0998	1.0050	0.3188
mouth_L	29.5±3.99 (18.1–42.8)	0.14	0.57	0.710 (0.615–0.805)	0.980	0.1699	0.42	0.6725	0.2971	0.5871
free_mouth	24.6±4.90 (12.3–37.4)	0.20		0.746 (0.660–0.833)	0.991	0.7912	1.26	0.2093	0.3203	0.5729
canine_L	2.5±0.73 (0.9–4.3)	0.30	3.87	0.650 (0.542–0.757)	0.982	0.2276	–0.05	0.9564	0.0205	0.8865

Note: Definitions of morphological traits are available from Table 1. A Shapiro–Wilk test (*W*) was used to calculate the normality of the data. The homogeneity of means, as well as homogeneity of variances, was between 1996 and 2002 values. 95% CI, 95% confidence intervals.

Fig. 3. Boxplots of the distribution of the main proboscis traits of southern elephant seals.



observed to copulate; Le Boeuf 1974). The three measures were strongly correlated (Pearson's *r*, with randomization test; FF/DAYS vs. MS_{100} = 0.869, P_{10k} = 0.0001; FF/DAYS vs. ENFI = 0.972, P_{10k} = 0.0001; MS_{100} vs. ENFI = 0.919, P_{10k} = 0.0001). We chose ENFI as our fitness measure for the selection analysis because it is the most proximate measure of individual fitness, and in practice is the best measure of reproductive success as judged by genetically determined paternities (Fabiani et al. 2004). Absolute fitness was transformed to relative fitness by dividing by yearly mean fitness.

Prior to selection analysis, we calculated the opportunity for selection (I = fitness variance/(mean fitness)^2), which represents an upper limit to phenotypic selection (Arnold and Wade 1984*a*). We used (*i*) a parametric method to test whether the observed I (I_{obs}) was greater than expected from random access to females (Sutherland 1987), comparing the observed distribution of ENFI to a Poisson distribution with mean equal to the observed mean ENFI (Banks and Thompson 1985), and (*ii*) a nonparametric method based on Monte Carlo simulation (McLain 1986). For each cycle of the simulation, each female was fertilized by one male chosen at random, and the resulting I (I_{sim}) was calculated. After 10 000 cycles, we calculated the proportion of cycles in which $I_{sim} > I_{obs}$.

We fitted nonparametric fitness functions for each morphological trait using cubic splines with the smoothing parameter chosen by cross validation (Schluter 1988). We then calculated 95% confidence bands for the fitness functions using a bootstrap procedure (10 000 samples).

We estimated univariate selection pressures on each trait by calculating selection differentials (*s*, i.e., the covariance between relative fitness and the trait) and selection intensities (*i*, i.e., the selection differential for the standardized trait). Selection differentials measure direct effects of selection on a trait plus indirect effects owing to selection on other traits correlated with the first (Arnold and Wade 1984*a*). Therefore, we also calculated selection gradients (β), which measure the selection pressures directly acting on a trait, with a multiple regression of relative fitness on standardized traits. The fitness measure, ENFI, had a skewed distribution with a very long right tail (g_1 = 2.90, g_2 = 9.67), and overdispersion (CV = 2.09). Therefore, we calculated standard error (SE) and confidence limits of selection

Table 3. Covariance and correlation matrix for proboscis traits of southern elephant seals.

	trunk_L	bump1_L	bump1_H	bump1_O	bump2_L	bump2_H	bump2_O
trunk_L	21.4	12.0	9.5	27.3	10.2	9.5	30.2
bump1_L	0.643**	16.2	7.0	23.8	3.79	3.54	9.49
bump1_H	0.824**	0.697**	6.21	17.3	3.11	3.94	12.7
bump1_O	0.824**	0.828**	0.969**	51.1	8.29	10.5	32.6
bump2_L	0.725**	0.311*	0.411**	0.383**	9.19	5.64	18.5
bump2_H	0.846**	0.363**	0.652**	0.608**	0.767**	5.88	18.7
bump2_O	0.794**	0.288*	0.619**	0.556**	0.742**	0.939**	67.4

Note: Covariances are above, variances are on, and Pearson's r correlations are below the diagonal. *, significant at $\alpha = 0.05$; **, significant at $\alpha = 0.01$ (sequential Bonferroni correction; see Materials and methods).

Table 4. Change in morphological traits of male southern elephant seals with age.

	Mean male age class (year)									
Trait	5 (N = 1)	6 (N = 5)	7 (N = 21)	8 (N = 19)	9 (N = 13)	10 (N = 9)	11 (N = 10)	12 (N = 3)	13 (N = 1)	14 (N = 1)
trunk_L	30.7	32.3	35.1	37.4	40.9	40.2	40.5	44.3	41.7	44.3
bump1_L	12.5	17.1	17.1	17.1	19.9	16.7	19.5	25.0	16.6	23.0
bump1_H	3.92	4.91	7.01	7.18	9.66	9.04	9.76	11.7	7.68	11.3
bump1_O	15.6	20.6	24.4	24.9	32.0	29.2	32.0	39.0	26.6	37.6
p_bump1	0.405	0.429	0.407	0.384	0.427	0.394	0.439	0.472	0.451	0.416
bump2_L	15.7	18.3	19.8	21.2	22.6	21.8	21.3	21.5	20.1	21.1
bump2_H	8.6	9.6	11.6	12.7	14.0	13.9	13.4	14.3	10.7	14.8
bump2_O	22.9	28.0	35.0	39.8	43.0	44.5	41.5	43.6	32.3	52.6
trunk_size	38.4	48.6	59.4	64.6	75.0	73.7	73.6	82.6	58.9	90.2
inflation1	1.24	1.22	1.44	1.47	1.60	1.78	1.66	1.58	1.60	1.66
inflation2	1.46	1.53	1.76	1.90	1.92	2.05	1.95	2.04	1.61	2.49
inflation	1.37	1.40	1.63	1.73	1.79	1.95	1.84	1.82	1.60	2.14
trunk_fall	1.27	2.71	3.95	4.92	6.93	6.21	6.05	8.26	2.17	10.2
mouth_L	28.2	26.8	28.8	28.4	29.1	30.6	32.7	28.8	36.2	38.8
free_mouth	26.9	24.1	24.8	23.5	22.2	24.4	26.6	20.5	34.1	28.7
canine_L	2.28	1.70	2.32	2.35	2.55	2.88	2.41	2.60	3.28	3.89

Fig. 4. Facial development of southern elephant seals with age. The pictures show different individuals belonging to different age classes, from juvenile to fully developed adults.

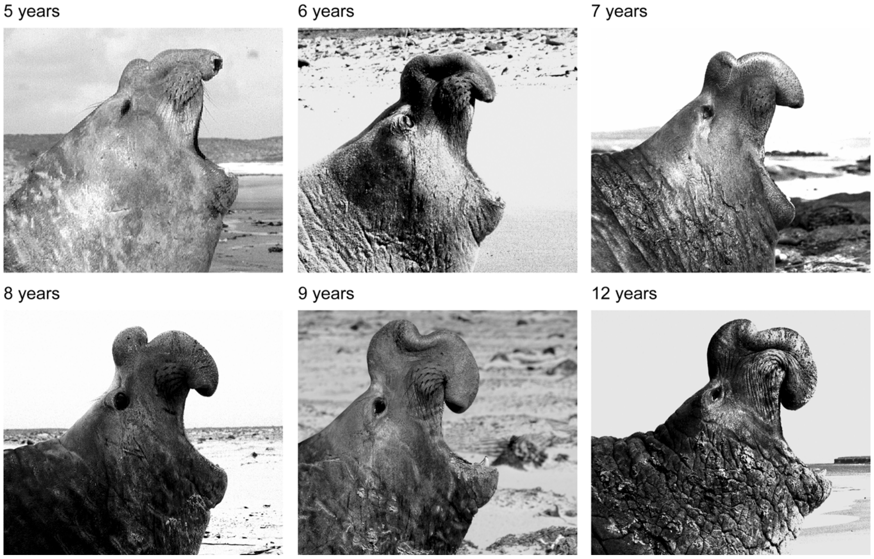


Table 5. Comparison of simple linear regression (two-parameters model) and piece-wise regression (four-parameter model) for facial traits of southern elephant seals using AIC_c (see Materials and methods).

	AIC_c		
Trait	Piece-wise regression	Linear regression	ΔAIC_c between models
trunk_L	214.4	216.4	**–2.0**
bump1_L	230.5	226	4.5
bump1_H	159.3	119	40.3
bump1_O	304.6	300.1	4.5
p_bump1	–476.5	–479.3	2.8
bump2_L	195.1	184.5	10.6
bump2_H	124.3	131.2	**–6.9**
bump2_O	322.7	330.9	**–8.2**
trunk_size	405.2	400.8	4.4
inflation1	–260.3	–255.8	**–4.5**
inflation2	–226.4	–225.8	–0.6
inflation	–258.2	–255.7	**–2.5**
trunk_fall	149.3	147.6	1.7
mouth_L	232.2	229.1	3.1
free_mouth	271.8	270.7	1.1
canine_L	–39.9	–52.7	12.8

Note: Differences in AIC_c (ΔAIC_c) between models for traits that were fitted better by the piece-wise regression (difference ≥2) are shown in boldface type.

Table 6. (A) Linear regression (coefficient of determination (R^2), slope or regression coefficient (b), standard error (SE), 95% CI) and (B) piece-wise regression (R^2, bending point (BP), intercept of regression line before BP (a), slope before BP (b_1), difference in the slope between regressions lines before and after BP (b_d), slope after BP (b_2)) models of growth of southern elephant seal facial morphology.

(A) Linear regression.

Trait	R^2	b ± SE (95% CI)	P
bump1_L	0.107	0.73±0.23 (0.264 to 1.186)	0.0025
bump1_H	0.350	0.81±0.12 (0.571 to 1.041)	0.0000
bump1_O	0.311	2.19±0.33 (1.530 to 2.856)	0.0000
bump2_L	0.072	0.45±0.16 (0.138 to 0.766)	0.0145
trunk_size	0.341	4.31±0.72 (2.891 to 5.738)	0.0000
inflation_2	0.187	0.07±0.02 (0.031 to 0.101)	0.0000
trunk_fall	0.207	0.67±0.16 (0.344 to 0.988)	0.0000
mouth_L	0.147	0.88±0.25 (0.388 to 1.381)	0.0003
free_mouth	0.006	0.22±0.33 (–0.444 to 0.880)	0.5140
canine_L	0.096	0.13±0.04 (0.044 to 0.211)	0.0050

(B) Piece-wise regression.

Trait	R^2	BP	a_0 (95% CI)	b_1 (95% CI)	b_d (95% CI)	b_2	t	P
trunk_L	0.433	9	17.5 (10.3 to 24.7)	2.51 (1.57 to 3.44)	–1.80 (–3.48 to –0.13)	0.71	–2.139	0.0354
bump2_H	0.290	9	1.64 (–4.28 to 7.56)	1.39 (0.58 to 2.20)	1.53 (–2.51 to –0.56)	–0.14	–3.145	0.0023
bump2_O	0.335	9	–4.59 (–24.1 to 15.0)	5.58 (2.91 to 8.26)	–5.67 (–8.88 to –2.46)	–0.09	–3.518	0.0007
inflation1	0.307	10	0.674 (0.260 to 1.087)	0.10 (0.05 to 0.16)	–0.14 (–0.23 to –0.04)	–0.03	–2.829	0.0059
inflation	0.297	9	0.613 (0.022 to 1.203)	0.14 (0.06 to 0.22)	–0.13 (–0.22 to –0.03)	0.02	–2.575	0.0118

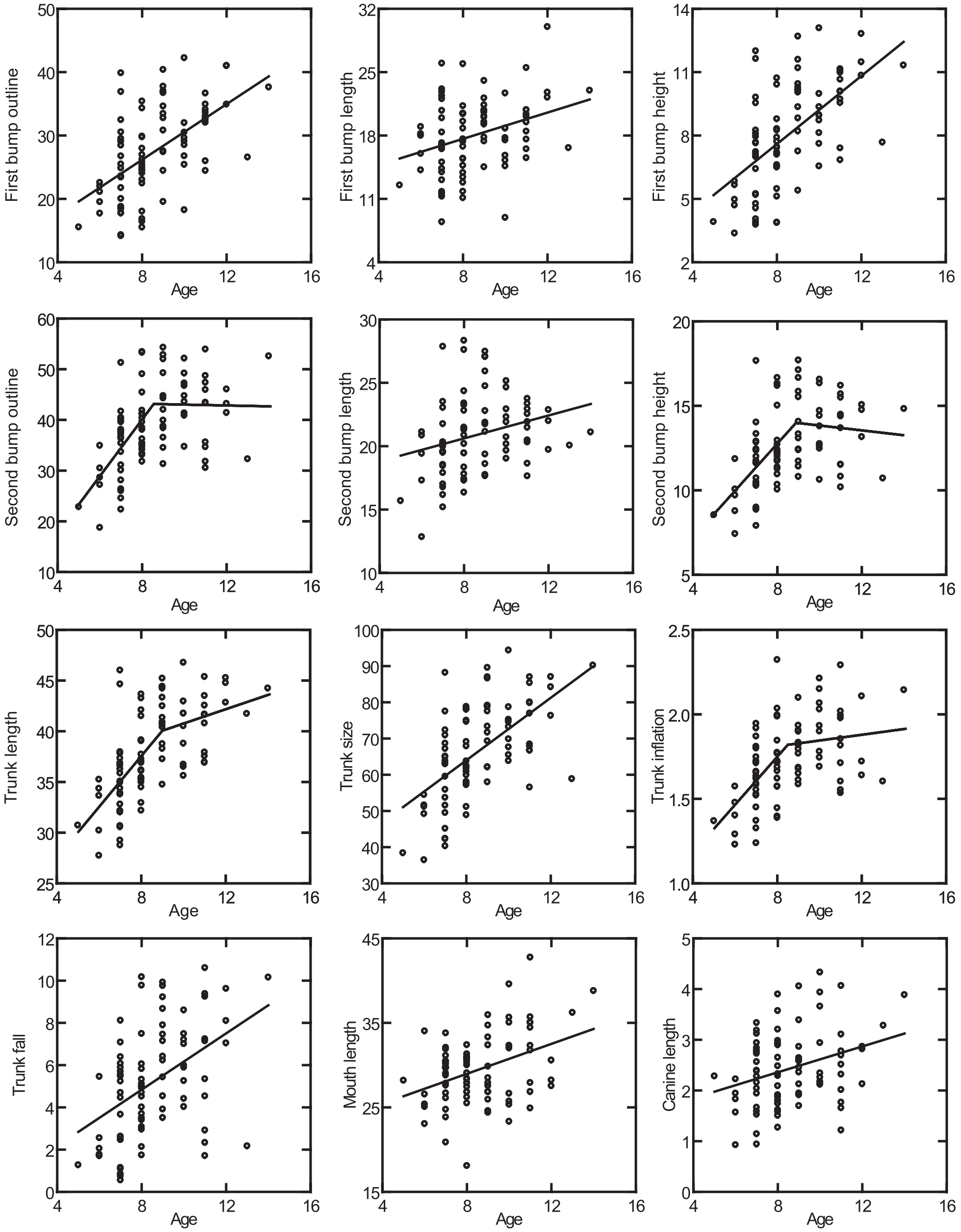
Note: P values indicate the significance of the regression coefficient (H_0: $b = 0$) in A and the significance of the change in slope after BP (H_0: $b_d = 0$) in B. For all traits and models, $N = 83$ males.

differentials and gradients using a jackknife delete-one procedure (Mitchell-Olds and Shaw 1987), and tested their difference from 0 with randomization (10 000 resamplings; Manly 1991). A problem with multivariate analysis of selection is the correlation among phenotypic traits (i.e., multicollinearity), because it may produce poor estimates of selection gradients (Mitchell-Olds and Shaw 1987). For each phenotypic trait and each regression model, we calculated a collinearity diagnostic, the variance inflation factor (VIF) = $1/(1 - R_j^2)$), where R_j^2 is the coefficient of determination of the linear regression of a trait j vs. all other traits included in the regression model. Values of VIF > 10 indicate a serious multicollinearity problem (Rawlings 1988).

Statistics

We present descriptive statistics as mean ± standard deviation (SD), and least-squares estimates as estimates ± SE.

Fig. 5. Scatterplots of some facial traits of southern elephant seals relative to age, with fitted linear regressions or piece-wise regressions (see Materials and methods).



We visually inspected distributions of variables using boxplots and tested normality using the Shapiro–Wilk test. We tested homogeneity of means between the 2 years of study using Student's *t* tests with randomization, and homogeneity of variances using the Brown–Forsyte test, again with randomization (Manly 1991). In case of multiple tests, we calculated adjusted probabilities using a sequential Bonferroni procedure (Hochberg and Benjamini 1990), with a required family-wise nominal level of $\alpha = 0.05$. In this procedure, calculated *P* values are examined in order from largest to the smallest. Adjusted *P* values were calculated using the following formula: adjusted $P_i = (n - i + 1)P_i$, where n is the number of *P* values, i is from 1 (largest) to n (smallest), P_i is the observed *i*th *P* value, and adjusted P_i is the adjusted *i*th *P* value. Adjusted *P* values were compared with the nominal level of choice. If adjusted *P* values were equal to or smaller than the nominal level, those values and all smaller observed *P* values were rejected at the nominal level. All statistical analyses were carried out with STATA® version 9 (StataCorp LP 2005). The number of resamplings in randomization tests is stated as the subscript of *P* labels; observed values of statistic were included in the resampled statistics (Manly 1991).

Results

Measurement error, repeatability, and statistics (Table 2)

Measurement error was <10% for all traits and was >5%

Table 7. Allometry of facial morphology of southern elephant seals (see Materials and methods), where *b* is the allometric coefficient.

Trait	*b* ± SE (95% CI)	Pearson's *r*	*P*
trunk_L	1.429±0.147 (1.170–1.745)	0.582	0.0001
bump1_L	3.018±0.363 (2.391–3.809)	0.311	0.0106
bump1_H	3.884±0.427 (3.105–4.860)	0.408	0.0008
bump1_O	3.442±0.370 (2.749–4.308)	0.402	0.0011
bump2_L	1.793±0.240 (1.417–2.269)	0.280	0.0225
bump2_H	2.251±0.246 (1.783–2.842)	0.310	0.0112
bump2_O	2.870±0.331 (2.274–3.623)	0.311	0.0105
trunk_size	2.568±0.286 (2.057–3.205)	0.427	0.0005
inflation1	1.176±0.141 (0.925–1.495)	0.195	0.1160
inflation2	1.230±0.134 (0.967–1.565)	0.179	0.1478
inflation	1.087±0.129 (0.856–1.381)	0.210	0.0864
trunk_fall	9.171±0.716 (7.239–11.618)	0.261	0.0197
mouth_L	1.840±0.206 (1.478–2.291)	0.452	0.0002
free_mouth	2.879±0.296 (2.266–3.657)	0.215	0.0416
canine_L	3.241±0.356 (2.550–4.120)	0.235	0.0588
Multivariate allometry	15.184±2.016 (11.942–19.306)	0.197	0.1167

Note: *P* values are the probabilities of the randomization test on the null hypothesis H_0: $r = 0$. For all traits, $N = 67$ males.

only for one variable (bump2_L). Measurement error for the outlines, which can be difficult to trace, was not greater than for linear measures. Repeatability of traits was high and significantly different from 0 for all traits. Size of trunk and of the first bump had the highest repeatability.

Trunk length averaged 37.6 cm, trunk size averaged 65.3 cm, and mouth opening averaged 29.5 cm. Distributions of variables were close to normal (Fig. 3, Table 2). The variables bump2_L and bump2_H differed significantly between years (1.95 and 1.3 cm longer, respectively, in 2002), but all other traits were homogeneous (Table 2). Variances were homogeneous between years (Table 2).

Correlations among proboscis traits

All correlations among proboscis traits were significantly positive, averaging Pearson's $r = 0.651$ (range 0.3–0.9; Table 3); however, as a whole, they were lower than expected from a set of morphologically integrated traits, with some correlations between 0.3 and 0.4. Relatively low correlations were found between the two bumps, indicating that their development was in part independent. Correlation matrices were homogeneous between years (standardized Mantel statistic = 0.9083, $P_{10k} = 0.9999$). The Bartlett test of sphericity was significant for each year (1996: $\chi^2_{[27]} = 556.4$, $P < 0.0001$; 2002: $\chi^2_{[27]} = 484.0$, $P < 0.0001$). In PCA, the first two PCs explained >93% of the variance of the seven original variables. Variables representing the two outlines had the highest loadings. Scores on the first two PCs were used as summary measures of proboscis size and shape (trunk_PC1 and trunk_PC2) for subsequent analyses.

Height, length, and outline were highly correlated (Pearson's $r > 0.9$) within each bump, so we ran PCAs to calculate overall measures of bump size. The first PC explained ~93% and ~95% of the variance of the original three traits for the first and second bumps, respectively, and its scores were retained as the new variables size_bump_1 and size_bump_2.

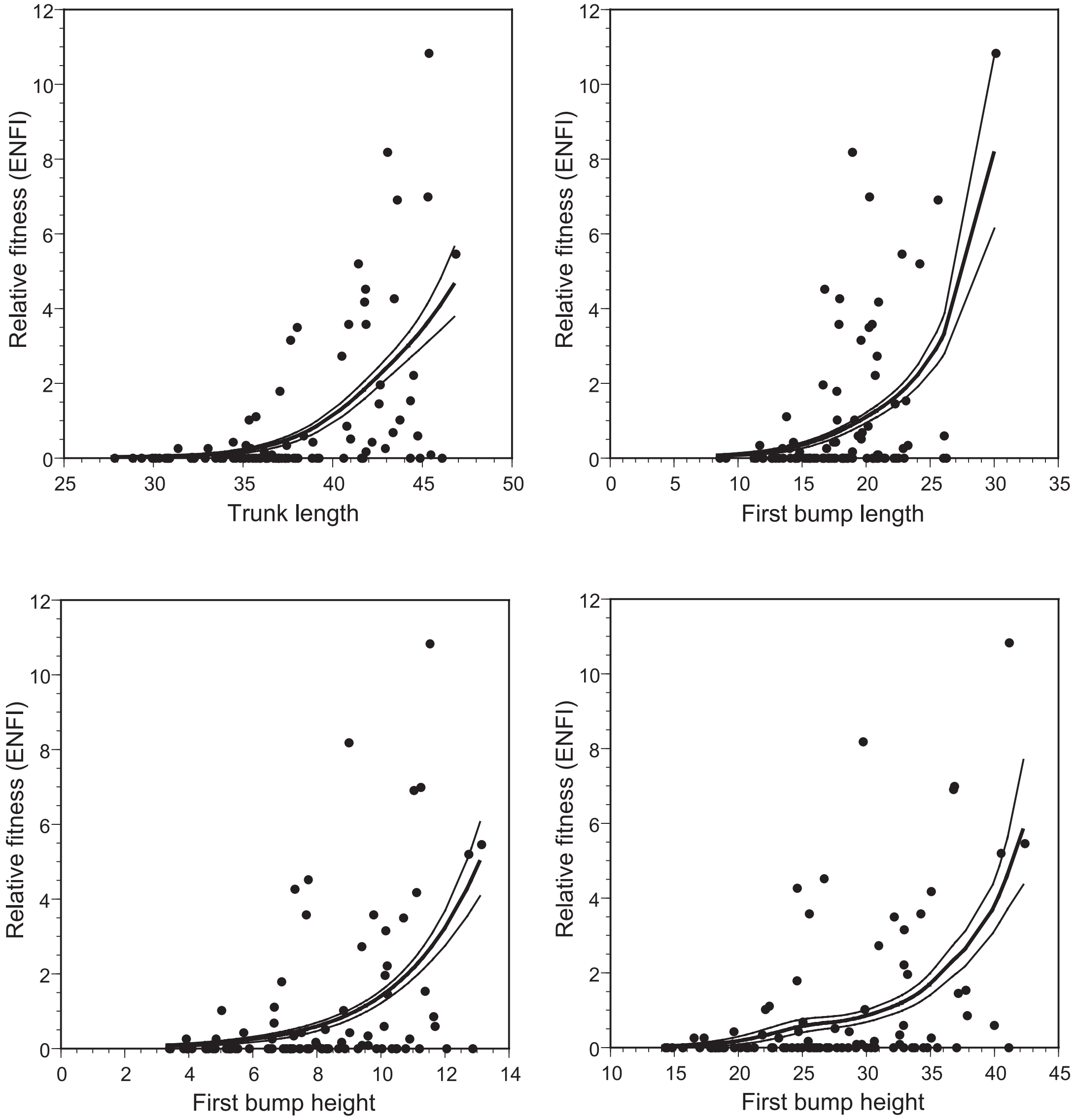
Age-related variation in facial morphology

Age-specific statistics of proboscis traits are listed in Table 4, and examples of the proboscis for different ages is shown in Fig. 4. The iterative Levenberg–Marquardt algorithm with least-squares loss function used to fit the logistic model achieved convergence for only 9 of 17 traits, showing that the logistic model (and asymptotic exponential models generally) were not adequate descriptions of proboscis growth. Although there was an apparent reduction in the slope of the age-specific variation of some proboscis traits around age 9, no trait showed a clear asymptote, little variance was explained by the logistic model for most traits (mean $R^2 = 0.327$), and SE of the *b* (SE_b) parameter was often very large. Estimated parameters had large correlations in most cases (in particular *b* and *k*), an indication of overparameterization. Therefore, we concentrated on linear models. The visual examination of scatterplots with LOWESS smoothers suggested that some traits increased almost linearly until approximately age 9, then growth slowed or stopped. Therefore we fitted a linear regression, then compared its fit with the fit of a piece-wise regression with an unknown bending point, using AIC_c (Table 5). For some traits, a better fit was obtained with the piece-wise model. In particular, trunk length, the second bump, and the trunk inflation showed a clear inflection point at age 9, whereas growth was linear for the first bump (Table 6, Fig. 5).

Allometry of facial morphology

SMA regression analysis showed high positive allometry on most traits of facial morphology (Table 7), and the 95% confidence interval (CI) did not include the isometric slope except for the three measures of proboscis inflation. Traits of the first bump had steeper allometric coefficients than traits of the second bump. Positive allometry also was suggested by the multivariate analysis (allometric coefficient >1); however, Pearson's *r* did not differ from zero (Table 7).

Fig. 6. Nonparametric univariate fitness functions of some proboscis traits of southern elephant seals (see Materials and methods).



Phenotypic selection

ENFI averaged 11.7 females and the opportunity for selection was 4.18 (N = 92 males). ENFI values showed a greater dispersion than for a Poisson distribution with the same mean, with a very long positive tail (Kolmogorov–Smirnov test with permutations: K–S statistic = 0.6836, P_{10k} = 0.0001). I_{obs} also was significantly greater than the expected I with random allocation of female fertilizations to males (I_{sim} = 0.076 ± 0.016; P_{10k} = 0.0001). Nonparametric fitness functions for some traits are shown in Fig. 6. These functions showed a slope close to zero in the first part of the range, where males had fitness close to zero, then a steep increase in the second part. Selection differentials and selection intensities are summarized in Table 8. Various traits, including all measures of size of the trunk, had positive and statistically significant selection differentials. In contrast, selection differentials on canine length were not significant.

Only trunk length had a statistically significant positive gradient (Table 9). Individual fitness in elephant seals is strongly related to body size, which is also related to trunk size. Therefore, we calculated selection gradients for a two-trait model that incorporated body length and trunk length. The main effect was due to body size (β = 1.022 vs. 0.703), but both selection gradients were significant (P_{10k} = 0.0001 vs. 0.0286).

Discussion

Characterization and measurement of the elephant seal proboscis are difficult because it is fleshy, and its size and shape depend on a male's behavior and motivational state. Our standardized stimulation of males, coupled with photogrammetry, provided highly repeatable measures of the proboscis during male agonistic displays. Measurement error was slightly higher than for conventional morphological traits (Yezerinac et al. 1992), but was low enough for our variables to be used as good phenotypic traits.

Facial differences between the sexes are widespread in pinnipeds (Miller and Boness 1979; Miller 1991, 2002), and

Table 8. Selection differentials (*s*) and selection intensities (*i*) on facial traits of southern elephant seals (see Materials and methods).

Trait	s ± SE (95% CI)	i	P_{10k}
trunk_L	4.847±1.253 (2.358 to 7.337)	1.047	0.0001
bump1_L	3.35±1.464 (0.442 to 6.259)	0.841	0.0001
bump1_H	2.076±0.613 (0.859 to 3.293)	0.827	0.0001
bump1_O	6.346±2.030 (2.315 to 10.378)	0.888	0.0001
p_bump1	0.018±0.012 (–0.007 to 0.042)	0.280	0.0960
bump2_L	2.161±0.782 (0.609 to 3.714)	0.556	0.0025
bump2_H	0.399±1.000 (–1.588 to 2.386)	0.046	0.3120
bump2_O	6.324±1.940 (2.470 to 10.177)	0.648	0.0003
p_bump2	–0.051±0.022 (–0.095 to –0.007)	–0.317	0.9934
trunk_size	14.012±3.892 (6.281 to 21.742)	0.795	0.0001
inflation1	0.066±0.041 (–0.016 to 0.149)	0.274	0.1002
inflation2	0.122±0.059 (0.005 to 0.239)	0.425	0.0296
inflation	–0.687±0.463 (–1.606 to 0.232)	–0.164	0.7582
trunk_fall	1.577±0.580 (0.426 to 2.728)	0.581	0.0031
mouth_L	3.287±0.930 (1.440 to 5.134)	0.823	0.0001
free_mouth	2.531±1.130 (0.286 to 4.776)	0.385	0.0250
canine_L	–4.007±2.570 (–9.112 to 1.098)	–0.171	0.7784

Note: P_{10k} values are the probabilities of the randomization test on the null hypothesis H_0: $s = 0$.

Table 9. Selection gradients (β) on proboscis traits of southern elephant seals (see Materials and methods).

Trait	β ± SE (95% CI)	P_{10k}
trunk_L	1.484±0.661 (0.232 to 2.859)	0.0321
bump1_L	0.556±0.897 (–1.197 to 2.367)	0.3886
bump1_H	0.483±1.363 (–2.188 to 3.228)	0.7280
bump1_O	–1.082±2.005 (–5.139 to 2.825)	0.5502
bump2_L	–0.484±0.487 (–1.473 to 0.464)	0.2628
bump2_H	0.568±0.751 (–0.978 to 2.007)	0.4414
bump2_O	–0.541±0.584 (–1.679 to 0.643)	0.4033

Note: P_{10k} values are the probabilities of the randomization test on the null hypothesis H_0: $\beta = 0$.

sexual differences in anatomy related to vocalization also occur (e.g., pharyngeal pouches of the walrus, *Odobenus rosmarus* (L., 1758); Tyack and Miller 2001). Facial morphology is a key component of threat communication in elephant seals — during agonistic contests, the proboscis is expanded, the mouth is opened, and the lower canine teeth are displayed (Sandegren 1976). The two most striking components of male elephant seal facial morphology are the proboscis and canines. The latter seem to not be under directional selection in the SLI population. Canine teeth are sexually dimorphic in many mammals, often resulting from intrasexual selection that favors the enlargement of canines for displays or fights between males (Harvey et al. 1978; Gittleman and Van Valkenburgh 1997). Sexual dimorphism in the size of the canine teeth also is widespread in pinnipeds (Lowry and Folk 1990), including both *Mirounga* species (Briggs and Morejohn 1975, 1976). Male elephant seals bite each other during agonistic contests, but it is doubtful that bites determine the outcome of contests (Haley 1994). At SLI (Braschi 2004) and in the Valdés Peninsula elephant seal population (Galimberti 1995), contests are determined by male strength and stamina, which in turn are related to body size; bites play only a secondary role.

The processes of intrasexual selection and selection by female choice may act together on the same male trait (Andersson 1994). Intrasexual selection is widely accepted to be an important evolutionary process for male elephant seals (Le Boeuf 1974; McCann 1981), resulting in the highest known opportunity for selection for any vertebrate (Galimberti et al. 2002). In contrast, the importance of intersexual selection is debated. The elephant seal mating system seems to offer few chances for females to choose mates directly (Galimberti et al. 2000): unlike other species, females move little between parturition and estrus, so almost always mate in the harem where they gave birth (compared with red deer, *Cervus elaphus* L., 1758; Clutton-Brock et al. 1982), and females play no role in the process of harem acquisition by males, which depends only on dominance relationships among males (compared with gelada baboon, *Theropithecus gelada* (Rüppell, 1835); Dunbar 1984). Moreover, at SLI, most matings and fertilizations involve harem-holding males (Galimberti et al. 2002; Fabiani et al. 2004). Therefore, the mating system severely constrains direct behavioral choice of mate by females (Beehler and Foster 1988), so the directional selection on proboscis size that we detected must be related to intrasexual selection. Secondary sexual traits usually are related to body size, which is a direct target of intrasexual selection in many species. Therefore, the direct effect of phenotypic selection on secondary sexual traits should be assessed by taking body size into account. When secondary sexual traits are the direct target of sexual selection, selection pressures may or may not be in the same direction as selection on size (Brown and Bartalon 1986; Feh 1990; Barki et al. 1991). At SLI, the selection gradient on proboscis size was positive and significantly different from zero even when the effect of body length was considered.

Most published statements about the functional role of the elephant seal proboscis in male competition are based on anecdotal or indirect evidence. For example, McCann (1981) stated that "The size of the proboscis increases with age but there is too much variation in its size among adult males for it to be used as a means of assessing relative dominance, as with the horns of some sheep species." Contrary to this conclusion, we showed that the growth of the proboscis and its two bumps is linear up to ~9 years of age. Therefore, it can reliably inform about age for at least some age groups, e.g., permitting discrimination between subadults and adults. Moreover, most proboscis traits are positively allometric relative to body size. Therefore, the proboscis can also inform about body size. Male southern elephant seals expand the proboscis when vocalizing, but otherwise have no special agonistic display for its exhibition. In species with specialized structures for communication, male agonistic behavior typically includes optical displays, e.g., the parallel walk of deer (Clutton-Brock et al. 1979; Barrette 1986; Braza et al. 1986; Jennings et al. 2003) and the antiparallel threat display of gray seals (*Halichoerus grypus* (Fabricius, 1791); Miller and Boness 1979). In elephant seals, a side-by-side posture that displays the proboscis best is very rare (<1% at SLI, unpublished data; Sandegren 1976). During most interactions, males are in front of one another, a position that does not permit effective display or assessment of proboscis size or shape. Therefore, it seems unlikely that the proboscis arose or functions mainly as an optical signal, apart from being a generic indication of male arousal (McCann 1981).

Vocalizations are a main component of elephant seal agonistic behavior (Sandegren 1976; Sanvito and Galimberti 2000), and vocalizations always are emitted with the proboscis expanded. Published statements regarding sound production in male elephant seals are anecdotal and contradictory. For the southern elephant seal, Laws (1953, 1956) suggests that air passes through the proboscis during vocalization, causing it to vibrate, and that sounds are altered by resonances in the proboscis diverticula. In contrast, McCann (1981) stated that “the proboscis does not appear to affect sound production”, but he did not provide any support for his statement. Similarly, for the northern elephant seal (*Mirounga angustirostris* (Gill, 1866)), Bartholomew and Collias (1962) stated that the proboscis has a fundamental role in sound production and that the development of the individual vocalization pattern depends on proboscis growth, but they provide no quantitative evidence. Later, Sandegren (1976) dismissed any role of the proboscis in sound production, again without any quantitative evidence. The acoustic properties of emitted sounds are structurally affected by size and shape of the vocal tract (Riede and Fitch 1999), and the proboscis, being connected to the main vocal tract, increases its length and changes its shape; on this basis, it is likely that the proboscis is involved in sound production. The relationship between vocal-tract size and body size explains how vocalizations can be honest signals of male phenotype (Fitch and Hauser 2002; Reby and McComb 2003). Recently, we have shown that the acoustic features determined by the main part of the southern elephant seal vocal tract are related to body size, but sound characteristics also are influenced by the proboscis, which acts as an extension of the vocal tract (Sanvito et al. 2007). The presence of a selection gradient on the proboscis independently of body size points to a selective advantage for a relatively large proboscis. An expanded proboscis might therefore permit dishonest communication about body size during vocal communication in this species.

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