

Skull allometry and sexual dimorphism in the ontogeny of the southern elephant seal (*Mirounga leonina*)

B.A. Tarnawski, G.H. Cassini, and D.A. Flores

Abstract: The southern elephant seal (*Mirounga leonina* (L., 1758)) is one of the most dimorphic mammals, but sexual dimorphism in its skull ontogeny is poorly known. We study ontogeny of sexual dimorphism by the allometric relationships between 21 measurements and its geometric mean. Based on 66 specimens (36 females, 30 males), the bivariate and multivariate analyses indicated that both approaches were congruent in most variables. We detected that sexual dimorphism was reached mostly by sexual shape differences in the ontogenetic trajectories of males and females. Twenty-four percent of variables were associated with intercept differences (pup size proportions), while 57% of variables were associated with slope intersexual differences (relative growth rates). Contrarily, sexual dimorphism was also achieved by size differences in adult stages (19% of variables), as males exhibited an extension of their common ontogenetic trajectories. Secondary growth spurt in males was detected for few variables. Our comparison with analogous data collected from southern sea lions (*Otaria byronia* (de Blainville, 1820)) indicated that in both species, sexual dimorphism was mostly associated with an enhanced ability to defend territories, which was linked to the polygynic behavior. However, discrepancies between both ontogenetic patterns of dimorphism were associated with interspecific differences in their life cycles.

Key words: *Mirounga leonina*, southern elephant seal, *Otaria byronia*, southern sea lion, allometric growth, cranium, morphometry, growth rate, pinniped.

Résumé : Si l'éléphant de mer austral (*Mirounga leonina* (L., 1758)) est un des mammifères les plus dimorphes qui soit, le dimorphisme sexuel de l'ontogénie de son crâne demeure méconnu. Nous étudions l'ontogénie du dimorphisme sexuel à la lumière des relations allométriques entre 21 mesures et leur moyenne géométrique. Des analyses bidimensionnelles et multidimensionnelles basées sur 66 spécimens (36 femelles, 30 mâles) indiquent que les deux approches sont congruentes pour la plupart des variables. Nous avons constaté qu'un dimorphisme sexuel est atteint principalement par des différences morphologiques selon le sexe dans les trajectoires ontogéniques des mâles et des femelles. Vingt-quatre pour cent des variables étaient associées à des différences associées aux points d'intersection (proportions des tailles des petits), alors que 57 % des variables étaient associées à des différences entre les sexes sur le plan de la pente (taux de croissance relatifs). En revanche, un dimorphisme sexuel découlait également de variations de la taille chez les stades adultes (19 % des variables), les mâles présentant un prolongement de leurs trajectoires ontogéniques communes. Une poussée de croissance secondaire chez les mâles a été détectée pour quelques variables. Notre comparaison avec des données analogues pour des otaries à crinière (*Otaria byronia* (de Blainville, 1820)) indique que, chez les deux espèces, le dimorphisme sexuel était principalement associé à une capacité accrue de défense du territoire, qui était elle-même associée au comportement polygynique. Des discordances entre les deux évolutions ontogéniques du dimorphisme étaient toutefois associées à des différences entre ces espèces sur le plan de leur cycle biologique. [Traduit par la Rédaction]

Mots-clés : *Mirounga leonina*, éléphant de mer austral, *Otaria byronia*, otarie à crinière, croissance allométrique, crâne, morphométrie, taux de croissance, pinnipède.

Introduction

Pinnipeds comprise a particular group of carnivorous mammals that alternate terrestrial environments (for reproduction, resting, and moulting) with marine environments (for feeding and displacements) during their life. This group contains 33 living species (Berta and Churchill 2012) included in the families Otariidae (sea lions and fur seals; 14 species), Phocidae (seals; 18 species), and Odobenidae (walruses; 1 species) from which several groups show the most spectacular examples of sexual size dimorphism in mammals (Lindenfors et al. 2002). In such species, females congregate in large colonies to breed and nurse their young (Haley et al. 1994; Trillmich 1996; Perrin et al. 2009). Otariids are universally dimorphic with large harems, whose young nurse over long periods of

up to 2 years (Kovacs and Lavigne 1992; Schulz and Bowen 2004). On the other hand, phocid young are more precocial (4–50 days weaning) and learn foraging skills after leaving their mothers (e.g., Riedman 1990; Hindell et al. 1999; Schulz and Bowen 2004). Phocids also exhibit a greater range of skull morphology than otariids, reflecting their great ecological diversity and more extreme specializations for feeding and reproduction (Jones and Goswami 2010). Although sexual dimorphism is not widespread in phocids, two of the most illustrative examples of the sexual selection theory through male–male competition are the northern and southern elephant seals of the genus *Mirounga* Gray, 1827 (Lindenfors et al. 2002). Male southern elephant seals (*Mirounga leonina* (L., 1758)) have been recorded to weigh 3700 kg, whereas

Received 6 May 2013. Accepted 8 November 2013.

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females only weighed between 400 and 800 kg, which makes this species the most sexually dimorphic mammal (Hindell and Perrin 2009).

In dimorphic species, different developmental processes affect the final adult size: growth rate, i.e., the speed of acquisition of adult characters and adult size, and growth duration (e.g., Gould 1977; Shea 1985, 1986; Stamps 1990; Cheverud et al. 1992; Teather and Weatherhead 1994; Stamps and Krishnan 1997; Smith and Leigh 1998; Badyaev et al. 2001). Males can get larger than females either by extending a common growth trajectory and maturing later than females ("bimaturism" sensu Leigh 1992) or by growing faster than females in a given period of time. Likewise, dimorphism can be achieved if females mature earlier than males or grow slower (Plavcan 2001). Additionally, Badyaev et al. (2001) stated that sexes can differ in other growth patterns, such as the size at birth, and phenotypic and genetic variations in growth patterns (and this related to a differential sensitivity to environmental conditions during growth). All these processes interact during the ontogeny to reach an adult performance that is maximized for intrasexual competition in males and successful breeding in females (e.g., Tarnawski et al. 2013). Such processes are also subject to selection, and their relative contribution to the sexual dimorphism of adults is informative about the direction and patterns of evolution of sexual dimorphism (Badyaev 2002). Comprehensive studies published on several aspects of cranial sexual dimorphism in otariid pinnipeds indicated that skull ontogeny varied intersexually (e.g. Brunner et al. 2004; Sanfelice and de Freitas 2008; Jones and Goswami 2010; Tarnawski et al. 2013). In all cases, sexual differences in cranial transformations led to a performance linked to male–male competition, producing characters highly associated with biting and fighting (e.g., Brunner et al. 2004; Tarnawski et al. 2013). Conversely, skull ontogenetic studies in phocids are scarce. Despite the extensive literature on the ecology and behavior related to sexual dimorphism in *M. leonina*, studies of its developmental basis, particularly in a comparative context, are rare. King (1972) and Briggs and Morejohn (1976) studied sexual dimorphism in adults using scarce cranial measurements in a univariate perspective. Jones and Goswami (2010), on the other hand, studied patterns of cranial morphology within otariids and phocids in a geometric morphometric framework. Although they included different ontogenetic stages of *M. leonina*, they examined a low number of specimens, highlighting the fact that this species is infrequent in osteological mammal collections.

Allometric growth trajectories represent the sum of all underlying molecular and cellular processes contributing to the growth of an organism. For example, the comparison of trait size with body size illustrates the underlying developmental processes regulating local versus global rates of growth (Cheverud et al. 1992; Klingenberg 1998; Sanger et al. 2013). Allometry, therefore, serves as a useful framework to compare the developmental bases of proportional differences between males and females (Sanger et al. 2013). In this study, we focus on the postnatal cranial growth of *M. leonina* to detect and quantify allometric patterns of sexual dimorphism during growth, using bivariate and multivariate approaches on a well-represented ontogenetic series of skulls of different inferred age stages. This statistical approach is possible thanks to the recent efforts of the Instituto Antártico Argentino (IAA) to collect dead carcasses. Together with the collections of other institutions, this makes the most complete ontogenetic series of specimens from the Atlantic population. In this study, we evaluated the morphological changes on their functional basis during a period of development in which critical changes occur. Interactions between neurocranial and splanchnocranial components during growth cause modifications in the function of the skull principally linked to the transition from juvenile to adult stages. Comparisons of different aspects of the skull morphology regarding each sex as a separate morphospecies are important for understanding the ecomorphological significance of the changes

detected in each sex (Dayan and Simberloff 1994). In this way, this work contributes to an increasing number of studies regarding growth and sexual dimorphism in pinnipeds.

Materials and methods

Study specimens and age stages

Mirounga leonina is relatively well represented by complete ontogenetic series deposited in mammal collections (see Appendix A, Table A1). The sample included 66 skulls of *M. leonina* (36 females, 30 males) that we divided into three broad categories (age groups; Figs. 1a–1f). Age groups were based on several criteria such as suture fusion (e.g., Morejohn and Briggs 1973), dentition (see Laws 1953; Carrick and Ingham 1962; Briggs and Morejohn 1975; McCann 1993; McMahan et al. 1997), and condylobasal length (CBL):

- (1) "Juveniles", with evident extraoccipital bones (sensu Doutt 1942; King 1976; Morejohn and Briggs 1973), which were in different fusion phases (from not fused to partially fused), permanent dentition in various erupting stages (from intra-alveolar to fully erupted, with exception of canine teeth), and CBL < 234 mm. Specimens had none or one external root ring on teeth (i.e., <1 year old (see McCann 1993); $n = 18$ females and 14 males);
- (2) "Subadults", defined by >50% fusion of extraoccipital bones, fully erupted permanent dentition with the exception of canine teeth (still erupting, reaching incisive teeth height), opened roots, and CBL < 260 mm. Specimens had two or three external root rings on teeth (i.e., between 2 and 3 years old; $n = 1$ female and 4 males); and
- (3) "Adults", with no visible extraoccipital bones and fully erupted permanent dentition with various degrees of tooth wear and root closure ($n = 17$ females, CBL > 276 mm, >4 years old; $n = 16$ males, CBL > 400 mm, >7 years old).

In the smallest specimens (i.e., female IAA 01-14, CBL: 155.0 mm; male LAMAMA ML004, CBL: 181.4 mm), deciduous dentition was completely functional. According to the available information (Morejohn and Briggs 1973; McMahan et al. 1997), the smallest specimens in our series were lactating pups between 1 and 3 weeks old.

Taking into account the extremely notable sexual dimorphism in this species, the same criterion was followed for southern sea lion, *Otaria byronia* (de Blainville, 1820) (Otariidae) (Tarnawski et al. 2013). The male sample was divided in two subsets (i.e., nonadults, including juvenile and subadult specimens, and other, including only adult specimens) to compare and detect different allometric growth patterns before and after the beginning of the secondary growth spurt. All samples were collected from the Atlantic population, mostly along Shetland Islands and the Argentine coast, in an attempt to avoid problems with ecogeographic variation in this species.

Study of growth and measurements

For the allometric analysis, 21 skull variables were used (Fig. 2) including neurocranial and splanchnocranial components. Variables and analytical methods were chosen to allow a direct comparison with a recent study of *O. byronia* (Tarnawski et al. 2013). They also overlap partially with those considered in other morphometric studies of carnivorous skulls, including otariids (e.g., Radinsky 1981; Brunner et al. 2004; Oliveira et al. 2005; Tanner et al. 2010; Giannini et al. 2010). However, because missing data are not allowed in multivariate analysis of allometry, the variables from the mandible were omitted to include a sample as large as possible in our analysis (see below).

According to Klingenberg (1996), ontogenetic allometry (or growth allometry) deals with covariation among characters during growth. The time frame is implicitly incorporated (size proxy)

Fig. 1. Skull lateral view of male (left, *a–c*) and female (right, *d–f*) southern elephant seals (*Mirounga leonina*). Ontogenetic series represent juvenile (*a, d*), subadult (*b, e*), and adult (*c, f*) specimens. Scale bars = 30 mm.



but not specified to describe relative modifications as the animal grows. To describe and analyze the skull ontogeny for each sex, two analytical techniques were used: bivariate regressions and multivariate allometry.

Bivariate analyses

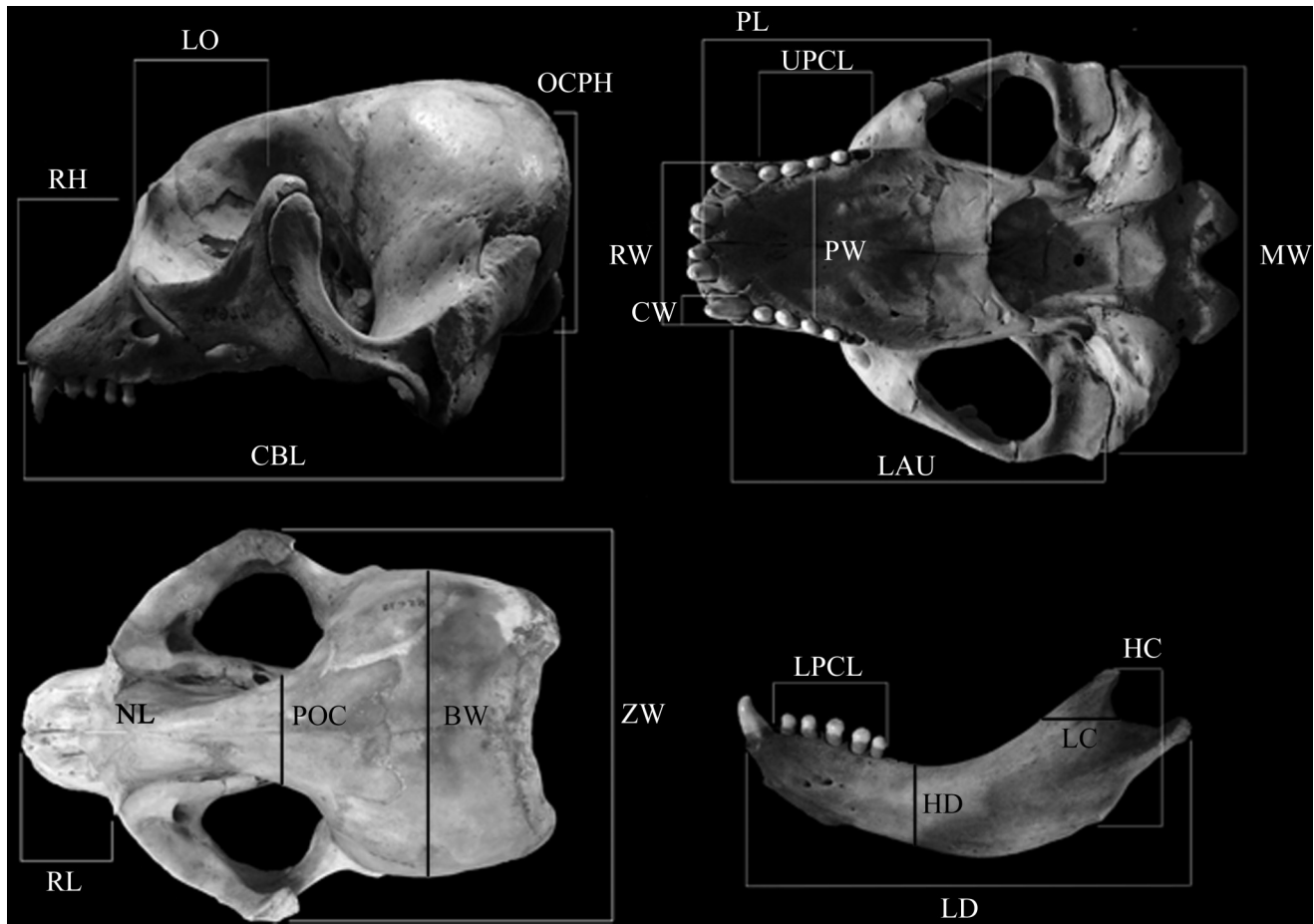
In bivariate comparisons of ontogenetic trajectories, there are three types of evolutionary change: ontogenetic scaling (overlapping trajectories; groups share slopes and intercepts but differ in their outputs), lateral shift (parallel trajectories; intercepts differ but slopes do not, indicative of change in the onset), and directional change (the slopes differ; indicative of novel modes of post-natal growth) (Weston 2003; Cardini and O'Higgins 2005; Marroig 2007). Sexual dimorphism occurs because of differences in size or shape between sexes. Ontogenetic scaling between sexes leads to adult size dimorphism through the modification of the duration of the systemic growth. On the one hand, similar patterns of adult shape dimorphism (different body proportions) can arise through early or late differentiation. Early differentiation is followed by parallel growth trajectories (lateral shift), indicating that differences in body proportions are present in early ontogenetic stages, and maintained along the trajectories. On the other hand, late differentiation is achieved through gradual changes in body proportions of males and females through sex-specific growth rate trajectories (a late divergence in shape by a directional change). In species that exhibit continual divergence, shape dimorphism is greatest when they reach their maximum size.

In growth studies, the allometry of a measurement can be strongly affected by the choice of the independent variable (Smith 1981; Wayne 1986), which is commonly the total length of the skull (e.g., common hippopotamus (*Hippopotamus amphibius* L.,

1758) and pygmy hippopotamus (*Hexaprotodon liberiensis* (Morton, 1849)); Weston 2003; mustelids: Suzuki et al. 2011; rodents: Kruska and Steffen 2013). In otariids, this measurement is not always isometric (see Brunner et al. 2004; Tarnawski et al. 2013) and consequently it precludes its use as an independent term. To avoid the problem, we used the geometric mean of all cranial measurements as the independent variable for the bivariate analyses (e.g. Mosimann 1970; Meachen-Samuels and Van Valkenburgh 2009; Tarnawski et al. 2013). The geometric mean is a size variable derived from the N th root of the product of N measurements, and it is a good predictor of the size of an individual. Consequently, it has the same dimensionality as skull measurements. The relationship between the two variables was isometric when the slope was equal to one (a value expected under geometric similarity between two variables with the same dimensionality; Peters 1993). The relationship of each variable to the overall size (geometric mean) was examined with the equation of allometry: $\log y = \log b_0 + b_1 \cdot \log x + \log e$, where y is any of the measured skull variables, $\log b_0$ is the y intercept or constant of normalization (and b_0 is the constant term of the growth function), b_1 is the slope of the line or coefficient of allometry, x is the geometric mean, and e is the error term (Alexander 1985; Calder 1996; West and Brown 2005). The standardized major axis (SMA) regression was used because it is more appropriate for dealing with allometric approaches than the ordinary least square (OLS) regressions (for an extensive overview on the subject see Warton et al. 2006).

As a first step, the significance of the coefficients of allometry was evaluated by a two-tailed t test at a significance level of $p = 0.01$. Deviations from isometry were assessed by comparing the allometric coefficient with the one expected under geometric

Fig. 2. Cranial measurements from a southern elephant seal (*Mirounga leonina*) used in the study. BW, braincase width; CBL, condylobasal length; CW, alveolus width of upper canine teeth; HC, coronoid height; HD, height of dentary (at the horizontal ramus); LAU, load arm length at upper canine; LC, length of coronoid process; LD, length of dentary; LO, length of orbit; LPCL, length of lower postcanine row; MW, mastoid width; NL, greatest nasal length; OCPH, occipital plate height; PL, palatal length; POC, postorbital constriction; PW, palatal width; RH, rostral height; RL, rostral length; RW, rostral width; UPCL, upper postcanine length; ZW, zygomatic width.



similarity (Alexander 1985). *F* tests were performed with the null coefficient set at 1.0 to assess significant deviations from isometry (Warton and Weber 2002). A coefficient value that was significantly <1.0 showed negative allometry, while a coefficient value that was significantly >1.0 showed positive allometry (Emerson and Bramble 1993). Testing for a common allometric coefficient (slope) among trajectories of sexes was the second step in the bivariate analysis. A likelihood ratio test for common SMA slope was used and compared against a χ^2 distribution (Warton and Weber 2002; Warton et al. 2006). When a common slope was shared between both subsets (i.e., absence of sexual dimorphism in the slope), the significance of a common constant of normalization (y intercepts) was compared using the Wald statistic for inference (Warton et al. 2006). Finally, if both slopes and y intercepts were shared by both sexes, data points were scattered around a common axis with no difference in elevation. All these coefficients, parameters, and statistical tests were performed in R software (R Development Core Team 2009) using the SMATR package (Warton and Weber 2002). If a variable exhibited a common slope between both male subsets, then the whole male sample was used in the female–male comparison. However, if nonadult males showed different slopes than adult males, then only the former subset was employed in the test among the sexes.

Multivariate analysis

Multivariate allometry is based on the generalization of the allometric equation proposed by Jolicoeur (1963). In this case, size

is considered a latent variable affecting all original variables simultaneously and the allometric relationships of all variables with the latent variable are expressed in the first eigenvector of a principal components analysis (PCA; extracted from a variance-covariance matrix of log-transformed variables). Briefly, under isometry, all variables respond in the same way to growth and the elements of the isometric unit eigenvector are equal to an expected value calculated as $1/p^{0.5}$, where p equals the number of variables (16 cranial variables for this analysis). The value of the eigenvector of the first principal component represents the observed multivariate coefficient of allometry of the corresponding variable. Comparison of each of the empirical elements of the first-unit eigenvector with the isometric eigenvector allowed the detection of negative (<0.25) and positive (>0.25) departures from isometry in each variable. Statistical departures from isometry were estimated using a jackknife procedure (Quenouille 1956; Manly 1997). For details regarding resampling see Giannini et al. (2004). The aim of this technique is to generate confidence intervals for the empirically obtained eigenvector elements. Herein, untrimmed and trimmed values were reported (for more details see Giannini et al. 2004), but the results with either the lower mean standard deviation or the lower bias were preferred. The multivariate statistical analysis (PCA + jackknife resampling) was programmed in R (R Development Core Team 2009); the author's script is available (Giannini et al. 2010).

Table 1. Test for common slope for both male subsets of southern elephant seal (*Mirounga leonina*).

Variable	Lr (df = 1)	p_{Lr}	Common slope	Growth trend
CBL	0.751	0.386	1.006	=
PL	1.281	0.258	1.483	+
PW	7.822	0.005*	NoAD > AD	NoAD: +; AD: =
ZW	5.244	0.022*	AD > NoAD	=
UPCL	0.406	0.524	1.250	=
OCPH	0.231	0.630	1.025	=
BW	0.056	0.812	0.810	=
RL	0.309	0.578	1.504	+
LO	2.903	0.088	1.298	=
RH	0.610	0.434	1.240	=
NL	3.89×10^{-4}	0.984	2.521	+
MW	7.76×10^{-3}	0.930	0.758	=
POC	7.69×10^{-4}	0.978	1.695	+
LAU	1.02×10^{-3}	0.974	1.140	=
RW	0.751	0.386	1.518	+
CW	10.655	0.001*	NoAD > AD	+
LD	0.554	0.456	1.060	=
HC	4.100	0.043*	NoAD > AD	+
LC	0.836	0.360	2.690	+
HD	11.974	5.39×10^{-4} *	NoAD > AD	NoAD: +; AD: =
LPCL	0.091	0.762	0.857	=

Note: Variable abbreviations as in Fig. 2. Shaded rows show significant regressions for common-slope parameters based on the likelihood ratio (Lr) test (Warton et al. 2006) and p value of the likelihood ratio test (p_{Lr}) (all significant except those with an asterisk). Growth trend is the summary allometry of each variable: isometry (=), negative allometry (-), and positive allometry (+). Asterisks indicate that differences are between the common-slope trend and the slope observed for each age group: adult (AD; $n = 16$) and nonadult (NoAD; $n = 14$).

The bivariate coefficients of allometry were interpreted as growth rates of a specific cranial variable, although they actually represent rates of size increase (Simpson et al. 1960; Gould 1966; Nelson 1978; Cassini et al. 2012). Thus, it was ultimately assumed that intraspecific allometry of size closely reflects true allometry of growth. To compare the bivariate allometric coefficients (BAC) with the multivariate allometric results, we followed Klingenberg (1996), who stated that multiplying principal component 1 (PC1) coefficients by the square root of p yields values (multivariate allometric coefficient, MAC) that can be interpreted as BAC. As for bivariate departures from isometry, F tests on the BAC values with the null coefficient set to the MAC value (for each variable) were performed to assess significant deviations of the SMA and OLS slopes from MAC values, as in a previous study on *O. byronia* (Tarnawski et al. 2013). Given the close geometrical similarity with the OLS regression, it is expected that the MAC would not differ significantly with the BAC from the OLS regression method.

Results

Bivariate analyses

Males

Intrasexual comparisons were performed between two male subsets: nonadults ($n = 14$) and adults ($n = 16$) (Table 1). The majority of variables showed high correlation values, although greatest nostril length (NL), mastoid width (MW), postorbital constriction (POC), and some mandibular variables showed low correlation values ($R^2 < 0.4$). We detected slope differences between both male subsets in 5 out of 21 characters (i.e., 24%). Of the five characters, palatal width (PW), alveolus width of the upper canine teeth (CW), coronoid height (HC), and height of dentary at the horizontal ramus (HD) showed higher slopes in nonadult males than in adult males, while the zygomatic width (ZW) showed a higher slope in adult males than in nonadult males. Consequently, for these five variables, intersexual comparisons (see Sexual dimorphism section below) were done using only nonadult males. In the remaining 16 variables (i.e., 76% of skull variables), we did not detect slope

differences between the trajectories of nonadult males and adult males.

Sexual dimorphism

We found that all of the variables had high correlation values, except for NL in females ($R^2 = 0.318$). In comparing slopes between males and females, we detected 10 common slopes for both sexes of *M. leonina* (Table 2). Common slopes for some characters associated with the feeding apparatus (i.e., rostral length (RL), rostral height (RH), length of the coronoid process (LC), and rostral width (RW)) showed positive allometric growth trends. In contrast, the upper postcanine tooth length (UPCL), the occipital plate height (OCPH), and the mastoid width (MW) showed negative allometric growth trends, whereas the remaining three variables (ZW, NL, and POC) were isometric in both sexes. Despite the absence of sexual dimorphism in their slopes, we found significant sexual differences in the intercepts or in the extensions of these common regression lines. On the one hand, five variables showed significant differences in female and male intercepts. Intercepts were higher in females than in males for RH, NL, RL, and UPCL. Similarly, intercepts were higher in males than in females for RW (Fig. 3a). On the other hand, both sexes shared common slopes and intercepts for OCPH, MW, POC, and LC (Fig. 3b), but additionally showed an extension in the growth trajectories of males. The ZW was an exception, as this variable did not show differences between sexes (females and nonadult males) in slopes, intercepts, or extensions of their regression lines. However, the detection of higher growth rates in adult males than in nonadult males could also be interpreted as higher growth rates in adult males than in females.

We also found statistical differences between slopes of both sexes corresponding to 11 skull characters (Table 2, Fig. 3c). We detected higher slope values in females than in males in seven characters, including braincase width (BW) and other six characters associated with skull lengths (e.g. CBL, palatal length (PL), orbital length (LO), load arm length at the upper canine (LAU), length of the orbit (LD), and lower postcanine tooth length (LPCL)).

Table 2. Test for common slope, common intercept, and shift along the regression axis for both sexes of southern elephant seal (*Mirounga leonina*).

Variable	Common slope				Common intercept			Shift	
	Lr _{b1}	p _{b1}	b ₁ com	Growth trend	W _{b0}	p _{b0}	b ₀ com	W _{shift}	p _{shift}
CBL	19.169	1.20×10 ⁻⁵	F > M	F: +; M: =					
PL	6.217	0.013	F > M	+					
PW*	6.793	0.009	M > F	+					
ZW*	3.006	0.083	1.007	=	2.254	0.133	0.351	3.084	0.079
UPCL	3.835	0.050	0.888	-	7.266	0.007	F > M		
OCPH	3.157	0.076	0.728	-	0.555	0.456	0.596	17.638	2.67×10 ⁻⁵
BW	14.738	1.24×10 ⁻⁴	F > M	-					
RL	3.670	0.055	1.275	+	4.986	0.026	F > M		
LO	5.274	0.022	F > M	F: =; M: -					
RH	0.847	0.357	1.245	+	4.492	0.034	F > M		
NL	2.827	0.093	0.969	=	8.986	0.003	F > M		
MW	0.450	0.502	0.751	-	2.206	0.137	0.776	18.065	2.14×10 ⁻⁵
POC	2.997	0.083	1.076	=	2.870	0.090	-0.380	14.099	1.73×10 ⁻⁴
LAU	11.590	6.63×10 ⁻⁴	F > M	+					
RW	1.389	0.239	1.339	+	25.906	3.59×10 ⁻⁷	M > F		
CW*	22.053	2.65×10 ⁻⁶	M > F	F: =; M: +					
LD	13.385	2.54×10 ⁻⁴	F > M	+					
HC*	7.896	0.005	M > F	+					
LC	0.153	0.696	1.420	+	0.433	0.510	-1.310	12.030	5.236×10 ⁻⁴
HD*	13.733	2.11×10 ⁻⁴	M > F	+					
LPCL	7.440	0.006	F > M	F: =; M: -					

Note: Variable abbreviations as in Fig. 2. Parameters: b₁ com, common slope from standardized major axis; b₀ com, common intercept from standardized major axis; Lr, likelihood ratio test (Warton et al. 2006); W, Wald statistic (Warton et al. 2006); p_{b1}, p value of Lr parameter; p_{b0}, p value of W(log b₀); p_{shift}, p value of W_{shift}. Growth trend is the summary allometry of each variable: isometry (=), negative allometry (-), and positive allometry (+). Differences are between the common-slope trend and the slope observed for each sex: F, females (n = 36); M, males (n = 30, except for variables marked with an asterisk where only nonadult males were employed and n = 14). Shaded rows show significant regressions for the common slope.

Furthermore, some of these variables showed different allometric growth trends in both sexes. For instance, LO and LPCL were negatively allometric in males but isometric in females (Table 2). Likewise, CBL showed isometry in males but positive allometry in females (Fig. 3c). In contrast, we found higher slopes in males than in females for PW and CW, as well as for HC and HD. Overall, comparisons of the bivariate results between both sexes of *M. leonina*, indicated that adult sexual dimorphism was achieved in 24% of skull variables by differences in intercepts, in 57% of variables by differences in growth rates (i.e., 81% of sexual shape dimorphism), and in 19% of variables by extensions of the ontogenetic trajectories of males (i.e., sexual size dimorphism).

Multivariate analysis

Males

The mean difference in the absolute bias favored untrimmed over trimmed analysis in both male subsets, with a 0.0167 mean absolute bias for the former and 0.0149 for the latter in nonadults (1.12 times higher), whereas in adult males the respective values were 0.0126 and 0.0102 (1.24 times higher). In this case, the multivariate analysis showed that most cranial variables (16 out of 21) showed common ontogenetic growth trends for both male subsets, while only four variables had different allometric trends. For instance, the PL showed no departure from isometry in nonadults and a positively allometric trend in adults, whereas the opposite trends were found for CW. The remaining two variables (ZW and UPCL) were isometric in adults and negatively allometric in non-adult males.

Sexual dimorphism

In both sexes of *M. leonina*, the mean difference in the absolute bias favored untrimmed over trimmed analysis, with a 0.0011 mean absolute bias for the former and 0.0041 for the latter in females (3.74 times higher), whereas in males the respective values were 0.0002 and 0.00089 (4.45 times higher). The multivariate analysis showed that half of the cranial characters considered (8 out of 16) had common ontogenetic growth trends in males and

females (Table 3). Three of such variables showed negative allometry (OCPH, BW, and MW), four showed positive allometry (PL, RL, LAU, and RW), and only POC scaled up isometrically when the general size increased.

We found sexual differences in the ontogenetic growth trends of the remaining eight variables. Among them, CBL was the only cranial variable that showed isometry in males and a positive growth trend in females. Conversely, the other seven variables showed allometry in males and isometry in females. ZW, UPCL, LO, and NL all scaled with negative allometry in males, whereas PW, RW, and CW showed positive allometry in males.

Bivariate vs. multivariate analyses

The comparison of bivariate and multivariate analyses of allometry in *M. leonina* indicated that most variables shared the same growth trends in both approaches. However, we observed differences in the signs of growth trends for PW and RH in females, as well as ZW, NL, and POC in males.

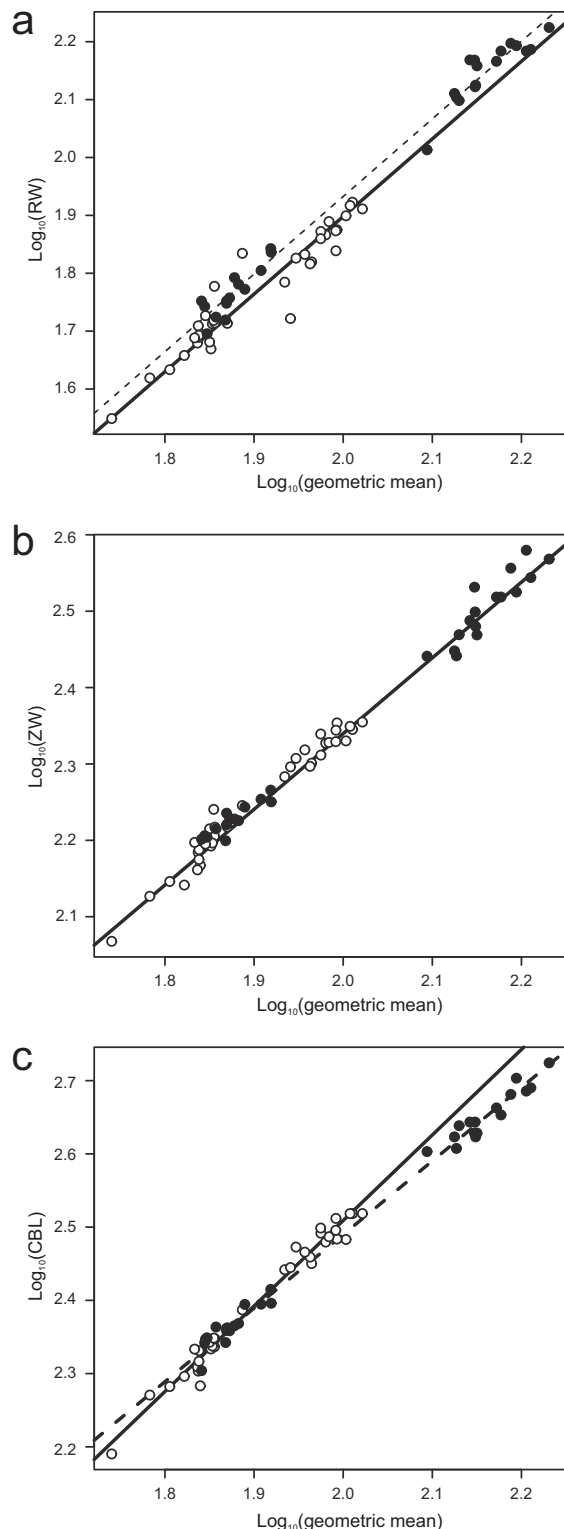
The statistical comparisons (F test; Table 4) between the SMA analysis and the multivariate analysis (untrimmed) showed significant differences for NL in both sexes; CW in females; and CBL, ZW, and LAU in males. Conversely, the statistical comparisons of the multivariate analysis and the OLS bivariate method showed no difference in females but four differences in males (CBL, ZW, NL, and LAU).

Discussion

Quantitative methods

As in Tarnawski et al. (2013), we found empirical support for equivalences between BAC and MAC. As stated by Klingenberg (1996), multiplying PC1 coefficients by the square root of *p* yields values that could be interpreted as BAC. We found more differences between the multivariate analysis and the SMA bivariate analysis than between the multivariate analysis and the OLS bivariate regressions. These differences could be the product of the differences between line-fitting methods (i.e., OLS vs. SMA). Addi-

Fig. 3. Plots of the bivariate standardized major axis (SMA) regressions. (a) Same slope and different intercepts between female and male southern elephant seals (*Mirounga leonina*); (b) same slope and intercepts for females and males; and (c) different slopes between the growth trajectories of males and females. Open symbols and solid lines are females, whereas solid symbols and broken lines are males. CBL, condylobasal length; RW, rostral width; ZW, zygomatic width.



tionally, our result also showed some discrepancies between the sexes, which could be related possibly to the degrees of freedom and amplitude of confidence intervals associated with sample size differences (females, $n = 32$; males, $n = 23$).

Sexual dimorphism in *M. leonina*

Our results suggested that the strong sexual dimorphism observed in *M. leonina* (Figs. 1a–1f) was reached following a pattern in which males and females share a large part of their ontogenetic growth trends. For instance, the bivariate analysis of allometry showed that both sexes shared slopes for 43% of cranial variables, whereas almost half of them (i.e., four out of nine variables) also had common male–female intercepts. However, in such cases, males exhibited an extension of their common ontogenetic trajectory compared with females (bimaturism), which is expected because of the extremely large size of males. This indicated that, in 19% of the skull variables analyzed, sexual dimorphism in skull proportions was related to size differences in adult stages (i.e., sexual size dimorphism), instead of sexual shape differences. Some of these variables (e.g., OCPH, MW) have been associated with the secondary growth spurt in the late development of otariid males (i.e., “biphasic growth”, e.g., Brunner et al. 2004). Indeed, Carrick et al. (1962) reported a double-sigmoid growth pattern in male elephant seals, with a secondary period of accelerated growth at 6–7 years of age, coinciding with puberty. However, we only found higher growth rates in adult males than in nonadult males for ZW. Irrespective of the mechanistic origin of these differences, the dimorphism of the reported variables (e.g., OCPH, MW, and ZW) could be related mostly to generate extra space for the temporal musculature and the neck musculature. This also supports the previous idea of secondary growth spurts in males because both muscle systems are extremely important for biting and head movements in battles during the breeding season (e.g. Brunner et al. 2004).

Alternatively, sexual shape dimorphism in *M. leonina* was reached by intersexual differences in intercepts (24% of total variables) and slopes (57% of total variables) of the ontogenetic trajectories of both sexes. Intercepts could be interpreted as differences in the initial proportions of the skull (i.e., early shape divergence), while slope differences could be interpreted as variations in growth rates relative to the overall skull size (i.e., the geometric mean; late shape divergence). On the one hand, considering intersexual differences in the intercepts, variables related to the rostrum (i.e., RL, RH, and NL) showed proportionally larger measurements in females than in males, having both similar skull sizes. Conversely, intercepts indicated that the rostrum exhibited wider dimensions (e.g., RW) in males than in females. Therefore, the differences detected in this anatomical region could indicate that sexual shape dimorphism is already present in early ontogenetic stages of *M. leonina* skulls. A rostral index could possibly be a noninvasive and useful tool for sex determination in skulls of young specimens. In fact, Carrick et al. (1962) determined that sexual dimorphism was almost externally indistinguishable (e.g., mass, total length) at birth and weaning pups. On the other hand, sexual shape dimorphism was also achieved by differences in relative growth rates. Slopes were higher in females than in males for CBL, PL, BW, LO, LAU, LD, and LPCL, which highlights the rapid development of some characters in females compared with those of males. Our results are consistent with those previously reported for elephant seals (e.g., northern elephant seal (*Mirounga angustirostris* (Gill, 1866)): Reiter et al. 1978; *M. leonina*: McMahon et al. 1997) in which female pups exhibited precocial tooth eruption and weaning. Indeed, Carrick et al. (1962) detected that females at McQuarie Island had the ability to breed at age 5.2 ± 1.8 years, whereas males may breed as late as 14 years of age. Therefore, female pups could be expected to develop earlier and faster than males. Delayed maturation in males was also associated with the avoidance of intrasexual competition between non-

Table 3. Results of the multivariate analysis of cranial allometry by sex of southern elephant seals (*Mirounga leonina*).

Variable	Sex	Untrimmed					Trimmed				
		Resampled coefficient	Bias	99% CI	Departure	Growth trend	Resampled coefficient	Bias	99% CI	Departure	Growth trend
CBL	F	0.282	-0.001	0.261-0.303	0.032	+	0.280	2.0×10 ⁻⁴	0.264-0.296	0.030	+
	M	0.241	-2×10 ⁻⁴	0.231-0.251	-0.008	=	0.240	5.0×10 ⁻⁴	0.232-0.248	-0.009	-
PL	F	0.319	-0.001	0.288-0.349	0.069	+	0.318	-0.001	0.296-0.340	0.068	+
	M	0.287	-3×10 ⁻⁴	0.270-0.304	0.037	+	0.286	-6×10 ⁻⁵	0.271-0.302	0.036	+
PW	F	0.281	-7×10 ⁻⁴	0.239-0.322	0.031	=	0.291	-0.006	0.260-0.322	0.041	+
	M	0.299	-2×10 ⁻⁴	0.281-0.318	0.049	+	0.299	-4.8×10 ⁻⁵	0.282-0.316	0.049	+
ZW	F	0.246	-0.001	0.225-0.267	-0.003	=	0.242	0.008	0.223-0.260	-0.007	=
	M	0.234	-2×10 ⁻⁴	0.221-0.247	-0.015	-	0.231	0.001	0.220-0.243	-0.018	-
UPCL	F	0.222	4×10 ⁻⁴	0.183-0.261	-0.027	=	0.2349	-0.005	0.207-0.262	-0.015	=
	M	0.197	-1×10 ⁻⁴	0.173-0.221	-0.052	-	0.1959	6×10 ⁻⁴	0.174-0.215	-0.054	-
OCPH	F	0.183	-6×10 ⁻⁴	0.162-0.203	-0.067	-	0.1817	8×10 ⁻⁵	0.163-0.199	-0.068	-
	M	0.166	-2×10 ⁻⁴	0.150-0.182	-0.083	-	0.164	8×10 ⁻⁴	0.152-0.176	-0.085	-
BW	F	0.139	-4×10 ⁻⁴	0.121-0.157	-0.110	-	0.139	-5×10 ⁻⁵	0.123-0.154	-0.111	-
	M	0.092	-2×10 ⁻⁴	0.072-0.111	-0.158	-	0.090	4×10 ⁻⁴	0.075-0.105	-0.159	-
RL	F	0.326	-0.001	0.284-0.367	0.076	+	0.330	0.003	0.299-0.362	0.080	+
	M	0.293	-2×10 ⁻⁴	0.268-0.318	0.043	+	0.293	-4×10 ⁻⁴	0.275-0.312	0.043	+
LO	F	0.225	-7×10 ⁻⁴	0.189-0.2619	-0.024	=	0.224	-2×10 ⁻⁴	0.191-0.257	-0.025	=
	M	0.193	-3×10 ⁻⁴	0.171-0.215	-0.056	-	0.194	-5×10 ⁻⁴	0.174-0.213	-0.055	-
RH	F	0.296	0.001	0.226-0.366	0.046	=	0.333	-0.016	0.299-0.367	0.083	+
	M	0.293	2×10 ⁻⁵	0.270-0.316	0.043	+	0.294	-6×10 ⁻⁴	0.275-0.313	0.044	+
NL	F	0.160	-0.002	0.029-0.292	-0.089	=	0.116	0.019	0.027-0.205	-0.133	-
	M	0.172	-3×10 ⁻⁴	0.107-0.237	-0.077	-	0.164	0.003	0.109-0.218	-0.086	-
MW	F	0.183	-0.001	0.151-0.214	-0.066	-	0.173	0.003	0.157-0.188	-0.076	-
	M	0.175	1.5×10 ⁻⁵	0.158-0.192	-0.074	-	0.178	-0.001	0.164-0.192	-0.071	-
POC	F	0.204	8×10 ⁻⁴	0.151-0.257	-0.045	=	0.210	-0.002	0.170-0.250	-0.040	=
	M	0.261	-2×10 ⁻⁴	0.221-0.301	0.011	=	0.263	-0.001	0.229-0.297	0.013	=
LAU	F	0.319	-0.001	0.291-0.348	0.069	+	0.318	-4×10 ⁻⁴	0.292-0.344	0.068	+
	M	0.276	-1×10 ⁻⁴	0.262-0.291	0.026	+	0.275	8×10 ⁻⁴	0.263-0.287	0.025	+
RW	F	0.301	-0.002	0.270-0.331	0.051	+	0.300	-0.001	0.275-0.326	0.050	+
	M	0.324	-2×10 ⁻⁴	0.306-0.341	0.074	+	0.324	-3×10 ⁻⁴	0.309-0.339	0.074	+
CW	F	0.218	-0.001	0.145-0.292	-0.031	=	0.206	0.004	0.144-0.268	-0.043	=
	M	0.348	-5×10 ⁻⁴	0.312-0.384	0.098	+	0.344	0.001	0.314-0.374	0.094	+

Note: Variable abbreviations as in Fig. 2. Jackknife results calculated with untrimmed and trimmed sets of pseudovalues. Resampled coefficient is the unbiased coefficient of the first-order jackknife value. Sex: F, females ($n = 36$); M, males ($n = 30$). Bias is the difference between the resampled coefficient and the observed coefficient (value obtained with all specimens included; not included in the table). The jackknife 99% confidence interval (CI) is provided. Allometric variables are those whose confidence interval excludes the expected value under isometry (0.25). Growth trend is the summary allometry of each variable: isometry (=), negative isometry (-), and positive allometry (+).

adult males and adult males. By delaying their growth spurt, males maintain juvenile or female morphology as long as possible, which may alleviate intermale competition during breeding seasons (Jarman 1983; Leigh 1992). In contrast, we detected higher relative growth rates in males than in females in four variables, including CW. Briggs and Morejohn (1975) found that canine growth seemed to be the primary force in remodeling the facial region of male skulls in *M. leonina*. During male dominance disputes, followed by ritualized bellowing and displays, blows are stuck with the upper canine teeth (see Le Boeuf and Peterson 1969). In contrast to this continual emphasis throughout most of the life of the male on the size and use of the feeding apparatus and neck musculature in social disputes, females primarily use such regions in nonsocial roles such as food procurement (e.g., Laws 1953). In this sense, the dimorphism in the breadth of the rostrum reflecting canine size and other bite-related variables are morphological expressions of the different social roles played by sexes at maturity (see also Morejohn and Briggs 1973). The detected differences in growth rates for CW suggested that sexual shape dimorphism in this character was achieved by a late divergence between sexes, which could be associated with late canine teeth eruption (i.e., adult stage; see Materials and methods section).

Ontogeny of sexual dimorphism in extremely dimorphic pinnipeds

The comparative study of the ontogeny of sexual dimorphism in representative species of two different families of pinnipeds is relevant because differences among taxa in sexual size and shape dimorphism of adults could result from changes in distinct developmental processes, and thus, those differences may reflect different evolutionary histories (Badyaev et al. 2001). Tarnawski et al. (2013) studied the skull ontogeny of *O. byronia* using the same methodology described for this study, which guarantees comparable results in two of the most dimorphic extant pinnipeds (e.g., Perrin et al. 2009; Cappozzo et al. 1991). According to Jefferson et al. (2008), both species compared here differed in the timing of life-history events and body growth.

The multivariate analyses indicated that 50% of cranial variables were dimorphic in *M. leonina*, whereas this percentage reached 67% in *O. byronia*. In both species, these analyses detected sexual differences in the allometric growth trends affecting both neurocranium and splanchnocranium, such as CBL, LO, RH, and CW. However, *M. leonina* exhibited additional sexual differences related to PW, ZW, NL (this measurement was not included in *O. byronia*), and UPCL. In contrast, sexual dimorphism in *O. byronia* was related to RL, RW, PL, OCPH, MW, and LAU.

Table 4. Comparisons between multivariate (multivariate allometric coefficient (MAC)) and bivariate (ordinary least squares (OLS) and standardized major axis (SMA)) analyses in the southern elephant seal (*Mirounga leonina*).

Variable	Sex	MAC	OLS		SMA	
			$F_{[1,n-2]}$	p	$F_{[1,n-2]}$	p
CBL	F	1.131	0.497	0.486	1.403	0.244
	M	0.966	8.594	0.007*	6.588	0.016*
PL	F	1.276	0.291	0.593	1.213	0.279
	M	1.149	4.108	0.052	3.788	0.062
PW	F	1.125	0.245	0.624	1.784	0.191
	M	1.199	3.226	0.083	3.083	0.090
ZW	F	0.986	0.375	0.544	1.332	0.256
	M	0.938	7.043	0.013*	4.282	0.048*
UPCL	F	0.891	0.264	0.611	2.325	0.137
	M	0.790	2.770	0.107	2.203	0.149
OCPH	F	0.732	0.284	0.598	1.611	0.213
	M	0.665	3.338	0.078	2.211	0.148
BW	F	0.559	0.228	0.636	1.734	0.197
	M	0.368	3.319	0.079	2.645	0.115
RL	F	1.304	0.097	0.758	1.487	0.231
	M	1.174	2.246	0.145	2.367	0.135
LO	F	0.902	0.104	0.749	1.949	0.172
	M	0.775	1.882	0.181	2.023	0.166
RH	F	1.186	0.294	0.591	2.788	0.104
	M	1.174	2.351	0.136	2.795	0.106
NL	F	0.643	0.016	0.900	20.571	6.82×10 ⁻⁵ *
	M	0.690	7.295	0.012*	4.889	0.035
MW	F	0.732	0.111	0.741	1.256	0.270
	M	0.702	1.333	0.258	2.689	0.112
POC	F	0.819	0.190	0.666	3.969	0.054
	M	1.047	1.816	0.189	2.191	0.150
LAU	F	1.280	0.331	0.569	1.444	0.238
	M	1.107	6.153	0.019*	4.631	0.040*
RW	F	1.205	0.103	0.750	1.350	0.253
	M	1.297	3.802	0.061	4.011	0.055
CW	F	0.874	0.015	0.904	5.284	0.028*
	M	1.395	2.919	0.099	1.884	0.181

Note: Variable abbreviations as in Fig. 2. Sex: F, females ($n = 32$); M, males ($n = 23$). p values of F test between MAC and SMA and OLS slopes are given and asterisks indicate significant p values.



The comparison of the bivariate analyses of allometry (Table 5) also highlighted interesting information regarding the ontogenetic processes that lead to sex differences in both species. Overall, sexual dimorphism in *O. byronia* was mainly composed of shape differences (i.e., 89% of total variables showed sex differences in intercepts and slopes), whereas 11% of variables showed size differences between sexes (i.e., shift along the trajectories of males) (Table 6). Similarly, in *M. leonina*, 81% of differences between males and females were a result of sexual shape dimorphism, and the remaining 19% of sexual differences were due to sexual size dimorphism (Table 6). Morphometric data suggested that sexual shape dimorphism in *O. byronia* and *M. leonina* was reached through differences in the growth rates of each variable (i.e., slopes) that led to proportionally greater LO and PL in females, but bigger canines in males. Similarly, the total length of the skull also showed higher growth rates in females than in males of both species. This fact could reflect a relatively conservative pattern of sexual shape differences in dimorphic pinnipeds, which is associated with rapid development of females relative to males. These interspecific and intraspecific comparisons are in agreement with previous studies on polygynous pinnipeds (e.g., Lindenfors et al. 2002; Brunner et al. 2004) whose females reach reproductive age much earlier than males (Table 6) but spend significant amounts of energy on their offspring. Alternatively, males do not provide any parental care, and thus allocate more energy to growth, developing all secondary sexual characters involved in fights. As a result, larger body and canine size are favored in males but not in females (Plavcan 2001). On the other hand, additional similarities were found in the OCPH, as males of both species exhibited an extension of their ontogenetic trajectory compared with females (i.e., bimaturism). In this case, differences between final adult morphologies were due to sexual size dimorphism (i.e., higher

Table 5. Comparison of sexual dimorphism detected in bivariate analyses for the southern sea lion (*Otaria byronia*) (Tarnawski et al. 2013) and southern elephant seal (*Mirounga leonina*) (this study).

Variable	<i>O. byronia</i>	<i>M. leonina</i>
LCB	Slope	Slope
PL	Slope	Slope
PW	Intercept	Slope
ZW	Intercept	Slope*
UPCL	Slope*	Intercept
OCPH	Shift	Shift
BW	Shift	Slope
RL	No difference	Intercept
LO	Slope	Slope
RH	Slope*	Intercept
NL	—	Intercept
MW	Slope*	Shift
POC	Slope	Shift
LAU	Slope	Slope
RW	Slope	Intercept
CW	Slope	Slope
LD	Intercept	Slope
HC	Intercept	Slope
LC	Slope	Shift
HD	Slope	Slope
LPCL	Slope*	Slope

Note: Variable abbreviations as in Fig. 2. Sexual dimorphism is expressed as differences between males and females in slopes, intercepts, or shift (i.e., extension along the ontogenetic trajectory). Asterisks indicate slope differences between females and adult males. "No difference" indicates the absence of sexual dimorphism between the entire trajectory of males and females. Shaded rows show similarities in sexual dimorphism between species.

Table 6. A comparison of southern elephant seal (*Mirounga leonina*) and southern sea lion (*Otaria byronia*) showing mean ages at important biological events and a summary of ontogeny of sexual dimorphism (SD) in both species.

	Weaning	Sexual maturity (years)	First breeding (years)	SD	
 <i>Mirounga leonina</i>	23 days	F: 3 M: 5–6	F: 5 M: >10	F: 57% slopes (5.9% only in adults) M: 24% intercepts M: 19% shift	} 81% SD in shape 19% SD in size
 <i>Otaria byronia</i>	10 months	F: 4 M: 5	F: 5 M: 9	F: 69% slopes (23.5% only in adults) M: 21% intercepts M: 11% shift	

Note: Biological events were extracted from the literature (Carrick et al. 1962; Perrin et al. 2009; Grandi et al. 2010) and indicate mean ages at weaning, sexual maturity, and first breeding in males and females of both species. Sexual dimorphism describes principal allometric results for *M. leonina* (this study) and *O. byronia* (Tarnawski et al. 2013). Values in the last column are percentages of variables with SD in shape (i.e. sum of SD in slopes and intercepts) and SD in size (i.e. shifts along the ontogenetic trajectories of males).

occiput in males as a result of male's bigger skull size, but this does not imply higher occiput proportions).

However, the bivariate analysis also indicated that both species showed differences in the acquisition of sexual dimorphism. Briefly, compared with females, males of *O. byronia* exhibited higher relative growth rates for POC and RW (i.e., late shape divergence for POC and RW), a relative bigger initial size for PW (i.e., early shape divergence for PW), and an extension of the development of BW (i.e., size dimorphism for BW). Alternatively, male *M. leonina* showed higher growth rates than females for PW, HC, and HD relative to the initial size differences in early postnatal life favoring RW in juvenile males, and an extension of the development of the skull breadths related to muscle insertion (i.e., MW, POC, and LC). It is interesting to note that the relative RL did not show different ontogenetic trajectories between sexes of *O. byronia* (Table 5), whereas we detected sexual shape dimorphism due to higher RL proportions in juvenile females than in juvenile males of *M. leonina*.

Conversely, it is noteworthy that some percentage of sexual shape dimorphism was restricted to adult stages in both species. *Otaria byronia* exhibited sexual shape dimorphism as a result of higher growth rates in adult males rather than in females in four skull variables (i.e., 23.5% of sexual shape dimorphism is attributable to late shape dimorphism) (Table 6). Likewise, *M. leonina* showed sexual shape dimorphism in adults just for ZW (i.e., 5.9% of sexual shape dimorphism is caused by differences only in late ontogenetic stages) (Table 6). This indicated that although both species exhibited similar percentages of sexual shape and size dimorphism (Table 6), an insight into sexual shape dimorphism could highlight interesting differences between these species. On the one hand, almost all shape differences (i.e., 94.1%) between males and females were distinguishable in nonadults stages of *M. leonina*. On the other hand, 76.5% of shape differences were present in early stages, while the remaining 23.5% of sexual shape dimorphism was acquired in older ontogenetic stages of *O. byronia* (Table 6). Ecological variables, such as weaning time, may cause the differences detected between species in these ontogenetic pathways. Sexual dimorphism in the initial skull proportions could be related to differences between families in pup development because phocids are more precocial than otariids (e.g., Schulz and Bowen 2005). For instance, *M. leonina* are weaned at 23 days old (Carrick et al. 1962; McCann 1980), while *O. byronia* are weaned at approximately 10 months old (King 1983; Jefferson et al. 2008) (Table 6). The nursing period is an ideal time for males and females to gain a competitive edge over their cohort members, as this is the time of most rapid growth (Reiter et al. 1978; Clutton-Brock et al. 1981), so two different strategies were acquired in each family. Sexually dimorphic characteristics could be notable probably in intrauterine stages in phocids, whereas it

could be achieved during the long lactating period in otariids. For instance, RW, which is influenced by canine eruption, reflected the importance of rapid tooth replacement in phocids where feeding independence occurs abruptly and in early ontogenetic stages, as well as in juvenile male–male encounters (e.g., McMahon et al. 1997). Following Jones and Goswami (2010), it was reasonable to expect that ecological variables (e.g., sexual size dimorphism, gestation and weaning times, environmental variables) have had a relatively greater influence than phylogeny on cranial morphology.

It is also interesting to note that interspecific ontogenetic differences in which males exhibited higher parameters (i.e., slope, intercept, shift) than females were linked to the agonistic male behavior (e.g., muscle mass development of males owing to an increase in MW, ZW, OCPH or canine size (reflected in RW); Figs. 1a–1f) in both species. As expected, both pinniped species showed extreme sexual dimorphism mostly associated with an enhanced ability to hold and defend territories (i.e., characters that increase the capacity of biting and structural strength). Nevertheless, sexual dimorphism in both species was achieved by different ontogenetic mechanisms (Table 5), which also have been detected in different species of big apes (Plavcan 2001). For instance, the bigger relative MW of males is due to growth extension in male adulthood of *M. leonina*, but is due to sexual shape dimorphism between adults of *O. byronia*. Similarly, the wider zygomatic distance of male skulls is acquired by higher growth rates in adults of *M. leonina*, but by higher initial proportions in *O. byronia*. According to Badyaev (2002), similar patterns of dimorphism in adults may be achieved through a variety of ontogenetic pathways, and variation among these pathways may reflect fundamental differences in social structure, ecological factors, or phylogenetic relationships. The polygynous behavior may have imposed similar pressures that led to similar adult phenotypes, which may have been reached by convergence in both species (e.g., Jones et al. 2013). A working hypothesis is that the polygynous behavior in pinnipeds leads to similar sexually dimorphic traits in adults, while pup development leads to differences in the ontogenetic pathways. According to our analyses of sexual dimorphism in *M. leonina* (this study) and *O. byronia* (Tarnawski et al. 2013), the polygynous behavior is a trait linked to specific patterns of sexual dimorphism in the skull. This convergent behavior (Jones et al. 2013) could be considered a mechanism for the development of similar patterns of skull dimorphism, independent of the growth trajectory followed by both species.

In summary, our work highlights sexual dimorphism in growth trends of *M. leonina*, an aspect that has been previously poorly studied. For instance, most studies of sexual dimorphism have focused on adult characters. However, sexual dimorphism in adults is necessarily a product of the different male and female

growth trajectories (Plavcan 2001). Our results suggested that most allometric differences between sexes are due to sexual shape dimorphism (intercepts and slopes), rather than sexual size dimorphism (shift along the growth trajectory). An interesting finding was the detection of differences in skull proportions in juvenile stages, which favored RL and RH in females, but RW in males. This fact could be useful for sex determination in pups using a noninvasive technique (e.g., rostral index, instead of canine extraction). Females also exhibited higher relative growth rates than males for skull lengths and BW, which are possibly associated with the rapid development of female *M. leonina* compared with male *M. leonina*. In contrast, males showed higher rates for canine width. This emphasizes the importance of canine development in males, which use canines as weapons during male-male combats. Other sexually dimorphic traits, associated with agonistic male behavior, showed an extension along the ontogenetic trajectories of males, indicating that differences between sexes in characters linked to muscle insertions are size-dependent. Secondly, our work also revealed ontogenetic similarities and differences between two illustrative dimorphic pinniped species. Our comparison provided relevant information on the acquisition of sexual dimorphism in phocids and otariids, and its interpretation was related to a phylogenetic and ecological context. Identifying the ontogenetic trajectories underlying sexual dimorphism of the skull is critical to better understand the links among function, development, phylogeny, and the evolutionary mechanisms regulating the expression of this complex morphological feature (Schwartz et al. 2005).

Acknowledgements

We thank D. Verzi and I. Olivares (MLP); E. Crespo and N. García (CNP); M.E. Marquez, J. Negrete, and J. Mennucci (IAA); N. Goodall and volunteers (AMMA); S. Bogan (CFA); S. Lucero (MACN); and S.M. Velázquez (ZOO-BA), who granted access to mammal collections and for making us very welcome during our visits. We are also grateful to N. Chapire and P. Ganchegui for their logistical support. This work was financed by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). This is a contribution to the Projects PICT 0143 to S.F. Vizcaino, PICT 1798 to N. Giannini of the Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT), PIP 1054 to S.F. Vizcaino of CONICET, and UNLu CDD-CD 281-09 to J.C. Fericola. We dedicate this paper to the memory of Alejandro Carlini for his devotion to Antarctic ecosystems, particularly marine mammals, and his kindness during our visits to the IAA collection.

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Appendix A

Table A1 contains a list of specimens of *M. leonina* that we examined.

Table A1. Specimens of the southern elephant seal (*Mirounga leonina*) examined in this study.

Collection number	Sex	Age class	CBL (mm)	Geometric mean
IAA 01-14	F	Juvenile	155.0	54.987
LAMAMA ML024	F	Juvenile	176.5	63.843
MACN 22615	F	Juvenile	186.5	60.676
IAA AA-7	F	Juvenile	191.6	63.887
IAA AA-2	F	Juvenile	192.0	69.129
IAA AA-8	F	Juvenile	197.8	66.332
IAA 10	F	Juvenile	198.1	63.193
LAMAMA ML001	F	Juvenile	201.1	116.076
IAA 02.23	F	Juvenile	207.4	68.886
IAA 02.24	F	Juvenile	215.5	68.126
IAA AA-11	F	Juvenile	215.6	71.056
IAA 02.29	F	Juvenile	217.1	71.701
IAA AA-9	F	Juvenile	217.6	71.320
IAA 02.20	F	Juvenile	220.2	70.816
IAA 02.25	F	Juvenile	222.3	70.061
IAA 02.28	F	Juvenile	222.6	71.782
CNP 037	F	Juvenile	223.1	92.915
MACN 49.52	F	Juvenile	230.4	74.131
LAMAMA ML015	F	Subadult	243.8	88.907
MACN 22611	F	Adult	276.6	85.984
IAA 00-9	F	Adult	278.5	87.272
IAA 96-1	F	Adult	282.0	92.175
MACN 22614	F	Adult	287.8	91.805

Table A1 (concluded).

Collection number	Sex	Age class	CBL (mm)	Geometric mean
LAMAMA ML031	F	Adult	292.3	86.710
IAA 08/09	F	Adult	297.0	88.517
MACN 22613	F	Adult	301.7	95.592
ZOO-BA M-0016	F	Adult	304.2	100.729
CNP 111	F	Adult	304.6	151.146
LAMAMA ML025	F	Adult	306.8	92.016
MACN 22612	F	Adult	310.3	94.396
LAMAMA ML035	F	Adult	313.1	226.602
IAA 03.4	F	Adult	315.3	94.355
IAA 02.12	F	Adult	325.0	98.142
CFA ML01	F	Adult	330.0	102.426
MACN 20434	F	Adult	330.0	105.091
IAA 03.5	F	Adult	330.0	101.796
IAA 02.14	M	Juvenile	201.4	69.350
IAA AA-n1	M	Juvenile	212.3	69.552
IAA 02.30	M	Juvenile	219.9	69.916
IAA AA-6	M	Juvenile	220.0	73.804
LAMAMA ML026	M	Juvenile	223.3	103.444
IAA 02.26	M	Juvenile	228.5	73.974
IAA02.19	M	Juvenile	230.0	73.984
IAA 02.18	M	Juvenile	231.0	71.988
IAA AA-n2	M	Juvenile	231.9	75.511
IAA 02.21	M	Juvenile	233.6	76.316
LAMAMA ML016	M	Subadult	248.0	97.267
IAA 02.16	M	Subadult	248.2	80.880
MACN 26.222	M	Subadult	248.9	83.032
LAMAMA ML021	M	Subadult	260.0	132.317
MACN 20608	M	Adult	401.0	124.188
MACN 24.92	M	Adult	405.0	133.984
MACN 24.91	M	Adult	420.0	140.798
MLP 1504	M	Adult	420.0	133.309
IAA 99-5	M	Adult	425.0	141.283
LAMAMA ML019	M	Adult	425.0	171.716
MLP 26.IV.00.13	M	Adult	435.0	134.911
LAMAMA ML017	M	Adult	440.0	212.652
CNP 04-1999	M	Adult	440.0	159.173
LAMAMA ML032	M	Adult	450.0	159.424
LAMAMA ML028	M	Adult	460.0	204.050
LAMAMA ML020	M	Adult	480.0	262.907
MLP 947	M	Adult	485.0	160.495
MACN 24.93	M	Adult	490.0	162.378
IAA 00-8	M	Adult	505.0	156.416
MACN 13.26	M	Adult	530.0	170.243

Note: CBL, condylobasal length. Institutional acronyms: CFA, Colección Fundación Félix de Azara (Buenos Aires, Argentina); CNP, Centro Nacional Patagónico (Puerto Madryn, Argentina); IAA, Instituto Antártico Argentino (Buenos Aires, Argentina); LAMAMA, Laboratorio de Mamíferos Marinos of the Centro Nacional Patagónico (Puerto Madryn, Argentina); MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia (Buenos Aires, Argentina); MLP, Museo La Plata (La Plata, Argentina); RNP, Museo Acatashun de Aves y Mamíferos Marinos Australes (Ushuaia, Argentina); ZOO-BA-M, Osteological Mammal Collection, Zoológico de Buenos Aires (Buenos Aires, Argentina). Sex: F, female; M, male.