

Allometry of the postnatal cranial ontogeny and sexual dimorphism in *Otaria byronia* (Otariidae)

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Abstract We studied the cranial postnatal ontogeny of *Otaria byronia* in order to detect sexual dimorphism in allometric terms, analyzing the rate of growth of functional variables linked to specific capacities as bite and head movements. We used 20 linear measurements to estimate allometric growth applying bivariate and multivariate analyses in females and males separately. Males were also analyzed in two partitioned subsets considering non-adult and adult stages, when the dimorphism is accentuated in order to reach optimal performance for intra-sexual competition. In the comparison of the employed techniques, we detected an empirical relationship between our multivariate results and the ordinary least square bivariate analysis. The quantitative analyses revealed different ontogenetic trajectories between non-adult and adult males in most variables, suggesting that the adult skull is not a scaled version of subadult skull. For instance, variables related with longitudinal dimensions decreased their allometric coefficients when the adult stage was reached, whereas those related with breadth or vertical dimensions increased their values. In adult males this could indicate that skull breadth and height are more important than longitudinal growth, relative to overall skull size. Conversely, inter-sexual comparisons showed that females and non-adult males shared similar ontogenetic growth trends, including more allometric trends than did males along their own ontogenetic trajectory. In general, adult males exhibited higher allometric coefficients than non-adult males in variables associated with bite and

sexual behavior, whereas in comparison to females the latter showed higher coefficients values in these variables. Such patterns indicate a complex mode of growth in males beyond the growth extension, and are in partial agreement with changes previously reported for this and other species in the family Otariidae.

Keywords Pinnipedia · South American sea lion · Skull · Growth rates · Morphometry

Introduction

The South American sea lion, *Otaria byronia*, inhabits on the coasts of Chile, Peru, Uruguay, Argentina and Southern Brazil (Cappozzo et al. 1991, Rosas et al. 1993 and Reyes et al. 1999). It is the single member of the genus *Otaria* and one of the most sexually dimorphic pinnipeds, in both size and shape (e.g. adult males ~350 kg, and adult females ~150 kg, with a ratio of 2.3:1, Jefferson et al. 2008). As in several species of pinnipeds, the marked sexual dimorphism in size is frequently used to illustrate theories of sexual selection (Lindenfors et al. 2002). Females congregate in large colonies to breed and nurse their young, giving some males the potential to increase mating success, and fostering male intrasexual competition (e.g. Trillmich 1996). As a result, larger body size is favored in males (Lindenfors et al. 2002), displaying phenotypic adaptations such as rapid early growth and delayed maturation (Weckerly 1998).

The degree of cranial shape maturity appears to be a remarkably good predictor of “ecological maturity” which makes it an excellent tool to infer life-history strategies (Zelditch et al. 2003). Some comprehensive studies published on several aspects of cranial sexual dimorphism in pinnipeds (e.g. King 1972; Chiasson 1957; Crespo 1984; Drehmer and Ferigolo 1997; Brunner et al. 2004; Sanfelice

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and Freitas 2008) indicate that skull shape during development of dimorphic species varies intersexually from neonates to adults. Brunner et al. (2004) found that in dimorphic otariids changes in the relative size of skull variables were associated with changes in form and function (e.g. the development of sagittal and occipital crests in males reflected changes in structure of the skull at social maturity, when males were actively defending territories from other males). However, the ontogenetic pattern in an allometric context as a cause of morphological divergence in sexual dimorphism in *O. byronia* is still unknown in several aspects. For instance, changes in the cranial allometric pattern during the growth spurt in adult males (when the sexual selection becomes an important factor on reproductive success) is unknown, as well as its comparison with those patterns detected in male subadults and females.

The two general developmental processes that produce sexual size dimorphism are sex-specific differences in growth rate and growth duration (bimaturism, *sensu* Leigh 1992; Cheverud et al. 1992). These processes themselves are the subjects of selection and their relative contribution to the dimorphism of adults is informative about the direction and patterns of sexual size dimorphism evolution (Badyaev 2002). Ontogeny of sexual dimorphism is relevant because sex differences among taxa could result from changes in such developmental processes (Badyaev et al. 2001) whose variation may reflect fundamental differences in social structure, ecological factors or phylogenetic relationships.

In this study, we focus on the postnatal cranial allometric growth of the South American sea lion, employing two quantitative approaches, bivariate and multivariate allometry. Allometry is used to study relative growth of the different cranial variables. With this information, we described sexual differences in allometric growth trends achieved during ontogeny (change in slopes, lateral transposition and ontogenetic scaling between growth trajectories of both sexes and age stages). We interpreted allometry coefficients as growth rates, although, in truth, they represented size rates. In view of the high sexual dimorphism in adult sea lions, product of the hypermorphosis and delayed maturation of males (e.g. Weckerly 1998), we expect to find differences in the cranial growth of adult males in comparison to the trajectory drawn by females and subadult males, as well as in the ways in which both sexes reach its adult morphology. Although discussions of our findings are based on functional grounds, previous studies employed different approaches (e.g. Hamilton 1934; Cappozzo et al. 1991; Rosas et al. 1993; Brunner et al. 2004; Sanfelice and de Freitas 2008) providing relevant information on sexual dimorphism and age-related changes in *O. byronia*, allowing comparisons with our results. In this way, this work is focused on the study of the allometric trends of specific cranial variables during growth, contributing to a growing

number of studies regarding ontogeny and dimorphism in pinnipeds.

Materials and methods

Study specimens

O. byronia is a species well represented by complete ontogenetic series deposited in mammal collections. We analyzed 149 skulls of *O. byronia* (52 females, 97 males; Appendix I). In our sample, 16 specimens (eight females; eight males) were juveniles with not fully adult permanent dentition. In the smallest specimen (female LAMAMA OF141, condylo-basal length, LCB 139.4 mm; male LAMAMA OF139, LCB 140.4 mm) deciduous dentition was functional. According to the available information (Hamilton 1934), the smallest specimens in our series were newborns. Our sample included also old specimens in both sexes (female GEMARS 1323, LCB 292.7 mm, male MLP 1332, LCB 375.0 mm), covering a well-represented onset and offset in the ontogenetic series. All samples were collected from the Atlantic population, mostly along the Argentine coast, in an attempt to avoid problems with ecogeographic variation.

Following Sanfelice and Freitas (2008) and Brunner et al. (2004), our studied specimens were aged on three broad categories. Juveniles included specimens with sutural index (*sensu* Sivertsen 1954) between nine to ten, with opened canine tooth root and a condilo-basal skull length less than 192 mm. Subadults included specimens with a sutural index between 11 and 13, permanent dentition fully erupted (except canines) and LCB <220 and <294 mm for females and males, respectively. Adult specimens had a sutural index higher than 13, closed roots of permanent teeth (except canines) with different stages of crown wear and a fully developed sagittal crest.

Study of growth and measurements

Allometry of growth explicitly considers timing of changes throughout the life of an individual (Kunz and Robson 1995; Prestrud and Nilssen 1995; Maunz and German 1996; Stern and Kunz 1998). By contrast, allometry of size compares changes against overall size along a growth series. According to Klingenberg (1996), ontogenetic allometry (or growth allometry) deals with covariation among characters during growth. Three types of data are usually used to study ontogenetic allometry: longitudinal data based on measurements of the same individuals at several developmental stages, cross-sectional data with different specimens in several known stages, and mixed cross-sectional data collected without information on ontogenetic stage (Cock 1966). In this case, the time frame is implicitly incorporated (size

proxy) but not specified to describe relative modifications as the animal grows. For the allometric analysis, we used 20 cranial and mandibular variables (Fig. 1) including length, width, and height of neurocranial (e.g. braincase, orbit) and splanchnocranial components (e.g. jaw length, tooth row length). The cranial dimensions analyzed herein partially overlap with those considered in other morphometric studies of carnivore skulls (e.g. Radinsky 1981; Molina-Schiller 2000; Brunner et al. 2004; Giannini et al. 2010; Tanner et al. 2010; Segura and Prevosti 2012), which allows efficient comparisons with other pinnipeds and carnivores in general.

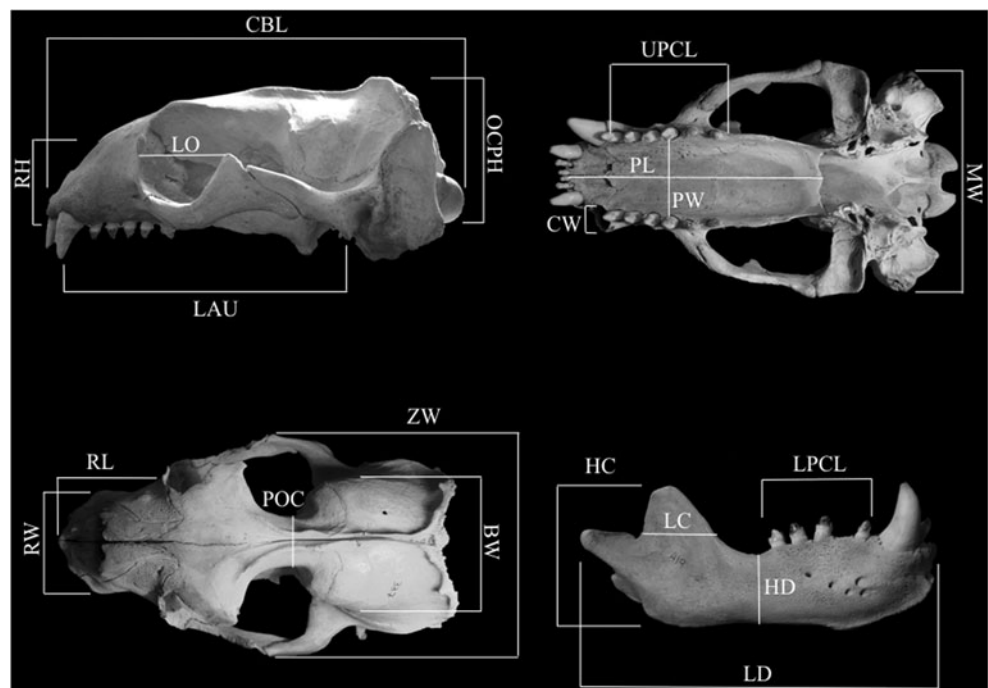
Two analytical techniques were used to describe and analyze ontogeny: bivariate regressions and multivariate allometry. Both techniques were applied for each sex in order to analyze the sexual dimorphism of growth in *O. byronia*.

Bivariate approach

In this analysis, the scaling of any measurement can be affected strongly by the choice of the independent variable (Smith 1981; Wayne 1986). In most of previous studies (e.g. Abdala et al. 2001; Flores et al. 2003; Giannini et al. 2004), researchers have taken the total length of the skull as a proxy of size and as an independent variable, because they demonstrated that it is isometric (see Janis 1990 and Cassini et al. 2012 for ungulates; Abdala et al. 2001 and Flores et al. 2003 for didelphid marsupials; Flores and Casinos 2011 for primates). We used the geometric mean as an independent variable and proxy of size (e.g. Mosimann 1970; Meachen-

Samuels and Van Valkenburgh, 2009) because we found that the total length of the skull was not isometric in both sexes (see “Results” section). The geometric mean is a size variable derived from the N th root of the product of N measurements, being a good predictor of individual size and skull measurements. Therefore, the relationship between the two variables was isometric when the slope is equal to one (value expected under geometric similarity between two variables that grows linearly; Peters 1993). The relation of each variable to overall size (geometric mean) was examined with the equation of allometry: $\log(y) = \log b_0 + b_1 \log(x) + \log(e)$; where y is any of the measured skull variables, $a = \log(b_0)$ is the y -intercept or constant of normalization (and b_0 is the constant term of power 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). The standardized major axis (SMA) regression determines an axis or line-of-best fit. The purpose of line-fitting is not to predict Y from X (as in ordinary least squares regression, OLS), but to summarize the relationship between two variables. The standardized major axis is the line that minimizes the sum of squares of the shortest distances from the data points to the line, calculated on standardized data, and rescaled to the original axes that allowed variation in both dimensions, so residuals were oblique with X and Y directions without equal weight when measuring departures from the line. The SMA regression is more appropriate than the OLS regression for dealing with allometric approaches (for extensive overviews on the subject, see Warton et al. 2006). Significance of allometry coefficients was evaluated by means of two-

Fig. 1 Cranial measurements of *O. byronia* used in this study. *BW*, braincase width; *CBL*, condylobasal length; *CW*, alveolus width of upper canine teeth; *HC*, coronoid height; *HD*, height of dentary (at 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



tailed t tests at a significance level set to $p=0.01$. Deviations from isometry were assessed by comparing the allometric coefficient with that expected under geometric similarity (Alexander 1985). We performed F tests with the null coefficient set at 1.0 to assess significant deviations from isometry (Warton and Weber 2002). Negative allometry refers to the case of a coefficient significantly less than expected by isometry, and positive allometry is when it is significantly higher (Emerson and Bramble 1993).

Adult males have greater dimensions (for each variable and geometric mean) than females. Bigger subadult males have the same or even greater sizes than the biggest females of our sample (Fig. 2). Brunner et al. (2004), identified a secondary growth spurt (= peak) in the late development of males in all the species considered, including also *O. byronia*, accentuating size differences between sexes in adult stages. So we decided to divide the male sample in two subsets, i.e. adults and non adults (juveniles and subadults) and testing for common allometric coefficient (slope) intra-sexually and then amongst the two sexes. We followed the recommendations of Warton et al. (2006) using a likelihood ratio test for common SMA slope, and compared it to a chi-squared distribution (Warton and Weber 2002). Then, if a common slope was shared (absence of sexual dimorphism in slope), we compared the significance of common constant of normalization (y -intercepts) using the Wald statistic (as described in Warton et al. 2006), in preference to the K statistic as they had received some attention in the literature. Finally, if both slopes and y -intercepts were shared by both sexes, then the data points were scattered around a common axis, with no difference in elevation. To test the hypothesis that there might be a shift along the axis we follow the Wald statistic following Warton et al. (2006). All these regression

coefficients, statistical parameters, and tests were performed using smart package of R software (Warton and Weber 2002).

Multivariate approach

This approach is based on the generalization of the allometry equation proposed by Jolicoeur (1963). In multivariate allometry, size is considered as 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 (extracted from a variance-covariance matrix of log-transformed variables). 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 (19 for this study because the postorbital constriction is enantiometric and eliminated in this analysis—see “Bivariate analysis” section). 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 us to detect negative (<0.229) and positive (>0.229) departures from isometry in each variable. Statistical departures from isometry were estimated using the application of jackknife (Quenouille 1956; Manly 1997). The aim of this technique is to generate confidence intervals for the empirically obtained eigenvector elements. Thus, pseudosamples are generated such that a new first unit eigenvector is calculated from a matrix with one individual removed at a time. Giannini et al. (2004, 2010) and Flores et al. (2006, 2010) followed Manly (1997) in using trimmed values for the calculation of pseudo-values. Trimming the largest and smallest pseudovalues for each variable significantly decreased the standard deviations. Herein, we reported untrimmed as well as trimmed values, opting for the results with either the lower average standard deviation or bias. The multivariate statistical analysis (PCA+jackknife resampling) was programmed in R (R Development Core Team 2009), and the script is available from the author (Giannini et al. 2010).

We interpreted the bivariate coefficients of allometry as growth rates of a specific cranial variable, although they actually represent rates of size increase (Simpson et al. 1960; Gould 1966; Nelson and Shump 1978; Cassini et al. 2012). Thus, we ultimately assumed that intraspecific allometry of size closely reflected true allometry of growth. On the contrary, some authors stated that allometric coefficients derived from principal components of skeletal measurements in a multivariate approach cannot be interpreted as growth rates (Jungers and Germans 1981). However, Klingenberg (1996) stated that multiplying PC1 coefficients by the square root of p yields values (multivariate allometry

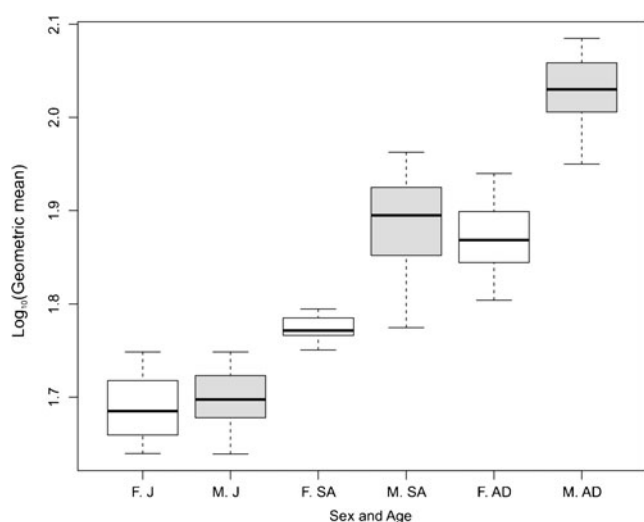


Fig. 2 Box-plot of log-transformed geometric mean of skull for both sex discriminating by age categories. Abbreviations: *F*, females; *M*, males; *J*, juveniles; *SA*, subadults; *AD*, adults

coefficient, MAC) can be interpreted as bivariate allometric coefficients (BAC) for each of the variables against a measure of overall size (a geometric mean of all variables). As we do for bivariate departures from isometry, we perform F tests on the BAC values with the null coefficient set at MAC value (for each variable) to assess significant deviations of the SMA and OLS slopes from MAC values. The first principal component geometrically corresponds to the direction of the longest axis through the scatter of data points (i.e. the direction that has maximal variance) and passes by the centroid (mean vector). So, the resultant line is that to which the sum of squared perpendicular distances (SSD) of each point are minimal. Also, the ratio between the SSD and $(n-1)$ correspond to part of the total variance not accounted by the PC1, (i.e., the residual variance) (Klingenberg 1996). Given the close geometrical similarity with the OLS regression, we expected that the MAC would not differ significantly with the BAC obtained by means of OLS regression method.

Results

Bivariate analysis

Regressions for *O. byronia* showed high values of correlation in all dependent variables, except in breadth of the braincase ($R^2=0.05$ in non-adult males; 0.206 in male adults and 0.01 in females) and postorbital constriction ($R^2=0.299$ in males of non-adult and adult stages, and 0.45 in females). Adult males also showed low values of correlation in the orbit and upper postcanine tooth lengths (0.44 and 0.4, respectively). Our analysis of the ontogenetic trajectories of males interpreted as two separated subsets (Table 1), considering non-adult and adult stages, detected that most variables changed their allometric trends when adult stage is reached (Fig. 3a, b). In the SMA analysis, only 5 out of 20 variables showed a common slope between male trajectories of non-adult and adult stages (Table 1, Fig. 3c). In four variables, the observed allometric trend was positive in both age groups: palatal, rostral and canine widths (PW, RW and CW), as well as for the length of coronoid process (LC). For the remaining variable, the orbital length (LO), both age stages showed a negatively allometric growth trend. Although the height of the coronoid process (HC) showed the same allometric trend in both male subsets, the coefficient of allometry (slope) was statistically higher in adults than in non-adults (Table 1). In contrast, slopes for the remaining variables showed different growth trends depending on the age stage. Only 5 out these 15 variables showed higher allometric trends in non-adult than in adult males (Fig. 3b), being all longitudinal measurements [condylo-basal length (CBL), palatal length (PL), rostral length (RL), load arm length at upper canine (LAU) and length of dentary (LD)]. Conversely, in the remaining nine

variables [zygomatic width (ZW), upper postcanine length (UPCL), occipital plate height (OPH), braincase width (BW), rostral height (RH), mastoid width (MW), postorbital constriction (POC), HC, height of dentary (HD) and length of lower postcanine row (LPCL)], the allometric coefficients were higher in adults than in non-adults (Fig. 3a).

The comparison of both sexes (i.e. all females with non-adult and adult males, Table 2) indicated that females and non-adult males shared more allometric trends than did males of non-adult and adult stages. For instance, 11 out 20 variables exhibited the same ontogenetic growth trend in non-adult males and the complete trajectory of females (Table 2), from which seven were negatively allometric (ZW, UPCL, OPH, BW, RH, MW and LPCL) and the remaining were positively allometric (PW, RL, LD and HC). Additionally, seven of these variables (UPCL, OPH, BW, RL, RH, MW and LPCL) showed also agreement among intercepts of the trajectories described by both sexes. Nevertheless, BW showed an extension of the ontogenetic offset in males. The remaining four variables showed significant sexual differences in their intercepts (Table 2).

The differences in slope values (i.e. coefficients of allometry or variable growth rates; Table 2) indicated that they were higher in females than those observed in males for CBL, LO and some characters of the muzzle, such as PL, RL, LAU, LC and HD. Conversely, males showed higher slopes for rostral and upper canine teeth widths (RW and CW, Fig. 3d). It is also remarkable that the POC showed enantiometry (*sensu* Huxley and Teissier 1936) in both groups, instead of the typical negatively allometric growth trend commonly registered in mammalian skulls. The latter was only detected for adult males of *O. byronia*.

Multivariate analysis

The mean difference in the absolute bias favored untrimmed over trimmed analysis in the three subsets (non-adult males, adult males, and females), which suggests that there are no extreme pseudovalues. For females, we obtained an average of 0.000094 in the absolute bias for the former analysis and 0.00018 for the latter (i.e. 1.91 times higher). In non-adult males the values were 0.000056 and 0.00023, respectively (4.19 times higher), whereas in adults, the average of absolute bias in untrimmed and trimmed analyses was 0.00011 and 0.00037, respectively (3.33 times higher). In only 4 out 19 variables under study, we found the same ontogenetic growth trends for all the subsets. HC showed positive allometry and PW isometry, whereas UPCL and BW showed negative allometry. Also, as reported in the bivariate analysis, the multivariate approach showed that the same ontogenetic trend was detected in females and non-adult male stages in most cranial variables (10 out 19) (Table 3). Palatal, rostral, dentary and coronoid lengths (PL, RL, LD and LC) were positively allometric in both groups, while five cranial

Table 1 Test for common slope for both male subsets of *O. byronia*

Variable	Lr ($df=1$)	p -Lr	Common slope	Growth trend
CBL	11.550	6.77E-04	NoAD>AD	NoAD: =; AD: -
PL	14.575	1.34E-04	NoAD>AD	NoAD: +; AD: =
PW	<i>1.380</i>	<i>0.239^a</i>	<i>1.228</i>	+
ZW	17.995	2.21E-05	AD>NoAD	NoAD: -; AD: +
UPCL	10.373	0.001	AD>NoAD	NoAD: -; AD: =
OCPH	20.492	5.99E-06	AD>NoAD	NoAD: -; AD: =
BB	10.131	0.001	AD>NoAD	NoAD: -; AD: =
RL	6.970	0.008	NoAD>AD	NoAD: +; AD: =
LO	<i>0.011</i>	<i>0.916^a</i>	<i>0.832</i>	-
RH	13.514	2.36E-04	AD>NoAD	NoAD: -; AD: +
MW	32.106	1.46E-08	AD>NoAD	NoAD: -; AD: +
POC	31.466	2.03E-08	AD>NoAD	NoAD: enant.; AD: +
LAU	7.750	0.005	NoAD>AD	NoAD: +; AD: =
LD	17.610	2.71E-05	NoAD>AD	NoAD: +; AD: =
HC	4.590	0.032	AD>NoAD	NoAD: +; AD: +
LC	<i>1.403</i>	<i>0.236^a</i>	<i>1.548</i>	+
HD	38.632	5.12E-10	AD>NoAD	NoAD: =; AD: +
LPCL	18.421	1.77E-05	AD>NoAD	NoAD: -; AD: =
RW	<i>3.597</i>	<i>0.057^a</i>	<i>1.329</i>	+
CW	<i>0.007</i>	<i>0.932^a</i>	<i>1.624</i>	+

Variable abbreviations as in Fig. 1

Italicized rows show significant regressions for common slope

Parameters: *Lr* likelihood ratio (Warton *et al.* 2006); *p-Lr* p value of likelihood ratio (all significant except those with an asterisk); *Growth trend* is the summary allometry of each variable presented in symbols: (=), isometry; (-), negative allometry; (+), positive allometry; *enant* enantiometric; *AD* adult, *NoAD* non-adult

^aDifferences are between the common slope trend and the slope observed for each age group: AD ($n=54$) and NoAD ($n=43$)

variables (ZW, OCPH, RH, MW and LPCL) scaled with negative allometry, and only one variable (HD) had no significant departure from isometry. Conversely, intra-male comparisons showed that they shared their allometric growth trends in only four skull variables. Orbit and condylo-basal lengths scaled with negative allometry, while rostral and canine widths overall growth scaled with positive slopes. Just one variable (LAU) showed different allometric trends in each group. In females there was no significant departure from isometry for six variables (CBL, PW, LO, HD, RW and CW), whereas in non-adult males three variables were isometric (PW, LAU and HD). Finally, adult males showed seven isometric variables (PW, ZW, OCPH, RW, MW, LC and LPCL).

Comparing our results of bivariate and multivariate allometry, we found high consistence regarding to the detection of different allometric trends in the partitioned analyses of males and females. In both analyses, several variables in non-adult males showed a behavior reflecting the trajectories (or trends) followed by females, with a completely different pattern of growth in adult males.

Discussion

Quantitative methods

In comparison to multivariate analyses, bivariate coefficients of allometry can be useful because they are less affected by

sample completeness (Giannini *et al.* 2004) and are more directly interpretable in terms of size-dependent functional relationships (Jungers and German 1981). In addition, bivariate coefficients can be derived from simple growth models of each measurement (Laird 1965; Wayne 1986). However, this technique implies a condition of isometry of the commonly considered independent variable (condylo-basal length), which does not necessarily occur as in our case. Therefore, a multivariate approach seemed to be more independent of such conditions, because size is considered as a latent variable affecting all variables simultaneously (e.g. Flores *et al.* 2006). The geometric mean used as an independent variable for the bivariate approach, provides relevant information that could not be obtained by multivariate analyses, such as significant differences between sexes in slopes and intercepts as well as growth period (onset and offset of the growth trajectory).

Our F tests on the BAC values with the null coefficient set at MAC value for each variable (performed to assess significant deviations of the SMA and OLS slopes from MAC values) did not detect significant differences between the multivariate analysis and the OLS bivariate analysis (Table 4). These findings support the suggestion of Klingenberg (1996) that multiplying PC1 coefficients by the square root of p yields values can be interpreted as bivariate allometric coefficients, but only with OLS regressions to the geometric mean. In our case, we found an empirical similarity between the OLS and the multivariate analysis. In this way, it is likely that differences between bivariate (SMA) and multivariate approaches in our

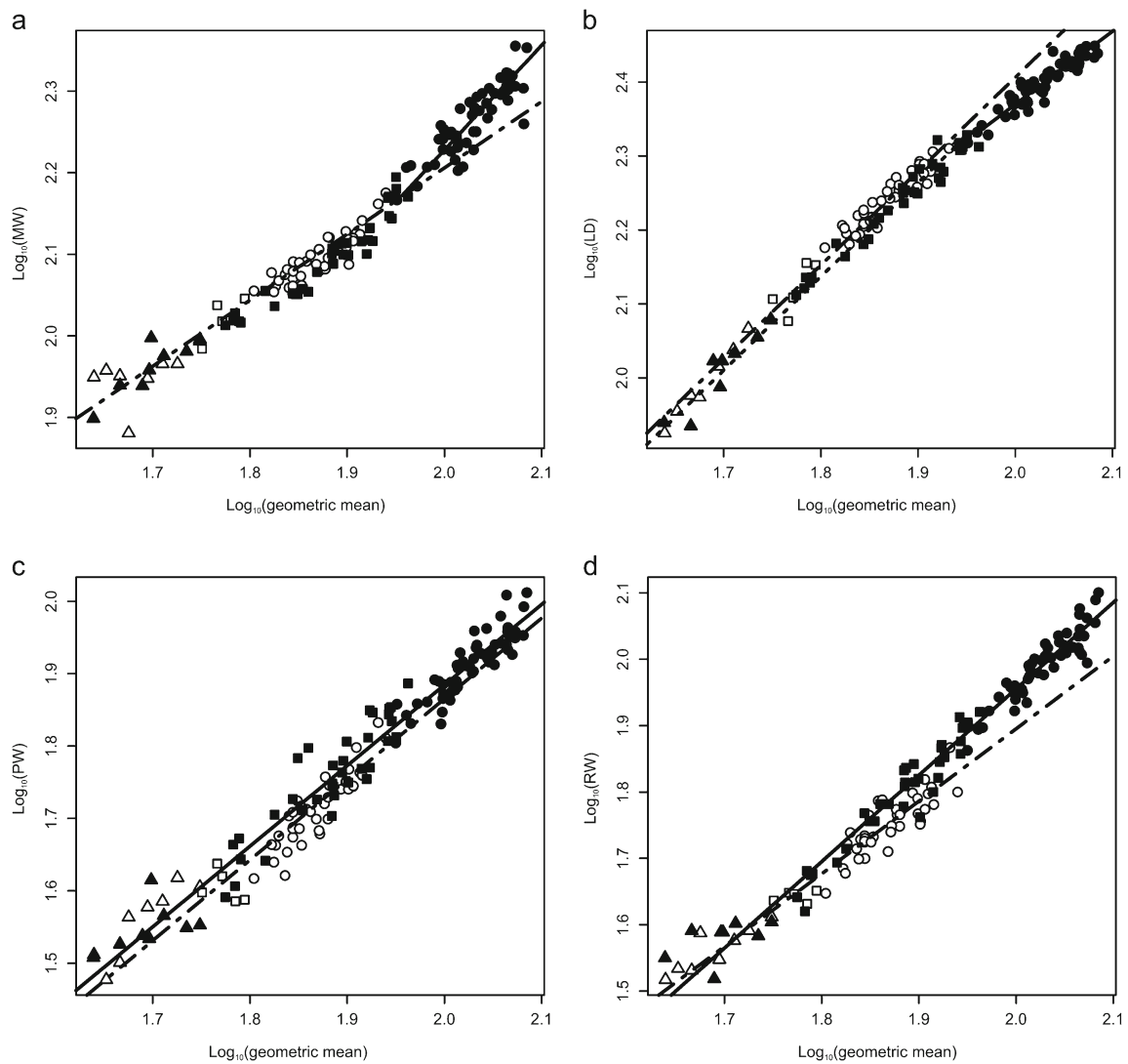


Fig. 3 Bivariate SMA regressions. **a** Same slope and intercepts for females and non-adult males, higher slope for adult males; **b** same slope and different intercepts between females and non-adult males, lower slope for adult males; **c** same slope and different intercepts between male trajectories; and **d** different slopes between the growth

trajectories of males and females. Symbols: *white symbols*—females; *black symbols*—males; *triangles*—juveniles; *squares*—subadults; *circles*—adults; lines SMA regression, *dot and dash line*—females; *dashed line*—non adult males; *solid line*—adult males. Abbreviations as in Fig. 1

analyses rely on the differences between line-fitting methods (i.e. OLS vs SMA) than in the dimensionality of the analyses (bi vs multivariate). In addition, as stated by Warton et al. (2006), bivariate OLS analyses are adequate for predictions, although SMA is commonly used in studies of allometry. In this way and according to the similarity detected between the OLS and the multivariate analysis, we suggest the use of a composed independent variable such as the geometric mean, instead of a single measurement in bivariate analyses of this species.

Allometric growth in *O. byronia*

Although numerous studies have provided a detailed description of sexual dimorphism in *O. byronia* (e.g. Crespo 1984;

Brunner et al. 2004; Sanfelice and de Freitas 2008), our understanding of the skull development in terms of allometry remains incomplete, as well as its interpretation as allometric differences in sexual dimorphism. Consequently, our approach is complementary to previous studies and contributes by incorporating additional analyses to the classic ontogenetic approaches. Ontogenetic studies have revealed that several developmental pathways may lead to sexual body size dimorphism in adults. In pinnipeds, males may grow faster than females from early stages, or males may display similar growth rates early and continue growing at a slow rate as adults, while females stop growing (Isaac 2005).

Sanfelice and de Freitas (2008), using two dimension geometrics morphometrics, have studied ontogenetic series of three species of otariid skulls, concluding that in both

Table 2 Test for common slope, common intercept and shift for both sexes of *O. byronia*

Variable	Common slope				Common intercept			Shift	
	Lr(b1)	P(b1)	b1 com	Growth trend	<i>W</i> (log.bo)	<i>P</i> (log.bo)	log.bo com	<i>W</i> shift	<i>P</i> (shift)
CBL	4.447	0.034	F>M	F: =; M: =					
PL	11.948	5.46E-04	F>M	F: +; M: +					
PW ^a	<i>2.815</i>	<i>0.093</i>	<i>1.114</i>	+	<i>12.241</i>	4.67E-07	<i>M>H</i>		
ZW	<i>0.786</i>	<i>0.375</i>	<i>0.954</i>	–	<i>25.610</i>	4.18E-07	<i>H>M</i>		
UPCL	<i>1.940</i>	<i>0.163</i>	<i>0.834</i>	–	<i>2.699</i>	<i>0.100</i>	<i>0.253</i>	<i>0.517</i>	<i>0.471</i>
OCPH	<i>0.802</i>	<i>0.370</i>	<i>0.675</i>	–	<i>0.582</i>	<i>0.445</i>	<i>0.678</i>	<i>1.308</i>	<i>0.252</i>
BW	<i>1.039</i>	<i>0.308</i>	<i>0.550</i>	–	<i>1.884</i>	<i>0.169</i>	<i>0.958</i>	<i>6.292</i>	<i>0.012</i>
RL	<i>1.190</i>	<i>0.275</i>	<i>1.322</i>	+	<i>2.940</i>	<i>0.086</i>	<i>–0.659</i>	<i>1.490</i>	<i>0.222</i>
LO ^a	26.933	2.11E-07	F>M	F: =; M: –					
RH	<i>0.539</i>	<i>0.462</i>	<i>0.913</i>	–	<i>3.283</i>	<i>0.070</i>	<i>0.032</i>	<i>1.961</i>	<i>0.161</i>
MW	<i>0.002</i>	<i>0.956</i>	<i>0.810</i>	–	<i>3.505</i>	<i>0.061</i>	<i>0.584</i>	<i>0.642</i>	<i>0.422</i>
POC	4.570	0.032	M>F	Enant.					
LAU	7.984	0.004	F>M	F: +; M: +					
LD	<i>2.617</i>	<i>0.105</i>	<i>1.269</i>	+	<i>25.625</i>	4.14E-07	<i>F>M</i>		
HC	<i>3.276</i>	<i>0.070</i>	<i>1.420</i>	+	<i>44.181</i>	2.99E-11	<i>F>M</i>		
LC	8.180	0.004	F>M	F: +; M: +					
HD	5.395	0.020	F>M	F: +; M: =					
LPCL	<i>2.060</i>	<i>0.151</i>	<i>0.733</i>	–	<i>1.114</i>	<i>0.291</i>	<i>0.326</i>	<i>1.514</i>	<i>0.219</i>
RW ^a	15.853	6.84E-05	M>F	F: +; M: +					
CW ^a	13.537	2.33E-04	M>F	F: =; M: +					

Variable abbreviations as in Fig. 1

Italicized rows show significant regressions for common slope

Parameters: *b1com* common slope from standardized major axis, *log.bo com* common intercept from standardized major axis (values are italics), *Lr* likelihood ratio (Warton et al. 2006), *W* Wald statistic (Warton et al. 2006); *P(b1)* *p* value of *Lr* parameter, (*p* values significant at 0.01 level are in bold); *P(log.bo)* *p* value of *W(log.bo)*; *P(shift)* *p* value of *W* shift; *Shift* shift along the regression axis. *Growth trend* is the summary allometry of each variable presented in symbols: (=), isometry; (–), negative allometry; (+), positive allometry; “enant.”, enantiometric. Differences are between the common slope trend and the slope observed for each sex: *F*, females (*n*=52); *M*, non-adult males (*n*=43), except for those variables with a superscripted letter “a” asterisk (^a) were the complete set of males was employed (*n*=97)

sexes of *O. byronia* the palate elongated, which is in partial agreement with the positive allometry of PL for both females and non-adult males in our results, although the trajectory of the palate exhibited a complex mode of growth in males, with coefficients values in adults lesser than those obtained for females and non-adult males. Other transformations detected in the cited work, as the narrowing of the rostrum and zygomatic width in females (but widening in males), are also partially in agreement with our bivariate and multivariate approaches. The positive allometry of the RL, and the lower allometric trend of the ZW, combined with the isometry of the condylo-basal length (CBL) in females and non-adult males, gives them a more slender skull appearance compared with adult males. In the latter, the rate of growth of the RL decreases and the coefficient of the ZW becomes positive (bivariate) or isometric (multivariate). Recently, Jones and Goswami (2010), using three-dimensional geometric morphometrics, stated that the basic shape transition from juveniles to adults in male otariids

involved enlargement of the rostral and palatal regions, and growth of the canines and mastoid process. In our partitioned study, the allometric growth trends of some variables with positive allometry in adult males (such as RW, CW and MW) also reflected largely the pattern reported, although our results indicate some contradiction with the conclusions of Jones and Goswami (2010), as PL and RL decreased their allometric growth trends compared with females and non-adult males.

In species with sexual size dimorphism, sex differences in growth strategies are thought to have evolved as a result of reproductive success. Growth spurts in male body mass and size in relation to sexual or social maturity have been widely observed in several species of pinnipeds (e.g. Bryden 1968; Payne 1979; McLaren 1993; Clinton 1994). Bryden (1972) detected periods of accelerated growth followed by a marked slowing or cessation of growth in males, associated to sexual or social maturation because energetic resources previously used for growth are directed towards reproductive development,

Table 3 Results by sex and age of the multivariate analysis of cranial allometry in *O. byronia*

Variable	Sex	Untrimmed					Trimmed				
		Resampled coefficient	Bias	99 % CI	Departure	Growth trend	Resampled coefficient	Bias	99 % CI	Departure	Growth trend
CBL	F	0.225	-1.38E-03	0.205-0.246	-4.12E-03	=	0.22	1.40E-03	0.204-0.235	-9.69E-03	=
	M-NoAD	0.210	-1.03E-03	0.192-0.229	-1.90E-02	-	0.205	1.67E-03	0.192-0.218	-2.44E-02	-
	M-AD	0.145	-9.83E-04	0.117-0.173	-8.43E-02	-	0.146	-1.59E-03	0.122-0.170	-8.31E-02	-
PL	F	0.295	-1.24E-03	0.272-0.318	6.54E-02	+	0.291	5.06E-04	0.272-0.311	6.19E-02	+
	M-NoAD	0.264	-9.54E-04	0.244-0.285	3.49E-02	+	0.259	1.87E-03	0.243-0.274	2.93E-02	+
	M-AD	0.185	-2.23E-03	0.146-0.224	-4.39E-02	-	0.19	-4.52E-03	0.162-0.218	-3.94E-02	-
PW	F	0.210	1.67E-04	0.177-0.244	-1.89E-02	=	0.211	-2.53E-04	0.183-0.240	-1.81E-02	=
	M-NoAD	0.245	3.05E-04	0.211-0.279	1.58E-02	=	0.255	-4.49E-03	0.230-0.280	2.54E-02	+
	M-AD	0.255	-6.24E-04	0.201-0.310	2.57E-02	=	0.26	-2.98E-03	0.214-0.306	3.04E-02	=
ZW	F	0.207	3.64E-04	0.188-0.226	-2.27E-02	-	0.213	-2.85E-03	0.200-0.226	-1.62E-02	-
	M-NoAD	0.203	-3.20E-04	0.189-0.218	-2.61E-02	-	0.203	-1.46E-04	0.190-0.215	-2.64E-02	-
	M-AD	0.250	-6.89E-04	0.212-0.288	2.08E-02	-	0.253	-2.04E-03	0.218-0.288	2.36E-02	=
UPCL	F	0.179	-5.20E-04	0.152-0.206	-5.06E-02	-	0.181	-1.73E-03	0.164-0.199	-4.82E-02	-
	M-NoAD	0.153	-5.16E-04	0.119-0.186	-7.67E-02	-	0.153	-7.10E-04	0.126-0.180	-7.63E-02	-
	M-AD	0.155	2.56E-04	0.089-0.222	-7.39E-02	-	0.145	5.69E-03	0.090-0.198	-8.48E-02	-
OCPH	F	0.134	5.22E-04	0.113-0.154	-9.56E-02	-	0.135	-1.89E-04	0.119-0.151	-9.42E-02	-
	M-NoAD	0.145	8.41E-05	0.131-0.160	-8.39E-02	-	0.145	2.98E-04	0.133-0.157	-8.44E-02	-
	M-AD	0.190	-7.52E-04	0.148-0.232	-3.94E-02	=	0.192	-1.64E-03	0.156-0.228	-3.76E-02	-
BW	F	0.005	1.71E-03	-0.038-0.048	-2.24E-01	-	-0.001	4.82E-03	-0.039-0.036	-2.30E-01	-
	M-NoAD	0.022	-3.98E-04	-0.012-0.055	-2.07E-01	-	0.017	1.72E-03	-0.012-0.047	-2.12E-01	-
	M-AD	0.089	-1.08E-04	0.019-0.158	-1.40E-01	-	0.098	-5.01E-03	0.042-0.154	-1.31E-01	-
RL	F	0.289	-1.37E-03	0.245-0.332	5.92E-02	+	0.292	-3.10E-03	0.264-0.320	6.26E-02	+
	M-NoAD	0.278	-3.30E-04	0.250-0.305	4.83E-02	+	0.276	4.70E-04	0.255-0.297	4.67E-02	+
	M-AD	0.152	-9.65E-04	0.107-0.198	-7.69E-02	-	0.15	1.94E-04	0.109-0.191	-7.93E-02	-
LO	F	0.202	-1.68E-03	0.173-0.231	-2.75E-02	=	0.198	1.54E-04	0.175-0.222	-3.11E-02	-
	M-NoAD	0.175	-1.24E-03	0.145-0.206	-5.41E-02	-	0.167	2.76E-03	0.144-0.190	-6.21E-02	-
	M-AD	0.119	-6.23E-04	0.070-0.169	-1.10E-01	-	0.123	-2.56E-03	0.082-0.165	-1.06E-01	-
RH	F	0.178	6.61E-04	0.128-0.228	-5.13E-02	-	0.182	-1.40E-03	0.141-0.223	-4.72E-02	-
	M-NoAD	0.186	3.36E-04	0.161-0.211	-4.35E-02	-	0.193	-3.02E-03	0.174-0.211	-3.68E-02	-
	M-AD	0.227	9.42E-04	0.163-0.290	-2.89E-03	=	0.242	-6.69E-03	0.192-0.292	1.23E-02	=
MW	F	0.168	3.51E-04	0.135-0.202	-6.11E-02	-	0.163	2.77E-03	0.143-0.184	-6.59E-02	-
	M-NoAD	0.172	-1.19E-04	0.151-0.193	-5.74E-02	-	0.177	-2.78E-03	0.165-0.190	-5.20E-02	-
	M-AD	0.251	-7.37E-04	0.201-0.301	2.19E-02	=	0.261	-5.43E-03	0.224-0.297	3.13E-02	=

Table 3 (continued)

Variable	Sex	Untrimmed					Trimmed				
		Resampled coefficient	Bias	99% CI	Departure	Growth trend	Resampled coefficient	Bias	99% CI	Departure	Growth trend
LAU	F	0.271	-9.43E-04	0.255-0.287	4.17E-02	+	0.267	1.26E-03	0.255-0.278	3.73E-02	+
	M-NoAD	0.247	-9.63E-04	0.229-0.265	1.77E-02	=	0.244	6.74E-04	0.229-0.259	1.44E-02	=
	M-AD	0.197	-1.51E-03	0.171-0.224	-3.21E-02	-	0.195	-5.41E-04	0.172-0.219	-3.40E-02	-
LD	F	0.283	-1.03E-03	0.269-0.297	5.35E-02	+	0.279	9.08E-04	0.268-0.290	4.96E-02	+
	M-NoAD	0.269	-7.42E-04	0.248-0.291	3.99E-02	+	0.263	2.23E-03	0.249-0.277	3.39E-02	+
	M-AD	0.204	-1.01E-03	0.180-0.228	-2.50E-02	-	0.203	-3.95E-04	0.181-0.225	-2.63E-02	-
HC	F	0.315	5.21E-04	0.288-0.341	8.52E-02	+	0.324	-4.09E-03	0.307-0.341	9.45E-02	+
	M-NoAD	0.296	-7.24E-04	0.273-0.318	6.63E-02	+	0.289	2.50E-03	0.273-0.306	5.99E-02	+
	M-AD	0.319	-2.72E-03	0.259-0.378	8.91E-02	+	0.328	-7.47E-03	0.281-0.375	9.86E-02	+
LC	F	0.333	-9.21E-04	0.277-0.389	1.03E-01	+	0.33	4.03E-04	0.281-0.379	1.00E-01	+
	M-NoAD	0.315	-3.95E-04	0.271-0.358	8.51E-02	+	0.312	6.84E-04	0.274-0.350	8.29E-02	+
	M-AD	0.281	4.12E-04	0.184-0.379	5.20E-02	=	0.299	-8.59E-03	0.225-0.374	7.00E-02	=
HD	F	0.255	2.00E-03	0.211-0.299	2.51E-02	=	0.262	-1.64E-03	0.225-0.299	3.24E-02	=
	M-NoAD	0.224	2.00E-04	0.197-0.251	-5.40E-03	=	0.229	-2.50E-03	0.209-0.250	5.86E-06	=
	M-AD	0.373	-1.27E-03	0.286-0.460	1.43E-01	+	0.357	6.96E-03	0.288-0.425	1.27E-01	+
LPCL	F	0.157	-3.01E-04	0.140-0.174	-7.25E-02	-	0.157	-5.40E-04	0.142-0.172	-7.20E-02	-
	M-NoAD	0.146	-8.19E-04	0.123-0.169	-8.37E-02	-	0.14	2.12E-03	0.124-0.156	-8.96E-02	-
	M-AD	0.182	-1.04E-03	0.121-0.242	-4.76E-02	=	0.185	-2.67E-03	0.133-0.237	-4.43E-02	=
RW	F	0.228	1.57E-04	0.203-0.253	-1.38E-03	=	0.231	-1.21E-03	0.215-0.247	1.35E-03	=
	M-NoAD	0.270	9.19E-04	0.234-0.307	4.09E-02	+	0.277	-2.20E-03	0.248-0.305	4.72E-02	+
	M-AD	0.298	-2.07E-03	0.246-0.349	6.81E-02	+	0.297	-1.84E-03	0.253-0.341	6.76E-02	+
CW	F	0.208	-1.55E-03	0.143-0.272	-2.17E-02	=	0.194	5.17E-03	0.151-0.237	-3.52E-02	=
	M-NoAD	0.329	2.27E-04	0.251-0.407	9.94E-02	+	0.306	1.17E-02	0.268-0.344	7.64E-02	+
	M-AD	0.304	-2.19E-03	0.234-0.373	7.40E-02	+	0.307	-3.73E-03	0.246-0.367	7.71E-02	+

Variable abbreviations as in Fig. 1. Jackknife results calculated with untrimmed and trimmed sets of pseudovalues. *Resampled coefficient* is the unbiased coefficient is the first-order jackknife value. The observed coefficient is the value obtained with all specimens included. Sex, *F* females ($n=52$), *M-No.AD* non-adult males ($n=43$), *M-AD* adult males ($n=54$). *Bias* is the difference between the resampled and observed coefficients. The jackknife 99 % confidence interval is provided; allometric variables are those whose confidence interval excludes the expected value under isometry (0.229). *Growth trend* is the summary allometry of each variable presented in symbols: (=), isometry; (-), negative allometry; (+), positive allometry.

Table 4 Comparisons between multivariate and bivariate (OLS-SMA) analyses in *O. byronia*

Variable	Sex	<i>n</i>	MAC	OLS		SMA	
				<i>F</i> (1, <i>n</i> -2)	<i>p</i> value	<i>F</i> (1, <i>n</i> -2)	<i>p</i> value
CBL	F	52	0.983	2.442	0.124	4.903	0.031
	M-NoAD	43	0.917	3.553	0.067	5.761	0.021
	M-AD	54	0.654	0.076	0.784	5.010	0.030
PL	F	52	1.303	1.464	0.232	3.264	0.077
	M-NoAD	43	1.157	3.584	0.065	5.667	0.022
	M-AD	54	0.850	0.160	0.691	1.974	0.166
PW	F	52	0.945	0.363	0.549	3.660	0.061
	M-NoAD	43	1.140	0.016	0.901	0.778	0.383
	M-AD	54	1.162	0.001	0.973	3.417	0.070
ZW	F	52	0.953	0.001	0.977	0.540	0.466
	M-NoAD	43	0.908	1.145	0.291	2.501	0.121
	M-AD	54	1.132	0.000	0.990	2.347	0.132
UPCL	F	52	0.810	0.013	0.909	2.060	0.157
	M-NoAD	43	0.685	0.093	0.762	3.411	0.072
	M-AD	54	0.646	0.584	0.448	34.723	0.000
OCPH	F	52	0.605	0.340	0.562	3.261	0.077
	M-NoAD	43	0.649	0.593	0.446	2.692	0.108
	M-AD	54	0.858	0.032	0.859	6.873	0.011
BW	F	52	-0.007	0.665	0.419	108423	0.000
	M-NoAD	43	0.078	0.188	0.667	406.448	0.000
	M-AD	54	0.440	0.029	0.866	43.450	0.000
RL	F	52	1.306	0.072	0.789	1.452	0.234
	M-NoAD	43	1.235	1.116	0.297	2.865	0.098
	M-AD	54	0.671	0.187	0.667	17.013	0.000
LO	F	52	0.887	0.349	0.557	3.002	0.089
	M-NoAD	43	0.748	1.606	0.212	5.439	0.025
	M-AD	54	0.551	0.005	0.942	17.535	0.000
RH	F	52	0.815	0.094	0.761	5.342	0.025
	M-NoAD	43	0.861	0.001	0.970	0.846	0.363
	M-AD	54	1.081	0.100	0.753	4.037	0.050
MW	F	52	0.731	2.346	0.132	7.158	0.010
	M-NoAD	43	0.793	0.018	0.893	0.354	0.555
	M-AD	54	1.166	0.140	0.710	2.207	0.143
LAU	F	52	1.193	2.452	0.124	4.537	0.038
	M-NoAD	43	1.091	1.729	0.196	3.372	0.074
	M-AD	54	0.874	0.152	0.698	3.626	0.062
LD	F	52	1.248	2.010	0.162	3.938	0.053
	M-NoAD	43	1.178	4.356	0.043	6.596	0.014
	M-AD	54	0.908	0.246	0.622	3.305	0.075
HC	F	52	1.449	0.006	0.941	0.462	0.500
	M-NoAD	43	1.294	2.306	0.137	4.617	0.038
	M-AD	54	1.467	0.296	0.589	1.850	0.180
LC	F	52	1.476	0.058	0.810	3.272	0.076
	M-NoAD	43	1.397	0.275	0.603	2.558	0.117
	M-AD	54	1.339	0.181	0.673	7.069	0.010
HD	F	52	1.171	0.062	0.804	2.448	0.124
	M-NoAD	43	1.026	0.006	0.938	1.148	0.290

Table 4 (continued)

Variable	Sex	<i>n</i>	MAC	OLS		SMA	
				<i>F</i> (1, <i>n</i> -2)	<i>p</i> value	<i>F</i> (1, <i>n</i> -2)	<i>p</i> value
LPCL	M-AD	54	1.594	0.234	0.630	7.638	0.008
	F	52	0.704	0.214	0.646	3.458	0.069
	M-NoAD	43	0.625	1.223	0.275	5.099	0.029
RW	M-AD	54	0.827	0.036	0.849	10.752	0.002
	F	52	1.032	0.250	0.619	2.269	0.138
	M-NoAD	43	1.237	0.031	0.861	0.885	0.352
CW	M-AD	54	1.329	0.015	0.902	2.635	0.111
	F	52	0.869	0.944	0.336	10.254	0.002
	M-NoAD	43	1.368	1.733	0.195	8.022	0.007
	M-AD	54	1.371	0.002	0.964	5.329	0.025

Variable abbreviations as in Fig. 1

Sex: *F* females, *M-NoAD* non-adult males, *M-AD* adult males; *n* sample size, *MAC* multivariate allometry coefficient, *OLS* ordinary least squares, *SMA* standardized major axis

p values of *F* test between MAC and SMA and OLS slopes are given

production of secondary sexual characteristics (other than size) and sexual behaviors. In a comprehensive study, Brunner et al. (2004) have studied skull allometry of sea lions, during the initial growth phase in both sexes, identifying a secondary growth spurt (i.e. biphasic growth) in the late development of the male in all species considered, including *O. byronia*, accentuating size differences between sexes in adult stages. In this work, we detected such secondary growth spurt for some variables related to bite, as zygomatic and mastoid widths, dentary and occipital plate heights. For this reason, the cranial morphotype of non-adult males resembles that of females in several variables, including those related to muzzle, dentition and muscle insertions. This pattern is expected by the high sexual competition between adult males of this species, in which young subadult males tend to avoid clashes with adults (e.g. Campagna et al. 1988). Although in males we detected the expected strong shift or hypermorphosis for all the variables considered in this work (i.e. greater skull dimensions), some specific measurements exhibited notable changes in the trajectories of adult males, reaching shorter dimensions than expected by the skull size. Consequently, this secondary growth spurt (i.e. growth extension or hypermorphosis) is not necessarily accompanied by growth acceleration of all the cranial variables because some specific measurements (such as CBL, PL, RL, LAU and LD) tend to acquire lesser growth rates, relative to overall skull size, compared to the those obtained for females and non-adult males. Differences in allometric trends between non-adult and adult males suggest that although the skull continues to grow in adult males, in general variables related with longitudinal dimensions decrease their allometric coefficients, whereas those variables related with breadth or vertical dimensions increase these values. This

determines a growth pattern in adult males in which skull breadth and height are more important than longitudinal growth, relative to overall skull size. Such increasing of the allometric trends of these variables can be attributed to the biphasic growth pattern in characters implied in the development of the masticatory and neck musculature of adult males. The higher values of allometric coefficients were precisely observed in measurements related to bite and neck movements in males (e.g. MW, ZW, RW, OCPH, CW), highly important in fight during intra-sexual competition, when males acquire a fully erupted dentition and develop an evident sagittal crest.

Our study also shows that the allometric trends of females are different in several aspects from the growth pattern detected in non-adult males. For instance, variables related with skull length, such as CBL, PL, LO, LAU and LC showed higher growth rates relative to overall skull size, than in non-adult males. This rapid growth pattern indicates an earlier optimal performance of females compared with males of the same size, which is in concordance with the earlier maturation of otariid females in comparison with males. However, our data showed that there is a strong dimorphism in variables related with canine size (as the positive allometry of the rostrum and upper canine alveolus width detected in both non-adult and adult males, in contrast with the isometry of females). Such sexual differences are related with canine tooth eruption, a character strongly dimorphic in this species (e.g. Crespo 1984). Considering that just 5 out of 20 variables shared common growth trajectories between non-adult and adult males (i.e. slopes and intercepts), and that 11 out of 20 variables shared growth trajectories between females and non-adult males, it could be argued that the skull of *O. byronia* exhibits a

sexually differentiated pattern of growth in which adult males do not represent a scaled version of the non-adult morphotype. This suggests that sexual dimorphism is achieved not only by a linear male hypermorphosis, but also via differences in allometric growth (slopes).

As also evidenced by Brunner (1998) for other otariid species, our results indicated that growth pattern in neurocranial and splachnocranial components were in most cases different, being mostly negatively allometric in neurocranial variables, but isometric or positively allometric in splachnocranial variables. This is related to the importance of sensorial capsules during early stages of development and late growth cessation of most variables related to trophic functions. Comparative studies of skull growth in several mammal species (e.g. Moore and Lavelle 1974; Emerson and Bramble 1993) have demonstrated that growth of the braincase, orbital cavities and otic capsules follows a pattern similar to that of the nervous system, which develops mostly during prenatal and early postnatal life. Also, the detection of enantiometry (i.e. reduction of the absolute size during growth) in the POC in both sexes suggests a complex way of growth in different regions of the braincase. Enantiometry is not commonly detected in morphometric studies, but it was also registered in the braincase growth of some primates (Corner and Richtsmeier 1991). This fact could be associated with the generation of extra space to accommodate temporal muscles, besides the growth of the zygomatic breadth. In adult males of *O. byronia*, the orbit size (as all variables) exceed that of females. However, in relation to overall skull size they are proportionally smaller adult males. Indeed, the allometric trends (both analyses) indicated that female orbits grow isometrically respect to overall skull size, whereas in males (non-adult and adult stages) their growth was negatively allometric. Berg and Pyenson (2008) have linked bony orbit size, a proxy for eye size, to pinniped diving capacity, detecting an increasing orbit size among all species with increasing skull size, although with negative allometric relationships, such that larger skulls, on average, have proportionately smaller eyes. Although the authors made an inter-specific approach, it is also in agreement with our intra-specific comparisons in the South American sea lion, as male adults dive deeper than females (e.g. Campagna et al. 2001) but diving capacity could also be determined by other variables, such as body size.

The length of the functional mandibular postcanine tooth row corresponds closely with that of the maxillary row. In order to achieve and preserve the occlusal relationships between upper and lower dental rows there must be a high degree of coordination between the rates of growth of upper and lower complex (Moore 1981), which is also demonstrated by the functionally coordinated trends in both analyses (Tables 2 and 3). This feature contributes to feeding as postcanine teeth which are specialized for diets of fish,

crustaceans and cephalopods from early age stages (note the negative allometric growth trends of both sexes). In otariids, there is an interval in which juvenile forage without fully developed canines, reflecting the importance of the postcanines at such early age stages (Brunner et al. 2004).

Overall, we propose the use of a composite independent variable in future allometric studies of *O. byronia* that employ bivariate regressions. The absence of isometry in CBL detected in both allometric approaches, as well as in previous multivariate analyses (e.g. Brunner et al. 2004), supports the idea that this measurement alone cannot be easily used as the independent variable, at least in this species. Further research of cranial ontogeny and dimorphism in related pinnipeds species is still required. Comparisons of ontogenetic trends in different age stages and sex would allow recognizing evolutionary patterns reflected in growth modes. Then, relating morphometric patterns with chronological age would provide much-needed information on ageing seals using non-invasive techniques. Finally, geographical variations of growth in other populations of *O. byronia* (as those inhabiting the Pacific Ocean) may provide better descriptions regarding the extent of inter-population variation in growth related with ecological parameters.

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Appendix I

Specimens examined in this study. CBL, condylo-basal length (millimetres). GM, geometric mean. Institution acronyms: CFA, Colección Fundación Félix de Azara (Buenos Aires, Argentina); CNP, Centro Nacional Patagónico (Puerto Madryn, Argentina); GEMARS, Grupo de Estudos de Mamíferos Marinhos (Porto Alegre, Brazil); LAMAMA, Laboratorio de Mamíferos Marinos of the Centro Nacional Patagónico (Puerto Madryn, Argentina); MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia (Buenos Aires, Argentina); MCN, Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (Porto Alegre, Brazil); MLP, Museo La Plata (La Plata, Argentina); MMPMa, Museo Municipal Lorenzo Scaglia

(Mar del Plata, Argentina); RNP, Museo Acatashun de Aves y Mamíferos Marinos Australes (Ushuaia, Argentina); UFSC, Universidade Federal de Santa Catarina (Florianópolis, Brazil); ZOO-BA-M, Osteological mammal collection, Zoológico de Buenos Aires (Buenos Aires, Argentina). Sex: F, female; M, male. Age: J, juvenile; SA, subadult; AD, adult.

Collection number	Sex	Age class	CBL.	GM.
LAMAMA 141	F	J	139.4	43.6
LAMAMA 140	F	J	141.1	44.907
LAMAMA 331	F	J	152.6	46.385
MACN 23574	F	J	154.7	47.347
MACN 21740	F	J	168.4	49.517
MLP 26.IV.00.5	F	J	179.7	56.044
MACN 21739	F	J	179.7	51.302
LAMAMA 620	F	J	187	53.146
LAMAMA 484	F	SA	197.2	56.318
LAMAMA 144	F	SA	200.6	58.386
LAMAMA 556	F	SA	202.3	59.086
LAMAMA 237	F	SA	211.5	62.32
LAMAMA 686	F	SA	218.9	60.962
LAMAMA 623	F	AD	225.6	63.69
LAMAMA 604	F	AD	227.6	67.045
LAMAMA 417	F	AD	230.7	67.534
LAMAMA 147	F	AD	233.8	66.394
LAMAMA 505	F	AD	234	66.752
RNP 2319	F	AD	234.8	69.914
RNP 21737	F	AD	236.6	70.601
LAMAMA 243	F	AD	237.7	69.85
MLP 7.VII.50.1	F	AD	238.1	69.205
LAMAMA 555	F	AD	239.3	68.555
LAMAMA 033	F	AD	240.7	71.171
LAMAMA 444	F	AD	243.8	72.14
LAMAMA 127	F	AD	244	68.903
MACN 21738	F	AD	244.9	69.854
LAMAMA 253	F	AD	246.5	69.894
LAMAMA 588	F	AD	247.2	69.84
LAMAMA 024	F	AD	247.3	71.323
MLP 1531	F	AD	250.9	70.934
MACN 25138	F	AD	251.7	76.159
MACN 20573	F	AD	252.2	72.833
MLP 1060	F	AD	252.6	75.909
LAMAMA 303	F	AD	253	74.462
LAMAMA 61	F	AD	253.4	75.435
LAMAMA 616	F	AD	254.4	75.287
LAMAMA 590	F	AD	255.2	74.326
LAMAMA 578	F	AD	255.3	73.841
LAMAMA 026	F	AD	257.3	75.924
LAMAMA 385	F	AD	259.6	78.256
MACN 20578	F	AD	265.5	81.179
GEMARS 565	F	AD	266	81.854
LAMAMA 453	F	AD	267.6	79.19
LAMAMA 029	F	AD	269.6	79.762
MACN 22853	F	AD	270.6	80.551
MLP 27.X.97.14	F	AD	272.3	79.272
RNP 2364	F	AD	273.3	79.679
MACN 13.11	F	AD	277.5	87.042
RNP 2416	F	AD	277.9	80.588
MLP 41	F	AD	278.3	82.29
GEMARS 1323	F	AD	292.7	85.486
LAMAMA 139	M	J	140.4	41.89
LAMAMA 142	M	J	150.4	44.598
LAMAMA 569	M	J	162.7	47.948
MACN 24731	M	J	164.4	51.513
MACN 30236	M	J	168	47.073
LAMAMA115	M	J	174.8	49.69
LAMAMA 134	M	J	187.1	52.584
LAMAMA 329	M	J	192	54.157
LAMAMA 606	M	SA	199	58.362
LAMAMA 053	M	SA	207.8	60.208
MACN 21744	M	SA	210.5	59.437
GEMARS 813	M	SA	212.3	58.625
LAMAMA 371	M	SA	213.5	59.644
MLP 26.IV.00.6	M	SA	229.5	65.155
LAMAMA 427	M	SA	233.1	64.491
LAMAMA 629	M	SA	239	68.895
MLP 8.X.01.8	M	SA	244	68.804
LAMAMA 031	M	SA	247.2	73.388
MACN 50.52	M	SA	247.7	70.585
MLP 26.IV.00.8	M	SA	250.9	71.011
UFSC 1341	M	SA	252.6	76.82
MACN 22608	M	SA	257.2	75.157
LAMAMA 605	M	SA	258.3	76.259
LAMAMA 487	M	SA	260	75.972
MACN 21743	M	SA	260.2	77.821
GEMARS 343	M	SA	260.8	76.985
LAMAMA 270	M	SA	262.8	76.441
MMPMa 4086	M	SA	268	83.315
GEMARS 967	M	SA	269.3	82.048
MLP 475	M	SA	269.6	77.904
GEMARS 799	M	SA	270.5	80.839
MLP 453	M	SA	273.3	82.869
LAMAMA 105	M	SA	274.2	77.9
GEMARS 196	M	SA	274.7	82.966
LAMAMA 43	M	SA	275.5	82.886
MACN 22609	M	SA	280.8	87.338
GEMARS822	M	SA	283.8	87.184
GEMARS 229	M	SA	285.9	91.019
GEMARS 812	M	SA	290.5	86.742
LAMAMA 032	M	SA	291.1	88.839

Collection number	Sex	Age class	CBL.	GM.
MACN 20420	M	SA	292.3	87.933
MACN 22852	M	SA	293.1	88.296
LAMAMA 419	M	SA	293.8	87.269
LAMAMA 337	M	AD	294.8	92.279
RNP 2068	M	AD	294.9	88.794
RNP 2396	M	AD	296.5	91.055
MLP 14.IV.48.9	M	AD	296.8	89.394
GEMARS 659	M	AD	300.9	92.967
GEMARS 434	M	AD	307.2	97.373
LAMAMA 60	M	AD	307.8	99.917
RNP 2477	M	AD	309.3	96.113
LAMAMA 152	M	AD	311.2	102.499
MLP 1532	M	AD	314.9	98.629
LAMAMA 030	M	AD	318.4	102.939
LAMAMA 151	M	AD	319.2	100.067
LAMAMA 027	M	AD	320.5	99.485
LAMAMA 213	M	AD	322	103.855
LAMAMA 245	M	AD	322	99.485
MMPMa 4013	M	AD	324	107.393
LAMAMA 028	M	AD	324	107.737
RNP 2371	M	AD	325	101.78
LAMAMA 022	M	AD	325	113.826
RNP 2683	M	AD	327	106.535
MLP 1526	M	AD	330	105.642
RNP 2464	M	AD	330	108.157
RNP 2475	M	AD	330	100.019
RNP 2457	M	AD	330	102.171
LAMAMA 155	M	AD	330	108.727
LAMAMA 244	M	AD	330	108.945
LAMAMA 492	M	AD	330	110.249
LAMAMA 479	M	AD	333	116.955
MACN 22851	M	AD	335	106.888
MACN 27.27	M	AD	335	102.864
ZOO-BA-M-15	M	AD	335	104.986
RNP 2072	M	AD	335	101.775
RNP 2395	M	AD	335	104.437
GEMARS 428	M	AD	340	115.926
LAMAMA 490	M	AD	340	117.731
MACN 21984	M	AD	341	110.283
MACN 21994	M	AD	343	108.668
GEMARS 171	M	AD	345	116.387
RNP 2456	M	AD	345	113.455
MACN 23.26	M	AD	350	117.671
RNP 2633	M	AD	350	111.505
RNP 2467	M	AD	350	117.261
LAMAMA 025	M	AD	350	110.91
LAMAMA 250	M	AD	350	113.498
LAMAMA 353	M	AD	350	118.937
MACN 25168	M	AD	355	114.984

Collection number	Sex	Age class	CBL.	GM.
RNP 2468	M	AD	355	116.355
RNP 2365	M	AD	359	103.024
MLP 1330	M	AD	360	114.998
MLP 26.IV.00.10	M	AD	360	121.887
RNP 2635	M	AD	368	118.265
MLP 26.XII.02.36	M	AD	370	118.717
LAMAMA 199	M	AD	370	121.907
MLP 1332	M	AD	375	121.16

References

- Abdala F, Flores DA, Giannini NP (2001) Postweaning ontogeny of the skull of *Didelphis albiventris*. *J Mammal* 82(1):190–200. doi:10.1644/1545-1542
- Alexander RM (1985) Body support, scaling and allometry. In: Hildebrand M, Wake DB (eds) *Functional vertebrate morphology*. Belknap Press of Harvard University Press, Cambridge, pp 27–37
- Badyaev AV (2002) Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. *Trends Ecol Evol* 17:369–378. doi:10.1016/S0169-5347
- Badyaev AV, Hill GE, Whittingham LA (2001) The evolution of sexual size dimorphism in the house finch: IV. Population divergence in ontogeny of dimorphism. *Evolution* 55:2534–2549
- Brunner S, Bryden M, Shaughnessy PD (2004) Cranial ontogeny of otariid seals. *Syst Biodivers* 2(1):83–110. doi:10.1017/S1477200004001367
- Brunner S (1998) Skull development and growth in the southern fur seals *Arctocephalus forsteri* and *A. pillosus* (Carnivora:Otariidae). *Aust J Zool* 46:43–66. doi:10.1071/ZO97019
- Bryden MM (1968) Control of growth in two populations of elephant seals. *Nature (Lond)* 217:1106–1108. doi:10.1038/2171106a0
- Bryden MM (1972) Growth and development of marine mammals. In: Harrison RJ (ed) *Functional anatomy of marine mammals*. Academic press, London, pp. 1–79
- Berg LM, Pyenson ND (2008) Osteological correlates and phylogenetic analysis of deep diving in living and extinct pinnipeds: what good are big eyeballs? *J Vertebr Paleontol* 28(Suppl):51A
- Campagna C, Le Boeuf BJ, Cappelozzo HL (1988) Group raids: a mating strategy of male southern sea lions. *Behav* 105:224–249
- Campagna C, Werner R, Karesh W, Martin AR, Koontz F, Cook R, Koontz C (2001) Movements and location at sea of South American sea lions (*Otaria flavescens*). *J Zool* 257:205–220
- Cassini GH, Flores DA, Vizcaino SF (2012) Postnatal ontogenetic scaling of Nesodontine (Notoungulata, Toxodontidae) cranial morphology. *Acta Zool* 93(3):249–259
- Cappelozzo HL, Campagna C, Monserrat J (1991) Sexual dimorphism in newborn southern sea lions. *Mar Mamm Sci* 7:385–394. doi:10.1111/j.1748-7692.1991.tb00113.x
- Cheverud JM, Wilson P, Dittus WPJ (1992) Primate population studies at Polonnaruwa. III. Somatometric growth in a natural population of toque macaques (*Macaca sinica*). *J Hum Evol* 23:51–77
- Chiasson RB (1957) The dentition of the Alaskan fur seal. *J Mammal* 38:310–319
- Clinton WL (1994) Sexual selection and growth in male northern elephant seals. In: Le Boeuf BJ, Laws RM (eds) *Elephant seals: population ecology, behaviour, and physiology*. University of California Press, London, pp 154–168

- Cock A (1966) Genetical aspects of metrical growth and form in animals. *Quart Rev Biol* 41:131–190
- Corner BD, Richtsmeier JT (1991) Morphometric analysis of craniofacial growth in *Cebus apella*. *Am J Phys Anthropol* 84:323–342. doi:10.1002/ajpa.1330840308
- Crespo EA (1984) Dimorfismo sexual en los dientes caninos y en los cráneos del lobo marino del sur, *Otaria flavescens* (Shaw) (Pinnipedia, Otariidae). *Rev Mus Argent Cienc Nat Bernardino Rivadavia* 25(8):245–254
- Drehmer CJ, Ferigolo J (1997) Osteologia craniana comparada entre *Arctocephalus australis* e *Arctocephalus tropicalis* (Pinnipedia, Otariidae). *Iheringia Ser Zool* 83:137–149
- Emerson SB, Bramble DM (1993) Scaling, allometry and skull design. In: Hanken J, Hall BK (eds) *The skull*. The University of Chicago Press, Chicago, pp 384–416
- Flores DA, Giannini NP, Abdala F (2006) Comparative postnatal ontogeny of the skull in an Australidelphian Metatherian, *Dasyurus albopunctatus* (Marsupialia: Dasyuromorpha: Dasyuridae). *J Morphol* 267:426–440. doi:10.1002/jmor.10420
- Flores DA, Giannini NP, Abdala F (2003) Cranial ontogeny on *Lutro-lina crassicaudata* (Didelphidae): a comparison with *Didelphis albiventris*. *Acta Theriol* 48(1):1–9. doi:10.1007/BF03194261
- Flores DA, Abdala F, Giannini NP (2010) Cranial ontogeny of *Caluromys philander* (Didelphidae, Caluromyinae): a qualitative and quantitative approach. *J Mammal* 91:539–550. doi:10.1644/09-MAMM-A-291.1
- Flores D, Casinos A (2011) Cranial ontogeny and sexual dimorphism in two new world monkeys: *Alouatta caraya* (Atelidae) and *Cebus apella* (Cebidae). *J Morphol* 272:744–757. doi:10.1002/jmor.10947
- Giannini N, Abdala F, Flores D (2004) Comparative postnatal ontogeny of the skull in *Dromiciops gliroides* (Marsupialia: Microbiotheriidae). *Am Mus Novit* 3460:1–17
- Giannini NP, Segura V, Giannini MI, Flores D (2010) A quantitative approach to the cranial ontogeny of the puma. *Mamm Biol* 75(6):547–554. doi:10.1016/j.mambio.2009.08.001
- Gould SJ (1966) Allometry and size in ontogeny and phylogeny. *Biol Rev* 41:587–638. doi:10.1111/j.1469-185X.1966.tb01624.x
- Hamilton JE (1934) The southern sea lion *Otaria byronia* (De Blainville). *Discovery Rep* 19:121–164
- Huxley JS, Teissier G (1936) Terminology of relative growth. *Nature* 137:780–781
- Isaac JL (2005) Potential causes and life-history consequences of sexual size dimorphism in mammals. *Mammal Rev* 35:101–115. doi:10.1111/j.1365-2907.2005.00045.x
- Janis CM (1990) Correlation of cranial and dental variables with body size in ungulates and macropodoids. In: Damuth J, MacFadden BJ (eds) *Body size in mammalian paleobiology: estimation and biological implications*. Cambridge University Press, Cambridge, pp 255–300
- Jefferson TA, Webber MA, Pitman RL (2008) *Marine mammals of the world: a comprehensive guide to their identification*. Academic Press, Elsevier
- Jolicoeur P (1963) The multivariate generalization of the allometry equation. *Biometrics* 19:497–499
- Jones KE, Goswami A (2010) Quantitative analysis of the influences of phylogeny and ecology on phocid and otariid pinniped (Mammalia; Carnivora) cranial morphology. *J Zool* 280:297–308. doi:10.1111/j.1469-7998.2009.00662.x
- Jungers WL, German RZ (1981) Ontogenetic and interspecific skeletal allometry in nonhuman primates: bivariate versus multivariate analysis. *Am J Phys Anthropol* 55:195–202. doi:10.1002/ajpa.1330550206
- King JE (1972) Observations on phocid skulls. In: Harrison RJ (ed) *Functional anatomy of marine mammals*. Academic Press, London, pp 81–115
- Klingenberg CP (1996) Multivariate allometry. In: Marcus LF, Corti M, Loy A, Slice D, Naylor G (eds) *Advances in morphometrics*. Plenum Press, New York, pp 23–48
- Kunz TH, Robson SK (1995) Postnatal growth and development in the Mexican free-tailed bat (*Tadarida brasiliensis mexicana*): birth size, growth rates, and age estimation. *J Mammal* 76(3):769–783
- Laird AK (1965) Dynamics of relative growth. *Growth* 29:249–263
- Leigh SR (1992) Patterns of variation in the ontogeny of primate body size dimorphism. *J Hum Evol* 23:2750. doi:10.1016/0047-2484(92)90042-8
- Lindenfors P, Tullberg BS, Biuw M (2002) Phylogenetic analyses of sexual selection and sexual size dimorphism in pinnipeds. *Behav Ecol Sociobiol* 52:188–193. doi:10.1007/s00265-002-0507-x
- Manly BFJ (1997) *Randomization, bootstrap, and Monte Carlo methods in biology*, 2nd edn. Chapman & Hall, London
- Maunz M, German RZ (1996) Craniofacial heterochrony and sexual dimorphism in the shorttailed opossum (*Monodelphis domestica*). *J Mammal* 77:992–1005
- McLaren IA (1993) Growth in pinnipeds. *Biol Rev* 68:1–79. doi:10.1111/j.1469-185X.1993.tb00731.x
- Meachen-Samuels J, Van Valkenburgh B (2009) Craniodental indicators of prey size preference in the Felidae. *Biol J Linn Soc* 96:784–799. doi:10.1111/j.1095-8312.2008.01169.x
- Molina-Schiller DM (2000) Age and cranial development of *Arctocephalus australis* in the coast of Rio Grande do Sul, Brazil. Master thesis. FURG
- Moore WJ (1981) *The mammalian skull*. Cambridge University Press, Cambridge
- Moore WJ, Lavelle CV (1974) *Growth of the facial skeleton in the hominoidea*. Academic Press, London
- Mosimann JE (1970) Size allometry: size and shape variables with characterization of log-normal and generalized gamma distributions. *J Am Stat Assoc* 65:930–948
- Nelson TW, Shump KA Jr (1978) Cranial variation in size allometry in *Agouti paca* from Ecuador. *J Mammal* 59:387–394
- Payne MR (1979) Growth in the Antarctic fur seal *Arctocephalus gazella*. *J Zool (Lond)* 187:1–20. doi:10.1111/j.1469-7998.1979.tb07709.x
- Peters TA (1993) The history and development of transaction log analysis. *Library Hi Tech* 11(2):41–66
- Prestrud P, Nilssen K (1995) Growth, size, and sexual dimorphism in arctic foxes. *J Mammal* 76:522–530
- Quenouille MH (1956) Notes on bias in estimation. *Biometrika* 43:353–360
- Radinsky LB (1981) Evolution of skull shape in carnivores. I. Representative modern carnivores. *Biol J Linn Soc* 15:369–388. doi:10.1111/j.1095-8312.1981.tb00770.x
- R Development Core Team (2009) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria
- Reyes LM, Crespo EA, Szapkievich V (1999) Distribution and population size of the southern sea lion (*Otaria flavescens*) in Central and Southern Chubut, Patagonia, Argentina. *Mar Mamm Sci* 15:478–493. doi:10.1111/j.1748-7692.1999.tb00814.x
- Rosas FCW, Haimovici M, Pinedo MC (1993) Age and growth of the South American sea lion, *Otaria flavescens* (Shaw, 1800), in Southern Brazil. *J Mammal* 74(1):141–147
- Sanfelice D, de Freitas RO (2008) A comparative description of dimorphism in skull ontogeny of *Arctocephalus australis*, *Callorhinus ursinus* and *Otaria byronia*. *J Mammal* 89(2):336–346. doi:10.1644/07-MAMM-A-344.1
- Segura V, Prevosti F (2012) A quantitative approach to the cranial ontogeny of *Lycalopex culpaeus* (Carnivora: Canidae). *Zoomorphology* 131(1):79–92. doi:10.1007/s00435-012-0145-4
- Simpson GG, Roe A, Lewontin RC (1960) *Quantitative zoology*. Harcourt, Brace and World Inc., New York
- Sivertsen E (1954) A survey of the eared seals (family Otariidae) with remarks on the Antarctic seals collected by M/K

- “Norvegia” in 1928–1929. Det Norske Videnskaps-Akademi 36:1–76
- Smith RJ (1981) On the definition of variables in studies of primate allometry. *Am J Phys Anthropol* 55:323–329
- Stern AA, Kunz TH (1998) Intraspecific variation in postnatal growth in the greater spear-nosed bat. *J Mammal* 79:755–763
- Tanner JB, Zelditch M, Lundrigan B, Holekamp K (2010) Ontogenetic change in skull morphology and mechanical advantage in the spotted hyena (*Crocuta crocuta*). *J Morphol* 271:353–365. doi:10.1002/jmor.10802
- Trillmich F (1996) Parental investment in pinnipeds. In: Rosenblatt JS, Snowdon CT (eds) *Parental Care: evolution, mechanisms, and adaptative significance*. Academic Press, London, pp. 533–577
- Warton DI, Weber NC (2002) Common slope tests for bivariate structural relationships. *Biometrical J* 44:161–174. doi:10.1002/1521-4036(200203)44:2<161::AID-BIMJ161>3.0.CO;2-N
- Warton DI, Wright IJ, Falster DS, Westoby M (2006) Bivariate line-fitting methods for allometry. *Biol Rev Camb Philos Soc* 81:259–291. doi:10.1017/S1464793106007007
- Wayne RK (1986) Cranial morphology of domestic and wild canids: the influence of development on morphological change. *Evolution* 40:243–261
- Weckerly FW (1998) Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *J Mammal* 79:33–52
- Zelditch ML, Sheets HD, Fink WL (2003) The ontogenetic dynamics of shape disparity. *Paleobiology* 29:139–156. doi:10.1666/0094-8373(2003)029<0139:TODOSD>2.0.CO;2