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## Allometry of the Postnatal Cranial Ontogeny and Sexual Dimorphism in *Otaria flavescens* (Otariidae)

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<b>Abstract:</b>	<p>We analyzed the cranial postnatal ontogeny of <i>Otaria flavescens</i> in order to detect sexual dimorphism in allometric terms, analyzing the rate of growth of functional components linked to specific capacities as mastication and head movements. We used 20 linear measurements to estimate allometric growth applying bivariate and multivariate analyses. The comparison of employed techniques detect and empirical relationship between our multivariate results and the ordinary least square bivariate analysis. The quantitative analyses reveal different patterns of growth in both sexes, detecting a dissociation of neurocranial and splachnocranial components. The skull growth is not conservative in <i>O. flavescens</i>. In general, females exhibit allometric coefficients higher than males, but males exhibit extension of the offset in growth trajectory. However, coefficients of variables associated to bite and sexual competence are higher in males. In general terms, the neurocranium exhibit little uniformity in its growth, as sexual dimorphism in the orbit was detected, being isometric in females and negatively allometric in males. In addition, we observed enantiometry of the postorbital constriction in both sexes, being the remaining variables associated to the braincase negatively allometric. Such patterns are in partial agreement with changes previously reported for this species and other species in the family.</p>
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**Allometry of the Postnatal Cranial Ontogeny and Sexual Dimorphism in *Otaria  
flavescens* (Otariidae)**

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**Short title**

Sea Lion cranial allometry

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**Abstract** We analyzed the cranial postnatal ontogeny of *Otaria flavescens* in order to detect sexual dimorphism in allometric terms, analyzing the rate of growth of functional components linked to specific capacities as mastication and head movements. We used 20 linear measurements to estimate allometric growth applying bivariate and multivariate analyses. The comparison of employed techniques detect and empirical relationship between our multivariate results and the ordinary least square bivariate analysis. The quantitative analyses reveal different patterns of growth in both sexes, detecting a dissociation of neurocranial and splachnocranial components. The skull growth is not conservative in *O. flavescens*. In general, females exhibit allometric coefficients higher than males, but males exhibit extension of the offset in growth trajectory. However, coefficients of variables associated to bite and sexual competence are higher in males. In general terms, the neurocranium exhibit little uniformity in its growth, as sexual dimorphism in the orbit was detected, being isometric in females and negatively allometric in males. In addition, we observed enantiometry of the postorbital constriction in both sexes, being the remaining variables associated to the braincase negatively allometric. Such patterns are in partial agreement with changes previously reported for this species and other species in the family.

### **Keywords**

Pinnipedia; South American sea lion; skull; growth rates; morphometry.

## Introduction

The South American sea lion, *Otaria flavescens*, inhabits on the coasts of Chile, Peru, Uruguay, Argentine 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 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 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. flavescens* is still unknown in several aspects.

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 methodological approaches, bivariate and multivariate allometry. In view of the high sexual dimorphism in adult, we expect that both sexes would exhibit differences in the mode of postnatal cranial ontogeny as well as in the ways in which they reach adult form. Previous studies employing different approaches (e.g. Hamilton 1934; Cappozzo *et al.* 1991; Rosas *et al.* 1993; Brunner *et al.* 2004; Sanfelice and Freitas 2008) have also provided relevant information on sexual dimorphism and age-related changes in *O. flavescens*, allowing comparisons with our results. In this way, this work contributes to a growing number of studies regarding growth and dimorphism in pinnipeds.

## Materials and methods

### Study specimens

*O. flavescens* is a species well represented by complete ontogenetic series deposited in mammal collections. We analyzed 149 skulls of *O. flavescens* (52 females, 97 males; Appendix I). In our sample, 16 specimens (8 females; 8 males) were juveniles with not fully adult permanent dentition. In the smallest specimen (female LAMAMA OF141, condylo-basal length –LCB– 139.4 mm; and 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 includes 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. The total sample analyzed was taxonomically uniform, consisting of specimens coming from populations genetically uniform (i.e. specimens coming from the Atlantic Ocean, mostly from argentine coasts). Therefore, the effects of ecogeographic variations were mostly avoided.

### Study of growth and measurements

Allometry of growth explicitly considers timing of changes throughout the life of an individual (Kunz *et al.* 1995; Prestrud and Nilssen 1995; Maunz and German 1996; Stern *et al.* 1998). By contrast, allometry of size

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5 compares changes against overall size along a growth series. The time frame is implicitly incorporated (size  
6 proxy) but not specified to describe relative modifications in structures as the animal grows.  
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9 For the allometric analysis, we used 20 cranial and mandibular variables (Fig. 1) including length, width, and  
10 height of neurocranial (e.g. braincase, orbit) and splanchnocranial components (e.g. jaw length, tooth row  
11 length). The cranial dimensions analyzed herein partially overlap with those considered in other  
12 morphometric studies of carnivore skulls (e.g. Radinsky 1981; Molina-Schiller 2000; Brunner *et al.* 2004;  
13 Giannini *et al.* 2010; Tanner *et al.* 2010; Segura and Prevosti 2012), which allows efficient comparisons with  
14 other pinnipeds and carnivores in general.  
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21 Two analytical techniques were used to describe and analyze ontogeny: bivariate regressions and  
22 multivariate allometry. Both techniques were applied for each sex in order to analyze the sexual dimorphism  
23 of growth in *O. flavescens*.  
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### 30 *Bivariate approach*

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32 In this analysis the scaling of any measurement can be affected strongly by the choice of the independent  
33 variable (Smith 1981; Wayne 1986). In most of previous studies (e.g. Abdala *et al.* 2001; Flores *et al.* 2003;  
34 Giannini *et al.* 2004) researchers have taken the total length of the skull as a proxy of size and as independent  
35 variable, because they demonstrated that it is isometric (see Janis 1990 and Cassini *et al.* 2012 for ungulates;  
36 Abdala *et al.* 2001 and Flores *et al.* 2003 for didelphid marsupials; Flores and Casinos 2011 for primates).  
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38 Because we found the total length of the skull is not isometric in both sexes (see results), we used the  
39 geometric mean as independent variable and proxy of size (e.g. Mosimann 1970; Meachen-Samuels and Van  
40 Valkenburgh, 2009). The geometric mean is a size variable derived from the  $N$ th root of the product of  $N$   
41 measurements, being a good predictor of individual size and growing linearly as the skull measurements.  
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43 Therefore, the relationship between the two variables was isometric when the slope is equal to one (value  
44 expected under geometric similarity between two variables that grows linearly; Peters 1993). The relation of  
45 each variable to overall size (geometric mean) was examined with the equation of allometry:  $\log(y) = \log b_0$   
46  $+ b_1 \log(x) + \log(e)$ ; where  $y$  is any of the measured skull variables,  $a = \log(b_0)$  is the y-intercept or constant  
47 of normalization (and  $b_0$  is the constant term of power growth function),  $b_1$  is the slope of the line or  
48 coefficient of allometry,  $x$  is the geometric mean, and  $e$  is the error term (Alexander 1985). The Standardized  
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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 for dealing with allometric approaches (for extensive overviews on the subject, see Warton *et al.* 2006).

In a first step, significance of allometry coefficients was evaluated by means of two-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 perform *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).

Testing for common allometric coefficient (slope) amongst two sexes lines was the second step in our analyses. In doing so, we follow the recommendations of Warton *et al.* (2006) using a likelihood ratio test for common SMA slope, and comparing it to a chi-squared distribution (Warton and Weber 2002). Then, if a common slope was shared (absence of sexual dimorphism in slope), we compare 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 has received some attention in the literature. Finally, if both slope and y-intercepts were shared by both sexes, then the data points are 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 *smatr* package of R software (Warton and Weber 2002).

#### *Multivariate approach*

It 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 results). 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 allows 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). Briefly (see Giannini *et al.* 2004 for details), 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 pseudovalues. Trimming the largest and smallest pseudovalues for each variable significantly decreased the standard deviations. Herein, we report 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 2008), and the script is available from the author (Giannini *et al.* 2010).

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interpreted the bivariate coefficients of allometry as growth rates, although they actually represent rates of size increase (Simpson *et al.* 1960; Gould 1966; Nelson *et al.* 1978). Thus, we ultimately assumed that intraspecific allometry of size closely reflects true allometry of growth. On the contrary, some authors stated that allometric coefficients derived from principal components of skeletal measurements in a multivariate approach can not be interpreted as growth rates (Jungers and Germans 1981). However, Klingenberg (1996) states that multiplying PC1 coefficients by the square root of  $p$  yields values (multivariate allometry 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 expect that the MAC did not differ significantly with the BAC obtained by means of OLS regression method.

## Results

### Bivariate analysis

Regressions for *O. flavescens* (Table 1) showed high values of correlation in all dependent variables, except in breadth of the braincase ( $R^2=0.108$  in females and  $0.041$  in males) and postorbital constriction ( $R^2=0.451$  in females and  $4.11e-07$  in males). In the SMA analysis, both females and males shared most of the ontogenetic trends. However, only four out 20 variables showed a common slope for both sexes. The observed allometric trend was positive in both sexes for eight variables: palatal length (PL), rostral length and width (RL, RW), load arm length at upper canine (upper out-lever, LAU), and most of mandible measurements (LD, HC, LC and HD, Table 1). In contrast, slopes for upper and lower postcanine tooth row length (UPCL, LPCL), occipital plate high (OCPH) and braincase width (BW) showed negative allometric trends in both sexes. When both sexes were pooled together, no variable showed isometry. The comparison of slopes and intercepts for males and females (Table 1) shows that both groups exhibit divergent patterns of cranial growth. For instance, although four out of 20 variables shared slope values, only half of them, rostral and coronoid height (RH, HC), showed agreement also among intercepts of the trajectories described in both sexes. Nevertheless, both variables showed an extension of the ontogenetic offset in males. The remaining two variables showed significant sexual differences in its intercepts, being statistically higher in females for HC, but higher in males for PW (Table 1; Fig. 2b).

In general, the differences in slope values (i.e. coefficients of allometry or growth rates; Fig. 2a) indicate that those were higher for females than those observed for males in condylo-basal length (CBL),

length of orbit (LO), braincase width (BW) and some characters of the muzzle, such as palatal length (PL), rostral length (RL), length of upper and lower postcanine rows (UPCL, LPCL), load arm length at upper canine (LAU), and mandible and coronoid lengths (LD, LC). On the other hand, males showed higher slopes for mastoid, zygomatic and rostral widths (MW, ZW, RW), height of the occipital plate (OCPH), and alveolus width of upper canine teeth (CW). It is also remarkable that the postorbital constriction (POC) showed enantiometry (*sensu* Huxley and Teissier 1936) in both sexes, instead the typical negative allometry (as most neurocranial components in Mammals, Emerson and Bramble 1993).

### Multivariate analysis

The mean difference in the absolute bias favors untrimmed over trimmed analysis in both sexes, with a 0.0004 average absolute bias for the former and 0.0014 for the latter in males (3.697 times higher), whereas in females the values were 0.0009 and 0.0018 respectively (2.017 times higher).

As in the bivariate analysis, the multivariate analysis showed that several cranial variables (11 out of 19 included in this analysis) shared the same ontogenetic trend in both sexes. Six cranial variables scaled with negative allometry (ZW, OCPH, LPCL, OCPH, BW, and RH), the palatal length as well as three mandibular characters (LD, HC, and LC) were positively allometric and the palatal width was isometric in both females and males.

In the remaining eight variables, males and females showed different ontogenetic trends (Table 2). In males there was no significant departure from isometry for mastoid width, rostral length and load arm for upper canine, whereas in females these variables scaled with positive (RL, LAU) and negative allometry (MW). Finally, the other five variables were isometric in females but showed allometry in males as development progressed.

Comparing our results of bivariate and multivariate allometry, we found 12 out of 19 agreements in the ontogenetic trends (i.e. CBL, PL, UPCL, OCPH, BW, LO, MW, LD, HC, LC, LPCL, and CW; Tables 1-2). From the remaining seven variables that showed different trends in both approaches, only one (ZW) occurred

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5 in both sexes, three differences were detected only in males (PW, RL and LAU) and three in females (RH,  
6 HD and RW).  
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## 10 11 12 13 **Discussion**

### 14 15 **Quantitative Methods**

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19 Bivariate coefficients of allometry can be extremely useful because they are less affected by sample  
20 completeness (Giannini *et al.* 2004) and are more directly interpretable in terms of size-dependent functional  
21 relationships (Jungers and German 1981). In addition, bivariate coefficients can be derived from simple  
22 growth models of each measurement (Laird 1965; Wayne 1986). However, this technique implies a condition  
23 of isometry of the commonly considered independent variable (condylo-basal length), which does not  
24 necessarily occur (as in our case; see results above). Therefore, a multivariate approach seemed to be more  
25 independent of such conditions, because size is considered as a latent variable affecting all variables  
26 simultaneously (e.g. Flores *et al.* 2006). The geometric mean used as independent variable for the bivariate  
27 approach (see methods), provides relevant information that could not be obtained by multivariate analyses,  
28 such as significant differences between sexes in slopes and intercepts as well as growth period (onset and  
29 offset of the growth trajectory).  
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43 Our *F*-tests on the BAC values with the null coefficient set at MAC value for each variable  
44 (performed to assess significant deviations of the SMA and OLS slopes from MAC values; see methods), did  
45 not detect significant differences between the multivariate analysis and the OLS bivariate analysis (Table  
46 3). These findings support the suggestion of Klingenberg (1996) that multiplying PC1 coefficients by the  
47 square root of  $p$  yields values can be interpreted as bivariate allometric coefficients (see methods), but only  
48 with OLS regressions to the geometric mean, indicating an empirical similarity between the OLS and the  
49 multivariate analysis. In this way, is likely that differences between bivariate (SMA) and multivariate  
50 approach in our analyses relay on the differences between line-fitting methods (i.e., OLS vs SMA) than in the  
51 dimensionality of the analyses (bi vs multivariate). In addition, as stated by Warton *et al.* (2006) bivariate  
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5 OLS analyses are adequate for predictions, although SMA is commonly used in studies of allometry. In this  
6 way, and according to the similarity between the OLS and the multivariate analysis in our case, we suggest  
7 the use of a composed independent variable (such as the geometric mean), instead of a single measurement in  
8 bivariate analyses.  
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### 17 **Allometric growth in *O. flavescens***

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20 Although a number of studies have provided a detailed description of sexual dimorphism in *O. flavescens*  
21 (e.g. Crespo 1984; Brunner *et al.* 2004; Sanfelice and Freitas 2008) our understanding of ontogeny remains  
22 incomplete in terms of growth trends interpreted as differences in sexual dimorphism during ontogeny.  
23  
24 Consequently, our approach is highly complementary to previous studies. Ontogenetic studies have revealed  
25 that several developmental pathways may lead to sexual size dimorphism in adult. In pinnipeds, males may  
26 grow faster than females from early stages, or males may display similar growth rates early and continue  
27 growing at a slow rate as adults, while females stop growing (Isaac 2005).  
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35 In a comprehensive study, Brunner *et al.* (2004) studied skull allometry of sea lions, during the  
36 initial growth phase in both sexes, identifying a secondary growth spurt (= peak) in the late development of  
37 the male in all species considered (including also *O. flavescens*). We found the same accelerated growth in  
38 males for several measurements related to bite (e.g. ZW, RW, CW) and some neurocranial components (e.g.  
39 MW, OCPH, Table 1). Unfortunately, our results are not completely comparable with those published in the  
40 cited work, because some adult stages were excluded and all otariid species were analyzed together. For  
41 instance, Brunner *et al.* (2004) report positive allometry for the total length of otariid skulls, whereas our  
42 analysis indicate that in *O. flavescens* this variable shows isometry (females) or negative allometry (males)  
43 relative to overall size (in our case, the geometric mean). Other differences were also detected in RW and LO  
44 which were negatively allometric in females, while the growth of MW and ZW in males resulted negative  
45 and isometric respectively. Anyway, the accelerated rate of growth detected in males for variables related to  
46 bite and neurocranium, reflects a way to reach an optimal adult morphology related to male competition.  
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6 Sanfelice and Freitas (2008), using two dimension geometrics morphometrics, studied ontogenetic  
7 series of three species of otariid skulls, concluding that in both sexes of *O. flavescens* the palate elongated,  
8 which is in agreement with the positive allometry of PL for both sexes in our results. Other transformations  
9 detected in the cited work, as the narrowing of the rostrum and zygomatic width in females (but widening in  
10 males), are also partially in agreement with our bivariate and multivariate approaches (Tables 1-2). The  
11 positive allometry of the RL, and the negative allometry of the ZW, combined to the isometry of the condylo-  
12 basal length (CBL) in females, gives a more slender skull appearance in adult females compared with males.  
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14 The strong shape and size differences between juveniles (both sexes) and later stages of development in *O.*  
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Sanfelice and Freitas (2008), using two dimension geometrics morphometrics, studied ontogenetic series of three species of otariid skulls, concluding that in both sexes of *O. flavescens* the palate elongated, which is in agreement with the positive allometry of PL for both sexes in our results. 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 (Tables 1-2). The positive allometry of the RL, and the negative allometry of the ZW, combined to the isometry of the condylo-basal length (CBL) in females, gives a more slender skull appearance in adult females compared with males. The strong shape and size differences between juveniles (both sexes) and later stages of development in *O. flavescens*, reveal transformations from early ontogeny, associated with those variables with rapid initial growth during early stages, but slowed in subadult and adult phases (i.e. negative allometry in this study; see Tables 1 and 2). Recently, Jones and Goswami (2010) 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 study, the allometric trends of some variables with positive allometry in males, such as rostral width, canine alveolus width, mastoid width (Table 1) also reflect largely the pattern reported.

According to our results, and considering that few variables shared common growth trajectories in both sexes (i.e. sharing slopes and intercepts, 2 out 20 variables), the skull growth is not conservative in *O. flavescens*. Sexual differences detected in almost all age stages suggest that sexual dimorphism is achieved from initial stages of growth (onset), although not only by extensions along the growth trajectories in males, but also by differences in allometric trends (slopes) and intercepts of each sex (Fig. 2). Females reach in general higher values of allometric trends than males, but males extend its growth trajectory by developing cranial characters linked with intra-specific competition in adult stages, denoting an evident higher offset of the male growth trajectories (Fig. 2c).

In species with sexual size dimorphism, sex differences in growth strategies are thought to have evolved as a result of sexual differences in the factors limiting reproductive success. Growth spurts in male body mass and size in relation to sexual or social maturity have been observed in several species of pinnipeds (e.g. Bryden 1968; Payne 1979; McLaren 1993; Clinton 1994). According to Weckerly (1998) female growth is characterized by early maturation, whereas males exhibit rapid early growth and delayed maturation. Such

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5 founding are also in agreement with the greater allometric coefficient values for most variables in females  
6 (Tables 1-2), and a noticeable offset extension in males (Fig. 2c). Periods of accelerated growth followed by  
7 a marked slowing or cessation of growth are associated with sexual or social maturation, because energetic  
8 resources previously used for growth are directed towards reproductive development, production of  
9 secondary sexual characteristics (other than size) and sexual behaviors (Bryden 1972). For instance, the  
10 increasing space generated for the temporal muscle (i.e. negative allometry of the braincase, enantiometry of  
11 POC, and positive allometry of ZW), and the development of the canines, are important for adult male-male  
12 encounters. Contrarily to the general trends favoring females, the higher values of allometric coefficients  
13 observed for measurements related to the masticatory apparatus in males (e.g. ZW, CW; Tables 1-2) are also  
14 in general agreement with the results obtained by Sanfelice and Freitas (2008) for *O.flavescens*, where the  
15 rate of growth in such specific functional dimensions were approximately three times faster in males than  
16 females.  
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31 Orbits in males exhibit the typical negative growth trend observed in mammals (Emerson and  
32 Bramble 1993), contrary to females that show isometric trend. This fact detects dissociation in the growth of  
33 a sensorial capsule in both sexes, although according to Brunner (1998) neurocranial components exhibit an  
34 intraspecific growth pattern usually conservative in pinnipeds. Such condition was also observed in other  
35 mammals like some groups of carnivorans (e.g. Giannini *et al.* 2010; Segura and Prevosti 2012) or primates  
36 (Flores and Casinos 2011). As also evidenced by Brunner (1998), our results indicate that growth pattern in  
37 neurocranial and splachnocranial components were in most cases different, being mostly negatively  
38 allometric in neurocranial variables (except the isometry in the female orbit, Table 1), but isometric or  
39 positively allometric in splachnocranial variables (except postcanine tooth length, see below, Table 1).  
40 However, the detection of enantiometry in the postorbital constriction in both sexes (a character detected in  
41 some primates, Corner and Richtsmeier 1991) suggests a complex way of growth in different regions of the  
42 braincase in, as enantiometry was not observed in the breadth of the braincase or height of the occipital plate  
43 (Tables 1-2).  
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58 The length of the functional mandibular postcanine tooth row in *O.flavescens* corresponds closely  
59 with that of the maxillary row. In order to achieve and preserve the occlusal relationships between upper and  
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5 lower dental rows there must be a high degree of coordination between the rates of growth of upper and  
6 lower complex (Moore 1981), which is also demonstrated by the functionally coordinated trends in both  
7 analyses (Tables 1-2). This feature contributes to feeding as postcanine teeth are specialized for diets of fish,  
8 crustaceans and cephalopods from early age stages. In otariids, there is an interval in which juvenile forage  
9 without fully developed canines, reflecting the importance of the postcanines at such early age stages  
10 (Brunner *et al.* 2004).  
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20 Further research of cranial ontogeny in related pinnipeds species is still required. Comparisons of  
21 ontogenetic trends would allow recognizing evolutionary patterns reflected in growth modes by using  
22 trajectories slopes and intercepts, and multivariate analyses of allometry for each sex and species groups.  
23 Also, an association of relative morphometric pattern with chronological age would provide much-needed  
24 information on ageing seals using non-invasive techniques. Finally, geographical variations of growth in  
25 other populations of *O. flavescens* (as those inhabiting the Pacific Ocean) may provide better descriptions  
26 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 (mm.). **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.

Collection number	Sex	CBL.	GM.
LAMAMA 141	F	139.4	43.600
LAMAMA 140	F	141.1	44.907
LAMAMA 331	F	152.6	46.385
MACN 23574	F	154.7	47.347
MACN 21740	F	168.4	49.517
MLP 26.IV.00.5	F	179.7	56.044
MACN 21739	F	179.7	51.302
LAMAMA 620	F	187.0	53.146
LAMAMA 484	F	197.2	56.318
LAMAMA 144	F	200.6	58.386
LAMAMA 556	F	202.3	59.086
LAMAMA 237	F	211.5	62.320
LAMAMA 686	F	218.9	60.962
LAMAMA 623	F	225.6	63.690
LAMAMA 604	F	227.6	67.045
LAMAMA 417	F	230.7	67.534
LAMAMA 147	F	233.8	66.394
LAMAMA 505	F	234.0	66.752
RNP 2319	F	234.8	69.914

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RNP 21737	F	236.6	70.601
LAMAMA 243	F	237.7	69.850
MLP 7.VII.50.1	F	238.1	69.205
LAMAMA 555	F	239.3	68.555
LAMAMA 033	F	240.7	71.171
LAMAMA 444	F	243.8	72.140
LAMAMA 127	F	244.0	68.903
MACN 21738	F	244.9	69.854
LAMAMA 253	F	246.5	69.894
LAMAMA 588	F	247.2	69.840
LAMAMA 024	F	247.3	71.323
MLP 1531	F	250.9	70.934
MACN 25138	F	251.7	76.159
MACN 20573	F	252.2	72.833
MLP 1060	F	252.6	75.909
LAMAMA 303	F	253.0	74.462
LAMAMA 61	F	253.4	75.435
LAMAMA 616	F	254.4	75.287
LAMAMA 590	F	255.2	74.326
LAMAMA 578	F	255.3	73.841
LAMAMA 026	F	257.3	75.924
LAMAMA 385	F	259.6	78.256
MACN 20578	F	265.5	81.179
GEMARS 565	F	266.0	81.854
LAMAMA 453	F	267.6	79.190
LAMAMA 029	F	269.6	79.762
MACN 22853	F	270.6	80.551



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MLP 27.X.97.14	F	272.3	79.272
RNP 2364	F	273.3	79.679
MACN 13.11	F	277.5	87.042
RNP 2416	F	277.9	80.588
MLP 41	F	278.3	82.290
GEMARS 1323	F	292.7	85.486
LAMAMA 139	M	140.4	41.890
LAMAMA 142	M	150.4	44.598
LAMAMA 569	M	162.7	47.948
MACN 24731	M	164.4	51.513
MACN 30236	M	168.0	47.073
LAMAMA115	M	174.8	49.690
LAMAMA 134	M	187.1	52.584
LAMAMA 329	M	192.0	54.157
LAMAMA 606	M	199.0	58.362
LAMAMA 053	M	207.8	60.208
MACN 21744	M	210.5	59.437
GEMARS 813	M	212.3	58.625
LAMAMA 371	M	213.5	59.644
MLP 26.IV.00.6	M	229.5	65.155
LAMAMA 427	M	233.1	64.491
LAMAMA 629	M	239.0	68.895
MLP 8.X.01.8	M	244.0	68.804
LAMAMA 031	M	247.2	73.388
MACN 50.52	M	247.7	70.585
MLP 26.IV.00.8	M	250.9	71.011
UFSC 1341	M	252.6	76.820

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MACN 22608	M	257.2	75.157
LAMAMA 605	M	258.3	76.259
LAMAMA 487	M	260.0	75.972
MACN 21743	M	260.2	77.821
GEMARS 343	M	260.8	76.985
LAMAMA 270	M	262.8	76.441
MMPMa 4086	M	268.0	83.315
GEMARS 967	M	269.3	82.048
MLP 475	M	269.6	77.904
GEMARS 799	M	270.5	80.839
MLP 453	M	273.3	82.869
LAMAMA 105	M	274.2	77.900
GEMARS 196	M	274.7	82.966
LAMAMA 43	M	275.5	82.886
MACN 22609	M	280.8	87.338
GEMARS822	M	283.8	87.184
GEMARS 229	M	285.9	91.019
GEMARS 812	M	290.5	86.742
LAMAMA 032	M	291.1	88.839
MACN 20420	M	292.3	87.933
MACN 22852	M	293.1	88.296
LAMAMA 419	M	293.8	87.269
LAMAMA 337	M	294.8	92.279
RNP 2068	M	294.9	88.794
RNP 2396	M	296.5	91.055
MLP 14.IV.48.9	M	296.8	89.394
GEMARS 659	M	300.9	92.967

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GEMARS 434	M	307.2	97.373
LAMAMA 60	M	307.8	99.917
RNP 2477	M	309.3	96.113
LAMAMA 152	M	311.2	102.499
MLP 1532	M	314.9	98.629
LAMAMA 030	M	318.4	102.939
LAMAMA 151	M	319.2	100.067
LAMAMA 027	M	320.5	99.485
LAMAMA 213	M	322.0	103.855
LAMAMA 245	M	322.0	99.485
MMPMa 4013	M	324.0	107.393
LAMAMA 028	M	324.0	107.737
RNP 2371	M	325.0	101.780
LAMAMA 022	M	325.0	113.826
RNP 2683	M	327.0	106.535
MLP 1526	M	330.0	105.642
RNP 2464	M	330.0	108.157
RNP 2475	M	330.0	100.019
RNP 2457	M	330.0	102.171
LAMAMA 155	M	330.0	108.727
LAMAMA 244	M	330.0	108.945
LAMAMA 492	M	330.0	110.249
LAMAMA 479	M	333.0	116.955
MACN 22851	M	335.0	106.888
MACN 27.27	M	335.0	102.864
ZOO-BA-M-15	M	335.0	104.986
RNP 2072	M	335.0	101.775

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5	RNP 2395	M	335.0	104.437
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7	GEMARS 428	M	340.0	115.926
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9	LAMAMA 490	M	340.0	117.731
10				
11	MACN 21984	M	341.0	110.283
12				
13	MACN 21994	M	343.0	108.668
14				
15	GEMARS 171	M	345.0	116.387
16				
17	RNP 2456	M	345.0	113.455
18				
19	MACN 23.26	M	350.0	117.671
20				
21	RNP 2633	M	350.0	111.505
22				
23	RNP 2467	M	350.0	117.261
24				
25	LAMAMA 025	M	350.0	110.910
26				
27	LAMAMA 250	M	350.0	113.498
28				
29	LAMAMA 353	M	350.0	118.937
30				
31	MACN 25168	M	355.0	114.984
32				
33	RNP 2468	M	355.0	116.355
34				
35	RNP 2365	M	359.0	103.024
36				
37	MLP 1330	M	360.0	114.998
38				
39	MLP 26.IV.00.10	M	360.0	121.887
40				
41	RNP 2635	M	368.0	118.265
42				
43	MLP 26.XII.02.36	M	370.0	118.717
44				
45	LAMAMA 199	M	370.0	121.907
46				
47	MLP 1332	M	375.0	121.160
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**Figure Captions**

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

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5 (at horizontal ramus); LAU, load arm length at upper canine; LC, length of coronoid process; LD, length of  
6 dentary; LO, length of orbit; LPCL, length of lower postcanine row; MW, mastoid width; NL, greatest nasal  
7 length; OCPH, occipital plate height; PL, palatal length; POC, postorbital constriction; PW, palatal width;  
8 RH, rostral height; RL, rostral length; RW, rostral width; UPCL, upper postcanine length; ZW, zygomatic  
9 width.  
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18 **Fig. 2** Bivariate SMA regressions. a. different slopes; b. same slope and different intercepts and c. same slope  
19 and intercepts, different shift. Symbols: white circles - females; black circles - males; solid line SMA  
20 regression of females and dashed line SMA regression of males.  
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Figure 1  
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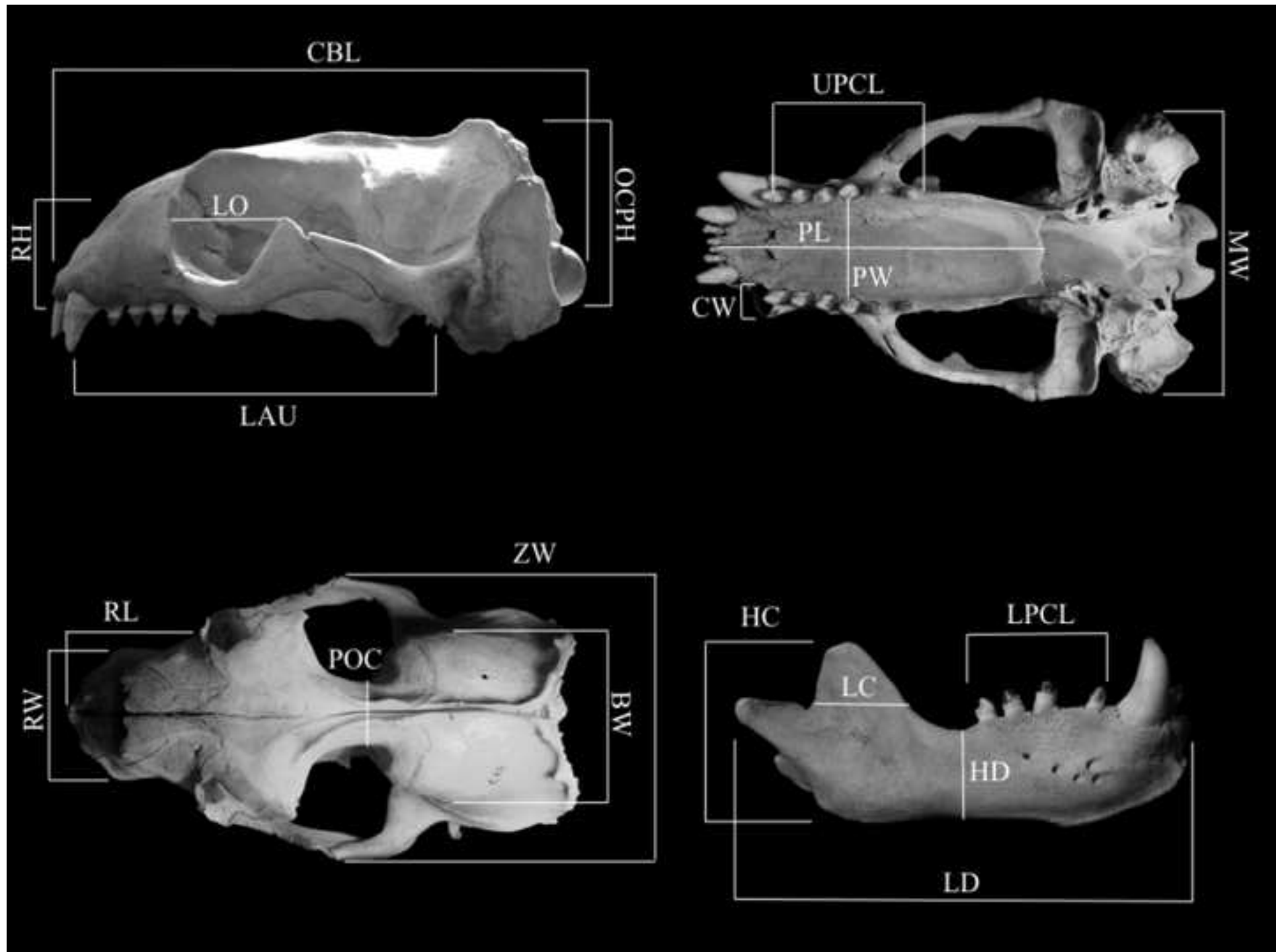
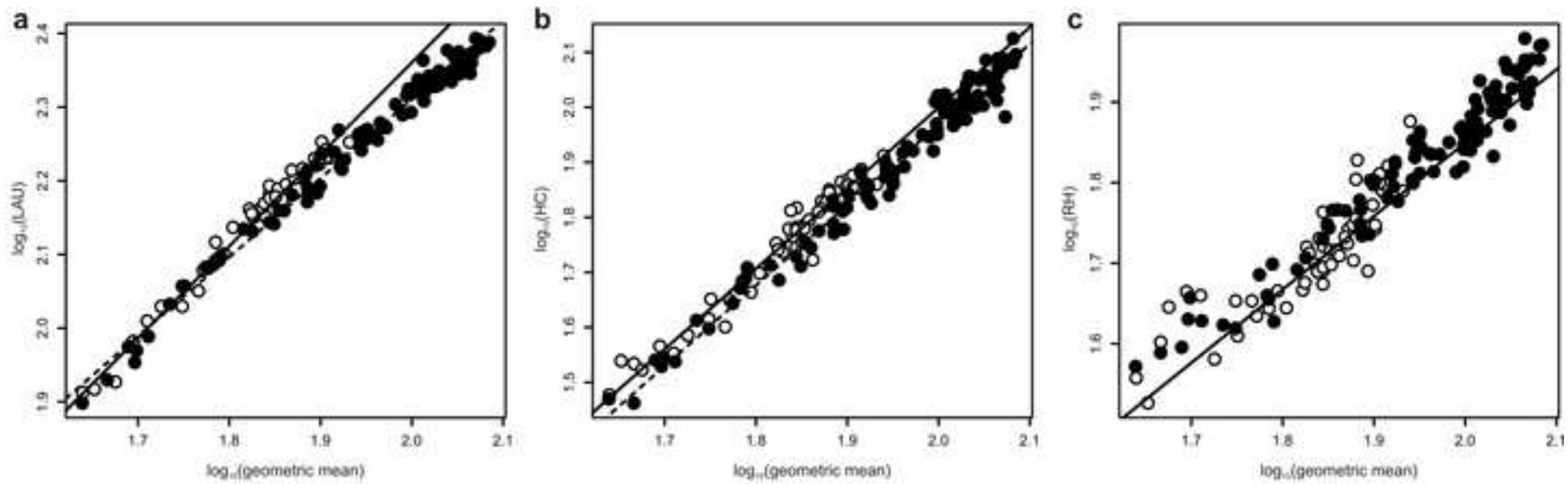


Figure 2  
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**Table 1** Test for common slope, common intercept and shift for both sexes of *O. flavescens*

Variable	Common slope			Growth Trend	Common intercept			Shift		
	Lr b1	P(b1)	b1 com		W (log(bo))	P (logbo)	log(bo)com	W -shift	P(shift)	shift
CBL	31.390	<b>2.11E-08</b>	F > M	F: =; M: -						
PL	35.702	<b>2.30E-09</b>	F > M	+						
PW	2.815	0.093	1.114	+	12.241	<b>4.67E-04</b>	M > F			
ZW	4.840	<b>0.028</b>	M > F	F: =; M: +						
UPCL	4.191	<b>0.041</b>	F > M	-						
OCPH	27.992	<b>1.22E-07</b>	M > F	-						
BW	10.497	<b>0.001</b>	F > M	-						
RL	20.406	<b>6.26E-06</b>	F > M	+						
LO	26.933	<b>2.11E-07</b>	F > M	F: =; M: -						
RH	0.507	0.477	0.911	-	1.480	0.224	0.0280	62.598	<b>2.55E-15</b>	M > F
MW	21.399	<b>3.73E-06</b>	M > F	F: -; M: =						
POC	11.848	<b>5.77E-04</b>	M > F	enant.						
LAU	31.137	<b>2.40E-08</b>	F > M	+						
LD	24.450	<b>7.63E-07</b>	F > M	+						
HC	0.159	0.690	1.463	+	40.508	<b>1.96E-10</b>	F > M			
LC	8.180	<b>0.004</b>	F > M	+						
HD	3.104	0.078	1.364	+	0.035	0.852	-1.067	60.520	<b>7.33E-15</b>	M > F
LPCL	5.210	<b>0.022</b>	F > M	-						
RW	15.853	<b>6.84E-05</b>	M > F	+						
CW	13.538	<b>2.34E-04</b>	M > F	F: =; M: +						



**Variable** abbreviations as in Figure 1. Parameters: **b1com**, common slope from standardized major axis; **log(bo)com**, common intercept from standardized major axis (values are in bold); **Lr**, likelihood ratio(Warton et al. 2006); **w**, Wald statistic (Warton et al. 2006); **Pb1**, p-value of Lrparameter, (p-values significant at 0.01 level are in bold); **Pb(logbo)**, p-value of W(logbo); **P(shift)**, p-value of Wshift; **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. Gray-shaded rows show significant regressions for common slope.

\*Differences are between the common slope trend and the slope observed for each sex (F, females; M, males).

**Table 2** Results by sex of the multivariate analysis of cranial allometry in *O. flavescens*

Variable	Sex	Untrimmed						Trimmed				
		Observed	Resampled coefficient	Bias	Departure	99% Confidence Interval	Growth trend	Resampled coefficient	Bias	Departure	99% Confidence Interval	Growth trend
CBL	F	0.245	0.225	-1.3E-03	-0.004	0.204-0.245	=	0.220	1.4E-03	-0.010	0.204-0.235	=
	M	0.240	0.189	-5.7E-04	-0.040	0.175-0.202	-	0.184	1.6E-03	-0.045	0.174-0.194	-
PL	F	0.246	0.295	-1.2E-03	0.065	0.271-0.318	+	0.291	5.0E-04	0.062	0.272-0.310	+
	M	0.240	0.248	-5.0E-04	0.018	0.235-0.260	+	0.244	7.9E-04	0.015	0.235-0.253	+
PW	F	0.234	0.210	1.6E-04	-0.019	0.176-0.244	=	0.211	-2.5E-04	-0.018	0.183-0.239	=
	M	0.237	0.242	-5.4E-05	0.013	0.226-0.257	=	0.244	-1.5E-03	0.015	0.231-0.257	+
ZW	F	0.243	0.207	3.6E-04	-0.023	0.187-0.225	-	0.213	-2.8E-03	-0.016	0.200-0.226	-
	M	0.240	0.179	-5.2E-04	-0.051	0.151-0.205	-	0.227	-7.6E-04	-0.002	0.218-0.235	=
UPCL	F	0.230	0.226	1.6E-04	-0.003	0.216-0.235	=	0.181	-1.7E-03	-0.048	0.163-0.198	-
	M	0.224	0.156	-1.5E-04	-0.074	0.140-0.171	-	0.156	-4.8E-04	-0.074	0.142-0.169	-
OCPH	F	0.237	0.134	5.2E-04	-0.096	0.113-0.154	-	0.135	-1.9E-04	-0.094	0.119-0.151	-
	M	0.237	0.187	5.0E-04	-0.042	0.172-0.201	-	0.189	-7.4E-04	-0.041	0.176-0.201	-
BW	F	0.032	0.005	1.7E-03	-0.225	(-0.038)-0.047	-	-0.001	4.8E-03	-0.231	(-0.038)-0.035	-
	M	0.047	0.014	-1.5E-04	-0.215	(-0.004)-0.032	-	0.013	1.9E-04	-0.216	(-0.003)-0.030	-
RL	F	0.240	0.289	-1.3E-03	0.059	0.2450-0.332	+	0.292	-3.1E-03	0.063	0.264-0.320	+
	M	0.235	0.238	-6.8E-04	0.009	0.2188-0.257	=	0.232	2.0E-03	0.003	0.216-0.246	=
LO	F	0.236	0.202	-1.6E-03	-0.028	0.1725-0.231	=	0.198	1.5E-04	-0.031	0.174-0.221	-
	M	0.230	0.150	-6.4E-04	-0.079	0.1320-0.168	-	0.145	1.9E-03	-0.085	0.130-0.158	-
RH	F	0.216	0.178	6.6E-04	-0.051	0.1279-0.228	-	0.182	-1.4E-03	-0.047	0.140-0.223	-
	M	0.235	0.192	9.4E-05	-0.037	0.1790-0.205	-	0.193	-8.8E-04	-0.036	0.182-0.204	-
MW	F	0.240	0.168	3.5E-04	-0.061	0.1347-0.201	-	0.163	2.7E-03	-0.066	0.142-0.184	-

	M	0.237	0.217	5.3E-04	-0.013	0.2017-0.232	=	0.221	-1.7E-03	-0.009	0.207-0.233	=
<b>LAU</b>	F	0.246	0.271	-9.4E-04	0.042	0.2551-0.287	+	0.267	1.2E-03	0.037	0.255-0.278	+
	M	0.241	0.234	-4.5E-04	0.005	0.2227-0.245	=	0.230	1.1E-03	0.001	0.221-0.239	=
<b>LD</b>	F	0.246	0.283	-1.0E-03	0.054	0.2686-0.297	+	0.279	9.1E-04	0.050	0.268-0.290	+
	M	0.242	0.249	-4.9E-04	0.020	0.2369-0.261	+	0.243	2.2E-03	0.014	0.234-0.251	+
<b>HC</b>	F	0.242	0.315	5.2E-04	0.085	0.2880-0.341	+	0.324	-4.1E-03	0.094	0.307-0.340	+
	M	0.238	0.316	-7.0E-06	0.087	0.3033-0.328	+	0.315	3.2E-04	0.086	0.303-0.326	+
<b>LC</b>	F	0.222	0.333	-9.2E-04	0.103	0.2766-0.388	+	0.330	4.0E-04	0.101	0.280-0.379	+
	M	0.229	0.287	-5.0E-04	0.058	0.2638-0.310	+	0.284	3.2E-04	0.055	0.265-0.303	+
<b>HD</b>	F	0.234	0.255	2.0E-03	0.025	0.2105-0.298	=	0.262	-1.6E-03	0.032	0.224-0.298	=
	M	0.231	0.294	9.1E-04	0.065	0.2676-0.321	+	0.297	-9.0E-04	0.067	0.274-0.318	+
<b>LPCL</b>	F	0.230	0.157	-3.0E-04	-0.073	0.1400-0.173	-	0.157	-5.4E-04	-0.072	0.142-0.172	-
	M	0.229	0.140	-2.1E-04	-0.089	0.1269-0.153	-	0.137	1.0E-03	-0.093	0.125-0.148	-
<b>RW</b>	F	0.237	0.228	1.5E-04	-0.001	0.2033-0.252	=	0.231	-1.2E-03	0.001	0.214-0.247	=
	M	0.239	0.282	2.6E-04	0.052	0.2641-0.299	+	0.284	-1.4E-03	0.055	0.269-0.298	+
<b>CW</b>	F	0.212	0.208	-1.5E-03	-0.022	0.1432-0.272	=	0.194	5.2E-03	-0.035	0.151-0.237	=
	M	0.234	0.295	-1.6E-04	0.066	0.2741-0.316	+	0.291	7.4E-03	0.062	0.271-0.310	+

Jackknife results calculated with untrimmed and trimmed sets of pseudovalues. The Observed coefficient is the value obtained with all specimens included (females,  $n=52$ ; males,  $n=97$ ).

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 3.** Comparison between multivariate and bivariate (OLS-SMA) analyses

<b>Variable</b>	<b>Sex</b>	<b>MAC</b>	<b>F_OLS</b>	<b>p_OLS</b>	<b>F_SMA</b>	<b>p_SMA</b>
<b>CBL</b>	F	1.0076	0.2924	0.5911	1.3224	0.2556
	M	0.8431	1.2611	0.2643	3.6222	0.0600
<b>PL</b>	F	1.3187	0.4769	0.4930	1.6096	0.2104
	M	1.1041	1.6633	0.2003	3.9751	0.0490
<b>PW</b>	F	0.9413	0.4616	0.5000	3.9893	0.0512
	M	1.0786	1.1866	0.2788	4.7697	0.0314
<b>ZW</b>	F	0.9244	1.2078	0.2770	3.4036	0.0710
	M	1.0078	2.6040	0.1099	5.5981	0.0200
<b>UPCL</b>	F	0.7993	0.1360	0.7139	2.9225	0.0936
	M	0.6942	0.3915	0.5330	6.7103	0.0111
<b>OCPH</b>	F	0.5982	0.6404	0.4274	4.1742	0.0463
	M	0.8330	1.2895	0.2590	5.5531	0.0205
<b>BW</b>	F	0.0213	0.2395	0.6267	10273	0.0000
	M	0.0630	0.0365	0.8488	689.19	0.0000
<b>RL</b>	F	1.2908	0.3438	0.5603	2.3670	0.1302
	M	1.0618	0.6169	0.4342	3.7880	0.0546
<b>LO</b>	F	0.9030	0.0329	0.8569	1.6772	0.2012
	M	0.6699	0.2787	0.5988	4.2739	0.0414
<b>RH</b>	F	0.7962	0.3478	0.5580	7.0328	0.0107
	M	0.8555	1.0114	0.3171	5.1466	0.0256
<b>MW</b>	F	0.7527	0.7295	0.3971	3.7275	0.0592
	M	0.9655	1.4828	0.2263	5.4184	0.0220
<b>LAU</b>	F	1.2128	0.6361	0.4289	1.7782	0.1884
	M	1.0427	2.0848	0.1521	4.4052	0.0385
<b>LD</b>	F	1.2654	0.6073	0.4395	1.7504	0.1918
	M	1.1113	2.3786	0.1263	4.6780	0.0331
<b>HC</b>	F	1.4073	0.7577	0.3882	2.7493	0.1036
	M	1.4083	1.7412	0.1902	4.5562	0.0354
<b>LC</b>	F	1.4879	0.0129	0.9102	2.7783	0.1018
	M	1.2792	0.3616	0.5491	4.1970	0.0433
<b>HD</b>	F	1.1384	0.6076	0.4394	4.6099	0.0367
	M	1.3109	0.9997	0.3199	5.5301	0.0208
<b>LPCL</b>	F	0.7016	0.2671	0.6075	3.6855	0.0606
	M	0.6234	0.4582	0.5001	5.4875	0.0212
<b>RW</b>	F	1.0198	0.6334	0.4299	3.3213	0.0744
	M	1.2548	1.9584	0.1649	4.9449	0.0285
<b>CW</b>	F	0.9287	0.0323	0.8580	4.9656	0.0304
	M	1.3721	0.3512	0.5549	4.1035	0.0456

Variable abbreviations as in Figure 1. Sex: F, females; M, males. MAC: multivariate allometry coefficient, P\_SMA, p-value of F-test between MAC and SMA slope; P\_OLS, p-value of F-test of MAC and slope.