



ORIGINAL INVESTIGATION

**A quantitative approach to the cranial ontogeny of the puma**

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Received 14 May 2009; accepted 3 August 2009

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**Abstract**

The cranial ontogeny of specialized mammals is relevant to the understanding of the connection of form and function in a developmental, ecological, and evolutionary context. As highly specialized carnivores, felids are of especial interest. We studied the postnatal ontogeny of the skull in *Puma concolor* (Mammalia: Carnivora: Felidae) using a quantitative approach. We interpreted our results in the light of a previous qualitative assessment of ontogenetic changes in the species. This represents one of the few integrative studies of skull development in any extant species of wild felids. We report patterns of multivariate allometry of 19 linear skull dimensions measured in 48 Argentine specimens. We examined the (jackknife resampled) departures from isometry as well as the interplay of isometric and allometric trends in shaping the puma skull. Both the qualitative and quantitative results indicate that the major ontogenetic changes are directly linked to cranial structures that support a developing masticatory apparatus and its associated jaw and neck musculature, which are essential for the action of canines and carnassials during the killing bite and slicing flesh. Sexual differences suggest allometric scaling (hypo- or hyper-morphosis) as key processes in the development of the puma skull.

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**Keywords:** Felidae; Skull ontogeny; Allometry; Hypermorphosis; Hypomorphosis

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**Introduction**

Mammalian carnivores display an extremely broad range of morphological and dietary diversity, from social insectivores to folivores to hypercarnivores

(Nowak 1999; Myers 2000). Felids are among the highly specialized predators. The felid lineage is composed functionally of two subgroups, sabretoothed cats and feline cats (Slater and van Valkenburgh 2008); the latter is characterized by impressive size variation within a remarkably conservative shape specialized in uniform powerful biting (Christiansen 2008). Thus, feline cats feature a number of morphological adaptations to a diet dominated by flesh obtained from prey they kill, of which craniodental characters stand prominently

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including a short face, anteriorly oriented orbits, large temporal fossa, large canines, specialized carnassials, and greatly reduced non-carnassial postcanines (Kitchener 1991).

In strict carnivores like felids, the transition from milk suckling to the demanding feeding habits of adults must be accompanied by pronounced modifications in morphology and behavior, as the juvenile masters the methods for hunting and killing prey required for leading an independent existence as a predator (Ewer 1973; Binder and van Valkenburgh 2000). The study of postnatal ontogeny of the felid skull is thus attractive given the potential to show how the suckling young develops the structures and functions of a highly specialized predator (Ewer 1973). Thus, important modifications in cranial shape and size are expected during the postnatal ontogenetic sequence. As summarized by Segura and Flores (2009), the cranial morphology in felids has been approached from three main points of view: descriptive (e.g., Kelson 1946; Ximénez 1974; Gilbert 1997; García-Perea 2002), taxonomic and phylogenetic (e.g., Collier and O'Brien 1985; Salles 1992; Johnson and O'Brien 1997; Mattern and Mc Lennan 2000; Mazák and Groves 2006; Slater and van Valkenburgh 2008), and functional (e.g., Emerson and Radinsky 1980; Martin 1980; Biknevičius 1996; Biknevičius et al. 1996; Antón et al. 2004; Christiansen and Adolfssen 2005; Christiansen 2008; Slater and van Valkenburgh 2008). However, the morphometric changes that occur in the skull of felids during the ontogeny are incompletely understood because the scope of the available studies is limited and few species have been studied in a morphological and/or morphometric context to date. Such species include *Panthera onca* (Stehlik 1971; Slaughter et al. 1974), *P. pardus* (Stander 1997), *Leopardus wiedii* (Volf 1972; Fagen and Wiley 1978; Petersen and Petersen 1978), *Lynx* (Crowe 1975; Johnson et al. 1981; Jackson et al. 1988; García-Perea 1996), *Acinonyx jubatus* (Broom 1949; Caro 1994), *Caracal caracal* (Stuart and Stuart 1985) and *Puma concolor* (Gay and Best 1996; Shaw et al. 2007; Segura and Flores 2009). However, these studies focused either on age estimation, functional analysis, or morphological description, including qualitative approaches to the ontogeny of some extant felids and felid-like fossils. The latter include analyses of comparative cranial anatomy of juvenile nimravids (see Bryant 1988, 1990; Peigné and de Bonis 2003).

Patterns of cranial ontogeny and mandible ossification, as well as its functional connection with tooth replacement, received attention in the puma (Biknevičius 1996; Biknevičius and Leigh 1997; Segura and Flores 2009). The ontogenetic changes and their functional consequences were investigated in a qualitative framework by Segura and Flores (2009), who showed that the morphological transformations and

interactions that occur in the neurocranium and splanchnocranium have a profound impact in the morphology and function of the skull of adults. Those ontogenetic changes paralleled the acquisition of a strictly carnivorous diet and affected mainly the trophic apparatus, the occiput and, presumably, their linked functions (feeding and head movements).

In this contribution, we build upon those findings and incorporate a quantitative analysis of growth in *Puma concolor* on the basis of multivariate linear allometry of functionally important variables of the skull. In this way, we aim at developing an integrated view of the skull ontogeny in this species.

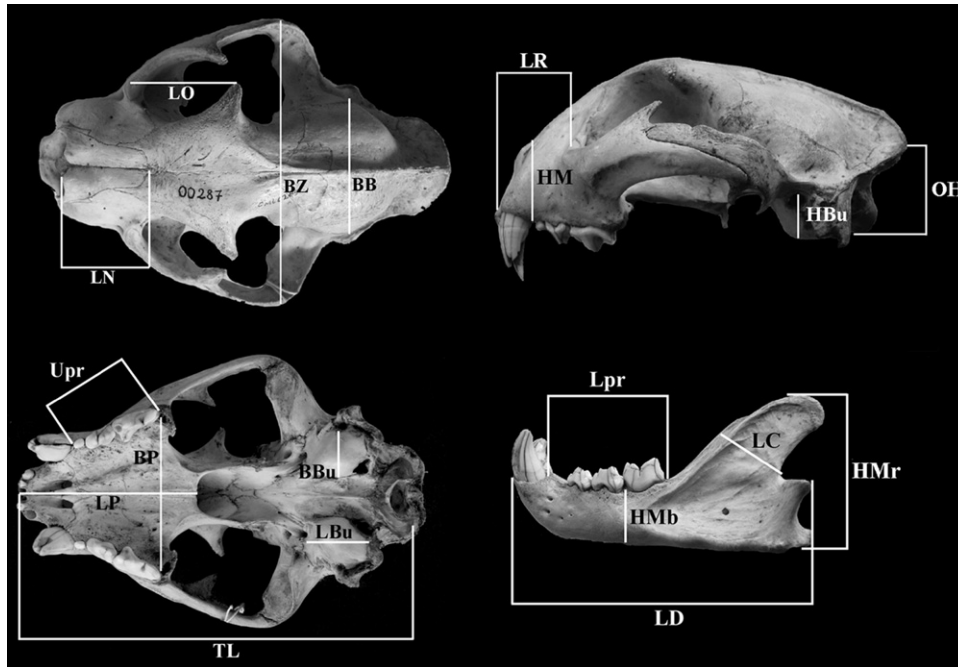
## Material and methods

### Study specimens

*Puma concolor* is a species frequently found in systematic collections. In this study, we analyzed a combined series of 48 skulls deposited at Colección Mamíferos Lillo (CML; Tucumán, Argentina) and Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN; Buenos Aires, Argentina). These are: CML 234, 235, 443, 650, 3726, 5484, 6285, 6355, 6356, 6357, 6360, 6363, and 7369; MACN 13045, 13046, 13047, 13048, 13059, 13328, 13330, 13342, 13345, 13346, 13457, 13458, 13460, 15307, 19244, 20.64, 24.19, 25.208, 25.61, 29.841, 30.19, 30.196, 30.214, 30.250, 3.15, 32.80, 36.939, 38.44, 39.208, 47.2, 48.344, 48.345, 49.296, 53.58, and 53.59. All the specimens were originally captured in Central, NE and NW Argentina. A few available specimens from Patagonia (*P. c. puma*) were excluded from the analysis due to the marked size difference that characterizes this form. Sixteen specimens were young with not fully erupted dentition, whereas the remainder of the sample comprised adults from different age classes. We took advantage of the correlation between tooth eruption chronology, and tooth wear, with absolute age to estimate the age of specimens of our sample (e.g., Eaton and Verlander 1977; Currier 1979, 1983; Laundré et al. 2000; Shaw et al. 2007). On this basis, our specimens ranged from c. 2 months (CML 7369) to c. 10 years (CML 6285).

### Allometry

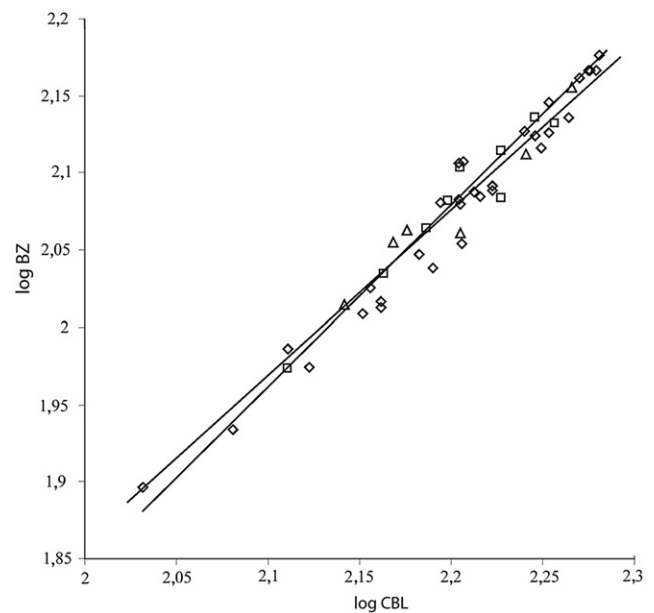
We used 19 linear measurements representing length, width or depth of skull structures (Fig. 1) to estimate allometric growth of skull components in *Puma concolor*. In this species, males tend to be larger than females of comparable age, as shown by variables such as the condylobasal length measured in selected adults of our sample ( $t=2,64$ , d.f.=18,  $P=0,013$ ).



**Fig. 1.** Cranial measurements of *Puma concolor* used in this study. Abbreviations: **BB** breadth of braincase; **BP** breadth of palate; **BZ** zygomatic breadth; **CBL** condylobasal length; **HMB** height of mandibular body; **HM** height of muzzle; **HO** height of occipital plate; **LC** length of coronoid process; **HMr** height of mandibular ramus; **LD** length of dentary; **LN** length of nasals; **LO** length of orbit; **Lpr** length of the lower postcanine row; **LP** length of palate; **Upr** length of upper postcanine row; **LR** length of the rostrum; **BBu** breadth of the bulla; **HBu** height of the bulla; **LBU** length of the bulla.

However, both males and females clearly exhibited the same ontogenetic trajectory (non-significant slope or intercept differences in bivariate analyses; see example in Fig. 2). Therefore, we pooled males and females of all ages in a single sample, which included ten specimens that died in captivity. The mensural differences between captive or domesticated animals and wild or feral populations may be significant in many respects (e.g., Hollister, 1917; O'Regan, 2001; O'Regan and Kitchener, 2005). However, in our data set those specimens did not appear as outliers that may bias the analysis of growth (Fig. 2). As a consequence, they were all included in the allometric analyses.

For the study of allometry, we took a multivariate approach based on the generalized allometry equation proposed by Jolicoeur (1963a, b). In multivariate allometry, size is regarded as a latent variable affecting all measured variables simultaneously (see applications of multivariate allometry in carnivorous marsupials in Giannini et al. (2004) and Flores et al. (2006)). The elements of the first eigenvector of a principal components analysis (PCA) expresses the allometric relationships among all variables with the latent size, provided that this eigenvector is extracted from a variance-covariance matrix of log-transformed variables and scaled to unity (i.e., with all elements scaled so that the sum of squared elements equals 1; Jolicoeur, 1963a). For a given variable, allometry is the statistical



**Fig. 2.** Bivariate scatterplot of zygomatic breadth (**BZ**) on condylobasal length (**CBL**) in males (diamonds) and females (squares) of *Puma concolor*. Triangles indicate specimens of unknown sex. Each line fits a least-squares regression model.

deviation of its corresponding eigenvector element from a hypothetical isometric value, which is expected to be equal for all elements if the global growth pattern is

isometric (size invariant). The isometric element value is calculated as  $1/p^{0.5}$  with  $p$  equal to the number of variables (0.229 for the present study). Statistical deviation from isometry was estimated using the application of jackknife (Quenouille 1956; Tukey 1956; Manly 1997) developed by Giannini et al. (2004); (see also Marroig and Cheverud, 2004). The purpose of this technique is to generate confidence intervals for each of the empirically derived first-eigenvector elements. The confidence interval may be inclusive of the isometric (null) value 0.229 and therefore statistically indistinguishable from isometry, or it may exclude such value and therefore be considered significantly allometric: either “positive” if the observed element is  $>0.229$ , or “negative” if the observed element is  $<0.229$  (i.e. with a higher, or lower, rate of change for the specific variable as compared to overall growth). To calculate this confidence interval,  $n$  pseudosamples are generated such that a new first unit eigenvector is calculated from a matrix with one puma specimen removed at a time (with  $n$  equal to the number of specimens). In each removal cycle, a pseudo value is calculated for each eigenvector element using the formula for the first-order jackknife:

$$\hat{e}_j^* = n\hat{e} - (n-1)\hat{e}_{-j}$$

where one pseudo value  $\hat{e}_j^*$  corresponds to the removal of specimen  $j$  from the sample of size  $n$ ,  $\hat{e}$  is the observed element of the unit eigenvector that corresponds to the multivariate coefficient of allometry of the skull variable  $x$ , and  $\hat{e}_{-j}$  is the value of the coefficient obtained with specimen  $j$  removed (Manly 1997). From the collection of  $n$  pseudo values, mean and standard deviation are calculated for each element corresponding to one skull variable. The mean represents the raw jackknife estimate of the multivariate allometry coefficient for that variable. The difference between this estimate and the actual value from the complete sample is a measure of bias; we report an unbiased jackknife estimate of the allometry coefficient that obtains from subtracting the bias from the raw estimate (Manly 1997). The standard deviation and the corresponding 99% and 95% confidence intervals (for  $n-1$  degrees of freedom) are calculated for each allometry coefficient.

Giannini et al. (2004) and Flores et al. (2006) followed Manly's (1997) suggestion of using trimmed pseudo values for the calculation of the confidence interval. Trimming the  $m$  largest and  $m$  smallest pseudo values for each variable may significantly decrease the standard deviations and allow for more realistic allometric estimations (see Giannini et al. 2004). If untrimmed and trimmed confidence intervals greatly differ in width, this can be taken as indication of extreme pseudo values affecting the standard errors. Here we report untrimmed as well as trimmed (with  $m=1$ ) calculations, opting for the results that in

combination reduce bias and interval width. The statistical analysis (PCA + jackknife resampling) was programmed in R (R Development Core Team 2004). The script is available on request.

## Results and discussion

### Allometric trends

The results of multivariate analyses of allometry are given in Table 1. For the wide (99%) confidence interval, untrimmed and trimmed values differed, albeit marginally, in two out of 19 variables. Specifically, the lengths of rostrum (LR) and upper postcanine row (Upr) were positively and negatively allometric, respectively, in the trimmed analysis, but the departure from isometry is weak (just c. 0.01 units above or below the expected value under isometry, 0.229). Narrowing the interval to 95% confidence confirms these trends in both untrimmed and trimmed analyses, with the addition of another three marginally allometric variables in the trimmed analysis. We choose to interpret the trimmed 99% results combining the conservative safety of a wide interval and the estimated bias in this analysis, which across variables averages slightly smaller in the chosen analysis (0.0002) than in other analyses (c. 0.0008). On the basis of this result, eleven variables significantly departed from isometry. These were the height of the occipital plate (HO), breadth of braincase (BB), length of orbit (LO), breadth of the auditory bulla (BBu), length of upper postcanine row (Upr), and length of lower postcanine row (Lpr; all negatively allometric), and breadth between zygomatic arches (BZ), length of rostrum (LR), length of dentary (LD), length of coronoid (LC), and the height of mandibular ramus (HMr; positively allometric).

These trends describe a pattern of postnatal growth in the puma skull that can be interpreted as follows. The condylobasal length, an accurate estimator of total skull length and an almost ubiquitous indicator of overall cranial (and body) size (van Valkenburgh 1990; Emerson and Bramble 1993; Christiansen and Harris 2005), conservatively grows at a rate indistinguishable from overall size change in the puma. The braincase grows at a slower pace than the skull, as estimated by the negative allometry of its two measured dimensions, breadth (BB) and height (HO), although they markedly differ in magnitude. The breadth of the braincase exhibits an extremely slow rate of growth (unbiased estimate = 0.050), whereas the height of the occiput is moderately negative (unbiased estimate = 0.193), so that the braincase of adults is proportionally higher than in young specimens. As in other mammals (e.g. *Didelphis*



**Table 1.** Summary of results of multivariate cranial allometry in *Puma concolor*<sup>a</sup>.

Cranial Variables	Variable code	Wide (99%) interval				Narrow (95%) interval	
		Untrimmed		Allometric trend	Trimmed (m = 1)		Trimmed (m = 1)
		Unbiased estimates	Confidence Interval		Confidence Interval	Allometric trend	
Condylobasal length	CBL	0.232	0.216-0.248	=	0.225-0.247	=	=
Height of occipital plate	HO	0.193	0.156-0.229	-	0.182-0.227	-	-
Breadth of braincase	BB	0.050	0.019-0.081	-	0.026-0.081	-	-
Interzygomatic breadth	BZ	0.259	0.241-0.276	+	0.250-0.277	+	+
Length of orbit	LO	0.180	0.144-0.215	-	0.147-0.204	-	-
Length of nasals	LN	0.201	0.165-0.237	=	0.177-0.237	=	=
Length of rostrum	LR	0.317	0.209-0.426	=	0.230-0.416	(+)	+
Height of muzzle	HM	0.300	0.215-0.386	=	0.225-0.311	=	+
Breadth of auditory bulla	BBu	0.085	0.052-0.118	-	0.058-0.117	-	-
Height of auditory bulla	HBu	0.194	0.126-0.263	=	0.125-0.235	=	-
Length of auditory bulla	LBu	0.196	0.141-0.250	=	0.155-0.237	=	-
Breadth of palate	BP	0.225	0.198-0.253	=	0.203-0.249	=	=
Length of palate	LP	0.234	0.215-0.253	=	0.219-0.246	=	=
Length of upper postcanine row	Upr	0.193	0.117-0.270	=	0.112-0.224	(-)	-
Length of mandible	LD	0.246	0.232-0.259	+	0.233-0.257	+	+
Height of mandibular body	HMb	0.197	0.161-0.233	=	0.178-0.236	=	-
Height of mandibular ramus	HMr	0.367	0.335-0.399	+	0.340-0.395	+	+
Length of coronoid process	LC	0.312	0.243-0.380	+	0.270-0.367	+	+
Length of lower postcanine row	Lpr	0.181	0.154-0.207	-	0.156-0.200	-	-

<sup>a</sup>The expected allometry coefficient under isometry is 0.229. See text for methodological specifics. Abbreviations for variables in Fig. 1. Allometric trends are coded using the symbols “=” (isometric), “+” (allometric, accelerated with respect to overall size or “positive”), and “-” (allometric, decelerated with respect to overall size or “negative”).

[Abdala et al. 2001], *Lutreolina* [Flores et al. 2003]), the length of the orbit scales negatively, although in australidelphian marsupials this pattern seems to be uncommon (see Giannini et al. 2004; Flores et al. 2006). Also as expected from other neurocranial components, the three dimensions of the auditory bulla grew with negative trends or nearly so (depending on the width of interval), but clearly the breadth is the dimension that grows the least (Table 1). As a consequence, the auditory bulla proportionally narrows as it grows. The temporal space, which contains the *temporalis* muscle, expands both outward and inward, by the combination of the positive allometry of zygomatic breadth with the strong negative allometry of the braincase. In relative terms, the palate preserves the length-width relationship of juveniles. Other dimensions of the facial skeleton (i.e. rostral height and length, and length of nasals), scale differently resulting in a modest elongation of the rostrum (the rostral length scaled positively, whereas the

height of rostrum and length of nasals were isometric). Both tooth rows were negatively allometric and grew at about the same relative rate (Table 1), clearly indicating a reduction in the relative postcanine space.

The mandible is modeled in a complex way during the ontogeny. The lower toothrow is negatively allometric, and so is the height of the mandibular body. By contrast, the mandible length and the two dimensions of the coronoid process are strongly positively allometric. This mosaic of allometric trends points to an elongation of the mandibular body and an enlargement of the mandibular ramus. This suggests a strong increase in the influence of masticatory musculature toward adulthood, via increased area of muscular insertion, specifically for the *temporalis* and *masseter* muscles. The negative allometry of the height of the mandible implies that high mechanic strength is achieved early in ontogeny, as suggested by a study on mandibular ossification in the puma (Biknevicius and Leigh 1997).

## Qualitative and quantitative estimations

The allometric trends in the ontogenetic series of *Puma concolor* are in close agreement with the qualitative interpretations made by Segura and Flores (2009). Our quantitative analyses showed that the occipital height grows faster (although negatively allometric) as compared with the braincase breadth, which generates a deep skull toward adulthood. Segura and Flores (2009) reported important qualitative changes, among which the most significant were the development of the lambdoid crest and the increased sculpturation of the surface of the occiput for insertion of *m. temporalis* anteriorly and cervical muscles posteriorly (Wickland et al. 1991; Richmond et al. 1992; Evans 1993; Duckler 1998; Antón et al. 2004). The latter include the *rectus capitis dorsalis*, *spinalis capitis*, and *splenius* (Evans 1993), which can be associated with specific head movements and also with the opening of the mandible as they elevate the skull (in combination with *m. digastricus*, which depresses the jaw; Biknevičius and van Valkenburgh 1996; Antón et al. 2004; Segura and Flores 2009). Probably, the change in orientation of the foramen magnum and the early fusion of the occipital elements contribute to the negative allometry of the occipital height (Segura and Flores 2009), which is in agreement with trends observed in other large felids (e.g. *Panthera tigris*; Mazák and Groves 2006).

In a qualitative context, Segura and Flores (2009) found that many of the important osteological changes represented the increase of surfaces for origin and insertion of the temporal, masseter and pterygoid muscles. Such transformations conform to a change in feeding behavior and diet toward adulthood (see also Peigné and de Bonis (2003) for inferences in young nimravids). The enlarged surface and depth of the temporal fossa increases the area of origin for the temporal muscle, thus accompanying the positive allometry of the zygomatic breadth and the negative allometry of the braincase that in combination create the space for such muscle. Also, the relative decrease in width of the postorbital constriction generates additional space for the increasing volume of the *m. temporalis* (Segura and Flores 2009).

The positive allometry of the rostral length and width (estimated by palate width), suggests an increase in the mechanic strength of this region, which becomes heavily involved during the killing bite. This pattern has been observed in the ontogeny of other predominantly carnivorous mammals, such as the marsupials *Lutreolina* (Flores et al. 2003) and *Dasyurus* (Flores et al. 2006). Overall, these changes suggest a highly integrated pattern of skull modeling (see Olson and Miller 1958; Vermeij 1973; Wagner 1996; Emerson and Hastings 1998; Goswami 2006).

## Sexual dimorphism and ontogenetic trajectories

As many felids, the puma is sexually dimorphic, with adult males tending to be larger than females (Currier 1983). Significantly, both sexes share both the intercept and the slope in bivariate analyses of allometry (see Fig. 2 for an example). Therefore, either males are peratypic with respect to females (with hypermorphosis as the specific developmental perturbation), or females are paedotypic with respect to males (with hypomorphosis as the specific developmental perturbation; terminology sensu Reilly et al. 1997). The specific process involved in the sexual differences in the puma can only be determined by outgroup comparison (Fink 1982; Reilly et al. 1997). With the caveat of using size as proxy of time as independent variable, the results strongly suggest that shifts in offset time may govern size and shape variation between sexes in the puma, whereas other processes (i.e., ac- or de-celeration [change in rate], or pre- or post-displacement [shift in onset], sensu Reilly et al. 1997) may be unimportant in relative terms.

## Conclusion

The skull of the puma exhibits complex allometric trends and qualitative changes. Negatively allometric trends affected neurocranial components as well as length of tooth rows, whereas zygomatic breadth, rostrum and dentary length, and the height of mandibular ramus grew at positive rates. Qualitative changes include development of braincase crests and surface sculpturation. Together these trends shape a deep and relatively long braincase, and wide zygomatic arches during development, which imply strengthening of structures for the action of masticatory and neck musculature, both associated to strong biting forces exerted during killing and eating prey. Many other details are also noteworthy. These include the effect of adult size dimorphism and the consequences of sharing slope and intercept by both sexes. A model of allometric scaling explains sexual differences.

## Acknowledgements

We thank Ruben Bárquez (CML) and Esperanza Varela (MACN) for access to specimens. Julio Rojo, Francisco Prevosti, and Fernando Abdala discussed earlier versions of the manuscript. We thank the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina, for funding this research.

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