Palaeogeography, Palaeoclimatology, Palaeoecology 453 (2016) 73–79

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Prediction of offspring in extant and extinct mammals to add light on paleoecology and evolution

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ARTICLE INFO

Article history:
Received 24 October 2015
Received in revised form 25 March 2016
Accepted 31 March 2016
Available online 9 April 2016

Keywords:
Fossil mammal
Life history
Offspring estimation
Paleobiology
Paleoecology

ABSTRACT

Reproductive strategies can be inferred from adult body mass, although offspring characteristics can give more accurate tools to predict life histories. In fossil mammals, adult body mass estimation incorporates error to the possible predictions, and additionally, there are not estimators of the offspring. Here I test the significance of two measurements, the inter-acetabulum width and the lumbar length, as predictors of offspring body mass, litter weight, and litter size in extant and fossil mammals. The inter-acetabulum width is the best measurement to estimate offspring body mass and litter weight, whereas litter size can be estimated from the division of litter weight on offspring body mass. The possibility of estimating these offspring variables gives a new approximation to study the history of life, paleoecology, and evolution of fossil species. Ecological aspects as developmental and maturity time, can be combined to study population growth, faunal interaction and evolution in fossil taxa. Some interpretative factors are proposed as start point to study fossil fauna taking into account offspring and reproductive information.

1. Introduction

Reproductive strategies can be classified in K and r selection. The K-selected individuals have been favored for their ability to make a large proportional contribution to a population that remain near to carrying capacity, while r-selected individuals have been favored for their ability to reproduce rapidly (Stearns, 1976, 1977). Following Stearns (Stearns, 1976, 1977), K-selected populations live in habitats that impose few random environmental fluctuations and populations are large and stable in which the offspring are relatively large, thus imposing high reproductive cost. Competition is intense among adults and determines their rates of survival and fecundity. Additionally, the young also have to compete and there are few opportunities for them to become established as breeding adults themselves. The predicted characteristics of these K-selected individuals are larger size, deferred reproduction, iteroparity, lower reproductive allocation and large but few offspring. By contrast, an r-selected population lives in habitats that are unpredictable, and populations are offspring size-insensitive with low reproductive costs. The mortality rates of both adults and juvenile are highly variable and unpredictable, and are frequently independent of population density or of body size or conditions of the individual concerned. The predicted characteristics of r-selected individuals are small size, early maturity, possible semelparity, large reproductive allocation and numerous but small offspring.

These reproductive strategies are well studied in extant mammals, and can be predicted from the adult body mass. However, the study of offspring provides more variables from which to predict reproductive strategies and life histories. These include pattern of growth, differentiation, storage and reproduction (Begon et al., 2006), offspring survival (Moyes et al., 2006a; Còté and Festa-Bianchet, 2001; Moyes et al., 2006b), future reproduction and survival of mother (Iason, 1990; Lambin and Yoccoz, 2001), investment per offspring (Charnov and Ernest, 2006), reproductive cost (Hamel et al., 2011), gestation period (Huggett et al., 1951; Sacher and Staffeldt, 1974; Economos, 1982a; Gillooly et al., 2002; Bueno and López-Urrutia, 2012), duration of parental care (Bueno and López-Urrutia, 2012), or rate of development (Gillooly et al., 2002; Bueno and López-Urrutia, 2012). As discussed below, offspring studies have the potential to illuminate paleoecological characteristics, such as variation of population sizes, relationships between species, their responses to environmental disturbances, and to seek general evolutionary trends. Although previous works have investigated trade-offs between adult and offspring in population ecology, population genetic, and evolutionary fitness (Messina and Fox, 2001) $^{\text{(and references therein)}}$, they have not considered osteological features that may constrain the variability of offspring size and number and the implications that these bony characteristics have for paleoecological studies. This work explores and tests the predictive value of some anatomical characters in regard to life history features.

In extant mammals a relation exist among adult body mass and offspring characteristics such as litter weight and offspring body mass (Sacher and Staffeldt, 1974; Millar, 1977; Blueweiss et al., 1978; Economos, 1982b); although litter size had not been related to body

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http://dx.doi.org/10.1016/j.palaeo.2016.03.033

mass (Sacher and Staffeldt, 1974; Blueweiss et al., 1978; Economos, 1982b; Leitch et al., 1959). Additionally, a trade-off between litter size and offspring body mass (Sibly and Brown, 2009), and between offspring number per year and offspring body mass (Sacher and Staffeldt, 1974) exists. Since body mass has predictive value in regard to life history strategies, one could make inferences regarding such features in extinct taxa. However, direct measure of body mass is not possible for fossil mammals, and must be estimated from various regression analyses (Damuth and MacFadden, 1990). Thus a double error of estimation may occur if offspring body mass and litter weight are predicted from such an estimate of mass. Therefore, some other direct measurement that could be taken from fossil material related to offspring body mass, litter weight and litter size is needed. To date, no such relationships have been developed. The major focus of this work is to seek and test the validity of osteological traits as they relate to offspring mass, litter weight, and litter size in placental mammals. Two traits are considered in this work as predictors of offspring body mass, litter weight, and litter size. These are the inter-acetabulum width (IAW), a trait related to the width of birth canal, and the lumbar length (LL), related to the uterine capacity (Fig. 1).

2. Materials and methods

2.1. Materials and measurements

Measures of inter-acetabulum width (IAW) and lumbar length (LL) were collected from fifty nine (59) specimens of extant mammals representing a broad range of placental mammal taxa within the orders Rodentia, Carnivora, Primate, Artiodactyla, Perissodactyla, and Proboscidea (SD Table 1). Only placental mammals were included because they give birth to developed offspring, turning significant the width of birth canal for limiting offspring body size. Xenarthras were excluded because of the high variability of their lumbar regions (vertebral fusion and vertebral number) that could result in the lumbar length being a measure that could not be reliably replicated. Species included in the work are these deposited in the most important museums of Argentina (further work with greater amount of data set can permit improve the results for specific taxonomic signification). Measurements were taken with digital caliper to the nearest 0.01 mm (and with tape-measure for measurements greater than 30 cm). IAW was measured as the distance between intern-sides of the acetabulum of the pelvis at the midpoint of the acetabular fosa, and the LL was measured as a right line from the anterior side of the most anterior lumbar vertebral body (centrum) to the posterior border of the most caudal lumbar centrum. The inter-acetabulum width is considered in the present work an estimator of the birth canal size, and the lumbar length as an estimator of the uterine capacity in pregnancy. Some caution need be considered in taking these measurements: IAW should be measured on articulated pelvis; LL: lumbar vertebrates should be without fusion with sacral region or with a clear suture that shows its extension, length should be taken as a right line between lumbar region ends, so anatomical space is represented although column can be curved, and all measurements should be taken without inter-vertebral disks.

These two variables were related to the average of offspring body mass (i.e. body mass of the new born young), the average of litter size, and the average of adult body mass for each taxon which were acquired from the literature (Nowak, 1999). Adult body mass was considered as the average between sexes when sexual dimorphism was present, because museum material frequently has not sexual identification. The mean value of the sexes is more representative of size if sex is not determined. However, future works with sex identification and sex specific body mass can improve estimations in extant mammals. The litter weight was calculated as the product between the average of offspring body mass and the average of the litter size of each taxon. The phylogenetic tree of the species included in the work used for performing the Phylogenetic Generalized Linear Models (PGLS see data analysis), was made with DNA sequences of CITb (GENbank) in Mega 6.60 (SD Fig. 1).

2.2. Data analysis

The phylogenetic signal (R version 3.1.3, 2015) was calculated on all the variables (SD Table 2). Variables were analyzed with PGLS; this function fits a linear model controlling for the non-independence between cases resulting from phylogenetic structure in the data (R version 3.1.3, 2015). The significant regressions were used to estimate offspring body mass and litter weight. Litter size was calculated from the division between the estimated litter weight on the estimated offspring body mass (i.e. litter size = litter weight/offspring body mass). The minimal and maximal values of the estimations were calculated from the residuals Standard Errors, and these values were used to calculate the limits of litter size. Limits of litter size were obtained in this work with the minimal and maximal values of offspring body mass and litter weight intercalated (i.e. min. litter size = max. offspring body mass/min. litter weight; max. litter size = min. offspring body mass/max. litter weight). All analyses were performed in R 3.1.3 (R version 3.1.3, 2015).

2.3. Fossil estimations and possible use of the estimated variables

Knowing offspring body mass and litter size in fossil mammals opens a new means to study and approach paleoecology and evolution. I propose how these variables can be used to describe population growth and I describe some indicator values (population growth factor, reproductive success factors, and variability factor) to predict

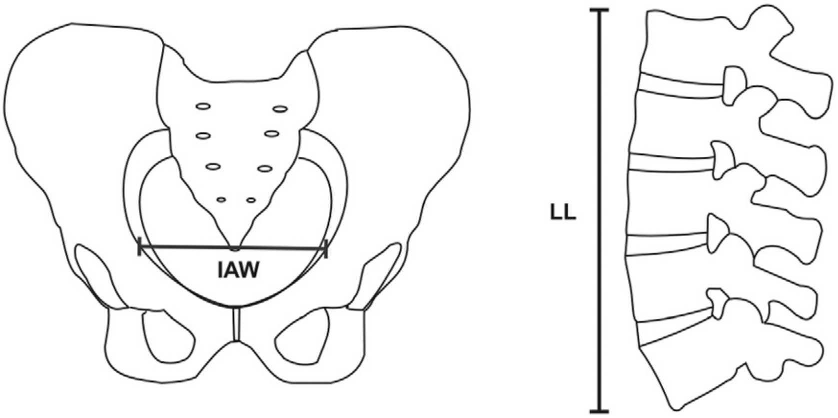

Fig. 1. Metric measurements considered in the work. Figure shows the metric measurements tested in the work to estimate offspring characteristics in extant and fossil mammals (figure of the example is in human bones). IAW: inter-acetabulum width, LL: lumbar length.