

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



Elissamburu Andrea

CONICET, Cátedra de Anatomía Comparada, Facultad de Ciencias Naturales y Museo, UNLP, Calle 64 s/n entre 120 y diagonal 113, 1900 La Plata, Buenos Aires, Argentina

## ARTICLE INFO

### Article history:

Received 24 October 2015

Received in revised form 25 March 2016

Accepted 31 March 2016

Available online 09 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.

© 2016 Elsevier B.V. All rights reserved.

## 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; Côté 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) (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

E-mail addresses: [aelissamburu@gmail.com](mailto:aelissamburu@gmail.com), [elissamburu@hotmail.com](mailto:elissamburu@hotmail.com).

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 those 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.

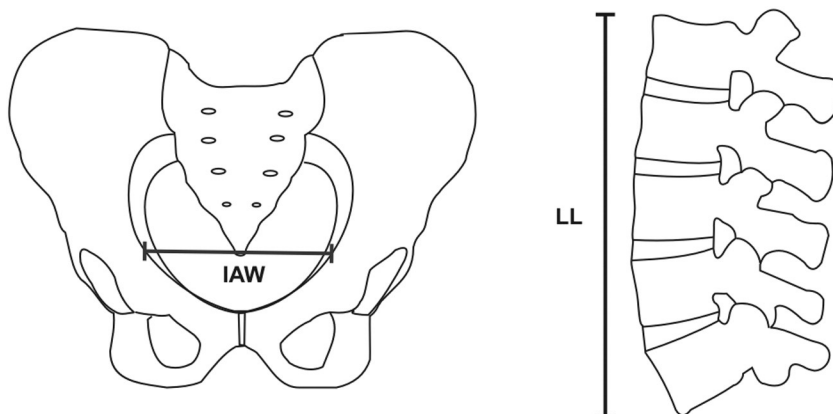
These two variables were related to the average of offspring body mass (i.e. body mass of the new born young), the average of litter size, and the average of adult body mass for each taxon which were acquired from the literature (Nowak, 1999). Adult body mass was considered as the average between sexes 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.

inter-specific and intra-specific trends front to different ecological situations through time (environment stability, competence, predation, availability of niches). This is only presented as a starting point to explore potentially meaning offspring variables in fossil mammals for advancing knowledge regarding paleoecology and evolution.

2.3.1. Population growth (Pg)

Population growth of extant mammals is generally investigated and discussed in terms of offspring number, survival, effort, density, fitness, fecundity, female age at first reproduction, among others (Winkler and Wallin, 1987; Sibly et al., 2005; Coulson et al., 2006; Hone et al., 2010; Sibly and Hone, 2002). Since these characteristics cannot be directly observed in extinct mammals, life history studies of fossils have been seriously constrained. However, offspring body mass, litter size and time of growth (time of gestation (Blueweiss et al., 1978) and time to get adult body mass (Gillooly et al., 2002)) can be inferred from offspring and adult body mass, and thus can provide a curve of population growth through time if all other biological and ecological variables are considered constant. This can provide a starting point to compare population growth between species. Population growth (measured as the increase of females into the population) is given as:

$$Pg_{(g)} = 1 + \left(\frac{\text{litter size}}{2}\right)^g + \left(pg_{(g-1)} * \frac{\text{litter size}}{2}\right) * \frac{gt}{edt};$$

where *g* = generation (1, 2, 3, etc.), and *Pg*(0) = 0. Additionally, *gt/edt* is the proportion of adult reproduction in generational time, it is expressed as the time of development from offspring to adult body mass (*gt*: generation time) divided the time of gestation (*edt*: embryonic development time).

2.3.2. Population growth factor (PgF)

To compare the population growth between two species a value that takes into account time and reproduction in a standardized form is needed. I propose to standardize the population growth as the input on one year (measured on females). Thus, *PgF* can be expressed as:

$$PgF = 1 + \left(\frac{\text{litter size}}{2}\right)^{365/gt} + \sum_{i=1}^{(365/gt)-1} \left(\frac{\text{litter size}}{2}\right)^{(365/gt)-1-i} * \frac{\text{litter size}}{2} * \frac{gt}{edt};$$

where 365/*gt*, and *gt/edt* must be expressed only as the integer part of the division.

2.3.3. Reproductive Success Factors (OARSF; AARSF; SRSF)

The value: 365/*gt* is defined as an indicator of Offspring Annual Reproductive Success (OARSF). The value: 365/*edt* is defined as an indicator of Adult Annual Reproductive Success (AARSF). The product between OARSF and AARSF is defined as an indicator of Species Reproductive Success (SRSF = OARSF\*AARSF). These can be compared between species.

2.3.4. Variability factor (VF)

Another important issue that can be represented is the variability (phenotypic and genotypic) on which selection acts through time. It can be expressed as the variability that a couple generates on one year (i.e, VF = 2\**PgF*), although to explore variability through time can be very useful.

Some extinct mammals (SD Table 1) were included to illustrate their offspring body mass, litter weight and litter size. For application example, *Actenomys priscus* (Rodentia: Ctenomyidae) and *Paedotherium* sp. (Notoungulata: Hegetotheriidae) were used to illustrate population growth and the proposed indicator values that can provide paleoecological information and predict evolutionary trends. Values of adult body

mass for these two taxa (required to calculate time of growth) were obtained from the literature (Elissamburu et al., 2011).

3. Results and discussion

3.1. Predictors of offspring body mass, litter weight and litter size

Table 1 summarize the regressions (PGLS) to predict offspring body mass and litter weight in placental mammals in general. The present data set includes the representative taxa from which the regression equations were derived. Nevertheless, future works with additional data sets can improve regressions for taxonomical specific applications, which could have more accurate predictions within specific groups. IAW is the best predictor of offspring body mass and litter weight, having the strongest relationships (*r*<sup>2</sup> > 0.85, *p* < 0.001). Additionally, IAW was highly correlated with adult body mass (ABM), a relationship that permits comparison of IAW to body mass attributes. Relationship of IAW to adult body mass is expected, because offspring characteristics are generally related to adult body mass (Sacher and Staffeldt, 1974; Millar, 1977; Blueweiss et al., 1978; Economos, 1982b). ABM regression was not as strongly related to IAW as offspring body mass, suggesting that IAW has a more direct association with offspring body mass than to adult body mass. Association between adult anatomy and offspring features permits to consider that some constraints or trade-off between adult anatomy and offspring exist, and these should be considered in studies of ecology and evolution. Additionally, relationship between IAW and adult body mass was not as strongly correlated as taxonomic specific regressions between adult body mass and limb or cranial bone measurements (e.g. (Damuth and MacFadden, 1990)). Future regressions of IAW within a variety of more inclusive clades could discern if IAW is more directly associated to offspring features or to adult body mass in specific taxonomic groups.

On the other hand, lumbar length (LL) has low regression values (0.59 < *r*<sup>2</sup> < 0.61, *p* < 0.001) with offspring body mass, litter weight, and body mass variables, and is thus considered to be a poor predictor of these variables. Even if LL is anatomically associated to uterine capacity during pregnancy, its relationship is imprecise and thus is of little value in estimating this capacity. This poor predictive value may be related to the fact that the lumbar region is involved in other of biomechanical and anatomical functions not related to uterine capacity (e.g., body structure, body support, visceral support, locomotion, flexibility, mobility of vertebral column). In any case, a more direct measurement of uterine capacity appears to be necessary.

Regressions between adult body mass and offspring body mass, and litter weight have highly significant values, following the results reported by Economos and Blueweiss (Blueweiss et al., 1978; Economos, 1982b) and the results herein. Fig. 2 shows the cited regressions of IAW and LL that have predictive value in regard to estimating offspring body mass and litter weight in extant and fossils mammals. As litter size did not demonstrate any significant regressions with the metric

Table 1

Regressions (PGLS) for the metric measurements IAW and LL. IAW: inter-acetabulum width, LL: lumbar length, OBM: offspring body mass, LW: litter weight, ABM: adult body mass.

Regressions (PGLS)				
Regressed variables	a (y-intercept)	B (slope)	r <sup>2</sup>	p
log(IAW) = a + b * log(OBM)	1.550	0.358	0.89	< 0.001
log(IAW) = a + b * log(LW)	1.121	0.409	0.86	< 0.001
log(LL) = a + b * log(OBM)	2.951	0.233	0.59	< 0.001
log(LL) = a + b * log(LW)	2.654	0.264	0.61	< 0.001
log(ABM) = a + b * log(IAW)	0.661	2.337	0.85	< 0.001
log(ABM) = a + b * log(LL)	-0.451	2.448	0.59	< 0.001
log(ABM) = a + b * log(OBM)	4.171	0.882	0.81	< 0.001
log(ABM) = a + b * log(LW)	2.706	1.034	0.87	< 0.001

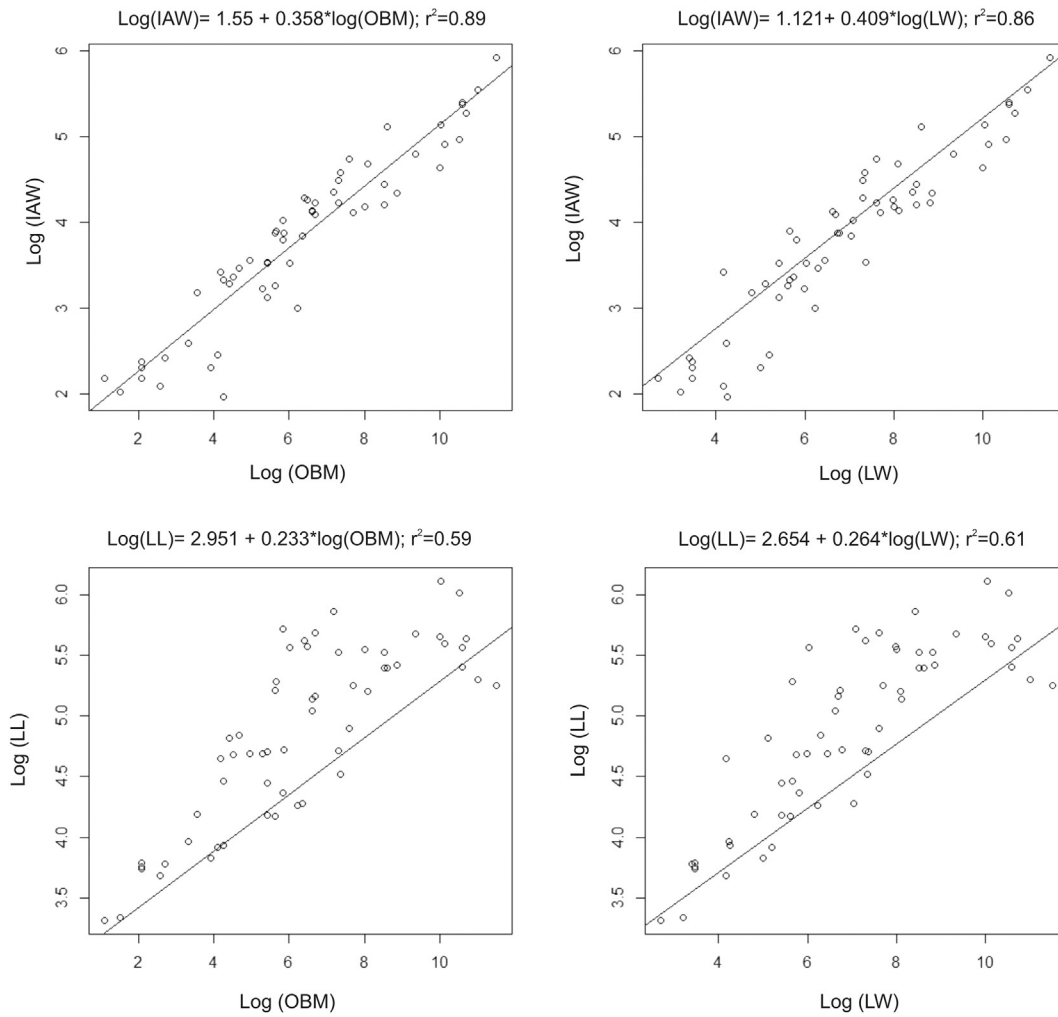


Fig. 2. Significant regressions in extant mammals (PGLS). Figure shows the significant regressions for the variables IAW and LL front to offspring body mass (OBM) and litter weight (LW).

variables, thus these are not graphed in Fig. 2 nor given in the regressions of Table 1.

### 3.2. Offspring characteristics in fossil mammals

Using extant placental mammals in a general framework to test regressions permits finding associations upon taxonomic classifications that can be representative of placental mammals. Thus, these regressions can be used for interpreting fossil taxa with or without extant relatives, taking into account proper use and that taxa with extant relatives into the tested regression are having more accurate estimations. Included fossil mammals are from Orders Xenarthra (if extant Xenarthra could be incorporated in the regression the estimation can

improve), Litopterna, Notoungulata, Carnivora and Rodentia. Table 2 summarizes the estimated values of offspring body mass, litter weight and minimal and maximal litter sizes for included extinct mammals. These estimations were obtained from the variable IAW. Litter sizes were obtained from dividing the estimations of litter weight on offspring body mass (see Methods section for detail).

Among the fossils included in the work, *Megatherium americanum* (Xenarthra, Megatheriidae), *Macrauchenia patachonica* (Litopterna, Macraucheniidae), and *Toxodon platensis* (Notoungulata, Toxodontidae) are predicted to have had only one offspring of 85.76 kg, 46 kg, and 99.5 kg respectively (values of offspring body mass are obtained from IAW using the regression of IAW–OBM of extant mammals). *Smilodon* sp. (Carnivora, Machairodontinae) could have had from one to two

**Table 2**  
Offspring estimations in fossil mammals. Estimated values of offspring body mass, litter weight and minimal and maximal litter sizes for some extinct mammals. IAW: inter-acetabulum width (mm), offspring body mass and litter weight are estimated in grams.

Taxon	IAW	Offspring body mass			Litter weight			Litter size		
		Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
<i>Macrauchenia patachonica</i>	220	45,984.83	35,949.61	58,821.35	34,413.62	24,601.22	48,139.79	0.75	0.42	1.34
<i>Megatherium americanum</i>	275	85,763.95	67,047.77	109,704.68	59,383.67	42,451.53	83,069.35	0.69	0.39	1.24
<i>Toxodon platensis</i>	290	99,478.92	77,769.74	127,248.14	67,617.6	48,337.7	94,587.45	0.68	0.38	1.22
<i>Smylodon</i> sp.	100.64	5174.81	4045.52	6619.34	5085.23	3635.27	7113.51	0.98	0.55	1.76
<i>Paedotherium</i> sp.	28.62	154.35	120.67	197.44	235.04	168.02	328.79	1.52	0.85	2.72
<i>Actenomys priscus</i>	11.73	12.78	9.99	16.35	26.55	18.98	37.14	2.08	1.16	3.72

offsprings of approximately 5 kg each. *Paedotherium* sp. could have had from one to three offsprings of 154 g each and *Actenomys priscus* could have had one to four offsprings of 12.8 g each.

Estimations of offspring characteristics open a new means to study paleobiology, paleoecology and evolution of fossil species. Because these data permit means to infer, at least with first order approximations, life history attributes, such as population growth, dynamics of faunal replacement, characteristic of occupation of niches related to environmental changes, and the tempo of evolution. Paleofaunal studies that integrate offspring data can give a more dynamic and realistic representation of the paleoecology and dynamics of the faunistic assemblages and communities. Such is exemplified in the follow section.

### 3.3. Improving paleoecological and evolutive studies

As an example of application of the present estimations, Fig. 3 shows the estimated offspring body mass and litter size, the gestation (Blueweiss et al., 1978) and development time (Gillooly et al., 2002), and the values of the proposed factors for the contemporaneous and ecologically related fossil taxa, *Actenomys priscus* and *Paedotherium* sp. Fig. 4 shows the population growth through time (measured as the increase of females into the population) for each species.

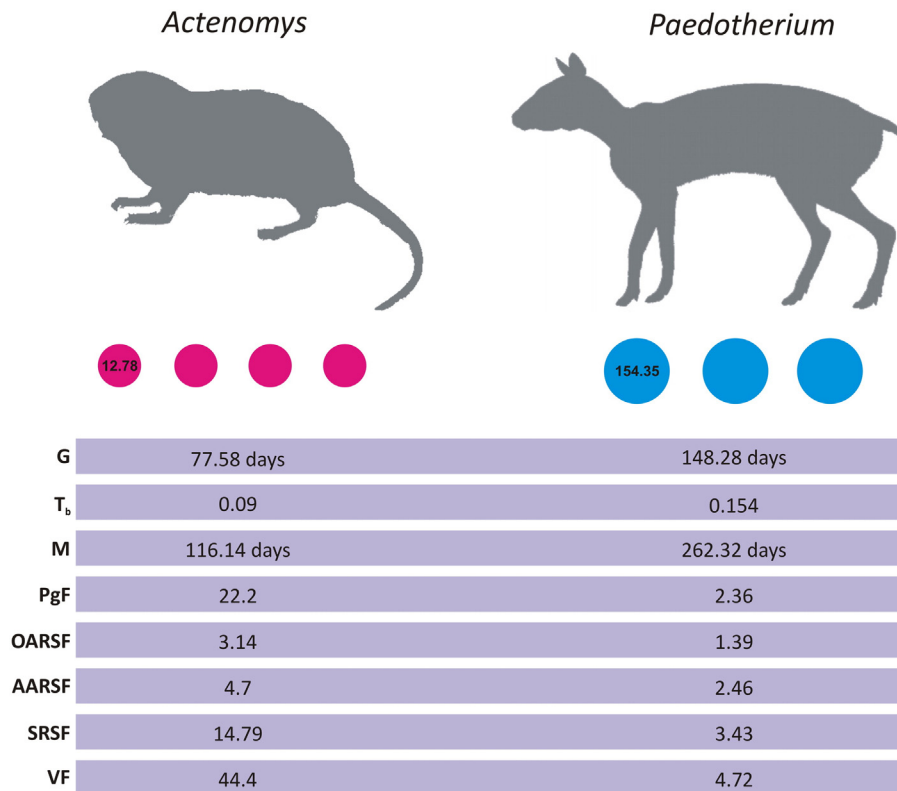
Life history attributes of two extinct taxa, *Actenomys priscus* (Rodentia: Caviomorpha) and *Paedotherium* sp. (Notoungulata: Typotheria) were inferred from the regression equations developed in this study based upon their pelvic skeletal traits. Both taxa are known from the Pliocene of Buenos Aires Province (Montehermosense, Chapadmalalense and Marplatense; Cione and Tonni, 1995a, 1995b). Both have been regarded as scratch diggers (Elissamburu, 2001; Elissamburu, 2004) and have been associated to trace fossils of burrows construction in the Chapadmalal Formation. *Actenomys priscus* is thought to have constructed burrows of 10–18 cm of diameter and *Paedotherium*

sp. having constructed others of 16–22 cm of diameter (Elissamburu et al., 2011). Additionally, these fossil burrows show some spatial and temporal differences in their distributions (Elissamburu et al., 2011), suggesting a degree of niche partitioning between the two taxa.

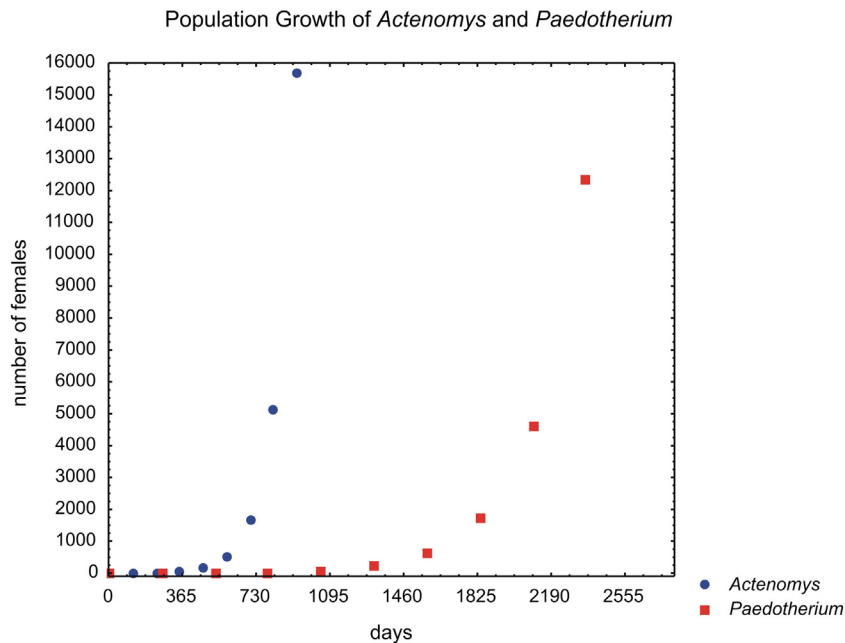
Estimated variables of life history of these taxa suggest that *A. priscus* had a gestation time of approximately 78 days, it giving birth to a maximum of four offspring that reach maturity around 116 days (time to reach adult body mass). On the other hand, *Paedotherium* sp. had a gestation time of approximately 148 days, having a maximum of three offspring that reached maturity in 262 days.

Population size increased faster in *Actenomys* than in *Paedotherium*; in two years *Actenomys* reaches population values that take five years to *Paedotherium* (Fig. 4). Population Growth Factor gives a comparative value to represent this disparity, with *Actenomys* having a value of 22.2 and *Paedotherium* having a PGF of 2.36. These differences in population growth permit inferring that *Actenomys* had a more dynamic population than *Paedotherium*. In these ecologically, temporally and spatially related mammals a more dynamic population could give an advantage for occupation of space (with construction and use of paleoburrows). Additionally, intra-specific competence could be higher, favoring the population dispersion and distribution. Spatial interaction in same soils could be supported if food resource were dissimilar for each species and inter-specific competence was reduced or if interaction favored another ecological factor for some of species (reducing predation, occupying constructed paleoburrows).

Additionally, *Actenomys* has high Adult Reproductive Success Factor (ARSF: 4.7) and Offspring Reproductive Success Factor (ORSF: 3.14), whereas *Paedotherium* has lower values, with ARSF (2.5) bigger than ORSF (1.4). These reproductive values show that in *Actenomys* both adults and offspring have high reproductive success; thus both ontogenetic stages have higher probability of survival, and in both could act selection pressure. On the other hand, in *Paedotherium* adults



**Fig. 3.** Life history estimated variables in *Actenomys* and *Paedotherium*. Litter size and offspring body mass for each taxon are represented by circles with its body mass values (expressed in grams) inside. G: gestation time (Blueweiss et al., 1978) ( $G = OBM/0.025 * OBM^{0.74}$ ; in the present work  $G = edt$ ), T<sub>b</sub>: biological time (Gillooly et al., 2002) ( $T_b = t(m/m_0)^{-1/4} * e^{-\alpha T_c/(1 + T_c/T_0)}$ ), M: maturity time (obtained from T<sub>b</sub> and the increase of body mass from offspring to adult), PgF: population growth factor, OARSF: offspring annual reproductive success factor, AARSF: adult annual reproductive success factor, SRSF: species reproductive success factor, VF: variability factor.



**Fig. 4.** Population growth of *Actenomys* and *Paedotherium* calculated as the increase of females from generation to generation. Population growth is calculated from estimated litter size, generation time and embryonic development time.

and offspring have lower values of reproduction, with lower values in offspring; thus offspring phase is more vulnerable because it required longer times to reach maturity and reproduction. In *Paedotherium* selection pressures on the offspring appeared to be greater. Species Reproductive Success Factor (which includes reproduction in all phases) is much higher in *Actenomys* (14.8) than in *Paedotherium* (3.4). While the reproductive factor is not decoupled in adult and offspring reproduction, it is still likely to be relevant in analyzing reproductive success between species in stable environment with high food availability.

Additionally, the variability factor of *Actenomys* in one year (44) is much greater than that of *Paedotherium* (4.7). This value allows to predict a higher probability of facing ecological and environmental changes, thus increasing the probability of adaptation and speciation in *Actenomys* than in *Paedotherium*.

#### 4. Conclusion

Knowledge of fundamental features of reproductive strategies is essential for understanding basic features of adaptations, life histories, and ecology of animals. Such fundamental data are generally lacking in paleoecological studies. However, this study suggests that at least some morphological features preserved in fossils can integrate life histories into the study of fossil taxa and thus provide clues regarding the lives of extinct animals that are absent in current studies. This study provides an example that illustrates possibilities, such as estimating offspring body mass and litter size in fossils mammals. Such opens a new means of study in paleoecology and evolution. Offspring body mass and litter size of fossil mammals can be a key to creating new tools that permit improving knowledge in these important issues.

Future taxonomic specific regressions and sex determined material can add more relevance for specific estimations. Finally, anatomical constraints of adults on offspring characteristics should be considered in future works.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2016.03.033>.

#### Acknowledgments

CONICET—Argentina financed the work. Thanks to M. Reguero and I. Olivares (Museo de Ciencias Naturales de La Plata, Argentina), to F. Scaglia and D. Romero (Museo de Ciencias Naturales de Mar del Plata, Argentina) and to S. Lucero (Museo de Ciencias Naturales Bernardino Rivadavia de Buenos Aires, Argentina) for the access to the respective collections. Thanks also to R. Lee Lyman and an anonymous reviewer for the very constructive and interesting comments that improved the work and to Bruce J. Shockey for help with the English and for the very useful and interesting comments that improved the work.

#### References

- Begon, M., Townsend, C.R., Harper, J.L., 2006. *Ecology: from Individuals to Ecosystems*. Blackwell Publishing, MA, USA.
- Blueweiss, L., et al., 1978. Relationships between body size and some life history parameters. *Oecologia* 37, 257–272.
- Bueno, J., López-Urrutia, A., 2012. The offspring-development-time/offspring-number trade-off. *Am. Nat.* 179 (6), 196–203.
- Charnov, E.L., Ernest, S.K.M., 2006. The offspring-size/clutch-size trade-off in mammals. *Am. Nat.* 167, 578–582.
- Cione, A.L., Tonni, E.P., 1995a. Los Estratotipos de los pisos Montehermosense y Chapadmalalense (Plioceno) del esquema cronológico sudamericano. *Ameghiniana* 32, 369–374.
- Cione, A.L., Tonni, E.P., 1995b. Chronostratigraphy and “Land-Mammal Ages” in the Cenozoic of Southern South America: principles, practices, and the “Uquian” problem. *J. Paleontol.* 69, 135–159.
- Côté, S.D., Festa-Bianchet, M., 2001. Birthdate, mass and survival in mountain goat kids: effect of maternal characteristics and forage quality. *Oecologia* 127, 230–238.
- Coulson, T., Benton, T.G., Lundberg, P., Dall, S.R.X., Kendall, B.E., Gaillard, J.M., 2006. Estimating individual contributions to population growth: evolutionary fitness in ecological time. *Proc. R. Soc. B* 273, 547–555.
- Damuth, J., MacFadden, B.J., 1990. *Body Size in Mammalian Palaeobiology: Estimation and Biological Implications*. Cambridge University Press, NY, USA.
- Economos, A.C., 1982a. Evolution of developmental rate in mammals. *Exp. Gerontol.* 7, 153–158.
- Economos, A.C., 1982b. Mammalian design and rate of living. *Exp. Gerontol.* 17, 145–152.
- Elissamburu, A., 2001. *Análisis Morfométrico y Morfofuncional del Esqueleto Apendicular de Paedotherium (Mammalia, Notoungulata) del Plioceno y Pleistoceno Temprano de la Provincia de Buenos Aires. Correlación con su Aptitud Fosorial*. (Tesis de Licenciatura en Ciencias Biológicas, FCEyN, UNMdP, Argentina).
- Elissamburu, A., 2004. Análisis morfométrico y morfofuncional del esqueleto apendicular de Paedotherium (Mammalia, Notoungulata). *Ameghiniana* 41 (3), 363–380.

- Elissamburu, A., Dondas, A., De Santis, L., 2011. Morfometría de Las Paleocuevas de la "Fm." Chapadmalal Y Su asignación a *Actenomys* (Rodentia). *Paedotherium* (Notoungulata) Y Otros mamíferos fósiles Hospedantes. *Mast. Neotrop* Vol. 18(2), pp. 227–238.
- Gillooly, J.F., Charnov, E.L., West, G.B., Savage, V.M., Brown, J.H., 2002. Effects of size and temperature on developmental time. *Nature* 417, 70–73.
- Hamel, S., Côté, S.D., Festa-Bianchet, M., 2011. Tradeoff between offspring mass and subsequent reproduction in a highly iteroparous mammal. *Oikos* 120, 690–695.
- Hone, J., Duncan, R.P., Forsyth, D.M., 2010. Estimates of maximum annual population growth rates ( $r_m$ ) of mammals and their application in wildlife management. *J. Appl. Ecol.* 47, 507–514.
- Huggett, A., StG., Widdas, W.F., 1951. The relationship between mammalian fetal weight and conception age. *J. Physiol.* 114, 306–317.
- Iason, G.R., 1990. The effect of size, age and cost of early breeding on reproduction in female mountain hares. *Holarct. Ecol.* 13, 81–89.
- Lambin, X., Yoccoz, N.G., 2001. Adaptive precocial reproduction in voles: reproductive cost and multivoltine life-history strategies in seasonal environments. *J. Anim. Ecol.* 70, 191–200.
- Leitch, I., Hytten, F.E., Billewicz, W.Z., 1959. The maternal and neonatal weights of some mammalia. *Proc. Zool. Soc. London* 133, 11–28.
- Messina, F., Fox, C., 2001. Offspring Size and Number. In: Fox, C.W., Roff, D.A., Fairbairn, D.J. (Eds.), *Evolutionary Ecology: Concepts and Case Studies*. Oxford University Press, New York, pp. 113–127.
- Millar, J.S., 1977. Adaptive features of mammalian reproduction. *Evolution* 31, 370–386.
- Moyes, K., et al., 2006a. Cumulative reproduction and survival cost in female red deer. *Oikos* 115, 241–252.
- Moyes, K., Coulson, T., Morgan, B.J.T., Donald, A., Morris, S.J., Clutton-Brock, T.H., 2006b. Cumulative reproduction and survival cost in female red deer. *Oikos* 115, 241–252.
- Nowak, R.M., 1999. *Walker's Mammals of the World*. The Johns Hopkins University Press, Baltimore.
- R version 3.1.3, 2015. (2015-03-09) "Smooth Sidewalk" Copyright (C). The R Foundation for Statistical Computing.
- Sacher, G.A., Staffeldt, E.F., 1974. Relation of gestation time to brain weight for placental mammals. *Am. Nat.* 108, 593–615.
- Sibly, R.M., Brown, J.H., 2009. Mammal reproductive strategies driven by offspring mortality-size relationships. *Am. Nat.* 173, 185–199.
- Sibly, R.M., Hone, J., 2002. Population growth rate and its determinants: an overview. *Philos. Trans. R. Soc. Lond. B* 357, 1153–1170.
- Sibly, R.M., Barker, D., Denham, M.C., Hone, J., Pagel, M., 2005. On the regulation of populations of mammals, birds, fish, and insects. *Science* 309, 607–610.
- Stearns, S.C., 1976. Life-history tactics: a review of the ideas. *Q. Rev. Biol.* 51, 3–47.
- Stearns, S.C., 1977. The evolution of life history traits: a critique of the theory and a review of the data. *Annu. Rev. Ecol. Syst.* 8, 145–171.
- Winkler, D.W., Wallin, K., 1987. Offspring size and number: a life history model linking effort per offspring and total effort. *Am. Nat.* 129, 708–720.