



## Splendid oddness: revisiting the curious trophic relationships of South American Pleistocene mammals and their abundance

RICHARD A. FARIÑA, ADA CZERWONOGORA and MARIANA DI GIACOMO

Universidad de la República, Laboratorio de Paleobiología, Facultad de Ciencias, Iguá 4225, 11400, Montevideo, Uruguay

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### ABSTRACT

The South American Pleistocene mammal fauna includes great-sized animals that have intrigued scientists for over two centuries. Here we intend to update the knowledge on its palaeoecology and provide new evidence regarding two approaches: energetics and population density and relative abundance of fossils per taxa. To determine whether an imbalance exists, population density models were applied to several South American fossil faunas and the results compared to those that best describe the palaeoecology of African faunas. The results on the abundance study for Uruguay and the province of Buenos Aires during the Lujanian stage/age reveal that bulk-feeding ground sloths (*Lestodon* and *Glossotherium*) were more represented in the first territory, while the more selective *Scelidotherium* and *Megatherium* were more abundant in the second. Although the obtained values were corrected to avoid size-related taphonomic biases, linear regressions of abundance vs. body mass plots did not fit the expected either for first or second consumers. South American Pleistocene faunas behave differently from what models suggest they should. Changes in sea level and available area could account for these differences; the possibility of a floodplain in the area then emerged could explain seasonal changes, which would modify the calculations of energetics and abundance.

**Key words:** abundance, megafauna, palaeoecology, population density, secondary productivity, Quaternary.

### INTRODUCTION

#### THE PECULIAR LUJANIAN MEGAFUNA

George Gaylord Simpson, probably the greatest 20<sup>th</sup> century vertebrate palaeontologist, openly declared his fascination for the large-mammal faunas of South America, as explicitly stated in the title of the book paraphrased in this paper (Simpson 1980). The appeal of these beasts relied, according to Simpson, on their diversity and special taxonomic composition, consequence, as he stated, of the post-Gondwanian isolation of the landmass in which

those mammals evolved. The attractiveness derived from the taxonomic oddness of the extinct South American mammalian faunas is valid for the whole of the Cenozoic and perhaps especially for the Lujanian stage/age (late Pleistocene-early Holocene). For instance, in the eponymous Luján local fauna, about half of the genera of those mammals with body masses above 10 kg were extinct xenarthrans, such as pampatheres, glyptodonts and ground sloths, and among the rest there were members of extinct and exclusively South American ungulate-like clades, such as litopterns and notoungulates, as well as proboscideans and very large camelids and sabretoothed felids.

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Correspondence to: Richard A. Fariña  
E-mail: [fari~a@fcien.edu.uy](mailto:fari~a@fcien.edu.uy)

There are also other reasons for why the Lujanian fauna causes fascination: one of its members, *Megatherium*, was studied under a modern palaeontological approach as early as the final years of the 18<sup>th</sup> century by Cuvier himself (Cuvier 1796) and, even before that, it was the first extinct vertebrate reconstructed in life position (Bru de Ramón 1784-1786). Only a few decades later did the megafauna become one of the major sources of inspiration for Darwin's ideas on evolution (Vizcaíno et al. 2009).

It should be added to former reasons the very large size of several of its members, as many species are proposed to have had adult body masses above one tonne (Fariña et al. 1998, 2013, Bargo et al. 2000, Vizcaíno et al. 2012). Moreover, their palaeoautecological traits are very peculiar and the studies on their palaeosynecology (Fariña 1996) have shown unexpected trophic relationships, as discussed below.

Remains of this fauna are common in the broadly distributed and abundant late Pleistocene loess or reworked loess sediments (Panario and Gutiérrez 1999, Zárate 2003) of mid-latitude South America, especially in Uruguay and the province of Buenos Aires, Argentina; many of such fossils were collected and housed in museums and personal collections as early as the end of the 19<sup>th</sup> century. The greatest South American palaeontologist, Florentino Ameghino, was the first author to make a comprehensive attempt to systematize the stratigraphy and faunal composition for the Lujanian age (see, for instance, Ameghino 1889). In this work we intend to update the knowledge on the palaeoecology of this fauna, and provide new knowledge in regard to two approaches: 1) energetics and population density, and 2) relative abundance of fossils per taxa. Our study focuses especially in the surrounding area of the Río de la Plata (Uruguay and the province of Buenos Aires, Argentina) but the first approach includes faunas from the rest of South America and the conclusions are largely valid for the whole of the landmass.

#### ENERGETICS AND POPULATION DENSITY

It was Darwin (1839) who first had a glimpse of the issue of so many large mammals living together and the ecological consequences of it. Indeed, the Chapter V of his journal of the Beagle's Voyage, was subtitled "*Large animals do not require luxuriant vegetation*" and included reflections on this subject in addition to commenting on the finding of remains of several large mammals in the Río de la Plata region. He then proceeded to compare the diversity and abundance of Lujanian and African faunas, drawing an interesting conclusion: although in India elephants and rhinos do dwell in fine forests, Brazilian jungles support mammals on average 25-fold smaller than those impressive mammals in the apparently less fertile African savannas and scrubs. According to Darwin's view, the numerous large mammals whose remains he found might not have been related to a much more luscious vegetation than that found today in the region, due to the lack of great physical changes which have not modified the features of the country (Darwin 1839). However, some physical change, unknown at the time of the great naturalist, did occur, as will be discussed below.

Inferences of past trophic ecology have become available since then and have greatly benefitted from modern ecological, taxon-free approaches (Damuth 1982) that determine which types of ecological properties and interactions are independent of the taxonomic composition (hence of phylogenetic legacy) and even of the time period studied, based both on trophic/energetic and biological size theory grounds. Those models were used by Fariña (1996) to make progress from Darwin's observations. In that paper, the body masses of the members of the fauna were estimated and their population density (measured as individuals per km<sup>2</sup>) was inferred following Damuth (1981) and other appropriate equations, yielding a proposal of a double imbalance: too many primary consumers for the inferred primary productivity and too few

carnivores for the secondary productivity. This led to the proposal of cryptic flesh-eaters. The giant ground sloth *Megatherium americanum* was considered an appropriate candidate, based on the potential fast extension of its forearm (hence having made possible an aggressive use of its large claws, Fariña and Blanco 1996), on the sharp dentition (useful for cutting fleshy food items and not so much for grinding hard grasses, Bargo 2001 a, b, 2003) and some marks on a rib of another megamammal that are congruent with the shape and dimensions of its dentition (Fariña 2002). Some time ago, one of the aspects of the imbalance, that of the flesh-eaters supported by the primary consumer biomass, was questioned by Prevosti and Vizcaíno (2006), for reasons to be discussed below.

#### ABUNDANCE

The palaeoecological context of the Lujanian megafauna can shed new light on their abundance. The just mentioned excess of trophic resources for carnivores and lack of them for herbivores (Fariña 1996) in the Luján local fauna (Tonni et al. 1985) could be related to taphonomic and temporal biases, although other local faunas of similar age with taphonomic and stratigraphic control (that also defined historically the Lujanian local one) show similar patterns (Bargo et al. 1986, Prado et al. 1987). In any case, actual relative abundance of current species or ecological diversity is frequently used to describe extant and fossil vertebrate communities of phylogenetically diverse members, as a means of identifying possible biases in the fossil record (Damuth 1982). The ecological validity of this distribution depends on taphonomic controls over the original abundance of this fauna; actualistic studies indicate the existence of important preservational biases related to body size (big vs. small taxa), habitat and mode of death of the organisms, that affect composition and relative abundance of species in bone assemblages (Palmqvist et al. 2003 and references therein).

Determination of the number of individuals per taxa present in a fossil assemblage is a prerequisite to perform many palaeoecological studies, especially those that involve relative or absolute abundance populations (Badgley 1986). Taphonomic context of an assemblage provides information to choose the appropriate quantification method: in this work the relative abundance in the Lujanian community will be assessed using Damuth's (1982) model, and such outcome will be integrated with those of the reanalysis just described above.

### MATERIALS AND METHODS

#### ENERGETICS AND POPULATION DENSITY

All of the taxa found in the Luján local Fauna and listed in Tonni et al. (1985) were classified according to their probable diet. Nomenclature and taxonomy were updated as per Prevosti and Vizcaíno (2006), Soibelzon et al. (2005) and other sources. The masses of the extinct taxa were taken from previous estimations in literature (Smith et al. 2003). Those species whose masses were estimated to have been less than 10 kg were not considered in order to avoid the problem of the biases in fossilisation, preservation, and collection (Behrensmeyer and Hill 1980, Damuth 1982, see Fariña 1996 for further discussion).

To estimate the population density of each herbivorous species, the general equation in Damuth (1981) was used:  $\log D = -0.75 \log m + 4.23$

where  $D$  is population density in number of individuals per square kilometre, and  $m$  is the body mass expressed in grams. This equation is empirical and was obtained from the study of many diverse modern ecosystems. The standard error of the slope is 0.026. If the average minus one s.e. were used rather than -0.75 there would be no important differences in the results.

The basal metabolic rate of these herbivores was recalculated, as per Fariña (1996), following the equation in Peters (1983):  $\log R = -0.25 \log m$

+ 0.6128 where  $R$  is the per-second mass-specific metabolic rate (in  $\text{J kg}^{-1} \text{s}^{-1}$ ), and  $m$  is the body mass expressed in grams.

Due to sound thermodynamical reasons related to the loss of free energy as the trophic level increases, and to biomechanical reasons related to limb bone strength allometry (Sorkin 2008), the modern Carnivora are known to be less abundant than their potential prey. Thus, a different equation must be used to estimate their population density; that obtained by Damuth (1993) for African flesh-eaters (same symbols as above):  $\log D = -0.64 \log m + 2.23$ .

The basal metabolic rate of species belonging to Carnivora is also described by a specific formula, because predators tend to consume more energy than herbivores, even at rest, and that, other things being equal, expenditure tends to be even higher as body size increases. Thus, an appropriate equation, also from Peters (1983), was used:  $\log R = -0.27 \log m + 0.6551$ .

Pleistocene: Apart from Luján, this model was also tested in other 14 South American faunas (see Fig 1). Faunal lists were obtained from the Paleobiology Database and the criterion for choosing them was the presence of at least two carnivore species within them. Body masses were obtained from Smith et al. (2003) and other sources (Casamiquela 1984, Hartwig and Cartelle 1996, Pomi 2008).

Four more models were also tested in these faunas. The first one was a modification of the calculation of population density for the carnivores, since this was an important issue of debate in Prevosti and Vizcaíno (2006). The equation was obtained from Carbone and Gittleman (2002):  $\log D = -0.88 \log m + 2.296$ , where  $D$  is the population density expressed in individuals per  $100 \text{ km}^2$  and  $m$  is the body mass in kg.

The second new model was a modification of the model in Fariña (1996) in the calculation of the secondary productivity. This was made following Western (1983):  $\log P = 0.67 \log m_s + \log N + 1.14$ , where  $P$  is the net productivity expressed in  $\text{kcal km}^{-2} \text{ year}^{-1}$ ,  $N$  is the population density (individuals

per  $\text{km}^2$ ) and  $m_s$  is the equivalent in kcal of the animal's body mass. In order to obtain  $M_s$ , the body mass in gr was multiplied by the caloric value of the mammalian body,  $1.5 \text{ kcal g}^{-1}$  (Banse and Mosher 1980, Western 1983). Production values were transformed into  $\text{J m}^{-2} \text{ year}^{-1}$  in order for them to be comparable to the values of the carnivore's energetic requirements.

The third new model was a mixture of both the first and second models. Population density of the carnivores was calculated following Carbone and Gittleman (2002) and secondary productivity was calculated following Western (1983).

The fourth new model changed the way population density was calculated, as well as the secondary productivity. The population density was calculated following Silva et al. (2001). The equations used were those for herbivores and carnivores:

$$\text{Herbivores: } \log D = 1.43 - 0.68 \log m$$

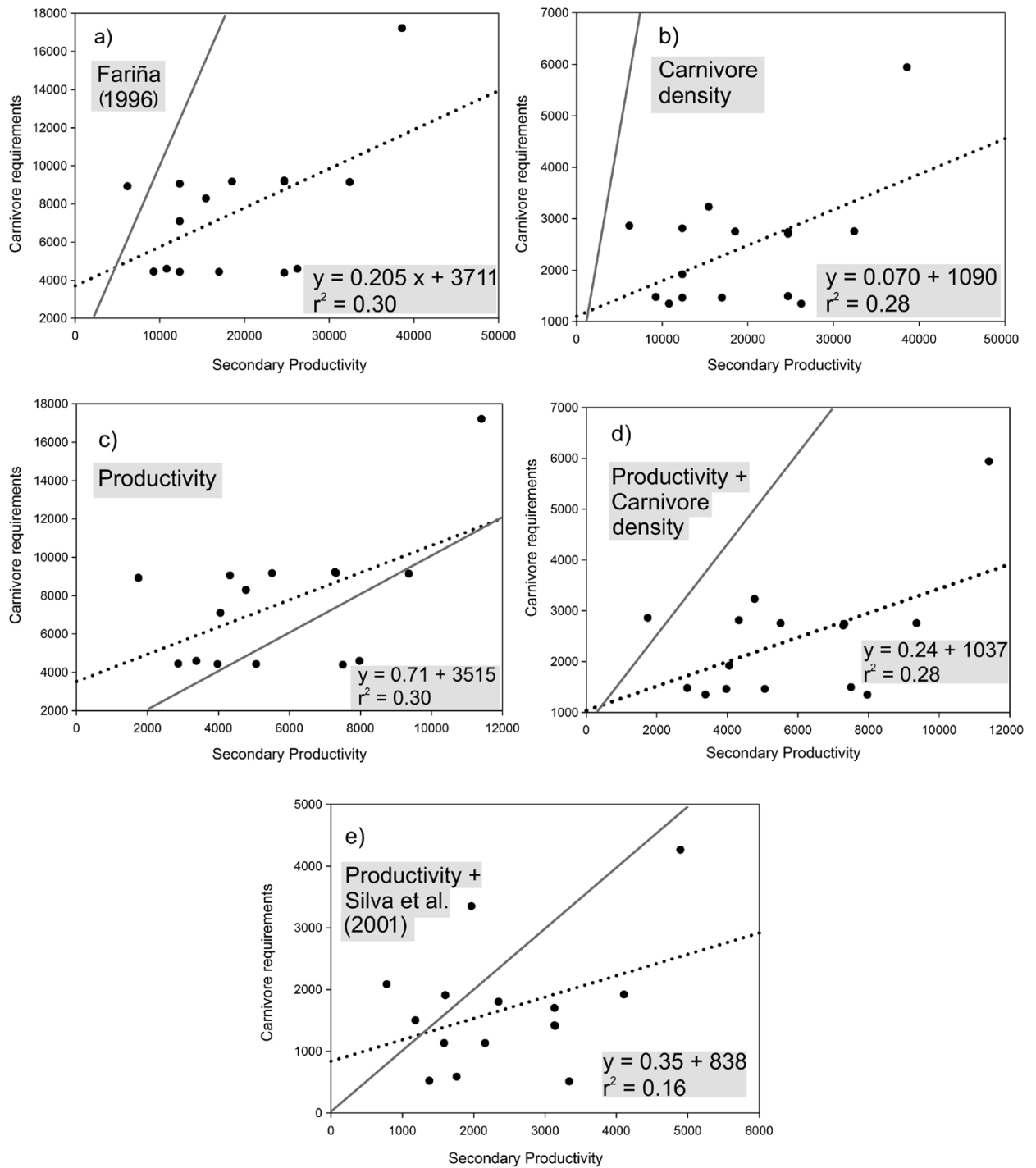
$$\text{Carnivores: } \log D = 1.41 - 1.83(\log m) - 0.34(\log m^2) + 0.28(\log m^3)$$

where  $D$  is the population density expressed in individuals per square km, and  $m$  their body mass in kg. Secondary productivity was calculated following Western (1983).

In all the models used, if there was a difference of 15% between the secondary productivity and the carnivores energetic requirements, the fauna was considered balanced.

#### ABUNDANCE

For the study of the relative abundance, the obtained distributions were corrected to avoid taphonomic biases dependant from body size and differential preservation, following Damuth (1982). In this study, we included those specimens assigned to the Lujanian of Uruguay, province of Buenos Aires (Argentina) and Arroio Chuí locality (Santa Vitória do Palmar, southern State of Rio Grande do Sul, Brazil) from the following museums: Museo Argentino de Ciencias Naturales



**Figure 1** - Linear regressions for the five models applied to the fifteen South American Faunas. All variables are given in  $J\ m^{-2}\ year^{-1}$ . Dotted line represents the regression and solid line the expected ratio (slope = 1).

“Bernardino Rivadavia”, Buenos Aires, Argentina (MACN), Museo del Hombre y la Tecnología de Salto, Uruguay (MACN-S), Museo de Geociencias

de Tacuarembó, Uruguay (MGT), Museo Histórico Departamental de Artigas, Uruguay (MHD-P), Museo Dr Carlos Torres de la Llosa, Instituto



Alfredo Vázquez Acevedo, Montevideo, Uruguay (MIAVA), Museo de La Plata, La Plata, Argentina (MLP), Museo Municipal de Colonia “Juan Bautista Rebuffo”, Colonia, Uruguay (MMC), Museo Municipal de Mar del Plata “Lorenzo Scaglia”, Mar del Plata, Argentina (MMMP), Museo Paleontológico Real de San Carlos “Armando Calcaterra”, Colonia, Uruguay (MPRSC); Museu Coronel Tancredo Fernandes de Mello, Jamil Pereira collection, Santa Vitória do Palmar, Brazil (MTFM-JP), Museo Nacional de Historia Natural, Montevideo, Uruguay (MNHNM), Museo Nacional de Historia Natural, Andrés Rinderknecht collection, Montevideo, Uruguay (MNHNM-AR, collection, in process of formalization, whose final destination will be the MNHNM). The fossils selected had precise geographic and stratigraphical provenance; also the remains without detailed geographic provenance that could be assigned to the studied region and temporal range of interest were also included. Specimens from the MTFM-JP were considered together with those from Uruguay, since they belong to a single assemblage located very near the Uruguayan-Brazilian border (Arroio Chuí). The Arroyo del Vizcaíno collection, Canelones, Uruguay (CAV) and the Vertebrate Palaeontology collection from the Facultad de Ciencias, Montevideo, Uruguay (FC-DPV) were also considered in the sample. For a complete list of the studied materials, see Czerwonogora (2010).

Regarding the remains from the province of Buenos Aires, two different counts were performed: one involving all the specimens assigned to the Lujanian age, and a differential one including only the remains from the local faunas of Luján, Paso Otero and Quequén Salado-Indio Rico. Each of these localities owns a characteristic local fauna that considered together define the typical faunistical association of the Lujanian.

The masses of the studied taxa were taken as per the energetics section and also from González (2001) and Toledo (1996).

In the abundance study, fossils that came from the Lujanian South American Land Mammal Age (SALMA) were included; the definition of this SALMA as divided in Bonaerian and Lujanian stages/ages follows Cione and Tonni (1999, 2001). In these works, the Bonaerian was proposed as a unit independent from the Lujanian, comprising the middle Pleistocene, between 780,000 and 130,000 years B.P. The Lujanian was considered as being from between 130,000 and 8500 years B.P. Finally, the *Ctenomys kraglievichi* biozone (Verzi et al. 2004), included in Cione and Tonni (2005), was the criterion to restrict the beginning of the Bonaerian to circa 400,000 years B.P. (Merino et al. 2007, Soibelzon et al. 2009).

The fossil material that was not possible to assign precisely to the Lujanian, was included in the Bonaerian-Lujanian lapse, involving the last 400,000 years B.P. (Merino et al. 2007, Soibelzon et al. 2009). Since the species level of fossil taxa is not always available along the entire record, the genus level was used to categorize the trophic structure of the palaeocommunity (Badgley and Behrensmeyer 1995). In the cases where the determination could not reach the genus level, the family level was used.

To estimate abundance the counts were based on the number of identified specimens (NISP), understanding that specimen refers to a bone, tooth or fragment (Klein and Cruz-Urbe 1984). MNI counts tend to diminish values of the most common species and overestimate those of odd species (Damuth 1982, Arribas and Palmqvist 1998). NISP counts did not consider glyptodont scutes nor cervid antlers.

## RESULTS

### ENERGETICS

The herbivorous mammals of body masses greater than 10 kilograms found in the Luján local Fauna are listed below. The original list from Tonni et al. (1985) including 30 species (more than half of them being xenarthrans) was updated considering the species if the genus was monospecific; in other cases the genus

was considered. There are 22 taxa: five glyptodonts (*Neothoracophorus*, *Plaxhaplous canaliculatus*, *Doedicurus clavicaudatus*, *Panochthus tuberculatus*, *Glyptodon*, one pampathere (*Pampatherium typum*), and four ground sloths (*Megatherium americanum*, *Scelidotherium leptocephalum*, *Glossotherium robustum*, *Lestodon armatus* (Czerwonogora and Fariña 2013). The list is completed with the addition of one rodent (the extinct giant capybara *Neochoerus sulcidens*), the extinct South American Order Notoungulata with the genus *Toxodon*, one litoptern (*Macrauchenia patachonica*), one perissodactyl (the horse *Equus (Amerhippus) neogeus*), seven artiodactyls (the tayasuids *Tayassu tajacu* and *Catagonus*, the camelids *Eulamaops parallelus*, *Hemiauchenia paradoxa* (Scherer et al. 2007), and *Lama guanicoe*, and the cervids corresponding to the genera *Morenelaphus* and *Antifer*), and the gomphothere proboscidean *Notiomastodon* (Mothé et al. 2012).

They range in mass from 22 kilograms, in the case of the peccary (one of the two living herbivorous species), to seven tonnes, in the case of the gomphothere *Notiomastodon*. The on-crop biomass for each species was obtained by multiplying the calculated population density by its body mass. The total on-crop biomass for these species was 10,350 kg km<sup>-2</sup>. The energy requirements for each species were obtained by multiplying its on-crop biomass by its basal metabolic rate. A typical assimilation efficiency of 50% (of the edible material) was assumed, and average actual maintenance metabolism was considered to be 2.5 times the basal rate (Peters 1983). Adding up the requirements of all the species considered, and converting the units, it follows that they must have needed some 1.2 MJ m<sup>-2</sup> year<sup>-1</sup> in habitat primary productivity.

The five large Carnivora species in the Luján local Fauna are the extinct canid *Dusicyon avus*, two living felids (jaguar, *Panthera onca* and cougar, *Puma concolor*), the extinct sabre-toothed felid *Smilodon populator*, and the extinct ursid

*Arctotherium*. They range in mass from 13 kg (*Dusicyon avus*) to 235 kg in the case of the average Lujanian species of *Arctotherium* (Soibelzon and Tarantini 2009). The on-crop biomass for each species was obtained by multiplying the calculated population density by its body mass. The total on-crop biomass for these carnivores was 63 kg km<sup>-2</sup>. The requirements for each species were obtained by multiplying its on-crop biomass by its basal metabolic rate. Adding up the requirements of all the large carnivore species, and converting the units, it follows that they must have needed about 11.2 kJ m<sup>-2</sup> year<sup>-1</sup> as habitat secondary productivity to bear their maintenance metabolism, if an assimilation efficiency of 50 % was assumed.

If the model used in Fariña (1996) is applied to fifteen South American faunas, including the Luján local fauna, and the secondary productivity is compared to the energetic requirements of the carnivores, then no faunas are ecologically balanced (Table I) and the relationship between these two variables is rather weak ( $r^2=0.3$ ; Figure 1a). The first new model applied here (modified from Fariña 1996) does not show any balanced faunas either, and the relationship between both variables is weak ( $r^2=0.28$ ; Table I, Figure 1b).

The Productivity model shows that there are only three balanced faunas in this continent (Table I). The regression shows that the secondary productivity and the carnivores' requirements are not closely related ( $r^2=0.3$ ; Figure 1c). The model that combines Productivity and Carnivore Density shows similar results to those obtained using the first model (Table I, Figure 2d).

The last model, i.e., Productivity + Silva et al. (2001), indicates that there are two balanced faunas in South America (Table I), and that the relationship between the variables is even worse than that seen in the other models ( $r^2=0.16$ ; Figure 1e). The present fauna of the Serengeti was included as an actualistic control and was found to be balanced with this model.

TABLE I  
Secondary Productivity of the herbivores and requirements of the carnivores  
for South American faunas. Coloured cells indicate balanced faunas.

Fauna	Fariña (1996)		Carnivore Density		Productivity		Prod. + Carnivore Density		Prod. + Silva et al. (2001)	
	Sec. Prod.	Req. Carn.	Sec. Prod.	Req. Carn.	Sec. Prod.	Req. Carn.	Sec. Prod.	Req. Carn.	Sec. Prod.	Req. Carn.
63515	10804.75	4586.6	10804.75	1347.84	3377.01	4586.6	3377.01	1347.84	1376.9	523.01
70673	38588.4	17207.8	38588.4	5942.12	11413.55	17207.8	11413.55	5942.12	4897.6	4260.64
70704	24696.6	9174.9	24696.6	2739.01	7311.4	9174.9	7311.4	2739.01	3133.07	1698.10
71274	26240.1	4590.2	26240.1	1345.00	7970.36	4590.2	7970.36	1345.00	3339.5	510.06
71298	16978.9	4427.04	16978.9	1459.90	5061.13	4427.04	5061.13	1459.90	2159.28	1130.82
71301	12348.3	4427.04	12348.3	1459.90	3973.03	4427.04	3973.03	1459.90	1585.47	1130.82
71303	32414.24	9140.32	32414.24	2752.19	9361.7	9140.32	9361.7	2752.19	4105.75	1917.06
71304	15435.35	8285.61	15435.35	3228.96	4772.95	8285.61	4772.95	3228.96	1967.08	3346.29
71313	12348.3	9047.58	12348.3	2812.65	4325.74	9047.58	4325.74	2812.65	1602.69	1906.39
71322	24696.57	9217.01	24696.57	2705.11	7285.91	9217.01	7285.91	2705.11	3131.9	1417.11
71332	24696.57	4384.91	24696.57	1493.81	7501.83	4384.91	7501.83	1493.81	3142.5	1411.81
71334	9261.21	4442.06	9261.21	1479.43	2863.37	4442.06	2863.37	1479.43	1183.46	1499.71
71335	18522.42	9161.84	18522.42	2749.94	5509.99	9161.84	5509.99	2749.94	2349.14	1800.91
71341	6174.14	8922.23	6174.14	2860.47	1744.5	8922.23	1744.5	2860.47	780.48	2083.68
71346	12348.3	7094.95	12348.3	1915.99	4055.99	7094.95	4055.99	1915.99	1762.17	585.02

#### ABUNDANCE

The Uruguayan sample analysed is composed of 1568 specimens (NISP), 81 of them juveniles. A percentage of 4.5% (71 specimens) was identified at the order level, while 20.7% (324 specimens) were classified at the family or subfamily level and the remaining 74.8% (1173 specimens) were classified at the generic level.

The sample from the province of Buenos Aires includes 1889 specimens (NISP), 51 of them juveniles. A percentage of 0.4% (7 specimens) was identified at the order level, 4.1% (77 specimens) were classified at the family or subfamily level and 95.5% (1805 specimens) were identified at the generic level.

*Lestodon* is the most represented taxon among the xenarthrans and also from the whole sample studied for Uruguay (Table II). The NISP of *Lestodon* from Uruguay represents 31% of the remains (479 specimens) and its abundance is 9% of the individuals present in the total studied fauna. Among the most represented sloths, *Glossotherium* follows, whose NISP corresponds to 4% of the total sample studied (57 specimens) and its

abundance represents 1.4% of the individuals. For *Megatherium* the NISP of the Uruguayan sample only represents 1% of the remains (9 specimens) and its abundance represents 0.1% of the individuals. *Scelidotherium*'s NISP is very small, 0.3% (5 specimens), and so its abundance was of 0.1%, although *Myiodon* presents even lower values, with a NISP of only 0.1% (2 specimens) and an abundance that represents 0.05% of the individuals of the studied fauna.

For the total remains studied from the province of Buenos Aires (Table III), the most represented taxon among the xenarthrans and among the whole analysed sample is *Scelidotherium* (NISP=293 specimens), since its remains constitute 15% of the studied fossils from the province and its abundance represents 9% of the individuals. The second most represented taxon of the whole sample is *Glossotherium*, whose NISP reaches 14% of the studied remains (274 specimens) and its abundance represents 7% of the individuals. *Megatherium*'s NISP corresponds to 9% of the remains (164 specimens, third place), and its



TABLE II

Taxa counts of primary (a) and secondary (b) consumers in the considered sample for Uruguay, including size category, estimated body mass, number of specimens (adults/juveniles, NISP) and estimated relative abundance.

a				
Taxon	Size category	Body mass (kg)	NISP	Total relative abundance
Cervidae indet	ii	50	185/16	17037
<i>Antifer</i>	ii	50	3	251
<i>Ozotoceros</i>	ii	32.5	6	589
<i>Morenelaphus</i>	ii	50	23	1917
<i>Paraceros</i>	ii	50	51	4250
Camelidae indet	ii	70	40/1	2934
<i>Catagonus</i>	ii	35	14	1336
<i>Hemiauchenia</i>	iii	191.5	67/2	3467
<i>Lama</i>	ii	100	6	501
<i>Tayassu</i>	ii	22	3	343
<i>Hippidion</i>	iii	476	20	708
<i>Equus (A.)</i>	iii	250	22	859
<i>Tapirus</i>	iii	250	14	634
<i>Stegomastodon</i>	iv	5946	22/3	315
<i>Mylodon</i>	iv	1000	2	53
<i>Lestodon</i>	iv	2590	440/39	9040
<i>Glossotherium</i>	iv	1302	46/2	1403
<i>Scelidotherium</i>	iii	826	5	144
<i>Megatherium</i>	iv	4584	6/3	145
<i>Glyptodon</i>	iii	633	19/1	642
<i>Panochthus</i>	iii	795	8	234
<i>Doedicurus</i>	iv	1041	2	52
<i>Propraopus</i>	iii	200	7	345
<i>Neuryurus</i>	iv	1000	1	27
<i>Pampatherium</i>	iii	200	5	246
<i>Dolichotis</i>	ii	12.5	2	282
<i>Holochilus</i>	i	0.35	1	549
<i>Lundomys</i>	i	0.37	7	2689
<i>Reithrodon</i>	i	0.086	3	2809
<i>Coendou</i>	i	2.95	3	1466
<i>Hydrochaerus</i>	ii	53	6	1304
<i>Neochoerus</i>	ii	63	16	458
<i>Myocastor</i>	i	7.5	7	857
<i>Cavia</i>	i	1	23	8923
<i>Galea</i>	i	0.45	10	4992
<i>Microcavia</i>	i	0.35	41	22517
<i>Lagostomus</i>	i	4.875	4	807
<i>Neolicaphrium</i>	ii	32.5	4	220
<i>Macrauchenia</i>	iii	909	20	554
<i>Toxodon</i>	iv	1415	127/9	3142
b				
Taxon	Size category	Body mass (kg)	NISP	Total relative abundance
<i>Smilodon</i>	iv	304	5	210
<i>Felis (Puma)</i>	ii	50.4	3	249
<i>Panthera</i>	iii	109	2	124

TABLE II (continuation)

b				
Taxon	Size category	Body mass (kg)	NISP	Total relative abundance
<i>Canidae indet</i>	ii	11.6	8	1163
<i>Duscicyon</i>	ii	14.7	7	930
<i>Pseudalopex</i>	i	8.5	5	817
<i>Lontra</i>	i	8.5	2	327
<i>Arctotherium</i>	iii	235	1	46
<i>Dasypus</i>	i	5.5	2	386

abundance is 3% of the individuals analysed in this fauna. Among sloths, *L. armatus* follows, whose NISP represents 4% of the studied remains (83 specimens) and its abundance corresponds

to 2% of the individuals of the analysed fauna. Finally, *Myiodon*'s NISP corresponds just to 2% of the studied remains (34 specimens) and its abundance to 1%.

TABLE III

Taxa counts of primary (a) and secondary (b) consumers in the considered sample for the province of Buenos Aires, including size category, estimated body mass, number of specimens (adults/juveniles, NISP) and estimated relative abundance.

a				
Taxon	Size category	Body mass (kg)	NISP	Total relative abundance
<i>Cervidae A</i>	ii	50	11	917
<i>Cervidae B</i>	ii	50	3	250
<i>Ozotoceros</i>	ii	32.5	2	196
<i>Morenelaphus</i>	ii	50	3	250
<i>Paraceros</i>	ii	50	1	83
<i>Hemiauchenia</i>	iii	191.5	13	650
<i>Lama</i>	ii	100	76/5	5256
<i>Tayassu</i>	ii	22	8	911
<i>Hippidion</i>	iii	476	44/2	1644
<i>Equus (A.)</i>	iii	250	115	5199
<i>Stegomastodon</i>	iv	5946	18/2	277
<i>Myiodon</i>	iii	1000	32/2	909
<i>Lestodon</i>	iv	2590	79/4	1559
<i>Glossotherium</i>	iv	1302	253/21	6726
<i>Scelidotherium</i>	iii	826	293/16	8970
<i>Catonyx</i>	iii	807	11	319
<i>Megatherium</i>	iv	4584	152/12	2493
<i>Glyptodon</i>	iii	633	59/6	2105
<i>Panochthus</i>	iii	795	30/2	945
<i>Doedicurus</i>	iv	1041	34	894
<i>Neosclerocalyptus</i>	iii	250	43/1	1999
<i>Plaxhplous</i>	iv	1300	1	24
<i>Tolypeutes</i>	i	1.53	2	627
<i>Eutatus</i>	iii	200	25	1230
<i>Chaetophractus</i>	i	1.44	4	1283
<i>Propraopus</i>	iii	200	1	49
<i>Pampatherium</i>	iii	200	1	49
<i>Dolichotis</i>	ii	12.5	11	1553

TABLE III (continuation)

a				
Taxon	Size category	Body mass (kg)	NISP	Total relative abundance
<i>Ctenomys</i>	i	0.4	17	8874
<i>Akodon</i>	i	0.0275	1	1444
<i>Calomys</i>	i	0.034	2	2664
<i>Holochilus</i>	i	0.35	2	1098
<i>Necromys</i>	i	0.55	9	4163
<i>Reithrodon</i>	i	0.086	15	14043
<i>Neochoerus</i>	ii	63	1	76
<i>Myocastor</i>	i	7.5	1	171
<i>Galea</i>	i	0.45	1	499
<i>Microcavia</i>	i	0.35	8	4394
<i>Lagostomus</i>	iv	4.875	52/7	10497
<i>Macrauchenia</i>	iii	909	50	1384
<i>Toxodon</i>	iv	1415	131/6	3065
b				
Taxon	Size category	Body mass (kg)	NISP	Total relative abundance
<i>Smilodon sp.</i>	iii	304	53/1	302
<i>Felis (Puma)</i>	ii	50.36	11	121
<i>Conepatus</i>	i	3.4	1	31
<i>Chrysocyon</i>	ii	23.4	1	15
<i>Canis</i>	ii	32.26	4	52
<i>Cerdocyon</i>	i	6.5	6	144
<i>Dusicyon</i>	iii	14.65	6	106
<i>Pseudalopex</i>	i	8.5	2	43
<i>Arctotherium</i>	iii	235	26/2	174
<i>Didelphis</i>	i	3.75	1	223
<i>Lestodelphis</i>	i	1.25	4	1354

With regard to the size categories in primary consumers, the most represented one in Uruguay was category ii (between 10 and 100 kg) including 13 taxa. In the province of Buenos Aires and the localities of Luján, Paso Otero and Quequén Salado-Indio Rico, the most represented body size category was the iii (between 100 and 1000 kg), with 13 and 12 taxa respectively.

#### DISCUSSION

The discussion will follow the main topics addressed in this paper (energetics and abundance) and other subjects that can provide additional information relevant to the results presented here: food preferences and abundance, size of predators and isotopes.

#### ENERGETICS

In the model employed in Fariña (1996), the Luján Local Fauna was not balanced. However, this model explained well the ecology of other local faunas: Venta Micena, Lower Pleistocene of Spain (Palmqvist et al. 2003), Chapadmalalan and Barranca de los Lobos, Plio-Pleistocene of Argentina (Vizcaíno et al. 2004), Puesto La Costa and Campo Barranca, Miocene of Argentina (Vizcaíno et al. 2010). As said above, these results rely on the condition of the models being taxon-free, hence independent of phylogenetical variables (although they are included in the inference of the basal metabolism). This is why a phororhacid (a large predatory Tertiary running bird) was

included in the energetic calculations of the Miocene faunas of Argentina studied in Vizcaíno et al. (2010).

It was also very useful as a starting point to develop other mathematical models that tried to explain the peculiar ecology of the megamammals that inhabited the continent.

Prevosti and Vizcaíno (2006) suggested that the approach used in Fariña (1996) was not accurate, since the carnivore population densities were not the ones found by this author. According to the authors, who compiled the information from several sources about carnivore population ecology, they stress that those populations are affected by several ecological factors that should have been taken into account, like prey abundance and diseases. These authors also suggested that the mylodontids should have been less abundant, given their low metabolic rates.

The model that best describes the palaeoecology during the Pleistocene (in Africa and other continents) is the one in which the population densities are calculated following Silva et al. (2001). The population densities for carnivores, obtained using the equation given by Carbone and Gittleman (2002), does not solve the ecological imbalances. The suggestion by Prevosti and Vizcaíno (2006) that carnivore densities are affected by ecological factors should not be taken into account, since the herbivores are affected by the same ecological factors (such as food availability and diseases). In any case, if the basic assumption made by Damuth (1981) to formulate his model is accepted, the average for population density depends exclusively on body size. Therefore, the increase in the number of individuals cannot be taken as permanent without violating his empirical, taxon-free model. Also, in these calculations the densities of the mylodontids were not reduced, since a low metabolism does not imply in a smaller population (Damuth 1981), a principle valid for mammals in general and, until otherwise demonstrated, also for xenarthrans as mylodontids. Actually, from a thermodynamical

point of view, it should imply in there being more (not less) individuals to be supported by the same primary productivity (for further discussion, see Peters 1983: 164-170).

It is important to address the fact that Prevosti and Vizcaíno (2006) studied only one side of the imbalance proposed by Fariña (1996), i.e., the relationship between the secondary productivity and the requirements of the carnivores. Fariña (1996) showed that there was another side to that imbalance, the primary productivity in the Luján Local Fauna having been too low for the herbivores to survive. Again in this case, it should be noted that these models are time-averaged (see below), i.e. they are instantaneous and not dynamic simulations, such as the evolutionary impact on species populations by a new predator (see, for instance, Alroy 2001). This issue was not considered in the models used, since there was not enough data on primary productivity in the different areas of the South American continent to make comparisons with.

#### ABUNDANCE

Even though the analysed faunas were corrected in order to avoid taphonomic biases, in all the studied cases the obtained values for the slope in the graph of abundance vs. body mass did not fit Damuth's (1982) model ( $-1.05 \pm 0.25$ ):  $\log A = -1.05 (\log m)$ .

In spite of those corrections, the obtained values for the slope in the graph of abundance vs. body mass did not fit the expected slopes. It should be noted that the terrestrial faunas of Pampean Pleistocene ecosystems have no analogues with modern ones (Tonni and Cione 1997). As Damuth pointed out: "It appears, then, that even some of our most promising assemblages present a badly distorted picture of original community structure" (Damuth 1982: 439). However, Damuth's tested assemblages (Rodeo, California, Late Pleistocene, and Brule Formation, South Dakota, Middle Oligocene) fit the model after the corrections had

been made to avoid taphonomic biases. A similar case can be described for the Pleistocene fauna of Venta Micena, in the Guadix-Baza basin, Spain, that shows adequate values for the slope of the graph of abundance vs. body mass described by Damuth's model (1982): for primary consumers  $\log A = -1.54x + 8.18$ ;  $r^2 = 0.62$  and for secondary consumers  $\log A = -0.93x + 5.19$ ;  $r^2 = 0.57$  (Arribas and Palmqvist 1998).

As proposed by Damuth (1982), the "assemblage" studied does not need to be very defined: the fauna of a whole formation can be considered as an assemblage if we suspect that it is the same community of individuals (again, vaguely defined). In this sense, the fossiliferous localities considered in the analysis for Uruguay and the province of Buenos Aires correspond to the studied temporal lapse; for this reason, it is assumed that the registered taxa are members of the same palaeocommunity. The specimens from the localities included in the counting, constitute a random sample of the then hypothetical living assemblage.

It must be taken into account that the classification of the studied taxa into certain ecological feeding categories following Miljutin (2009), where within the primary consumers we include the herbivorous and the frugivorous taxa, and within the secondary consumers the animalivorous taxa, reflects an a priori categorization that might imply some difference with the real habits of the taxa. For example, *Conepatus*, described as an omnivorous mainly insectivorous (González 2001) was included within the secondary consumers.

Vizcaíno et al. (2006) suggested that in most xenarthrans dentary occlusal surfaces are smaller than expected for extant herbivores of equivalent size, except for *Megatherium*. This might suggest for herbivorous xenarthrans other than *Megatherium* (or even megatheriids) a low efficiency for oral food processing in the buccal cavity, which should have been compensated with a slower transit and a higher fermentation capability in the digestive

tract in addition to lower metabolic requirements (Vizcaíno et al. 2006). Prevosti and Vizcaíno (2006:407) stated that "the very low metabolism proposed for the mylodontids (Vizcaíno et al. 2006) also suggests that they were probably not so abundant and that they did not need as much food as originally calculated by Fariña (1996)", which, as mentioned above, is not ecologically accurate. The alternative hypothesis proposed by these authors for the imbalance in Luján local fauna is that the density of carnivores depends on the density of herbivores; for this reason, if a great amount of herbivorous biomass was available, a high density of carnivores could have been supported.

Regarding the abundance of secondary consumers presented in this work, all the registered genera in the studied region were counted (9 for the analysed sample from Uruguay, Table IIb, and 11 for the province of Buenos Aires sample, Table IIIb), resulting in a greater number of studied taxa than in the original analysis (Fariña 1996). This increment is also due to the inclusion of minor size taxa such as *Dusicyon* and *Lontra*, which results in a higher number of secondary consumers than the registered in South American Tertiary faunas and is also consistent with observations in extant South American faunas (Prevosti and Vizcaíno 2006 and their references).

Another aspect that deserves attention is the aforementioned time averaging of the sample, in order to exclude it as the source of biasing the obtained results on abundance. For example, the Río Luján local fauna includes fossil remains from the Guerrero Member of the Río Luján Fm. These fossils are characteristic of the *Equus (Amerhippus) neogeus* Lund 1840 Biozone, defined by Cione and Tonni (1999, 2001) as the biostratigraphic base of the Lujanian. The latest radiocarbon dating, by Tonni et al. (2003), restricted the deposition period of the Guerrero Member of the Río Luján Fm. to ages between  $10,290 \pm 130$  years B.P. and  $21,040 \pm 450$  years B.P. Considering these ages, the Río Luján local fauna is between 11,000 and 21,000 years B.P.



The Rancho La Brea local fauna represents a required reference for late Pleistocene North American megafauna. La Brea tar pits contain a collection of fossils from a particular sedimentary environment. A taphonomic analysis of a single tar seep, Pit 91, revealed a complex history of deposition and diagenesis for specimens found there. Radiometric dating of 46 bones from Pit 91, documents at least two episodes of deposition, one from 45,000 to 35,000 yr BP and another, shorter interval, from 26,500 to 23,000 yr BP. The law of superposition of strata was not upheld consistently in this case study, as some younger bones were found at a greater depth than older bones, showing a clear case of time averaging, comprising at least 30,000 years (Frischia et al. 2008).

A similar case occurs in Sopas Fm. regarding its estimated ages (Guidon 1989, Ubilla 2001) that spans an interval time of at least 30,000 years. The fossil sample studied for Uruguay represents the greatest time averaging of the samples studied, that could exceed the 30,000 years. As seen for Rancho La Brea (Frischia et al. 2008), this time interval is within the reasonable and should not represent a concern for the interpretation of the obtained results. The presented examples allow for the exclusion of time averaging, as the source for biasing the obtained results for the application of Damuth's model (1982).

Finally, in the studied sample for Uruguay *Lestodon armatus* is the most represented taxon (NISP = 31%) and its abundance corresponds to 9% of the studied fauna. The records of *Megatherium* and *Scelidotherium* in Uruguay are scarce: NISP of the sample reaches only 1 and 0.3% of the studied specimens, respectively, and its abundances 0.1 and 0.05% of the individuals of the studied fauna. In contrast, in the province of Buenos Aires, *Scelidotherium* is the most represented taxon of the sample (NISP = 15%) and its abundance is similar to that observed for *L. armatus* in Uruguay (9%), whereas *Megatherium* constitutes the third

most represented taxon (NISP = 9% of the studied specimens) and its estimated abundance is 3% of the individuals analysed in this fauna, hardly greater than the observed for *L. armatus* (2%).

#### FOOD PREFERENCES AND ABUNDANCE

Sloths muzzle analyses developed by Bargo (2001a) and Bargo et al. (2006 a, b) propose that in *Megatherium americanum* and *Scelidotherium leptocephalum* narrower muzzles are indicative of selective or mixed feeder habits, and their prehensile lips were used to select plants or parts of plants. McDonald (1997, cited in Bargo et al. 2006b) stated that *S. leptocephalum* probably looked for buried food with the help of its forelimbs, even if it could also feed on other vegetation closer to the substrate level.

Biomechanical analyses of Bargo et al. (2000) and Vizcaíno et al. (2001) indicate that the forelimb of this sloth was capable of digging and the hypsodonty index found suggests abundance of grit in the food (Bargo et al. 2006a), which is consistent with the possibility of them being subterranean or close to the substrate in relatively open habitats. Bargo et al. (2006a) concluded that *S. leptocephalum* was a selective feeder specialized in succulent vegetal material, such as fruits, buds and tubercles, although it was capable of browsing on shrubs and grasses.

For *L. armatus*, Bargo et al. (2006a, b) proposed that muzzle shape suggests that it was not directly involved in the search for food; on the other hand, its wide and robust mandibular symphysis could have been used to take food from the substrate. The wide muzzle, shovel shaped, indicates that *L. armatus* was capable of taking a great quantity of food in one bite (Bargo 2001a). The dominant landscape inferred for the province of Buenos Aires in the considered period (psammophytic steppe) and the existence of the delta of the Palaeoparaná, perhaps with seasonal floods, suggest that this might have been a more

favourable environment for *L. armatus*, whose anatomy indicates its capability to exploit the tender grasses that grew in this more humid microclimate. In this sense, recent biogeochemical analyses show new evidences on the preferred vegetation for this sloth (Czerwonogora et al. 2011; see below). The results of the abundance study reveal that in the late Pleistocene, sloths considered as bulk feeders (*Lestodon* and *Glossotherium*) were more represented in Uruguay, while the more selective feeder sloths (*Scelidotherium*, *Megatherium*) were more abundant in the province of Buenos Aires.

#### SIZE OF PREDATORS

The Pleistocene evolution of *Arctotherium* in South America differs from the evolutionary trajectory of bears. According to the different moments of their extinction in North America and Europe, different selective pressures operated in the first in comparison to the second and third. Size decrease in *Arctotherium* could have been related to selective pressures due to the GABI, particularly the abundance of herbivores and the relative paucity of large carnivores in the early Pleistocene (Soibelzon and Schubert 2011 and their references). Over time, the post-GABI large carnivore guild increased in diversity and *Arctotherium* species shifted their diets towards more herbivory and decreased in size. These authors suggest higher degrees of omnivory and herbivory to avoid growing competition with other large carnivores: for example, *Arctodus simus*, traditionally considered a fast-running super-predator or a specialized scavenger, was reinterpreted recently (Figueirido et al. 2010) as a colossal omnivorous bear whose diet probably varied according to resource availability. For this reason, the pressures that ruled the late Pleistocene/early Holocene ecosystems must have favoured less specialized taxa than those with more specialized morphologies and of very large sizes (Soibelzon and Schubert 2011).

As said above, another source of error could be the lack of knowledge about the physiology and

energetic needs of most extinct xenarthrans, whose metabolic rates could have been lower than those expected for mammals of their sizes, as estimated from their energetics (McNab 2008, Bargo and Vizcaíno 2008) and tooth surface (Bargo 2001a, Vizcaíno et al. 2006). There is also the problem of comparing the hypselodont (i.e., evergrowing) teeth of xenarthrans with the hypsodont teeth of ungulates, which complicates the comparison of occlusal tooth area and other teeth and cranial dimensions. As was already pointed out in the previous section, Bargo et al. (2006a) suggested the difficulty for mylodontid ground sloths to perform an efficient oral processing of the food due to the relatively small occlusal teeth areas, and the different strategies to compensate this inefficiency (Vizcaíno et al. 2006).

#### ISOTOPES

Preliminary observations of growth lines on glyptodont teeth suggest the potential for reconstruction of many aspects of the life history of these mammals, including the search for seasonal periodicities and growth rhythms.

Furthermore, the fact that xenarthrans lacked enamel renders difficult the comparison of biogeochemical results obtained from teeth with those of other South American indigenous megamammals. For example, for *Toxodon* and *Macrauchenia*, a pure C4 grazing niche and a mixed feeding diet on both C3 leaves and C4 grasses have been inferred, respectively, using the carbon-isotope ratio ( $\delta^{13}\text{C}$ ) of tooth enamel (MacFadden and Shockey 1997, MacFadden 2008). However, more recent studies on late Quaternary toxodonts (MacFadden 2005) suggest, based on the mean  $\delta^{13}\text{C}$  data, a broader range of dietary adaptations. In the case of xenarthrans the isotopic analyses ( $^{13}\text{C}$ ,  $^{15}\text{N}$ ) should be based on bone collagen (Palmqvist et al. 2003). In addition, the analysis of bone collagen opens the possibility of measuring both carbon- and nitrogen-isotope ratios, which provide valuable indications

of the animal's overall diet for the last few years of life (the information obtained from enamel carbon-isotopes is more limited, since it only records the diet during the time the teeth were formed).

The averages of the obtained values of  $\delta^{13}\text{C}$  for *Lestodon armatus* from Uruguay (-18.8%, Czerwonogora et al. 2011) and *Glossotherium robustum* from the province of Buenos Aires (-20.5%, Czerwonogora et al. 2011) indicate a preference for C3 vegetation and rather open environments, similar to those currently found in northern Patagonia. Those results are compatible with the ones obtained in modern primary consumers in open habitats (DeNiro and Epstein 1978).

On the other hand, there is an evolutionary advantage for grazers to increase body size, which would promote digestion of high-fibre, relatively low nutritive value grasses by relatively longer residence times in the gut (Owen-Smith 1988). This trend could be extended to the "bulk feeder" giant sloths. The results for  $\delta^{13}\text{C}$  for *L. armatus* and *G. robustum* are comparable to those obtained for other mylodontid such as *Paramylodon harlani* from the North American Pleistocene site of Rancho La Brea (average -21.0 ‰, Coltrain et al. 2004), and from the results for *Megalonyx jeffersoni* of Saltville (-20.66 ‰, France et al. 2007).

The  $\delta^{15}\text{N}$  composition of collagen has proven useful for estimating the feeding and habitat preferences of extinct mammals, given that each trophic level above herbivore is indicated by an increase in  $\delta^{15}\text{N}$  of ~3.4‰ (Robinson 2001).  $\delta^{15}\text{N}$  values are also useful for estimating the palaeoenvironment, because herbivores from closed habitats exhibit lower  $\delta^{15}\text{N}$  values with respect to those from open grasslands as a consequence of soil acidity in dense forest and physiological adaptations for concentrating urea in animals inhabiting arid regions (see review in Gröcke 1997). The results of  $\delta^{15}\text{N}$  for *L. armatus* and *G. robustum* (+9.5 and +10.5 on average, respectively, Czerwonogora et al. 2011) are rather

high for a herbivore. However, as Amundson et al. (2003) pointed out, the  $\delta^{15}\text{N}$  in soil and plants systematically decreases with increasing mean annual precipitation and with decreasing mean annual temperature. These results are also congruent with those results obtained for the sloths *Paramylodon harlani* from Rancho La Brea (Coltrain et al. 2004) and *Megalonyx jeffersoni* from Saltville Valley (France et al. 2007): +7.9 and +4.65, respectively (see Czerwonogora et al. 2011 for a discussion).

#### OTHER EVIDENCE

Moreover, those high values of  $^{15}\text{N}$  are congruent with some marks found in a fragmentary left rib of a very large mammal, probably a giant sloth or a mastodont. The spacing of the damage marks fits well with the distance between the mesiodistal lophs of the teeth (Fariña 2002).

Complementary hypotheses could be assessed to contribute towards explaining the observed differences for the slope in the graph of abundance vs. body mass in Damuth's (1982) model with respect to the expected results. In the first place, during the pleniglacial and some millenia afterwards the sea level was about 120 metres below the current sea level (Lambeck et al. 2003). As a consequence, the Paraná River was extended to below the actual Río de la Plata (constituting a huge floodplain) and the Atlantic Ocean in front of the Rocha department coast in Uruguay and the south of the Brazilian state of Rio Grande do Sul. We could think of an extension of land, not available today as a terrestrial ecosystem, which could have accommodated a high primary productivity due to the income of rich nutrient sediments contributed by the possible seasonal floods (Sanchez-Saldías and Fariña 2014). This region between 33° and 37°S, bounded by the Pleistocene sand fields on the west and the current coast of the Río de la Plata (actually a large estuary) and the Atlantic Ocean on the east, has an area of nearly 300,000 km<sup>2</sup>. The emerged land would have

been about 480,000 km<sup>2</sup> with the aforementioned sea level, which represents an increase of 60% over present land area. The retraction of the coast line tens or hundreds kilometres from its present place and the increase in area itself suggest a very different palaeoecological scenario. For instance, the areas sampled in the abundance study now corresponding to the province of Buenos Aires, for which a psammophytic steppe was inferred (Prieto 1996, 2000, Quattrocchio et al. 1988, 1995) would have been hundreds of kilometres away from the coast and consequently under the continental effect that should have increased aridity (Tonni and Cione 1997, 1999). The emerged region would not only augment the available region for the fauna, but also its primary productivity would also have been increased in the low and humid lands of the delta and its vicinity.

#### CONCLUSIONS

Of the models used to study the energetics of the communities none could explain the dynamics of South American mammalian faunas during the Pleistocene. The model used for calculating the population densities according to Silva et al. (2001) did not show good results in this continent, even though it did in Africa. The main reason for this difference in the results could be that the great majority of the South American faunas did not have enough taxa in them, which meant that they did not properly represent the original mammalian communities composition in the Pleistocene. This is due to relative paucity of well-studied palaeontological sites in the whole of the continent, which could mean that many of the mammals that lived in them are yet to be discovered.

African mammalian faunas in the Pleistocene are very similar (if not identical) to those existing today, so the model that best explains their dynamics could be the starting point used to study other faunas in the rest of the continents. The South American mammals that lived in the

Pleistocene are different from those existing today, so the model may have to be modified to address this issue. However, this cannot be done until the faunas in the Paleobiology Database are improved both in number of species and in quantity.

The obtained results on relative abundance of primary and secondary consumers among the Lujanian palaeocommunity in Uruguay, in the province of Buenos Aires, Argentina and also in southern Rio Grande do Sul, Brazil, are consistent with previous ones and suggest that late Pleistocene South American assemblages should have been very different from extant faunas and from many other fossil mammalian faunas. In spite of the proposal of Prevosti and Vizcaino (2006), this new quantitative faunal analysis in the considered localities does not rule out the imbalance between the two trophic levels as a problem. The results show that in the studied localities during Late Pleistocene those ground sloths considered as bulk feeders (*Lestodon* and *Glossotherium*) were more represented in Uruguay, while those considered as selective feeders (*Scelidotherium* and *Megatherium*) were more abundant in the province of Buenos Aires.

One could then speculate on the possibility that mammals might have experienced seasonal migrations, which would have resulted in a more efficient usage of vegetation by the herbivores. The dramatic reduction of the available area subsequent to the end of the glacial period, together with the effects of the end-Pleistocene human arrival in the Americas, must have been crucial factors in the extinction of this fauna.

All these approaches open new and exciting possibilities for future research on the unique and bizarre mammals from South America, whose design and evolutionary history captivated George Gaylord Simpson and many others like us.

#### RESUMO

A fauna de mamíferos do Pleistoceno da América do Sul inclui animais de grande tamanho que têm despertado



o interesse dos cientistas durante mais de dois séculos. Aqui tencionamos atualizar o conhecimento da sua paleoecologia e disponibilizar nova evidência a respeito de dois enfoques: energética vs. densidade populacional e abundância relativa de taxa fósseis. Para determinar se as faunas estavam balanceadas, modelos de densidade populacional foram aplicados a várias faunas sul-americanas e os resultados comparados com os que melhor descrevem a paleoecologia das faunas africanas. Os resultados dos estudos de abundância para a o Uruguai e a província de Buenos Aires durante o piso/idade Lujanense revelam que as preguiças comedoras de vulto (*Lestodon* e *Glossotherium*) foram mais abundantes no primeiro território. No entanto, os mais seletivos *Scelidotherium* e *Megatherium* eram mais abundantes no segundo. Embora os valores obtidos tinham sido corrigidos para evitar tendenciamentos tafonômicos de tamanho, as regressões lineares de abundância vs. massa corporal não se ajustaram ao esperado para consumidores primários e secundários. As faunas do Pleistoceno da América do Sul se comportam diferentemente do que os modelos atualistas sugerem. Mudanças no nível do mar e, portanto, da área disponível poderiam dar conta dessas diferenças; a possibilidade de que uma grande planície aluvial na área hoje submersa poderia explicar mudanças estacionais, o que poderia modificar os cálculos da energética e da abundância.

**Palavras-chave:** abundância, megafauna, paleoecologia, densidade populacional, produtividade secundária, Quaternário.

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