

Paleoecology of the large carnivore guild from the late Pleistocene of Argentina

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The paleoecology of the South American fossil carnivores has not been as well studied as that of their northern relatives. One decade ago Fariña suggested that the fauna of Río Luján locality (Argentina, late Pleistocene–early Holocene) is not balanced because the metabolic requirements of the large carnivores are exceeded by the densities and biomass of the large herbivores. This conclusion is based on the calculation of densities using allometric functions between body mass and population abundance, and is a consequence of low carnivore richness *versus* high herbivore richness. In this paper we review the carnivore richness in the Lujanian of the Pampean Region, describe the paleoecology of these species including their probable prey choices, and review the available information on taphonomy, carnivore ecology, and macroecology to test the hypothesis of “imbalance” of the Río Luján fauna. The carnivore richness of the Río Luján fauna comprises five species: *Smilodon populator*, *Panthera onca*, *Puma concolor*, *Arctotherium tarijense*, and *Dusicyon avus*. Two other species are added when the whole Lujanian of the Buenos Aires province is included: *Arctotherium bonariense* and *Canis nehringi*. With the exception of *D. avus* and *Arctotherium*, these are hypercarnivores that could prey on large mammals (100–500 kg) and juveniles of megamammals (>1000 kg). *S. populator* could also hunt larger prey with body mass between 1000 and 2000 kg. The review of the “imbalance” hypothesis reveals contrary evidence and allows the proposal of alternative hypotheses. If high herbivore biomass occurred during the Lujanian, a higher density of carnivores could be supported than as inferred from the power function of body size and population density.

Key words: Carnivora, paleoecology, population densities, Pleistocene, South America.

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Introduction

Although the paleoecology of South American Pleistocene mammals has been little researched, some reconstructions of the large carnivore guild have been made. For instance, Berta (1988), partly following Marshall's (1977) scheme, divided the fossil South American carnivores into generalists (omnivorous species with varied diet) and specialists (species that feed mostly on other mammals), using body size and craniodental characters (e.g., relative size of carnassials). She subdivided the “generalist” category into “adaptive zones”, i.e., small–medium omnivores (e.g., foxes, procyonids) and medium–large omnivores (e.g., *Chrysocyon brachyurus* (Illiger, 1815), bears and large procyonids). Likewise the “specialist” category was divided into small carnivores (e.g., ferrets and small felids) and medium-sized/large carnivores (e.g., *Canis* Linnaeus, 1758, *Theriodictis* Mercerat, 1891, *Smilodon* Lund, 1842). Additionally, this author recognized three strategies within the latter adaptive zone: (1) species that ambush their prey (e.g., felids); (2) species that actively pursue their prey (e.g., *Canis*); and (3) scavenger species (*Protocyon* Giebel, 1855 and partially *Theriodictis*) (Berta 1988).

More recently, Van Valkenburgh (1991) analyzed the Quaternary carnivores using estimations of body mass and

craniodental indexes from living species to generate a multivariate space in which the ecological niches of extinct species can be identified. She differentiated the presence of large hypercarnivorous canids (e.g., *Canis*, *Theriodictis*, and *Protocyon*), large omnivorous carnivores (i.e., *Chrysocyon brachyurus*), and large hypercarnivorous felids, e.g., *Smilodon populator* Lund, 1842, *Panthera onca* (Linnaeus, 1858), *Puma concolor* (Linnaeus, 1771). According to this author, the paucity of other large carnivores would have permitted the evolution of several canid species with these adaptations (Van Valkenburgh 1991).

Later, Berman (1994) discussed the alimentary habits of some fossil carnivores of the Pampean region, mainly on the basis of anatomical descriptions. He suggested that *Canis gezi* Kraglievich, 1928 was hypercarnivorous and eat bones frequently, whereas *Arctotherium* Burmeister, 1879 and *Chapalmalania* Ameghino, 1908 were omnivorous and scavengers, and *Smilodon* hunted large mammals, but only juvenile megamammals. This author counted the number of specimens for each species from an Ensenadan bed in the Pampean region, and found that the most abundant species were the notoungulate *Mesotherium cristatum* Serres, 1867 (259 specimens), the ground sloth *Scelidotherium* Owen, 1839 (116 specimens), the glyptodont *Sclerocalyptus* Ameghino, 1891

(69 specimens), *Smilodon* (43 specimens), and *Arctotherium* (39 specimens). Based on the abundance and body size of these species, he suggested that *M. cristatum*, *Scelidotherium* sp., and *Sclerocalyptus* sp. were important items in the diet of *Smilodon* sp. during the Ensenadan (Berman 1994).

More recently, new paleoecological studies were carried out on the Lujanian fauna of the Pampean region (Fariña 1996). This author calculated the biomass and energetic requirements of herbivores and carnivores on the basis of species richness and their estimated body mass, and concluded that the community was out of balance because the biomass of large herbivores greatly exceeded the energetic requirements of the large carnivores. This reconstruction is based on the use of interspecific formulas obtained from Damuth's (1993) regression analyses between body mass and population density/basal metabolic rate of living mammals. This approach was similar to the one used by Damuth (1982); however, the latter contrasted expected *versus* observed densities in a fossil bed with the goal of identifying the existence of taphonomic biases (i.e., associations departing from the expected; Damuth 1982). The imbalance in the Pampean Lujanian arises from the low richness and abundance of large carnivores in contrast to a remarkable diversity of megaherbivores (Fariña 1996).

Until now, the scenario proposed by Fariña (1996) has only been questioned by Soibelzon (2002), who proposed that the specific richness of carnivores was higher than Fariña's (1996) estimation (but see below) and that a reassessment of that hypothesis was necessary.

The goal of this work is to provide a discussion of the paleoecology of large carnivores (body mass >10 kg) of the Lujanian (Late Pleistocene – early Holocene, 130–8.6 ka) of the Pampean region. For this purpose, the number of occurring species is established and the existing paleoecological information on these species is integrated so as to permit the inference of ecological relationships within this fossil vertebrate community (e.g., Damuth 1992; Palmqvist et al. 2003). The specific richness of Lujanian large carnivores is established in accordance with the most recent systematic revisions (e.g., Berman 1994; Soibelzon 2002, 2004). In addition, an attempt at the recognition of potential prey species within the Lujanian faunal assemblage and possible interactions among the carnivores is provided. Lastly, the usefulness of interspecific body mass/population density formulas is discussed in light of recent criticisms (e.g., Blackburn and Gaston 1996; Smallwood 1999, 2001) and the available ecological information for populations of living carnivores.

Institutional abbreviations.—MLP, Departamento Científico Paleontología, Vertebrados Museo de La Plata, La Plata, Argentina; MACN Pv, Colección Nacional de Paleovertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MCNSC, Museo de Ciencias Naturales de Santa Clara del Mar "Pachamama", Santa Clara del Mar, Argentina.

Other abbreviations.—D, population densities; FLRL, Río Luján local fauna; M, body mass; MPM, maximum prey

size; PE%, percentage prediction error of allometric equation; R², coefficient of determination; RGA, relative grinding area of the lower molars; SE, standard error of the estimate; TPM, typical prey size.

Material and methods

Species richness of large carnivores and herbivores of the Río Luján fauna and the Lujanian of the Pampean Region.

—The number of species of large carnivores occurring in the Río Luján fauna ("Fauna Local Río Luján", hereafter referred to as the FLRL) and the entire Lujanian of the Pampean region was established by means of bibliographical revision, mainly based on the works of Ameghino (1889), Tonni et al. (1985), Berman (1994), Cione et al. (1999), and Soibelzon (2002, 2004) (Tables 1–3). The list of herbivores was also taken from these authors (Table 3). Body mass values for Lujanian herbivores were taken from Fariña (1995, 1996) and Fariña et al. (1998). For those cases in which no estimation of body mass was available, we used the data from closely related and morphologically similar species. Three size categories were established: medium-sized mammals (10–100 kg), large mammals (100–1000 kg), and megamammals (>1000 kg). In effect, the "large" category comprises mainly the 100–500 kg range, as only one species of this group had greater body mass.

Paleoautecological and paleosynecological inferences.

—The paleoecology of extinct South American large carnivores is poorly developed, especially when compared to the studies of North American species. Three of the extinct South American taxa (*Canis nehringi* Ameghino, 1902, *Arctotherium* spp., *Smilodon populator*) are closely related and very similar to North American taxa (i.e., *Arctodus* Leidy, 1854, *Canis dirus* Leidy, 1858, *Smilodon fatalis* Leidy, 1868, respectively). This allows, *prima facie*, an extrapolation of the paleoecological inferences from the Neartic forms to the South American ones (see below), although future studies should contrast these with direct inferences for the latter. The information so gathered and produced permits the delineation of an "ecological profile".

Thus, the paleoecological inferences for fossil species were compiled mainly from bibliographical sources, but some estimations (e.g., body mass, typical, and maximum prey size) were made to achieve better characterization of these species.

For a synthesis of feeding habits of these carnivores we used the index of relative lower molar grinding area (RGA): (square root of occlusal surface [length * width] of the talonids of m1 + m2 + m3)/length of m1 trigonid (see Van Valkenburgh 1991; Table 1). Species with lower values are those with more carnivorous diets, with little (or no) grinding area and proportionally longer slicing blades in the lower molars; conversely, species with higher values are omnivorous.

Body mass for the carnivores was estimated using equations published in Van Valkenburgh (1990) and Turner and

Table 1. Estimated body mass (M) in kg, and relative lower molar grinding area index (RGA) for Lujanian large carnivores. Between parentheses are the observed ranges. FLRL: species occurring in the Río Luján fauna. The calculation of body mass [M, expressed in kilograms] for *Panthera onca* (Linnaeus, 1758) and *Dusicyon avus* (Burmesiter, 1966) were made according to the formulas in Van Valkenburgh (1990: table 10), for felids and canids respectively, based on condylobasal skull length (LCB), distance between condyles and anterior orbital border (LOO) and length of first lower molar (m1). For *P. onca* we also used the intraspecific formula (i.e., $M [kg] = 1.122 * LCB [cm] - 184.88$) of Turner and O'Regan (2002). The mean body mass of *Smilodon populator* Lund, 1842 were estimated from the weighted values estimated by Christiansen and Harris (2005), and the range is following this authors. The values of body size of *Arctotherium* spp. and *Puma concolor* came from Soibelzon (2002) and Sunquist and Sunquist (2002), respectively.

| | Mass | RGA |
|---|------------------------|------|
| <i>Smilodon populator</i> Lund, 1842 (FLRL) | 304.45 (220–400) | 0 |
| <i>Puma concolor</i> (Linnaeus, 1771) (FLRL) | 50.36 (22.70–80.00) | 0 |
| <i>Panthera onca</i> (Linnaeus, 1758) (FLRL) | 119.66 (95.00–137.71) | 0 |
| <i>Canis nehringi</i> (Ameghino, 1902) | 32.26 (28.69–38.54) | 0.64 |
| <i>Dusicyon avus</i> (Burmeister, 1866) (FLRL) | 14.65 (12.07–19.15) | 0.79 |
| <i>Arctotherium tarijense</i> Ameghino, 1902 (FLRL) | 139.42 (102.00–189.00) | 1.68 |
| <i>Arctotherium bonaeriense</i> (Gervais, 1852) | 110.17 (106.00–122.00) | 1.55 |

Table 2. Typical and maximum prey size (TPM and MPM, in kg) for Lujanian large carnivores $\pm 95\%$ prediction intervals. The values corrected for logarithmic de-transformation bias are shown in parentheses, and the values obtained from independent phylogenetic contrasts are shown in brackets. FLRL: species occurring in the Río Luján fauna. See the text for more details.

| | TPM | MPM |
|---|-------------------------------------|--|
| <i>Smilodon populator</i> Lund, 1842 (FLRL) | 764.16 \pm 4.91 (783.88) [763.08] | 1871.56 \pm 3.71 (1968.89) [1470.48] |
| <i>Puma concolor</i> (Linnaeus, 1771) (FLRL) | 26.90 | 366.00–500.00 |
| <i>Panthera onca</i> (Linnaeus, 1758) (FLRL) | 135.68 \pm 4.84 (139.18) [116.76] | 564.62 \pm 3.69 (594.98) [582.47] |
| <i>Canis nehringi</i> (Ameghino, 1902) | 23.16 \pm 29.71 (49.84) | 268.00 \pm 4.23 (303.12) [272.75] |
| <i>Dusicyon avus</i> (Burmeister, 1866) (FLRL) | 4.84 \pm 28.67 (10.42) | 59.95 \pm 4.17 (67.73) [60.82] |
| <i>Arctotherium tarijense</i> Ameghino, 1902 (FLRL) | 100.00 | 300.00 |
| <i>Arctotherium bonaeriense</i> (Gervais, 1852) | 100.00 | 300.00 |

Regan (2002) (Table 1), with the exception of *Smilodon populator* and the ursids. For these species we took the estimations of Christiansen and Harris (2005) and Soibelzon (2002), respectively. All these estimations should be verified in the future because it was not possible to control for the existence of phylogenetic correlation in the raw data used by the authors to construct the used functions. The mean values (see Table 1) were used to estimate other parameters and for graphical proposes.

The values for typical and maximum prey size were calculated using data from Van Valkenburgh and Koepfli (1993) and Van Valkenburgh and Hertel (1998) (see also Hemmer 2004). In the case of canids, a regression was made based on the values of body mass and prey size provided in Van Valkenburgh and Koepfli (1993), using the highest values for each species. We used the following formulas: typical prey size (in kilograms) = $1.97 * M - 1.60$ ($R^2 = 0.56$, $p < 0.001$; SE = 0.6689); maximum prey size (in kilograms) = $1.88 * M - 0.4052$ ($R^2 = 0.90$, $p < 0.001$; SE = 0.2669). For the felids we used the data from body mass and prey size provided in Van Valkenburgh and Hertel (1998), and the following formulas were calculated: TPM = $(1.86 * M) - 1.74$ ($R^2 = 0.90$, $p < 0.001$; SE = 0.3019); MPM = $1.29 * M + 0.075$ ($R^2 = 0.88$, $p < 0.001$; SE = 0.2409). As the known Lujanian *Puma concolor* specimens are fragmentary and fall within the size range of living specimens, no estimations of body

mass, TPM or MPM were made, but instead the information available from living specimens was used (see below).

The structure of the Lujanian carnivore community was compared with three recent communities: Serengeti (Tanzania), Chitawan (Nepal), and Yellowstone (USA), mainly following Van Valkenburgh (1985), and with the fauna from the late Pleistocene site Pit 91 of Rancho La Brea (USA, see Spencer et al. 2003). We used the body size of carnivores and their maximum prey size to do the comparisons. The typical prey size show the same pattern, thus for the sake of brevity we only present the analysis with maximum prey size.

All the regression analyses were calculated as simple linear regressions (least squares) of the log-10 transformed data. Because the predicted values from a logarithmic transformed arithmetic data are estimates of the geometric mean of the dependent variable, rather than the arithmetic mean, and as the geometric mean is always less than the arithmetic mean, detransformed predictions will underestimate the real values. Smith (1993a) reviewed several methods to correct the logarithmic transformation bias, and we follow this author in the correction of this bias. The predictive power of the allometric equations was tested by means of percentage predictive error (PE%) (see Van Valkenburgh 1990).

Estimation of population densities.—With the goal of confirming the results of the regression analyses of mammalian densities *versus* body mass made by previous authors (i.e.,

Table 3. Faunal list of large (>10 kg) non carnivore mammals in the Lujanian of the Pampean region with their estimated body size (kg). M: middle-sized mammal; G: large mammal; Me: megamammal. FLRL: species occurring in the "Fauna Local Río Luján".

| | Taxon | | M | Mass Category |
|-----------------|---|--------|--------|---------------|
| Camelids | <i>Hemiauchenia paradoxa</i> Gervais and Ameghino, 1880 | (FLRL) | 1000 | Me |
| | <i>Eulamaops parallelus</i> (Ameghino, 1884) | (FLRL) | 150 | G |
| | <i>Lama guanicoe</i> Müller, 1776 | (FLRL) | 90 | M |
| | <i>Lama gracilis</i> (Gervais and Ameghino, 1880) | (FLRL) | 50 | M |
| Cervids | <i>Paraceros fragilis</i> (Ameghino, 1888) | | 50 | M |
| | <i>Morenelaphus lujanensis</i> (Ameghino, 1888) | (FLRL) | 50 | M |
| Tayassuids | <i>Catagonus</i> Ameghino, 1904 | | 35 | M |
| | <i>Pecari tajacu</i> (Linnaeus, 1758) | (FLRL) | 30 | M |
| Mastodonts | <i>Stegomastodon platensis</i> (Ameghino, 1888) | (FLRL) | 7580 | Me |
| Equids | <i>Hippidion principale</i> (Lund, 1845) | | 511 | G |
| | <i>Equus (Amerhippus) neogeus</i> Lund, 1840 | (FLRL) | 300 | G |
| Toxodonts | <i>Toxodon platensis</i> Owen, 1837 | (FLRL) | 1642 | Me |
| | <i>Toxodon burmeisteri</i> Giebel, 1866 | (FLRL) | 1100 | Me |
| Macraucheniiids | <i>Macrauchenia patachonica</i> Owen, 1838 | (FLRL) | 988 | G |
| Armadillos | <i>Eutatus seguini</i> Gervais, 1867 | (FLRL) | 200 | G |
| | <i>Propraopus grandis</i> Ameghino, 1881 | | 200 | G |
| | <i>Pampatherium typum</i> Ameghino, 1875 | (FLRL) | 200 | G |
| Glyptodonts | <i>Sclerocalyptus migoyanus</i> Ameghino, 1889 | (FLRL) | 250 | G |
| | <i>Neothoracophorus depressus</i> (Ameghino, 1881) | (FLRL) | 1100 | Me |
| | <i>Neuryurus</i> Ameghino, 1889 | | > 1000 | Me |
| | <i>Panochthus morenoii</i> Ameghino, 1881 | | 1100 | Me |
| | <i>Panochthus frenzelianus</i> Ameghino, 1889 | | 1100 | Me |
| | <i>Panochthus tuberculatus</i> (Owen, 1845) | (FLRL) | 1061 | Me |
| | <i>Doedicurus clavicaudatus</i> (Owen, 1847) | (FLRL) | 1468 | Me |
| | <i>Plaxaplous canaliculatus</i> Ameghino, 1884 | (FLRL) | 1300 | Me |
| | <i>Glyptodon clavipes</i> Owen, 1839 | (FLRL) | 2000 | Me |
| | <i>Glyptodon reticulatus</i> Owen, 1845 | (FLRL) | 862 | G |
| Ground sloths | <i>Megatherium americanum</i> Cuvier, 1796 | (FLRL) | 6073 | Me |
| | <i>Glossotherium myloides</i> (Gervais, 1855) | (FLRL) | 1200 | Me |
| | <i>Glossotherium robustum</i> (Owen, 1842) | (FLRL) | 1713 | Me |
| | <i>Lestodon trigonidens</i> Gervais, 1873 | (FLRL) | 3397 | Me |
| | <i>Mylodon darwini</i> Owen, 1843 | | >1000 | Me |
| | <i>Scelidotherium leptocephalum</i> Owen, 1839 | (FLRL) | 1057 | Me |
| Rodents | <i>Nechoerus aesopi</i> (Leidy, 1853) | (FLRL) | 63 | M |

Damuth 1993), we performed a regression analysis of tropical African carnivores. Unfortunately, the raw data used by Damuth (1993) are not included in his work, therefore we used the data on population density (expressed as individuals per square kilometer) and body mass for tropical African living carnivores from Damuth (1987). However, Damuth (1993) only included 12 species in the regression analysis for African carnivores, whereas his 1987 work included 13 species of carnivores that currently inhabit tropical Africa. Based on the maximum and minimum body mass values given by Damuth (1993), we can deduce that both *Panthera leo* (Linnaeus, 1758) and *Galerella sanguinea* (Rüppell, 1836) were included in his analysis, but we have no way to identify which of the re-

maining eleven species was excluded. For this reason we performed several regressions alternatively excluding each species, but none of the results was identical to those of Damuth (1993), and therefore the original 13 species were included. These species are: *Panthera leo*, *Panthera pardus* (Linnaeus, 1758), *Felis silvestris* Schreber, 1775, *Acinonyx jubatus* (Schreber, 1775), *Galerella sanguinea*, *Ichneumia albicauda* (Cuvier, 1829), *Genetta genetta* (Linnaeus, 1758) *Crocota crocuta* (Erxleben, 1777), *Lycan pictus* (Temminck, 1820), *Canis aureus* Linnaeus, 1758, *Canis adustus* Sundevall, 1847, *Canis mesomelas* Schreber, 1775, and *Canis simensis* Rüppell, 1840. Since *L. pictus* is an "outlier", it was excluded from the final regression analysis.

Phylogenetic comparative analysis.—The correlation between the variables used in the regression analysis and the phylogenetic scheme of the studied species was contrasted by means of the Serial Independence Test using the program Phylogenetic Independence 2.0 (Reeve and Abouheif 2003; see also Abouheif 1999). The supertree of living carnivores was taken from Bininda Emonds et al. (1999) and modified according to the most recently published phylogenies (Mattern and McLennan 2000; Koepfli and Wayne 2003; Yoder et al. 2003; Marmi et al. 2004; Yu et al. 2004; Zrzavý and Řičánková 2004). As the raw data for body mass and typical and maximum prey size of living carnivores used to estimate the value of the last two variables in fossil species, are correlated with their phylogeny, the relationship between these variables was explored by means of Independent Phylogenetic Contrasts (Harvey and Pagel 1991) using the program PDTREE of the software package PDAP version 5.0 (Garland et al. 2003). The adjustment of branch length was checked using the ratio of standardized values of the contrasts *versus* their standard deviations (see Garland et al. 2003). The estimations of TPM and MPM for fossil *Panthera onca* specimens were obtained by re-rooting the tree in the *P. onca* branch (see Garland and Ives 2000).

Studied material.—*Panthera onca*: MLP 10-3, MLP 10-9, MLP 82-IV-7-1, MLP 53-III-19-4; *Smilodon populator*: MACN Pv 46; *Dusicyon avus* (Burmeister, 1866): MLP Pv 95-V-2-1; MACN Pv 53, MACN Pv 51; *Canis nehringi*: MACN Pv 500; *Arctotherium bonariense* (Gervais, 1852): MACN Pv 2668; MCNSC 1099; *Arctotherium tarijense* Ameghino, 1902: MACN Pv 2667.

Results

Specific richness of carnivores and distribution of herbivore body mass.—Fariña (1996) lists four large carnivores in the FLRL, but Soibelzon (2002) stated that four additional species should be added, because three *Arctotherium* species are recorded in the Lujanian. However, only two of these are present in the Lujanian of the Pampean region, and only *Arctotherium tarijense* was found in FLRL (Soibelzon 2004). Additionally, *Puma concolor* was mentioned by Tonni et al. (1985) but not by Fariña (1996; see Soibelzon 2002).

The species of large carnivores recorded in FLRL and the entire Lujanian of the Pampean region comprise five and seven species, respectively (Table 1). Fossil remains of a bear (*Arctotherium tarijense*), a canid (*Dusicyon avus*) and three large felids (*Panthera onca*, *Puma concolor*, and *Smilodon populator*) were recorded in FLRL. If the analysis is expanded to include the entire Lujanian (130–8.6 ka) of the Pampean region, it should include three additional species, namely *Arctotherium bonaeriense*, *Canis nehringi*, and *Homo sapiens* Linnaeus, 1758, which entered the Pampean region towards the end of the Pleistocene (11–10 ka; Miotti 2003). In this case the time averaging is much more marked and is influenced mainly

by the increase in the scale of the analysis, with higher biomass overestimation. The number of carnivores in the Río Luján fauna is lower than in recent communities and the Pit 91 of Rancho La Brea, but not very different than in Chitawan (six species). In comparison to recent communities, the Lujanian has less species with body size between 50 and 10 kg, and maximum prey size lower than 200 kg, but possess more species with body size above 100 kg and maximum prey size over 200 kg (Fig. 1). In Yellowstone there are several species with maximum prey size above 200 kg, too. Additionally, the Lujanian differ in the presence of a very large taxon (>300 kg) with maximum prey mass over 1000 kg. The fauna of the Pit 91 of Rancho La Brea shows the same differences with recent communities, but is more diverse than the Lujanian carnivore fauna (Fig. 1).

The Pampean Lujanian fauna of large herbivores and mega-herbivores comprises 36 taxa including cervids, camelids, equids, tayassuids, native ungulates, and several xenarthran groups (Table 3). The number of these mammals is somewhat lower in FLRL (26) but the faunistic composition is basically the same. The body mass of herbivores is concentrated mainly within the 10–2000 kg range (Fig. 2). The distribution is not uniform within this 1000 kg range; rather, most of the species have body masses between 10 and 300 kg and only three species fall within the 300–1000 kg range (Fig. 2; Table 2).

There are no significant differences in the distribution of herbivore body mass between FLRL and the entire Lujanian of the Pampean region. Most of the non-carnivorous mammals with body mass greater than 10 kg that have been so far recorded in the Lujanian of the Pampean region can also be found in the Río Luján fauna, with the exception of few species and genera: *Eutatus seguini* Gervais, 1867, *Propaopus grandis* Ameghino, 1881, *Neothoracophorus depressus* (Ameghino, 1881), *Panochthus frenzelianus* Ameghino, 1889, *Neuryurus* Ameghino, 1889, *Panochthus morenoi* Ameghino, 1881, *Mylodon darwini* Owen, 1840, *Paraceros fragilis* (Ameghino, 1888), *Catagonus* Ameghino, 1904, *Hippidion principale* (Lund, 1845) (Table 3), and the distribution of body mass for these mammals is basically the same in both assemblages (see above).

Paleoecological inferences.—The size of *Smilodon populator* separates it from other carnivores by a large gap near to 150 kg (Table 1, Fig. 3). *Arctotherium tarijense*, *Panthera onca*, and *Arctotherium bonariense* follow *S. populator* in size, with body masses above 100 kg (Table 1, Fig. 3). *Puma concolor* is the largest of the other three species, followed by *Canis nehringi*, and last by *Dusicyon avus* (Table 1, Fig. 3). The body mass of *C. nehringi* duplicates the size of *D. avus*, but the two ursids have a similar size (Table 1, Fig. 3). The values of typical prey size are ordering these carnivores in a similar way, but *Panthera onca* have higher values than the ursids (Table 2). The pattern of the maximum prey size is similar to the TPM, with the exception that *Puma concolor* has a higher value than the species of *Arctotherium* (Table 2, Fig. 3).

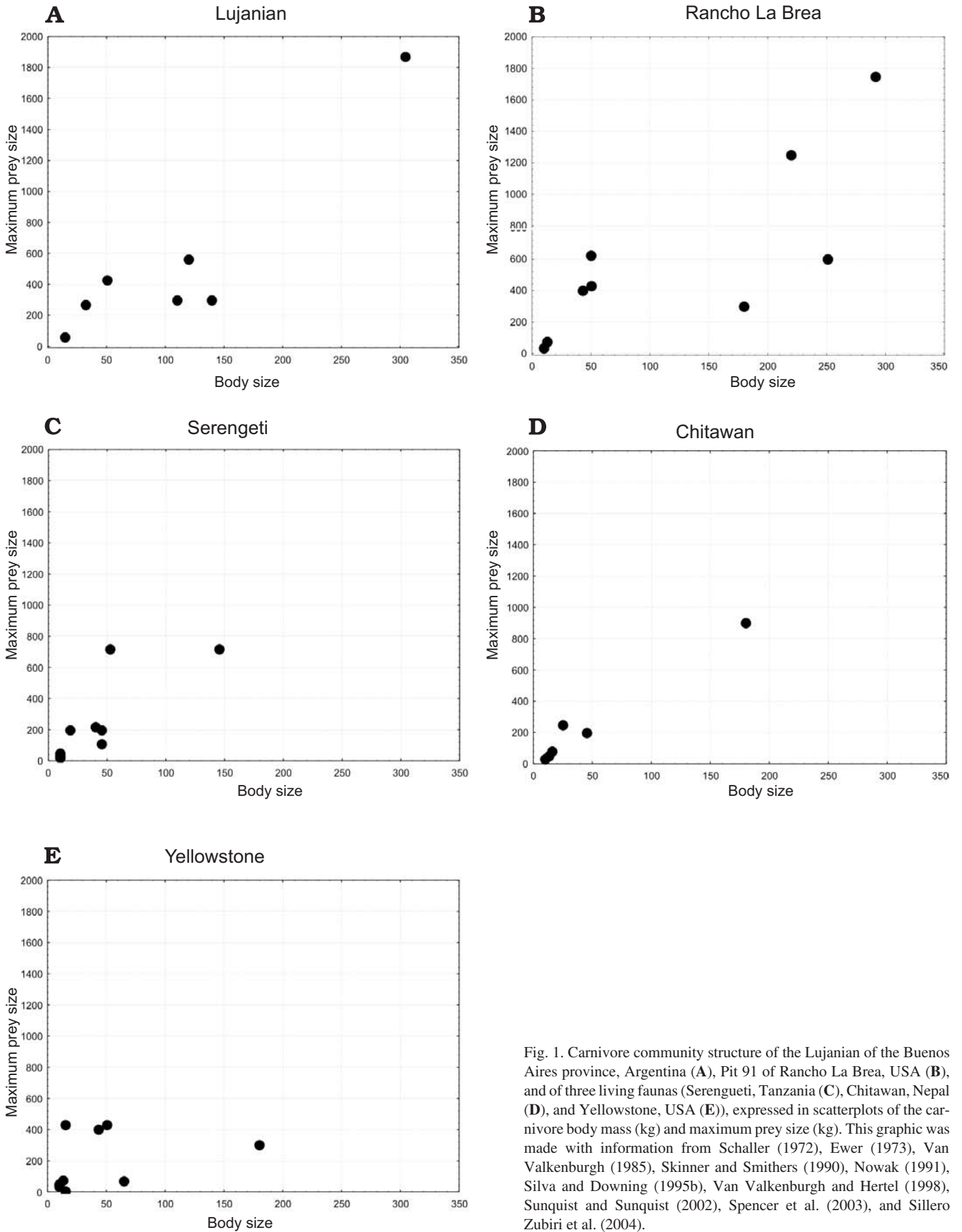


Fig. 1. Carnivore community structure of the Lujanian of the Buenos Aires province, Argentina (A), Pit 91 of Rancho La Brea, USA (B), and of three living faunas (Serengeti, Tanzania (C), Chitawan, Nepal (D), and Yellowstone, USA (E)), expressed in scatterplots of the carnivore body mass (kg) and maximum prey size (kg). This graphic was made with information from Schaller (1972), Ewer (1973), Van Valkenburgh (1985), Skinner and Smithers (1990), Nowak (1991), Silva and Downing (1995b), Van Valkenburgh and Hertel (1998), Sunquist and Sunquist (2002), Spencer et al. (2003), and Sillero Zubiri et al. (2004).

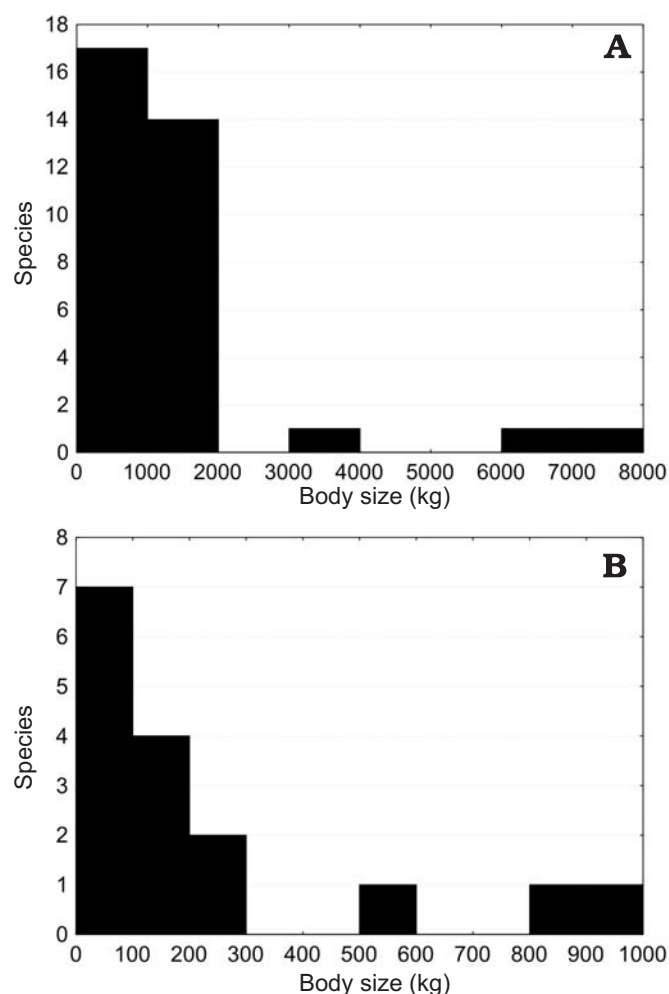


Fig. 2. Frequencies of herbivore body mass (>10 kg) from the Lujanian of the Pampean Region (Argentina). A. Total sample. B. Herbivores with body mass between 10–1000 kg.

The RGA ordered the species with higher values (more omnivorous) in one extreme of the distribution (*Arctotherium* spp.), and the more carnivorous species represented by the felids, that lack m1 talonid and post-carnassial molars, in the other (Table 1; Fig. 3). The canids are situated in between with intermediate values; among these, *Dusicyon avus* has the highest value. The species of *Arctotherium* present lower RGA than *Ursus arctos* Linnaeus, 1758 and *Ursus americanus* Pallas, 1780 (1.76–2.12), but overlap with *Ursus maritimus* Phipps, 1774 (1.58–1.71) and *Tremarctos ornatus* (Cuvier, 1825 in Geoffroy and Cuvier 1825) (1.67). *Arctotherium bonariense* and *Arctotherium tarijense* have similar values, but *A. bonariense* reaches the lowest index (1.68–1.43) of the studied ursids (see Table 1). The value of *C. nehringi* is lower than *D. avus* and falls in the range of modern hypercarnivorous canids (0.51–0.72). On the other hand, the RGA of *D. avus* (0.76–0.82) overlaps the range of *Dusicyon culpaeus* (Molina, 1782) (0.77–0.91) but one specimen possesses a lower index indicating more carnivorous habits.

The function used to estimate TPM of canids showed high PE% and bias generated by the logarithmic de-transformation (272.34 and 2.15 respectively), and very broad prediction intervals (see Table 2). Moreover, the function was no longer significant after the data were adjusted according to the phylogeny. The PE% was low for the equations used to estimate MPM of felids and canids (15.23 and 10.81, respectively), but it was somewhat high for the TPM function of felids (77.73).

All the variables used in the regressions to estimate MPM and TPM values were significantly correlated with the phylogeny ($p. <0.05$). The analysis of independent phylogenetic contrasts (with the exception of TPM-canid body size) showed that even after controlling for phylogenetic effects, the TPM and MPM values are positively correlated to M and that the calculated regression lines fall within the 95% confidence interval of the lines obtained from the raw data. The TPM values estimated from the contrasts are similar to those obtained from the raw data, but the MPM for *Smilodon populator* is more than 500 kg lower, which could be due to the far away position of this species from the recent ones.

The published ecological and paleocological information agrees with these ecological inferences of *Dusicyon avus* and *Canis nehringi*. *D. avus* presents craniodental features interpreted as adaptation to more carnivorous habits than recent foxes (Berman and Tonni 1987). The diet of its recent relative *Dusicyon culpaeus* with a typical prey mass of 2 kg, and a maximum prey size of 27 kg (see Sillero Zubiri et al. 2004), is in concordance with estimated values for the extinct taxon.

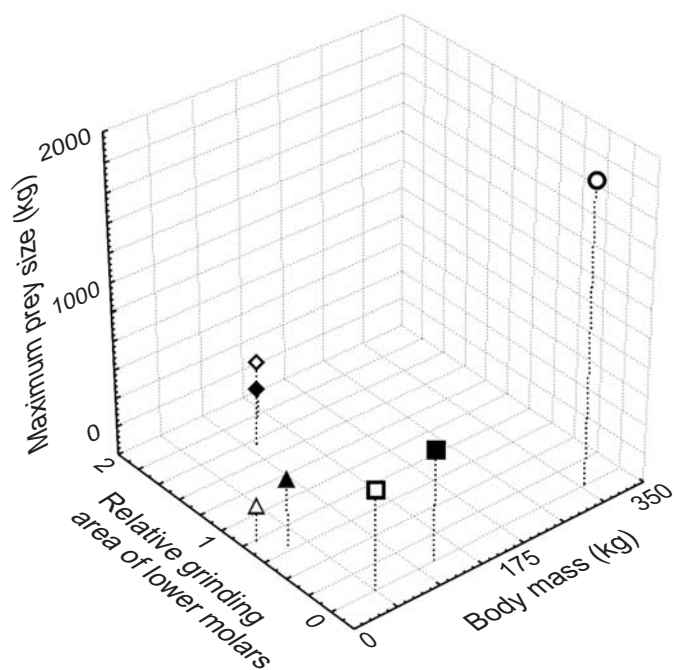


Fig. 3. Threedimensional distribution of Lujanian large carnivores according to their maximum prey size, relative grinding area of lower molars and body mass values. White circle: *Smilodon populator* Lund, 1842; black square: *Panthera onca* (Linnaeus, 1758); white square: *Puma concolor* (Linnaeus, 1771); black triangle: *Canis nehringi* (Ameghino, 1902); white triangle: *Dusicyon avus* (Burmeister, 1866); black diamond: *Arctotherium tarijense* Ameghino, 1902; white diamond: *Arctotherium bonaeriense* (Gervais, 1852).

The calculated body mass values overlap with the highest values for *Dusicyon culpaeus*, but are higher than the mean weight for the latter species. The identification of *C. nehringi* as a hypercarnivorous canid was previously made by Van Valkenburgh (1991). Additionally, the relative if not conspecific with *Canis dirus*, hunted in packs and preyed on ruminants and other large herbivorous, with a typical prey size around 300 kg and a maximum of 600 kg (Van Valkenburgh 1991; Van Valkenburgh and Hertel 1998; Coltrain et al. 2004). The bite force, dental morphology, and dental pathologies suggest that could hunt larger prey and consumed larger amount of bones than the living *Canis lupus* Linnaeus, 1758 (e.g., Kurtén and Anderson 1980; Van Valkenburgh and Ruff 1987; Van Valkenburgh and Hertel 1993; Biknevicius and Van Valkenburgh 1996; Van Valkenburgh and Sacco 2002; Wroe et al. 2005; Therrien 2005a). Recent isotopic analysis (Matheus, 1995; Barnes et al. 2002) suggest that *Arctodus simus* Cope, 1879 was a highly carnivorous species adapted to scavenge, in contraposition to the early omnivorous or herbivorous hypotheses (Van Valkenburgh and Hertel 1998) but in more concordance with the opinion of (Kurtén 1967). Unfortunately the studies of South American species (*Arctotherium* spp.) are much scarcer, but the possession of secodont carnassials teeth (at least more secodont than in living ursines and *Tremarctos ornatus*) and the dental wear pattern/pathologies suggest that they have a broad omnivore diet but with a large carnivorous component, that include the consumption of bone (Soibelzon 2002). Using craniodental and postcranial measurements and Van Valkenburgh's (1991) and Anyonge (1993) formulas for ursids, Soibelzon (2002) estimated the body mass of *Arctotherium tarijense* in 102–189 kg (mean: 139.42 kg) and that of *Arctotherium bonaeriense* as 106–122 kg (mean: 110.17 kg; Table 1; Fig. 3). The values of the relative grinding area of lower molar are not completely in accordance with a strict carnivore diet (Matheus 1995; Barnes et al. 2002) and because the presence of a large relative area are more consistent with a more omnivorous regimen. But it is possible that this index is not very good to predict diet in ursids, because two species with very different diet (the strict carnivorous *Ursus maritimus* versus the mostly herbivorous *Tremarctos ornatus*) posses overlapping indexes. Sacco and Van Valkenburgh (2004) found that the carnivorous ursids present a low morphological specialization in comparison to other carnivorous carnivores, thus the relative large grinding area of lower molars, in comparison to other carnivores, could be due to different hunting strategies or phylogenetic legacy. Unfortunately no formulas are available for the estimation of typical and maximum prey size of bears, but taking into account the body mass of *A. tarijense* and *A. bonaeriense* and the estimations for *Arctodus simus* (Van Valkenburgh and Hertel, 1998) it is probable that the South American species could prey on mammals of up to 300 kg, with a typical prey size around 100 (Table 2; Fig. 3). The jaguar (*Panthera onca*) and the puma (*Puma concolor*) are felids that prey in the present on large and middle-sized mammals using ambush or stalk-short chase strategies (Eisenberg and Redford, 1999). The jag-

uar diet includes approximately 5% small mammals (<1 kg), and 95% mammals greater than 1kg (López González and Miller 2002). The size of the typical prey varies with their availability, between 19–30 kg [*Pecari tajacu* (Linnaeus, 1758), 3–4 kg (*Dasybus novemcintus* Linnaeus, 1758), and 63 kg (*Hydrochaerus hydrochaerus* (Linnaeus, 1766)]. They also prey occasionally on larger mammals like tapirs (*Tapirus terrestris* Linnaeus, 1758, 177 kg) and cattle (*Bos taurus* Linnaeus, 1758, 361–500 kg) (Hoogesteijn and Mondolfi 1993, 1996; Medellín et al. 2002; Sunquist and Sunquist 2002). Estimated maximum prey size are somewhat higher than those currently observed (Table 2, Fig. 3; and see above) in accordance with the higher inferred body mass. On the other hand the current absence of larger prey in South America could restrict the MPM of the living representatives. The puma is smaller than the jaguar but posses a similar diet, with a mean prey mass that decreases towards the tropics (e.g., 29 kg in Patagonia and 0.4 kg in Belize) and is positively correlated with the body mass of the puma, a variable that also increases with higher latitudes (Iriarte et al. 1990; Gay and Best 1996). In South America it could prey on large mammal like deer (e.g., *Odocoileus Rafinisque*, 1832, 50–120 kg), tapirs (177 kg) and bovine cattle (366–500 kg). Several lines of evidences (functional morphology, stable isotopes, pattern of dental wear/pathologies, dental microwear) indicate that *Smilodon* preyed on large mammals, stalking and captured it after a short chase (Muñiz 1845; Akersten 1985; Van Valkenburgh and Hertel 1993; Anyonge 1996a, 1996b; Biknevicius and Van Valkenburgh 1996; Van Valkenburgh and Hertel 1998; Wroe et al. 2005; Therrien 2005b). As showed the analysis of ¹³C and ¹⁵N isotopes, *Smilodon fatalis* ate mainly ruminants in Rancho La Brea (Coltrain et al. 2004). Finally, its little dimorphism and its endocephalic morphology suggest that it was solitary rather than gregarious and did not have developed social behavior (Van Valkenburgh and Sacco 2002; McCall et al. 2003). Recently, Christiansen and Harris (2005) estimated that the body size of *Smilodon populator* was between 220–360 kg, and that some occasional specimens could reach or exceed the 400 kg. The TPM and MPM values are congruent to some extent with those estimated by Van Valkenburgh and Hertel (1998), although the value for the first of these indexes is higher than suggested by these authors to *Smilodon fatalis* (300–599 kg; Table 1; Fig. 3). On the contrary, the MPM values fall within the range estimated by these authors (1000–2000 kg; Table 2; Fig. 3). In any case, these values should be considered with caution, as they are only provisional figures and represent extrapolations.

Estimation of population densities for fossil carnivores.—The function obtained from the 12 African carnivores of Damuth (1987) shows that there is significant negative correlation between body mass and population density, and is expressed as: $D = -0.52 M + 1.82$ (Fig. 4). R^2 is 0.455 and SE is 0.4229. This function is very similar to the one that in Damuth (1993), although the latter has greater slope (–0.64), lower R^2 (0.36) and higher SE (0.6171); however, the line obtained by

Table 4. Body size (M, in kg), observed and estimated density (D, in individuals/km²) for five species of African large mammals, calculated from Schaller (1972). Values corrected for logarithmic de-transformation bias are shown in parentheses. PI: 95% prediction interval.

| | M | Observed D | Stimulated D D ± 95% PI |
|--|--------|------------|----------------------------|
| <i>Lycaon pictus</i> (Temminck, 1820) | 18.50 | 0.012 | 0.400 ± 9.10 (0.522) |
| <i>Panthera leo</i> (Linnaeus, 1758) | 145.00 | 0.072 | 0.136 ± 9.15 (0.180) |
| <i>Panthera pardus</i> (Linnaeus, 1758) | 45.00 | 0.036 | 0.251 ± 9.11 (0.329) |
| <i>Crocota crocuta</i> (Erxleben, 1777) | 52.50 | 0.140 | 0.231 ± 9.12 (0.303) |
| <i>Acinonyx jubatus</i> (Schreber, 1775) | 45.00 | 0.009 | 0.251 ± 9.11 (0.329) |

this author (Damuth 1993) falls within the 95% confidence intervals of the regression line obtained here (Fig. 4).

The correction factors estimated using three methods are higher than those considered acceptable (see Smith 1993b): 1.61 (“quasi-maximum likelihood estimator”), 1.45 (“smearing estimate”) and 1.30 (“ratio estimator”), indicating that the regression don’t have a good prediction power. The latter value was used to correct the bias of logarithmic de-transformation. PE% is also very high (224.84).

The 95% confidence and prediction limits that were obtained are wide and range from unrealistic values (negative densities) to relatively high values (e.g., densities >9 individuals per km²), spanning several orders of magnitude (Table 4).

According to the Serial Independence Test, neither the body mass values (0.11, $p = 0.2745$) nor the densities values (0.24, $p = 0.1126$) used here are significantly correlated with the phylogeny, and therefore the “raw” data could be used without applying any comparative method.

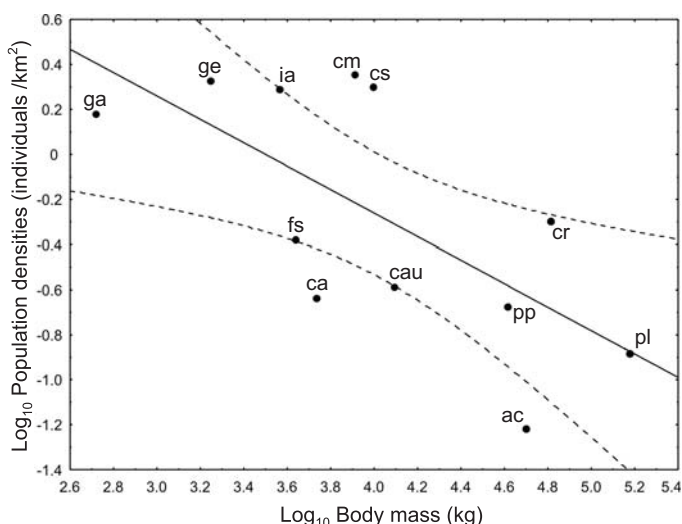


Fig. 4. Bivariate plot of log-transformed body size vs. population density for 12 species of African carnivores. Full lines: regression line (least squares adjustment) Dotted lines: 95% confidence intervals. pp: *Panthera pardus* (Linnaeus, 1758); pl: *Panthera leo* (Linnaeus, 1758); ac: *Acinonyx jubatus* (Schreber, 1775); cr: *Crocota crocuta* (Erxleben, 1777); fl: *Felis silvestris* Schreber, 1775; gs: *Galerella sanguinea* (Rüppell, 1836), ia: *Ichneumia albicauda* (Cuvier, 1829); ge: *Genetta genetta* (Linnaeus, 1758); cau: *Canis aureus* Linnaeus, 1758; *Canis adustus* Sundevall, 1847; cm: *Canis mesomelas* Schreber, 1775; cs: *Canis simensis* Rüppell, 1840.

Discussion

Carnivore specific richness and time averaging of the Río Luján fauna.—The FLRL comprises the fossil remains found in the Guerrero Member of the Río Luján Formation. These fossils have been collected throughout more than 100 years in the vicinity of the town of Luján, in the Luján river watershed (see Tonni et al. 1985).

The Guerrero Member is a flood-plain deposit that occurs extensively in association with river and stream beds in Buenos Aires province (Fidalgo 1992). The vertebrates found within it are typical of the *Equus (Amerhippus) neogeus* Lund, 1840 Biozone (Tonni et al. 1999), the basis for the Lujanian Stage/Age. Several radiocarbon dates restrict the age of this member to between 10.29 ± 0.13 and 21.04 ± 0.45 ka (Tonni et al. 2003). Taking this information into consideration, the age of the FLRL fauna is probably between 11 and 21 ka, thus comprising a wide temporal span that includes both the maximum peak of the last glaciation and the subsequent deglaciation (Thompson 2000). According to dating of the Guerrero Member from another locality (i.e., Arroyo Tapalqué), this fossil assemblage probably represents a time averaged span of approximately 8 kyr (see Tonni et al. 2003). Unfortunately, there are few dates available for this member in the Luján river bed, but dates for the overlying member (Río Salado Member) indicate that it is older than 10.04–11.06 ka (Prieto et al. 2004). A recently published paper about the geology of the Río Luján in the Luján area, suggests that the Guerrero Member comprise two independent stratigraphic beds and dates the base of this sequence at >40 ka (Toledo 2005). If this study is confirmed, the time averaging of this fauna is greater than 20 ka.

On the other hand, these fossils were collected without taphonomic control, thus is not possible to recognize the existence of preservation bias in this fossil assemblage (e.g., Behrensmeyer and Hook 1992; Aslan and Behrensmeyer 1996; Behrensmeyer et al. 2000).

According to the faunal list compiled by Fariña (1996), large carnivores are represented in the Río Luján fauna by *Smilodon populator*, *Arctotherium tarijense*, *Panthera onca*, and *Dusicyon avus*; to which *Puma concolor* must be added (see above). If the hypothesis that these species were sympatric and contemporaneous is accepted, their number is relatively low, and lowest than in living communities (see above; Fig. 1), although the total number of carnivorous mammal

species (including smaller ones, like mustelids and small foxes) recorded within this “local fauna” (eight) is clearly higher than the amount in South American Tertiary faunas, and falls within the range observed for living South American faunas (Croft 2001; see also Van Valkenburgh 1999). The Lujanian presents more large carnivores species than recent faunas, especially when complete sample of the Lujanian Age in the Buenos Aires province is considered (Fig. 1). On the other hand, the late Pleistocene large carnivore richness of South America is one of the highest worldwide in regard to the continental area (Wroe et al. 2004).

Potential prey and intraguild competition.—The paleoecological information obtained show that the Lujanian fauna contain three hypercarnivorous felids, one large hypercarnivorous canid with bone cracking abilities, a medium-sized canid with moderate carnivorous capabilities, and two ursids with carnivorous habits.

Taking into account the typical and maximum prey size values obtained from the raw body mass values, as well as those obtained from independent contrasts, in addition to the estimation of other paleoecological parameters, it becomes possible to establish approximate prey size ranges for the Lujanian carnivores. Thus, it is possible to identify potential prey for each of these carnivores within the faunal assemblage of this age (Table 1; Fig. 5). Medium-sized rodents (e.g., *Myocastor* Kerr, 1792, *Dolichotis* Desmarest, 1820) and armadillos (e.g., *ChaetophRACTUS villosus* (Desmarest, 1804)) were probably frequently preyed upon by *Dusicyon avus*, while small rodents and more sporadically larger mammals could be hunted by this species (e.g., deers, camelids). The diet of *Canis nehringi* would have comprised mainly middle-sized mammals such as camelids, deer, peccary, armadillos (large and small), and medium and large rodents. Pack-hunting behavior would have permitted it to prey on large herbivores such as equids [*Hippidion principalis* (Lund, 1845)], large camelids (*Eulamaops parallelus* Ameghino, 1884), and small glyptodonts [*Sclerocalyptus migoyanus* (Ameghino, 1889)], but it probably preyed only on juvenile megamammals. The diet of *Puma concolor* and *Panthera onca* would comprise mainly middle-sized mammals, but also including large mammals of up to 600 kg. Given the larger size of the fossil jaguar (see also Cabrera 1934; Kurtén 1973; Seymour 1993), this species could have fed on preys that were somewhat larger than those hunted by living individuals. It is also highly probable that it preyed upon juvenile megamammals. The size and morphology of *Smilodon populator* indicate that it preyed habitually on middle-sized mammals such as large armadillos, equids, small glyptodonts (e.g., *Sclerocalyptus migoyanus*), and large camelids, but it would also be able to hunt megamammals weighing approximately 1000 to 2000 kg, as well as juveniles of the larger species (i.e., *Megatherium americanum* Cuvier, 1796). According to extant paleoecological synthesis (see above), the species of *Arctotherium* were carnivorous (Soibelzon 2002), and the potential prey could be in the range of 10–300 kg body mass (see Table 2).

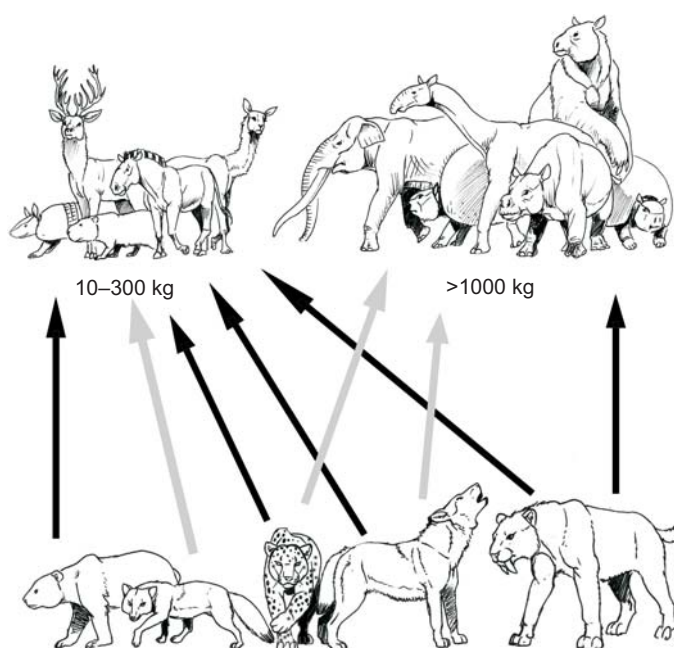


Fig. 5. General trophic relationships between the Lujanian carnivores and their main prey grouped by size classes. Black arrows: frequent preys; Grey arrows: occasional preys. The reconstructions are not drawn to scale (see the text for body mass estimations). Upper section (from left to right): a giant armadillo (*Pampatherium typum* Ameghino, 1875), a deer [*Morenelaphus lujanensis* (Ameghino, 1888)]; a capybara [*Neochoerus aesopi* (Leidy, 1854)]; a horse [*Hippidion principale* (Lund, 1840)]; a guanaco (*Lama guanicoe* Müller, 1776); a mastodon [*Stegomastodon platensis* (Ameghino, 1888)]; a glyptodont [*Panochthus tuberculatus* (Owen, 1845)]; a litoptern (*Macrauchenia patachonica* Owen, 1838); a toxodont (*Toxodon platensis* Owen, 1837); and the giant ground sloth (*Megatherium americanum* Cuvier, 1796). Lower section (from left to right): short faced bears (*Arctotherium bonariense* (Gervais, 1852) and *Arctotherium tarijense* Ameghino, 1902); a large fox [*Dusicyon avus* (Burmeister, 1866)]; large conical toothed felid [*Panthera onca* (Linnaeus, 1758) and *Puma concolor* (Linnaeus, 1771)]; a wolf [*Canis nehringi* (Ameghino, 1902)]; and a sabertoothed cat [*Smilodon populator* (Lund, 1842)].

On the other hand, in the absence of good living analogues of glyptodonts, the vulnerability of these forms to predation by the carnivores is unclear, since their large size and the possession of hard shell and, in some species, a robust club-shaped tail, could have been efficient defenses (Alexander et al. 1999). Gillette and Ray (1981) interpret that the presence of a carapace, the preference for muddy lowland habitats and a gregarious behavior, protected the adults of *Glyptotherium texanus* Osborn, 1903 from predators, but young individuals were vulnerable. The anterior facial region and the distal limbs are free of protection, and one skull of an adult specimen of *Glyptotherium texanus* has two carnivore punctures on its braincase, showing that they were not invulnerable to predators (Gillette and Ray 1981). Clearly this subject needs more study and development.

These inferences, along with the distribution of frequencies of herbivore body mass, indicate that all these carnivore species preyed upon species in the 10–300 kg range, but *Canis nehringi*, *Panthera onca*, *Puma concolor*, and *Smilo-*

don populator were able to hunt mammals weighing around 500 kg (e.g., *Hippidion principale*), while only the last species was able to hunt mammals with greater body mass.

The low number of carnivore species, and the differences in their body mass and relative grinding area of lower molars (see above) would indicate that the overlap in prey choice was low (e.g., Rosenzweig 1966; Dayan et al. 1992). The two species of bears, with similar size and morphology (see above) could be the exception, but so far they have not been found within the same faunal assemblage. However, using the studies of living communities as reference (e.g., Palomares and Caro 1999), there probably was some intraguild competition and predation. In this case, the large size of the bears and of *Smilodon populator* would have allowed these species to displace (or hunt) smaller carnivores and snatch their prey. The social behavior of *Canis nehringi* could have allowed this species to confront these large carnivores, if the number of pack members was high enough. Similarly, the species *Puma concolor* and *Panthera onca* could have displaced *Dusicyon avus*, and *P. onca* could have displaced *Puma concolor* as it does at present (Iriarte et al. 1990).

Population densities of carnivores and the “imbalanced” Río Luján fauna.—The relationship between carnivore densities and body size calculated from the raw data is consistent with the observations appearing in classical analyses (e.g., Damuth 1981, 1987 1993; Peters 1983; Peters and Raelson 1984; Robinson and Eisenberg 1990), in which species density decreases with the increasing mass. As in these regressions, the SE value and the amount of variance not explained by mass are high (e.g., Robinson and Eisenberg 1990; Smallwood 1997; Hemmer 2004) and result in extremely broad prediction and confidence intervals. Thus the allometric equation is not a good predictor of population densities, specially at a local scale. This can be seen in the Table 4 where the allometric equation is used with a recent community. On the other hand the real carnivore densities (Schaller 1972) depart from the values expected according to the allometric equation, because some larger carnivores (i.e., *Panthera leo* and *Crocota crocuta*) are more abundant than other smaller species (i.e., *Lycaon pictus*, *Acinonyx jubatus*).

The high levels of error and unexplained variance of these functions could be explained by the differences of variance between these variables, as the variance is much higher for the densities than for the body mass (Silva and Downing 1995a; Smallwood 1997). For instance, in the case of the puma, densities range from 0.0044 to 0.1303 (Smallwood 1997), whereas body mass values for adult individuals range only between 36 and 103 (Nowak 1991). The error occurring in these functions has been linked to the existence of additional factors that were not included in the analyses (e.g., Peters 1983; Brown 1995; Silva and Downing 1995a; Silva et al. 2001). This agrees with the available ecological information on living carnivores, which demonstrates the presence of several factors affecting the densities of these mammals in a local scale: climate, prey density and availability, presence of competitors and predators, epidemics, population genetic diversity (e.g.,

Schaller 1972; Ewer 1973; Bertram 1979; Handy and Biggot 1979; Macdonald 1983; East 1984; Johnson et al. 1996; Mills and Gorman 1997; Gorman et al. 1998; Palomares and Caro 1999; Vucetich and Creel 1999; Creel 2001; Creel et al. 2001; Fuller and Sievert 2001; Carbone and Gittleman 2002; Wayne et al. 2004; Höner et al. 2005).

For example, it is worth mentioning that there can be temporal and spatial variations in population densities within a species, and these can be a consequence of the interaction of diverse factors. For instance, Packer et al. (2005) found that the density of Serengeti lions exhibit a pattern of variation in a large temporal scale (decades) comprising 10 to 20 year periods of stability punctuated by abrupt increases. This pattern would result from the interaction between prey abundance and vegetation, but would be determined by the population structure. In other cases (e.g., Smallwood 1997) the variation of intraspecific densities seems not to be related to biological causes but rather be a methodological artifact. Furthermore, the positive relationship between carnivore density and prey abundance was found for several carnivores in different habitats (e.g., Bertram 1979; Handy and Biggot 1979; Macdonald 1983; East 1984; Creel et al. 2001; Fuller and Sievert 2001; Carbone and Gittleman 2002; Höner et al. 2005), which is an important observation for the imbalance hypothesis of Fariña (1996; see below).

Apart from that, several criticisms and observations on interspecific density-body mass relationships of mammals have been made, ranging from suitability of different regression models, to sampling errors and biases, non-linearity of the relationship, phylogenetic influence, and use of average values for each species, to authors suggesting that the observed relationship between the variables is an artifact and as such does not represent a biological pattern (e.g., Silva and Downing 1995a; Blackburn and Gaston 1996; Smallwood and Schonewald 1998; Griffiths 1998; Smallwood 1999, 2001; Silva et al. 2001). Clearly these observations argue against the use of allometric equations between living carnivore densities and body mass to estimate the densities of fossil communities.

Another relevant information to the “imbalance” hypothesis comes from recent studies of the dental occlusal surface area (Vizcaíno et al. 2006) of fossil xenarthrans. These authors demonstrated that this trait is smaller in most fossil xenarthrans than the expected for extant herbivorous mammals of equivalent body size, with the exception of *Megatherium americanum*, whose dental occlusal surface area is equal to or even higher than expected for a mammal of its size. This suggests low efficiency in oral food processing that was probably compensated by intense fermentation in the digestive tract, or lower metabolic requirements, or a combination of both adaptations. Moreover, 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).

The ecological information available and discussed above (e.g., Bertram 1979; Handy and Biggot 1979; Fuller and

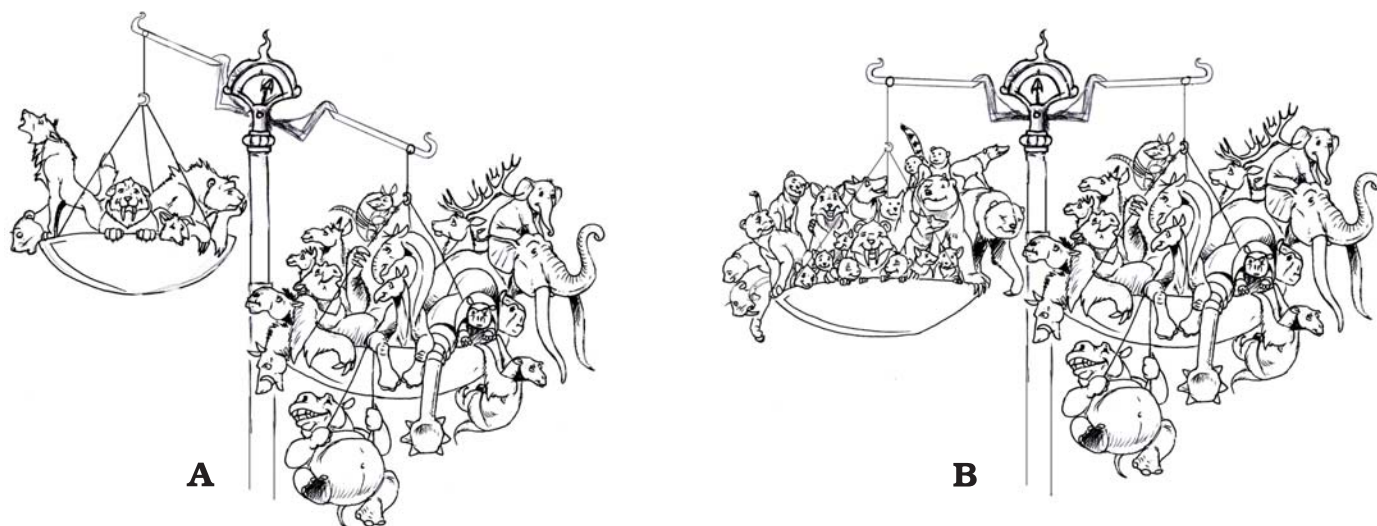


Fig. 6. Schematic representation of the “imbalance” hypothesis (A) and an alternative hypothesis (B).

Sievert 2001; Höner et al. 2005) allows for an alternative hypothesis to the imbalance proposed by Fariña (1996), namely that the density of carnivores depends on the density of herbivores (Fig. 6). Thus, in case there was high herbivore biomass, a high density of carnivores could be supported (Fig. 6), as is the case in some recent ecosystems. Either an increased density of all carnivore species or, more likely, of some dominant species (e.g., *Smilodon populator*) could account for the high biomass of carnivores in this scenario. Then again, other elements, including climate, competitors, predators, and possibly non-deterministic factors (e.g., Bell 2001; Brown 1995), might be coupled and affect the temporal changes of species densities in this locality.

The strong phylogenetic constraints that affected the evolution of autochthonous lineages of mammals in South America that lack modern analogues, such as the xenarthrans, notoungulates and litopterns, underscore the importance of undertaking biomechanical, morpho-geometrical, ecomorphological, and biogeochemical analyses for a better understanding of their paleobiology (Bargo 2003; Palmqvist et al. 2003; Vizcaíno and De Iuliis 2003; Vizcaíno et al. 2006). Comprehensive biostratigraphic, taphonomic, and taxonomic studies of the Pleistocene deposits of the continent are needed for testing previous hypotheses and generating new sound ones.

Conclusions

Five large carnivores (*Smilodon populator*, *Panthera onca*, *Puma concolor*, *Arctotherium tarijense*, and *Dusicyon avus*) occur in Río Luján fauna, and two more species (three with the inclusion of *Homo sapiens*) have been recorded in other Lujanian localities in the Pampean region (*Canis nehringi*, *Arctotherium bonariense*). Although the species richness of the group is lower than in the late Pleistocene of other continents (e.g., North America, see Kurtén and Anderson 1980)

the number of large placental mammals was always low in South America, possibly due to the relative isolation of this subcontinent.

The three felids and *C. nehringi* were hypercarnivorous species that preyed upon middle-sized and large mammals, although *S. populator* could also have preyed on megamammals. *D. avus* would have been moderately carnivorous, a hunter of small and middle-sized mammals, although in all probability its diet also included a small proportion of plant matter or insects. The *Arctotherium* species would have been omnivorous, even though vertebrate flesh was an important food item in their diet and they were probably able to hunt prey of less than 200 kg body mass. *Arctotherium tarijense*, *A. bonariense*, and *C. nehringi* could certainly have scavenged mammal carcasses that were available in these ecosystems.

These considerations, along with Vizcaíno et al.'s (2006) observations of the presence of lower metabolism and lower densities in the ground sloths, would present a more balanced scenario than the one put forward by Fariña (1996; Fig. 6). The available information concerning the ecology of living carnivores, the most recent studies of the relationship between densities and body mass, and a reanalysis of the function used by this author, do not support his estimations of population densities. Accordingly, there is no evidence that the densities of Lujanian carnivores were imbalanced with respect to the abundance of herbivores.

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