# Paleoecology of the mammalian predator guild of Southern Patagonia during the latest Pleistocene: Ecomorphology, stable isotopes, and taphonomy

Francisco J. Prevosti [a,c,]*, Fabiana M. Martin [b]

[a] *División Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" — CONICET, Av. Angel Gallardo 470, C1405DJR Buenos Aires, Argentina*
[b] *Centro de Estudios del Hombre Austral, Instituto de la Patagonia (UMAG). Av. Bulnes 01890, Punta Arenas, Chile*
[c] *Departamento de Ciencias Básicas, Universidad Nacional de Luján - Ruta 5 y Avenida Constitución - 6700 Luján, Buenos Aires, Argentina*

## ARTICLE INFO

## ABSTRACT

During the late Pleistocene, Patagonia had a rich fauna of large mammals including some megamammals such as ground sloths (*Mylodon darwini*), horse (*Hippidion saldiasi*), and camelids (e.g., *Lama guanicoe*). The carnivore guild was represented by several extinct taxa such as the sabretooth cat (*Smilodon*), the Patagonian Panther (*Panthera onca mesembrina*), a short-faced bear (*Arctotherium tarijense*) and a large fox (*Dusicyon avus*), but also by the extant puma (*Puma concolor*). In order to reconstruct the relationships within the predator guild and between these carnivores and their potential prey, body size, prey size and diet habits of each predator were estimated. These results are complemented with stable isotopic analyses and taphonomic information. Results indicate that the guild was composed of three felids that were large hypercarnivores, two of which (*Smilodon*, *P. onca*) could prey on most large mammals. Morphology suggests that the short-faced bear was mainly an omnivore that may have scavenged and occasionally hunted medium-large mammals like camelids and horses. *D. avus* was slightly larger and more carnivorous than the living culpeo fox (*Lycalopex culpaeus*), and preyed mostly on small mammals (rodents) but occasionally on camelids. Stable isotopes ($\delta^{13}$C and $\delta^{15}$N) are congruent with these interpretations, although they indicate that *Arctotherium* and *D. avus* were highly carnivorous. This could be explained by scavenging habits. Stable isotopes also indicate that *P. o. mesembrina* ate larger proportions of *Hippidion* and *Lama gracilis*. Taphonomic studies showed that *P. o. mesembrina* gnawed bones of *Mylodon*, *Hippidion* and camelids, a result that suggests that these taxa were common prey, and agrees with the ecomorphological and stable isotope interpretations. The diversity of potential prey is lower than that observed in lower latitudes (e.g., Pampean Region) while the number of predators is similar, a relationship that could be explained by the high latitude where these mammals lived.

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## 1. Introduction

The paleoecology of South American Late Pleistocene carnivores is a topic with very few publications. Most of the studies are limited to only a few species or groups, and to the inference of diet and estimation of body mass (e.g., Van Valkenburgh, 1991; Prevosti and Palmqvist, 2001; Christiansen and Harris, 2005; Oliveira et al., 2005; Prevosti, 2006; Figueirido and Soibelzon, 2009; but see Cartelle and Langguth, 1999; Prevosti, 2006 for locomotory inferences in extinct canids). Previous to these works, paleontological comments were made on the base of descriptive and qualitative studies (e.g., Marshall, 1976; Berta, 1989). Fewer studies explore paleosinecological aspects of the terrestrial carnivore guilds in South America, and are mostly limited to the potential prey of extinct canids, and their potential competitive relationships with other carnivores (e.g., Prevosti and Palmqvist, 2001; Prevosti, 2006; Prevosti et al., 2009). The only exception is the study of the paleoecology of the carnivore guild of the Lujanian of Buenos Aires province (Argentina), in which the diversity of carnivores and other mammals, and potential predator–prey relationships were inferred (Prevosti and Vizcaíno, 2006). This study refuted the hypothesis that the Lujanian fauna was not balanced (i.e., there were not enough predators for the high diversity of large mammals and megamammals) proposed by Fariña (1996).

* Corresponding author. División Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" — CONICET, Av. Angel Gallardo 470, C1405DJR Buenos Aires, Argentina.
E-mail address: protocyon@hotmail.com (F.J. Prevosti).

Southern Patagonia had a rich fauna of large mammals, as well as some megamammals (body size above one tonne), which during the late Pleistocene included a ground sloth (*Mylodon darwini*), horse (*Hippidion saldiasi*), lytopterns (*Macrauchenia* sp.) and some species of camelids (*Lama guanicoe, Lama gracilis, "Lama owenii"*) (see Roth, 1899, 1904; Nami and Menegaz, 1991; Esteban, 1996; Borrero, 1997; Latorre, 1998; Miotti and Salemme, 1999; Mol et al., 2003; Labarca et al., 2008; Martin, 2008, in press; Labarca and Prieto, 2009; Orlando et al., 2009; Prieto et al., 2010). The carnivore guild was represented by several extinct taxa such as a sabretooth cat (*Smilodon*), the Patagonian panther (*Panthera onca mesembrina*), a short faced bear (*Arctotherium tarijense*, but see below), a large fox (*Dusicyon avus*), and the extant puma (*Puma concolor*) (Canto, 1991; Borrero, 1997, 2009; Latorre, 1998; Mol et al., 2003; Prevosti et al., 2003; Barnett et al., 2005; Amorosi and Prevosti, 2008; Labarca et al., 2008; Martin, 2008, in press; Prieto et al., 2010). There is abundant contextual information that includes taxon dates, stable isotopes, taphonomic information, and palynological results (Markgraf, 1985, 1991, 1993; McCulloch et al., 2000; Sagredo et al., 2011), which is adequate to study paleoecological relationships.

## 2. Material and methods

### 2.1. Sites and areas

The studied fossils came from 10 sites located in three areas of Southern Chile: Ultima Esperanza (Cueva del Milodón; Cueva del Medio; Cueva Chica; Cueva Escondida; Cueva Lago Sofía 1; Cueva Lago Sofía 4), the Pali Aike Lava Field (Cueva Fell; Cueva de los Chingues; Cueva del Puma) and Tierra del Fuego island (Tres Arroyos 1) (see Table 1 for more details). The Ultima Esperanza area was covered by a glacial lobe during the Last Glacial Maximum (LGM), after which there was a glacial readvance synchronous with the Antarctic Cold Reversal (ACR) (Fowgill and Kubik, 2005). After the retreat of the ice, a proglacial lake was formed in this area (Stern et al., 2011: 89; Sagredo et al., 2011). The lake was formed before 13,560 ± 180 BP, with an important lake level drop ca. 12,235 ± 40 BP, again reaching high stands before 12,125 ± 85 BP, and finally emptying into the Pacific ca. 9210 ± 40 BP. Pollen analysis indicates the existence of open environments between 10,700 and 10,100 BP (Moore, 1978; Markgraf, 1985; Heusser et al., 1992; Villa-Martinez and Moreno, 2007).

**Table 1**
Details and information about the sites where the studied fossils were recovered.

| Site name | Area | Geographic coordinates | Radiocarbon dates | Size and characteristics | Site interpretation |
|---|---|---|---|---|---|
| Cueva del Milodón | Ultima Esperanza | 51° 33′ 54″ S; 72° 37′ 13″W | 13.6 and 10.2 ka BP (Borrero, 1997; Borrero and Martin, 2012) | Large cave of about 150 m by 180 m, with a large carpet of ground sloth dung (Hauthal, 1899) | Is mainly a paleontological site, with minimal evidence for human exploitation of Hippidion saldiasi (Martin, in press) |
| Cueva del Medio | Ultima Esperanza | 51° 35′ S; 72° 38′ W | 11.0 and 9.5 ka BP (Nami, 1987; Nami and Menegaz, 1991; Nami and Nakamura, 1995) | Large cave of ca. 87 m by 41 width (Nami, 1985–1986). | Have human Late Pleistocene occupations include both extinct and modern faunas |
| Cueva Chica | Ultima Esperanza | 51° 34′ 23.9″ S; 72° 35′ 09.7″ W | 14.8 and 10.7 ka BP (see Martin et al., 2013) | Cave about 70 m long and 17 m wide | Paleontological Site |
| Cueva Escondida | Ultima Esperanza | 51° 33′ 13.9″ S; 72° 37′ 49.9″ W | 13.8 and 10.9 ka BP (Martin et al., 2012). | Dark cave with a restricted and narrow entry, with a length of about 34 m and a width between 6 and 2 m | Carnivore den (Martin et al., 2012) |
| Cueva lago Sofía 1 | Ultima Esperanza | 51° 31′ 54″ S; 72° 34′ 12″ W | 9.7 and 12.9 ka BP (Prieto, 1991; Massone and Prieto, 2004; Steele and Politis, 2009) | Cave measuring 30 by 8 m (Prieto, 1991) | Late Pleistocene human occupations and a lower paleontological level (Prieto, 1991; Massone and Prieto, 2004; Steele and Politis, 2009) |
| Cueva lago Sofía 4 | Ultima Esperanza | 51° 31′ 54″ S, 72° 34′ 12″ W | 13.4 and 10.8 ka BP (Borrero et al., 1997; Martin, 2008; Weinstock et al., 2009) | Dark cave which measures ca. 6.0 m by 2.5 m (Prieto, 1991) | Carnivore den (Borrero et al., 1997) |
| Cueva Fell | Pali Aike | 52° 02′ 40″ S; 70° 03′ 23″ W | 11.0 and 10.0 ka BP (Bird, 1988; Martin, in press) | Small cave of about 11 m by 8.5 m (Bird, 1988) | Archaeological remains including extinct and modern faunas (Bird, 1988; Martin, in press) |
| Cueva de los Chingues | Pali Aike | 52° 05′ 37″ S; 69° 44′ 31″ W | 12.1 and 10.1 ka BP (San Román et al., 2000; Martin, 2008, in press | Small lava tube located within a maar of ca. 10 m by 3 m, with a restricted access (San Román et al., 2000) | Large felid den with minimal evidence of human activities (Martin, 2008, in press) |
| Cueva del Puma | Pali Aike | 52° 1′ 12.6″ S; 69° 58′ 41.2″ W | 11.5 and 10.3 ka BP (Martin et al., 2004; Martin, 2008) | Large dark cave with a very small entry, with several chambers of varied size and shape (Martin, 2008) | Carnivore den (Martin et al., 2004; Martin, 2008) |
| Tres Arroyos 1 | Tierra del Fuego | 53° 23′ S; 68° 41′ W | 12.5 and 10.1 ka BP (Borrero, 2003; Massone, 2004) | Small rock shelter of ca. 6 m by 4 m (Massone, 1987, 2004) | Paleontological levels dated in 12.5–10.5 ka BP and upper levels with human evidence dated between 10.6 and 10.1 ka BP (Borrero, 2003; Massone, 1987, 2004) |

The aim of this paper is to reconstruct the structure of the late Pleistocene terrestrial carnivore guild in South Patagonia inferring body size, prey size, diet, and potential prey of its members, and also to compare this reconstruction with the available taphonomical information for some of the studied sites (Fig. 1).

The late glacial ice advance recorded at the western end of the Strait of Magellan coincides with the ACR (Blunier et al., 1997; McCulloch et al., 2005). The available palynological information indicates that steppe or Patagonian tundra environments dominated the Pali Aike region during post-glacial times, starting ca. 14,000 BP
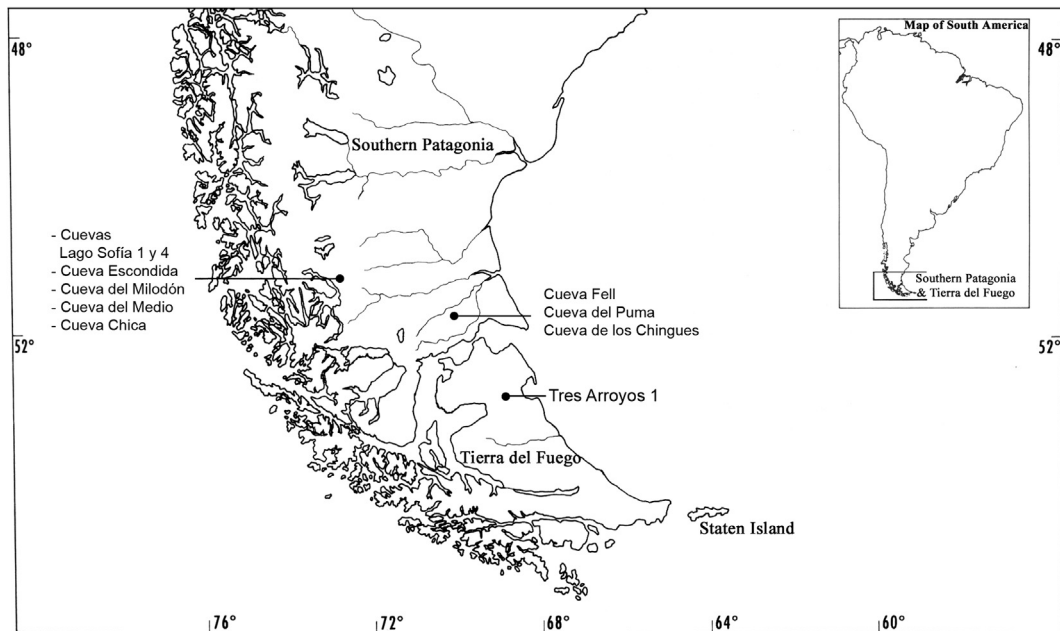
**Fig. 1.** Map of Southern Patagonia showing the sites studied in this paper.

(Markgraf, 1988; Clapperton, 1993; Heusser, 2003; McCulloch et al., 2005; Zolitschka et al., 2006). A change from mesic to xeric climates that appears to be related with an increase in temperature is recorded ca. 11,000–10,000 BP (Markgraf, 1988; Prieto et al., 1999).

The island of Tierra del Fuego was still connected to the continent at the time of the initial human occupations of Tres Arroyos 1 (McCulloch et al., 1997). A proglacial lake was formed between the ice front and the Second Narrows when glacial advances obstructed the western strait (McCulloch et al., 2005; Sugden et al., 2005).

### 2.2. Specimens

Study included fossil specimens deposited at the following collections: American Museum of Natural History (AMNH), USA; Centro de Estudios del Hombre Austral, Instituto de la Patagonia (CEHA), Chile; Evolutions Museet, University of Uppsala (UUZM), Sweden; Museo de La Plata (MLP), Argentina; Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Argentina; Zoological Museum of Amsterdam (ZMA), Netherlands (see Supplementary data 1). When it was possible we inferred body size, prey size and diet from specimens collected in each of the areas, but when that was not possible due to presence of fragmentary specimens that inhibited the analysis, we used estimates from specimens from other areas. For *Arctotherium* we used data of prey size obtained from the literature, specifically from Prevosti and Vizcaíno (2006).

### 2.3. Body size estimation

Using a non parametric regression method (Quantile Regression, see Koenker and Hallock, 2001; Cade and Noon, 2003) and after controlling for the lack of independence due to phylogenetic patterns (see Supplementary data 2), we used previously published data (Van Valkenburgh, 1990; Christiansen and Harris, 2005) to generate new allometric equations. The use of the predictor was based on the maximization of the inclusion of fossil specimens. Quantile Regression is a robust method that it is not biased by normality and homoscedasticity assumptions, and to the log transformation bias in the case of predictions (Cade and Noon, 2003). The Phylogenetic Eigenvector Regression (Diniz-filho et al.,

1998) was used to "control" the phylogenetic pattern using the topologies published by Johnson et al. (2006) for felids and Lindblad-Toh et al. (2005; see also Prevosti, 2010) for canids.

For canids and felids, we used the length of the lower carnassial (Lm1) and the body mass (BM) reported by Van Valkenburgh (1990), and also the anteroposterior width of the diaphysis of the humerus (HDap), mediolateral width of the diaphysis of the tibia (TDml), and body mass of living felids published by Christiansen and Harris (2005). The TDml regression did not include the living species *Lynx lynx* (see Christiansen and Harris, 2005). Because we could not have access to the raw data used by Anyonge (1993) we used the formula published by this author, created only with bears and the length of the femur (FL): body mass (BM) = (FL*3.85) − 7.62. All variables were log10 transformed prior to the analyses. All the analysis were done using the software R 2.15.1 (R Development Core Team, 2012) and PAST (Hammer et al., 2001).

### 2.4. Maximum and typical prey mass

We followed the methodology described for body mass estimations, and the data published by Van Valkenburgh and Koepfli (1993) and Van Valkenburgh and Hertel (1998) for typical and maximum prey size (TPM and MPM), and predator body mass, for canids and felids, respectively. For *Arctotherium* we followed the inference made by Prevosti and Vizcaíno (2006), because there was no available equation, and it was virtually impossible to obtain one (see Van Valkenburgh and Hertel, 1998). Information about the presence of potential prey in this region and their body mass was taken from the literature (Fariña, 1996; Borrero, 1997, 2009; Fariña et al., 1998; Latorre, 1998; Prevosti and Vizcaíno, 2006; Vizcaíno et al., 2012; Martin, in press).

### 2.5. Dental morphology and diet

We used a simple morphometric index based on the relationship between the lower carnassial trigonid length (the cutting part of the tooth) and the talonid of the tooth (representing the grinding area of the lower carnassial). We used a modification of the relative lower molar grinding area index (RGA; see Van Valkenburgh, 1991), that

took low or 0 values in hypercarnivores (e.g., felids), and increased its values in omnivores (e.g., ursids, procyonids). It is calculated as the square root of occlusal surface [length*width] of the talonid of m1/ length of m1 trigonid (cf. Van Valkenburgh, 1991; Prevosti and Vizcaíno, 2006). A recent study calculated values for living South American carnivores, plus some carnivores from other continents and several marsupials, and found that hypercarnivores that eat mainly flesh of other vertebrates have values below 0.48, and that omnivores have values above 0.54 (Prevosti et al., in press). Meso-carnivores (that consume mainly small mammals, but also some proportion of arthropods and vegetables) span the gap between 0.48 and 0.54, but some have values that fall within the omnivore range.

### 2.6. Isotopes and diet

The use of $\delta^{13}C$ and $\delta^{15}N$ to reconstruct the diet and trophic relationships between extinct mammals is widely established (e.g., Bocherens and Drucker, 2003; Fox Dobbs et al., 2007; Palmqvist et al., 2008). Within a community there is an increase in the $\delta^{13}C$ and $\delta^{15}N$ values in the more carnivorous diets, and lower values in herbivores (e.g., Bocherens and Drucker, 2003; Fox Dobbs et al., 2007; Palmqvist et al., 2008). The sample must be studied in the context of the different species of the assemblage and with the background knowledge available for each of them. We report $\delta^{13}C$ and $\delta^{15}N$ values obtained from collagen based on teeth with two exceptions (see Table 2 for more details about the samples). The existence of a temporal pattern in $\delta^{13}C$ was tested through bivariate graphs ($\delta^{13}C$ vs. $^{14}C$ dates), using the Spearman correlation index (only for the species with more than 3 specimens: Hippidion saldiasi, Mylodon darwini, P. onca mesembrina; Table 2). There were few $\delta^{15}N$ values to test this temporal pattern. As we did not find a clear geographic pattern in the signal of these stable isotopes, we pooled the sample for these analyses.

**Table 2**
Specimens included in the stable isotopic analyses, with non calibrated $^{14}C$ taxon dates, and $\delta^{13}C–\delta^{15}N$ information.

| Code | Taxa | Source | Area | Site | Date | $^{13}C$ | $^{15}N$ | Source |
|------|------|--------|------|------|------|------|------|--------|
| GX-32665 | Arctotherium | Atlas | PA | Cueva de los Chingues | 11.360 ± 70 | −19 | 10 | This paper |
| Ua-21033 | Arctotherium | Femur | PA | Cueva del Puma | 10.345 ± 75 | −20 | | Martin et al., 2004 |
| OxA-13717 | Smilodon | Radius | UE | "Milodon Cave" ZMA | 11.265 ± 45 | −19 | 10.4 | Barnett et al., 2005 |
| OxA-14457 | Smilodon | Radius | UE | "Milodon Cave" ZMA | 11.420 ± 50 | −19 | 9.6 | Barnett et al., 2005 |
| Ua-24687 | P. o mesembrina | Mandible | UE | Cueva del Medio | 11.410 ± 80 | −18 | 8.2 | Martin, 2008. this paper; Isotope code: CNR-113826 |
| GX-31643 | P. o mesembrina | Mandible (juvenile) | UE | Cueva Lago Sofía 4 | 10.840 ± 60 | −19 | | Martin, 2008. Martin, in press |
| OxA-9248 | P. o mesembrina | Metatarsal | TF | Tres Arroyos 1 | 11.085 ± 70 | −18.6 | 6.59 | Massone and Prieto, 2004; Steele and Politis, 2009 |
| Beta-288228 | P. o mesembrina | Fibule | UE | Cueva Chica | 11.520 ± 50 | −19 | 7.6 | Martin et al., 2013 |
| Beta-284439 | P. o mesembrina | Rib | UE | Cueva Chica | 12.890 ± 60 | −18 | | Martin et al., 2013 |
| Beta-309450 | P. o mesembrina | Coxal | UE | Cueva del Milodón | | −18 | 7.6 | This paper |
| OxA-9245 | Dusicyon avus | Tooth | TF | Tres Arroyos 1 | 10.575 ± 65 | −19.4 | 8.18 | Massone and Prieto, 2004; Steele and Politis, 2009 |
| OxA-9505 | Dusicyon avus | Mandible | UE | Cueva Lago Sofía 1 | 10.140 ± 120 | −19.5 | 7.7 | Massone and Prieto, 2004; Steele and Politis, 2009 |
| GX-32663 | Dusicyon avus | Mandible | PA | Cueva de los Chingues | 10.490 ± 80 | −18 | 10.1 | This paper |
| OxA-9319 | Hippidion saldiasi | Third tarsal | UE | Cueva Lago Sofía 1 | 10.780 ± 60 | −20.3 | 2.73 | Massone and Prieto, 2004; Steele and Politis, 2009 |
| Oxa-9504 | Hippidion saldiasi | Incisive | UE | Cueva Lago Sofía 1 | 10.310 ± 160 | −20.6 | 2.1 | Massone and Prieto, 2004; Steele and Politis, 2009 |
| Beta-147744 | Hippidion saldiasi | Second phalange | PA | Cueva de los Chingues | 11.210 ± 50 | −20.7 | | San Román et al., 2000; Martin, in press |
| Ua-24685 | Hippidion saldiasi | Distal humerus | PA | Cueva de los Chingues | 11.990 ± 90 | −21.1 | | Martin, 2008; Martin, in press |
| Beta-247710 | Hippidion saldiasi | Distal sesamoid | PA | Cueva Fell | 10.680 ± 40 | −20 | 3 | Martin, in press; This paper |
| OxA-9247 | Hippidion saldiasi | First phalange | TF | Tres Arroyos 1 | 10.685 ± 70 | −20.5 | 0.92 | Massone and Prieto, 2004; Steele and Politis, 2009 |
| GX-32666 | Hippidion saldiasi | Right scapula | PA | Cueva de los Chingues | 10.650 ± 50 | −20 | 3.7 | Martin, in press; This paper |
| Beta-310944 | Hippidion saldiasi | Lunar | UE | Cueva Escondida | | −20 | 1.6 | This paper |
| Beta-284437 | Mylodon darwini | Nasal | UE | Cueva Chica | 13.970 ± 70 | −20 | | Martin et al., 2013 |
| OxA-9506 | Mylodon darwini | Bone indet | UE | Cueva Lago Sofía 1 | 12.250 ± 110 | −20.1 | 4.4 | Steele and Politis, 2009 |
| Gx-31641 | Mylodon darwini | Rib | UE | Cueva Lago Sofía 1 | 9.700 ± 100 | −21.5 | | Martin, in press |
| Ua-32861 | Mylodon darwini | Osteoderm | PA | Cueva de los Chingues | 12.165 ± 80 | −19.7 | | Martin, 2008. Martin, in press |
| Ua-34249 | Mylodon darwini | Coxal | PA | Cueva Fell | 10.295 ± 65 | −21.8 | | Martin, in press |
| Beta-288230 | Mylodon darwini | Vertebra | UE | Cueva Chica | 14.240 ± 60 | −20 | 3.1 | Martin et al., 2013 |
| Beta-288227 | Mylodon darwini | Vertebra | UE | Cueva Chica | 10.780 ± 50 | −22 | 7.7 | Martin et al., 2013 |
| Beta-309451 | Mylodon darwini | Skin | UE | Cueva del Milodón | | −20 | 3.1 | This paper |
| Beta-310936 | Mylodon darwini | Osteoderm | UE | CB007 | | −20 | | This paper |
| Beta-310938 | Mylodon darwini | Osteoderm | UE | CB009 | | −20 | 2.8 | This paper |
| Beta-310940 | Mylodon darwini | Osteoderm | UE | Cueva Escondida | | −21 | 5 | This paper |
| Ua-24684 | Rheidae | Tibiotarsal | PA | Cueva de los Chingues | 10.165 ± 70 | −20 | 5.5 | Martin, 2008; This paper; Isotope code: CNR-113824 |
| GX-32667 | Rheidae | First phalange | TF | Tres Arroyos 1 | 9.960 ± 50 | −21 | 4.9 | Martin et al., 2009 |
| Beta-310941 | Camelidae | Humerus | UE | Cueva Escondida | | −19 | 5.3 | This paper |
| Beta-310943 | Camelidae | Second phalange | UE | Cueva Escondida | | −19 | 2.8 | This paper |
| GX-32664 | Camelidae | Radio-ulna | PA | Cueva de los Chingues | 10.890 ± 60 | −20 | 5.8 | Martin, in press; This paper |
| GX-31644 | Camelidae | Cuboid | UE | Cueva Lago Sofía 4 | 12.340 ± 80 | −21 | | Martin, in press |
| OxA-8635 | Lama guanicoe | Diaphysis indet | UE | Cueva Lago Sofía 1 | 10.710 ± 70 | −20.2 | 3.84 | Massone and Prieto, 2004; Steele and Politis, 2009 |
| Beta-288231 | Lama gracilis | Astragale | UE | Cueva Chica | 14.870 ± 70 | −19 | 5.2 | Martin et al., 2013 |
| OxA-9246 | Lama gracilis | Bone indet | TF | Tres Arroyos 1 | 10.630 ± 70 | −20 | 3.32 | Massone and Prieto, 2004; Steele and Politis, 2009 |

We explored prey predator relationships with bivariate graphs ($\delta^{13}$C vs. $^{14}$C dates; $\delta^{13}$C vs. $^{15}$N) and using an isotopic mixing model under a Bayesian statistic framework with the SIAR package (Parnell and Jackson, 2012, Phillips, 2012) of the R 2.15.1 program (R Development Core Team, 2012). We used $\delta^{13}$C and $\delta^{15}$N mean and standard deviation values of potential prey (*Hippidion saldiasi*, *Mylodon darwini*, *L. gracilis*, *L. guanicoe*, Rheidae, Camelidae). For cases in which there was a single value for a taxon we put a very low "standard deviation" value (i.e., 0.001). Enrichment factors from herbivores to predators of 1 and 2 for $\delta^{13}$C and 2.8, 4, and 5.7 for $\delta^{15}$N were observed in actualistic studies (see Bocherens, 2000; Bocherens and Drucker, 2003; Fox Dobbs et al., 2007; and literature there cited). Thus we included

*Smilodon* (ZMA collection): $\approx$ 322 kg, *Puma concolor* (ZMA collection): $\approx$ 145 kg; *P. onca*: $\approx$ 190 kg (Table 2; Supplementary data 1).

### 3.3. Diet and prey sizes

The morphometric index (RGA) indicated that *D. avus* had a mesocarnivorous diet, but some specimens had values in the range of hypercarnivores (mean: 0.49, range: 0.53–0.42). *Arctotherium* had a RGA typical of omnivorous species (mean RGA: 0.70, range: 0.65–0.73; Table 3; Prevosti and Vizcaíno, 2006; Table 3; Supplementary data 1). On the other hand, felids were in the hypercarnivore extreme, without talonids in the lower carnassial, and a RGA of 0.

**Table 3**
Estimated relative grinding area of lower carnassial (RGA), body size (BM, in kg), and typical (TPM in kg) and maximum (MPM, in kg) prey size. The figures are mean estimation $\pm$ standard deviation.

| | RGA | BM | TPM | MPM |
|---|---|---|---|---|
| *Puma concolor* | 0 | 145.27 ± 21.98 | 259.86 ± 59.41 | 698.47 ± 105.44 |
| *Panthera onca mesembrina* | 0 | 190.04 ± 57.71 | 403.61 ± 185.51 | 912.99 ± 258.71 |
| *Smilodon* | 0 | 402.56 ± 114.26 | 771.33 ± 152.28 | 1415.48 ± 181.62 |
| *Dusicyon avus* | 0.49 ± 0.03 | 15.84 ± 1.68 | 3.98 ± 0.75 | 62.90 ± 9.29 |
| *Arctotherium* | 0.70 ± 0.05 | 363.99 | 100 | 300 |

the enrichment factors so that the mean $\pm$ standard deviation covered this range (i.e., 1.5 $\pm$ 0.5 for $\delta^{13}$C, and 4.25 $\pm$ 1.45 for $\delta^{15}$N). Uninformative prior probabilities were used. Isotopic values were obtained with the same procedure of $^{14}$C dating process performed in different laboratories (see Table 2).

## 3. Results

### 3.1. Diversity and taxon dates

*P. onca mesembrina* and *D. avus* were the most common carnivores in the region, and they are present in the three areas (Table 2, Supplementary data 2; Latorre, 1998; Martin, 2008, in press). *Arctotherium* was present in Ultima Esperanza and Pali Aike (Prevosti et al., 2003; Martin et al., 2004; Martin, in press), while *Smilodon* was only present at Ultima Esperanza (Canto, 1991; Labarca et al., 2008; Prieto et al., 2010). In addition, we included unpublished *Smilodon* records from Tierra del Fuego (Prevosti and Martin, pers. obs.). Taxon dates for *P. onca* indicated that they were present in UE between 10.8–12.9 ka, and $\approx$ 11 ka in TF, while *D. avus* was present around 10.5 ka in the three areas. The dates of the *Smilodon* specimens from the ZMA collection were between 11.3 and 11.4 ka (Barnett et al., 2005), but there was a taxon date of 11.1 $\pm$ 0.08 ka from Cueva del Medio (Prieto et al., 2010). Remains of *Arctotherium* were dated in 10.4–11.4 ka in the PA area, and previously were assigned to *A. tarijense* (Soibelzon, 2004), but the fossils were very fragmentary (isolated teeth or postcranial bones at best) and did not have diagnostic features (see discussion in Prevosti et al., 2003). Thus we prefer to assign them to *Arctotherium* sp., but we recognise that they belong to a smaller sized species than *A. angustidens*.

### 3.2. Body mass

The equations obtained for body mass are presented in Supplementary data 2, and have a relatively high determination coefficient (except the Canidae equation based on the m1) and low PE% (percentage of prediction error). The estimated body mass for *D. avus* is $\approx$ 16 kg, and 364 kg for *Arctotherium* (Table 2; Supplementary data 1). The felids had the following values:

Typical and Maximum prey size followed the pattern of predator body size distribution. The larger carnivore (*Smilodon*) had the larger prey (mean TPM: 879 kg; mean MPM: 1543 kg), followed by the Patagonian Panther (mean TPM: 404 kg; mean MPM: 913 kg), the puma (mean TPM: 260 kg; mean MPM: 699 kg), *Arctotherium* (TPM: 100; MPM: 300; see Prevosti and Vizcaíno, 2006), and finally *D. avus* (mean TPM: 4 kg; mean MPM: 63 kg) (see Table 3). The TPM equation overestimated the TPM of large living felids by $\approx$ 55%, something that did not occur with the MPM equation. The TPM equation for canids had a very large PE% (Supplementary data 2), but it failed mainly in the sub-estimation of TPM for large hypercarnivorous living species (e.g., *Canis lupus*, *Lycaon*, *Cuon*) and the results obtained for *D. avus* (Table 2, Supplementary data 1) are consistent with those expected for a canid of its size and anatomy (see Prevosti and Vizcaíno, 2006).

### 3.4. Stable isotopes

In the whole sample there is a tendency to a decrease of $\delta^{13}$C values from 15 to 9 ka BP (Spearman R: 0.70, $p < 0.042$), which can be observed in the bivariate plot of most species, but only is significant for *Mylodon darwini* (Spearman $R = 0.81$, $p < 0.02$). In fact, *Mylodon* showed two steps in the distribution of the values of $\delta^{13}$C over time: around $-20$ between 14.5 and 12 ka BP, and $-21.5$ between 11 and 9.5 ka BP.

As is common in living communities and other fossil assemblages, the $\delta^{13}$C values of carnivores were higher than the values of herbivores (with the exception of the camelid *L. gracilis* and three samples of Camelidae; Table 2). Predators had wide overlapping values for this isotope, and considering the apparent temporal pattern and an enrichment factor of 1 for $\delta^{13}$C (see above), it appeared that *P. onca mesembrina* and *Smilodon* may have eaten meat from *Hippidion*, Camelidae, and *L. guanicoe*, and Rheidae in the case of *Arctotherium* and *D. avus* (Table 2). If *L. guanicoe* and Rheidae were present in older times (i.e., 11–14 ka BP), and the values obtained are representative of the $\delta^{13}$C signal of these taxa, they may have been part of the diet of *Smilodon* (Table 2). In the same way, *L. gracilis* may have been part of the diet of all the predators if its $\delta^{13}$C value is interpolated to the time span between the dated specimens. *P. onca mesembrina* also may have consumed

*Mylodon* with an enrichment factor of 1 for $\delta^{13}C$. With an enrichment factor of 2 for $\delta^{13}C$, all the prey may have been part of the diet of the recorded predators.

In the $\delta^{13}C/\delta^{15}N$ graph (Fig. 2) it was possible to separate a group of predators with higher $\delta^{15}N$, composed by *Arctotherium*, one specimen of *D. avus* and *Smilodon*, that may have had a diet composed of *Mylodon*, Camelidae and *L. gracilis* with an enrichment factor of 2.8–4 for $\delta^{15}N$, and also by Rheidae and *Hippidion* with a factor of 5.8. *P. onca mesembrina* may have consumed *Hippidion*, camelids, *Mylodon*, and Rheidae. The same was applicable to two specimens of *D. avus* that had $\delta^{15}N$ values similar to *P. onca mesembrina*, but with lower $\delta^{13}C$.

The Bayesian analysis gave similar results; *Arctotherium*, *D. avus* and *Smilodon* had a similar pattern where most species could be part of the diet, but in low proportion (posterior probability ≈ 0.20). *Mylodon*, Rheidae, and *L. guanicoe* (except for *D. avus*) had a slightly higher contribution to the diet of these carnivores (Fig. 3). Most prey species had a low contribution to the diet of *P. onca* (posterior probability below 0.20), but *Hippidion* and *L. gracilis* had a clearly higher contribution (median posterior probability of 0.35; Fig. 3).

## 4. Discussion

### 4.1. Diversity and temporal distribution

The fossils recovered and the available taxon dates indicate that some predators (*D. avus*, *P. onca mesembrina*) and prey (*Hippidion*, *Mylodon*, Camelidae) were present in the three studied areas during the late Pleistocene (Borrero, 1997; Latorre, 1998; Martin, 2008, in press). Other taxa had more restricted distributions. Among the predators, *Smilodon* was restricted to the UE and TF areas, *Arctotherium* was restricted to UE and PA, and *Puma concolor* to UE. In the prey groups, Rheidae was only recorded in PA and TF, *Macrauchenia* was present only in UE, *L. guanicoe* in UE, "*L. owenii*" in UE, and *L. gracilis* in the three areas (F. Martin, pers. obs.). *L. gracilis* was also present in Late Pleistocene of extra Andean Patagonia of Southern

Argentina (Santa Cruz Province; Menegaz and Ortiz Jaureguizar, 1995; Miotti et al., 1999; Paunero, 2003).

Using the range of the taxon dates obtained for each taxa (Table 2), there was an overlap between *Smilodon*, *P. onca mesembrina*, *Arctotherium*, *Mylodon*, *Hippidion*, Camelidae, *L. gracilis*, and also *L. guanicoe* (except with *Smilodon*). *Arctotherium* was detected in a similar time frame as Rheidae (Table 2). The same happens with the temporal range of *D. avus* against the ranges of *Arctotherium*, *Mylodon*, *Hippidion*, Rheidae, Camelidae, *L. gracilis*, and *L. guanicoe*, but not with *Smilodon* and *P. onca mesembrina* (Table 2). We cannot discount that the observed absence of these taxa in any area, or temporal window is a real phenomenon, but we believe that it is highly probable that a contributing factor is sampling bias due to a low number of specimens (for some taxa), and the low number of taxon dates, and low number of stable isotopes analyses. Pooling the all sample, we find that there were four large predators (*D. avus* is a medium sized canid), and seven other large vertebrates, of which two could be considered megamammals (i.e., *Macrauchenia*, *Mylodon*). This is clearly a much more diverse fauna than that of modern Patagonia (one large predator and three large vertebrates) or other biomes of South America (e.g., Pampean Region; Redford and Eisenberg, 1992; Prevosti, 2006; see also Miotti and Salemme, 1999). The abundance of large predators and other mammals is similar to that observed in other high latitude areas like Beringia, where Fox-Dobbs et al. (2008) reported 5 predators and 6 large potential prey for a wider time span (50–10 ka), or 6 potential large mammalian prey for the period 18–10 ka BP (Guthrie, 2006; see also; Harington, 2011). A similar situation was present in the Late Pleistocene "Mammoth Steppe Fauna" of northern Eurasia (see Vereshchagin and Baryshnikov, 1992). The comparison with other assemblages of the Late Pleistocene of South America was more difficult, because most of them lacked robust chronological data (there were very few taxon dates) and taphonomic control. The exceptions were assemblages that clearly had a large time averaging (e.g., Río Lujan Fauna in Argentina and Minas Gerais Caves in Brazil, see Auler et al., 2006; Prevosti and Vizcaíno, 2006, respectively). Several localities of higher latitudes (e.g., Talara in Peru; La Carolina in Ecuador; Camet Norte localities in the Buenos Aires province of Argentina) differed only in the presence of more than 10 mammalian species above 10 kg (Hoffstetter, 1952; Lemon and Churcher, 1961; Pardiñas et al., 1998; Cartelle, 1999; Martinez and Cadenillas, 2004; Prevosti, 2006). These comparisons indicated that even when it was not very diverse, this vertebrate assemblage had a "good balance" in terms of the number of large predators versus number of prey (see Fariña, 1996; Prevosti and Vizcaíno, 2006).

### 4.2. Paleoecological inferences

The obtained body mass estimates are in general agreement with previous inferences (see Christiansen and Harris, 2005; Prevosti and Vizcaíno, 2006; Soibelzon and Tartarini, 2009). However, we detected that estimates based in the m1 and humerus diaphysis gave excessive body masses for *Puma concolor* and *P. onca mesembrina* in comparison to the expected for these two felids (see below). This is in part because the m1 and humerus measurements were greater than in living relatives and similar to larger living felids (*P. leo*, *P. tigris*). The m1 equation of body mass for larger living felids has large confidence intervals, and these ranges overlap with the values obtained with other functions (humerus and tibia). The humerus equation has narrower confidence intervals, but we cannot discard that there are subtle differences in the way that we and Christiansen and Harris (2005) have taken this measurement, something that could inflate the estimations for larger felids. We believe that it is better not to include in the following discussion the
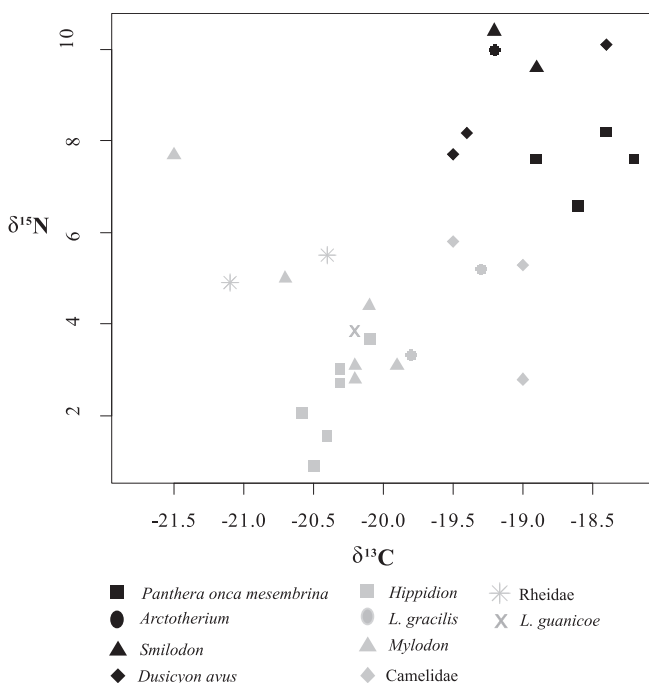


**Fig. 2.** Distribution of $\delta^{13}C$ and $\delta^{15}N$ values of the species recorded in the Late Pleistocene of Southern Patagonia.
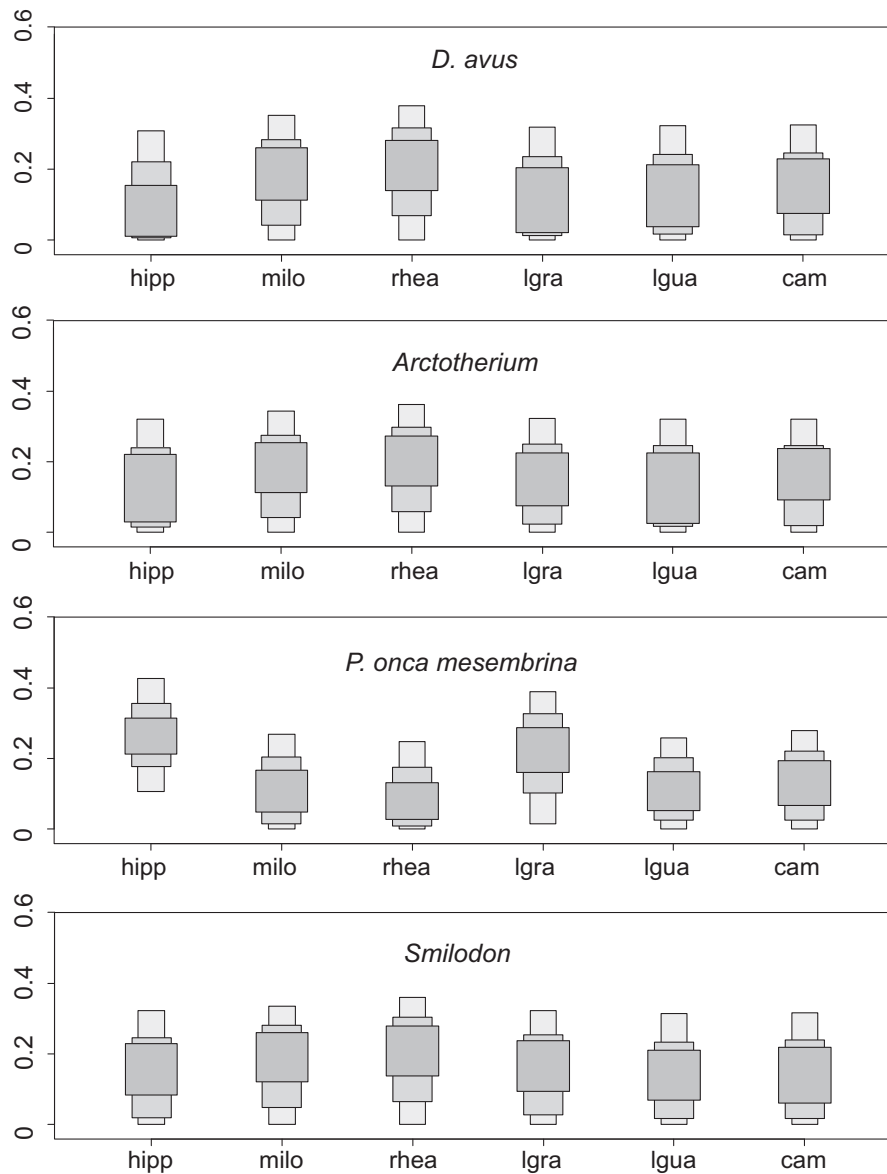
**Fig. 3.** Bayesian isotopic model indicating the posterior probability distribution of the potential contribution of each prey to the diet of each carnivore. The colors of the boxes indicate the credibility intervals of 95% (dark gray), 75% (gray), and 25% (light gray). hipp: *Hippidion*; milo: *Mylodon*; cam: Camelidae; lgra: *L. gracilis*; lgua: *L. guanicoe*; rhea: Rheidae.

estimates based on m1 and humerus for *Puma concolor* and *P. onca mesembrina*. We included the estimate of *Smilodon* body mass based on the m1 because it was below the estimate based on the femur, and it was congruent with the estimates published by Christiansen and Harris (2005). Thus, we think that the following estimates provide a better reconstruction of the fossil specimens of *Puma concolor*: 121 kg, and *P. onca mesembrina*: 140 kg. Similarly, the TPM equation, gave overestimates for larger living felids. In this case the lower limit of the 95% confidence interval (95%IC) was a better predictor for larger felids (Supplementary data 1). Following these observations, we considered that TPMs of 121, 150, 390 kg and MPMs of : 584 (95%IC: 336−1033), 670 (95%IC: 363−1246), 1415 (95%IC: 519−3836) kg were better inferences for *Puma concolor*, *P. onca mesembrina*, and *Smilodon*, respectively.

The estimates of body mass, prey size, and dental morphology suggested that there was a robust segregation between the predators of the Late Pleistocene Southern Patagonia. In one extreme there was a medium sized canid, *D. avus* ($\approx$ 15 kg) with a mesocarnivorous diet,

and an omnivorous bear (body mass $\approx$ 360 kg). The others were hypercarnivores that were mainly separated by body size, from the smaller *Puma concolor* ($\approx$ 121 kg), to *P. onca mesembrina* ($\approx$ 140 kg), and the larger *Smilodon* ($\approx$ 400 kg) (Table 2, Supplementary data 1).

Typical and maximum prey size inferences indicated that *D. avus* could have hunted mainly medium sized rodents (e.g., *Dolichotis*, *Myocastor*) and armadillos (e.g., *Chaetophractus, Zaedyus*), but that it also could have hunted *L. gracilis,* Rheidae, and juveniles of larger ungulates (See Supplementary data 3). These metrics indicated that the bulk of *Puma concolor* diet was composed of camelids (*L. guanicoe* also is a common prey of the puma in Patagonia at the present), but also could hunt equids, and juveniles of larger prey (see Wilson, 1984; Bank and Franklin, 1998; Bank et al., 2002; Borrero et al., 2005; Zanón Martínez et al., 2012). The *P. onca mesembrina* diet may have included by large camelids (e.g., "*L. owenii*", large individuals of *L. guanicoe*), *Hippidion*, and juveniles of larger prey. Due to its large body mass and hypercarnivore specializations, *Smilodon* was the top predator of these assemblages,

and if we consider the upper 95%IC limit of the MPM estimate, it surely hunted *Hippidion*, *Macrauchenia*, and *Mylodon*. Besides these estimates, and due to the opportunistic habits of carnivores (see Wilson and Mittermeier, 2009), these predators also hunted smaller prey than the predicted ones. The inference of prey size for *Arctotherium* is a complicated task. With the exception of *Ursus maritimus*, which is specialized to hunt pinnipeds, living bears are not active predators (Sacco and Van Valkenburgh, 2004; Christiansen, 2007), thus it was not possible to obtain an allometric function to estimate prey size (see Van Valkenburgh and Hertel, 1998; Prevosti and Vizcaíno, 2006). But it is clear that several species of bears preyed on large mammals, and some populations of *Ursus arctos* consume a high proportion of meat (Bojarska and Selva, 2012). Even the herbivorous spectacled bear (*Tremarctos ornatus*), the closest living relative of *Arctotherium* (Krause et al., 2008) occasionally hunt and consume livestock (e.g., *Bos taurus*; Castellanos, 2012; García-Rangel, 2012). Dental anatomy (see above and Table 2) indicated that *Arctotherium* was omnivorous (see also Prevosti and Vizcaíno, 2006, and cited bibliography), and a geometric morphometric analysis indicated that Late Pleistocene species of this genus were in part herbivorous (Figueirido and Soibelzon, 2009). Thus the morphological evidence suggests that *Arctotherium* was a non active hunter, at least for the species of the Late Pleistocene, but the empirical evidence does not invalidate that it occasionally could have hunted or scavenged large mammals like equids and camelids.

*Smilodon, D. avus*, and *Arctotherium* have similar isotopic signals, that indicate they could have eaten all the analyzed potential prey (i.e., prey specialization is not evident). But, based on prey size estimation and beyond the occasional hunting event, it is not probable that Rheidae and *L. gracilis* were a common prey of *Smilodon*. On the other hand, *P. onca mesembrina* consumed more *Hippidion,* and *L. gracilis* showed a slightly more specialist strategy (Fig. 3). Following these analyses *Arctotherium* and *D. avus* had hypercarnivorous diets were not congruent with inferences based on morphology (see above; Prevosti and Vizcaíno, 2006), except for some *D. avus* especimens that have RGA values that fall in the hypercarnivore range. One explanation is that they scavenged prey that was hunted by other predators.

Stable isotope studies in the North American *Arctodus simus*, a relative of *Arctotherium*, also pointed to a carnivorous diet (Bocherens et al., 1995; Matheus, 1995; Barnes et al., 2002; Fox-Dobbs et al., 2008; but see; Sorkin, 2006), and a caribou hunter specialist (Fox-Dobbs et al., 2008) or a scavenger (Matheus, 1995). The hunter or scavenger hypotheses also could be applied to *Arctotherium*, but in this case we prefer the latter because it is more congruent with morphological studies (see above, Berman, 1994; Figueirido and Soibelzon, 2009). Another hypothesis is that the extinct fox and bear ate a large proportion of freshwater or marine resources, as it happens with some population of *U. arctos* that eat salmon, or some *C. lupus* that live on marine islands (Mowat and Heard, 2006; Darimont et al., 2009). This could be plausible for Ultima Esperanza Area, where a proglacial lake was present between ca. before 13.5 and 9.2 ka BP (Sagredo et al., 2011; Stern et al., 2011), but is not likely for the Pali Aike area or Tres Arroyos 1, because they were too far away (>30 km) from the sea coast or large freshwater bodies during the latest Pleistocene-early Holocene (see Ponce et al., 2011). The closest large water body was the Magellan Strait, where there was a proglacial lake between 10.3 and 12.7 ka (McCulloch et al., 2005; Ponce et al., 2011). Additional isotopic analyses will allow us to test this hypothesis, and to correct the bias that could be introduced by the presence of temporal variation in $\delta^{13}C/\delta^{15}N$ values.

Another source of evidence is the taphonomic analyses of several caves bone assemblages by one of us (F. Martin), that indicates

that some of them (Cueva de los Chingues, Cueva Lago Sofía, Cueva del Puma) were *P. onca mesembrina* dens (Martin, 2008, in press). In general terms sites Lago Sofía 4, Cueva de los Chingues and Cueva del Puma were interpreted as carnivore dens, places where panthers were the main bone accumulation agents. Carnivore marks were frequent present on bones of both horses and camelids of different sizes and the marks pattern was attributed to panthers (Martin, 2008). This information together with the synchronic presence of adult and sub-adult panther bones clearly supported the den interpretation. Another characteristic of these assemblages is that they exhibit a rich faunal record which is dominated by camelids, followed by horse and finally *Mylodon* (Borrero et al., 1997; San Román et al., 2000; Martin et al., 2004; Martin, in press). Except at Cueva Lago Sofía 4 *Mylodon* bones were practically restricted to osteoderms, while the horse bones were relatively abundant and marked by carnivores (Martin, 2008). The high frequency of camelid bones indicated that these resources were heavily consumed. On the other hand, the horse remains were also relatively abundant at Cueva de los Chingues, but relatively scarce at Cueva Lago Sofía 4 and Cueva del Puma. The study by Borrero et al. (1997) at Cueva Lago Sofía 4, interpreted this site as a carnivore den, and showed that camelids were well represented in contrast with the scarcity of horse remains. This is interesting in view of the fact that horse bones were more resistant to destruction (Alberdi and Prieto, 2000; Martin, 2008). The *Lama* sp. specimens include low density bones, which are highly fragmented and marked by carnivores. The paucity of horse specimens probably indicates the selective introduction of its parts. Some horse specimens preserved carnivore marks. It must be emphasized that the smaller elements like carpals, tarsals, and phalanges were corroded by gastric acids. This suggests their introduction by carnivore scats.

Bone assemblages at Cueva del Milodón and Cueva Chica are different in that *Mylodon* remains dominate, many of which exhibit carnivore marks. It was suggested that Cueva del Milodón was a place where panthers hunted ground sloth, given the pattern of marks recorded in their bones (Martin, 2008, in press). The case of Cueva Chica, where the bone assemblage was dominated by *Mylodon* and panther, can also be interpreted as a panther den. This site is interesting due to the absence of horse remains, which were present at the rest of the sites, and the scarcity of camelid remains (see Martin et al., 2013).

## 5. Conclusions

The late Pleistocene fauna of Southern South America had four large and one medium size predators, a guild diversity that is correlated to a richer diversity of other large mammals.

The predator guild was structured mainly by body size differences, but also by prey selection. *Arctotherium* and *D. avus* were more omnivorous, but based on their isotopic signal they may have had a scavenger role. *Smilodon*, *Puma concolor* and *P. onca mesembrina* hunted large mammals, and their trophic segregation surely was based on their body mass differences, with *Smilodon* probably more focused on the larger prey, like *Mylodon*, *Macrauchenia*. *P. onca mesembrina* was likely preying on *Hippidion* and camelids, while *Puma concolor* was probably preying on camelids and Rheidae. Bayesian isotopic analysis differs because it indicates that *Arctotherium*, *D. avus* and *Smilodon* did not have a preferred prey, but that *P. onca mesembrina* included in its diet a larger proportion of *Hippidion* and *L. gracilis*. More isotopic data, especially the inclusion of other taxa present in these sites, is needed to test these reconstructions. Finally, the published taphonomic information about *P. onca mesembrina* generally agrees with our results, but also suggests that *Mylodon* could be a more frequent prey than the expected from isotopic and prey size estimations.

In conclusion the late Pleistocene Southern Patagonia had a rich fauna of large mammals including some megamammals. The carnivore guild had three felids that were large hypercarnivores, and two of them (*Smilodon*, *P. onca*) that could prey on most large mammals. The diversity of potential prey is lower than that observed in lower latitudes (e.g., Pampean Region), while the number of predators is similar.

## Acknowledgments

## Appendix A.  Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quaint.2012.12.039.

## References

Alberdi, M.T., Prieto, A., 2000. Hippidion (Mammalia, Perissodactyla) de las cuevas de las provincias de Magallanes y Tierra del Fuego. Anales del Instituto de la Patagonia (Serie Ciencias Humanas) 28, 147–171.

Amorosi, T., Prevosti, F.J., 2008. A preliminary review of the canid remains from Junius Birds excavations at Fell's and Pali Aike caves, Magallanes, Chile. Current Research in the Pleistocene 25, 25–27.

Anyonge, W., 1993. Body mass in large extant and extinct carnivores. Journal of Zoology 231, 339–350.

Bank, M.S., Franklin, W.L., 1998. Puma (Puma concolor) feeding observations and attacks on guanacos (Lama guanicoe). Mammalia 62 (4), 599–605.

Bank, M.S., Sarno, R.J., Campbell, N.K., Franklin, W.L., 2002. Predation on guanaco (Lama guanicoe) by southernmost mountain lions (Puma concolor) during a historically severe winter in Torres del Paine National Park, Chile. Journal of Zoology 258, 215–222.

Barnes, I., Matheus, P., Shapiro, B., Jensen, D., Cooper, S., 2002. Dynamics of Pleistocene population extinctions in Beringian brown bears. Science 295, 2267–2270.

Barnett, R., Barnes, I., Phillips, M.J., Martin, L.D., Harington, C.R., Leonard, J.A., Cooper, A., 2005. Evolution of the extinct Sabretooths and the American cheetah-like cat. Current Biology 15 (15), R589–R590.

Berman, W.D., 1994. Los carnívoros continentales (Mammalia, Carnivora) del Cenozoico en la provincia de Buenos Aires. Ph.D. thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina.

Berta, A., 1989. Quaternary Evolution and Biogeography of the Large South American Canidae (Mammalia: Carnivora), vol. 132. University of California Publication in Geological Sciences, pp. 1–149.

Bird, J., 1988. Travels and Archaeology in South Chile. University of Iowa Press, Iowa.

Blunier, T., Schwander, J., Stauffer, B., Stocker, T.F., Deallenbch, A., Ndermumle, A.I., Tschumi, J., Chppellaz, J., Raynaud, D., Barnova, I.J.M., 1997. Timing of the Antarctic Cold Reversal and the atmospheric $CO_2$ increase with respect to the Younger Dryas event. Geophysical Research Letters 24, 2683–2686.

Bocherens, H., 2000. Preservation of isotopic signals ($^{13}C$, $^{15}N$) in Pleistocene mammals. In: Ambrose, S.H., Katzenberg, M.A. (Eds.), Biogeochemical Approaches to Paleodietary Analysis. Kluwer Academic/Plenum Publishers, New York, pp. 65–88.

Bocherens, H., Drucker, D., 2003. Trophic level isotopic enrichments for carbon and nitrogen in collagen: case studies from recent and ancient terrestrial ecosystems. International Journal of Osteoarchaeology 13, 46–53.

Bocherens, H., Emslie, S.D., Billiou, D., Mariotti, A., 1995. Stable isotopes ($^{13}C$, $^{15}N$) and paleodiet of the giant short-faced bear (Arctodus simus). Comptes Rendus de l'Académie des Sciences, Série II 320, 779–784.

Bojarska, K., Selva, N., 2012. Spatial patterns in brown bear Ursus arctos diet. Mammal Review 42 (2), 120–143.

Borrero, L.A., 1997. The extinction of the megafauna: a supra-regional approach. Anthropozoologica 25, 209–216.

Borrero, L.A., 2003. Taphonomy of the Tres Arroyos 1 rockshelter, Tierra del Fuego, Chile. Quaternary International 109–110, 87–93.

Borrero, L.A., 2009. The elusive evidence: the archaeological record of the South American extinct megafauna. In: Haynes, G. (Ed.), American Megafaunal Extinctions at the End of the Pleistocene. Springer, Amsterdam, pp. 145–168.

Borrero, L.A., Martin, F., 2012. Ground Sloths and humans in southern Fuego-Patagonia: taphonomy and archaeology. World Archaeology 44 (1), 102–117.

Borrero, L.A., Martin, F.M., Prieto, A., 1997. La cueva Lago Sofía 4, Ultima Esperanza: una madriguera de felino del Pleistoceno tardío. Anales del Instituto de la Patagonia (Serie Ciencias Sociales) 25, 103–122.

Borrero, L.A., Martin, F.M., Vargas, J., 2005. Tafonomía de la interacción entre pumas y guanacos en el Parque Nacional Torres del Paine, Chile. Magallania 33 (1), 95–114.

Cade, B.S., Noon, B.R., 2003. A gentle introduction to quantile regression for ecologists. Frontiers in Ecology and the Environment 1, 412–420.

Canto, J., 1991. Posible presencia de una variedad de Smilodon en el Pleistoceno tardío de Magallanes. Anales del Instituto de la Patagonia (Serie Ciencias Sociales) 20, 96–99.

Cartelle, C., 1999. Pleistocene mammals of the Cerrado and Caatinga of Brazil. In: Eisemberg, J.F., Redford, K.H. (Eds.), Mammals of the Neotropics. The Central Neotropics, vol. 3. The University of Chicago Press, Chicago and London, pp. 27–46.

Cartelle, C., Langguth, A., 1999. Protocyon troglodytes (Lund): um canídeo intertropical extinto. Anais de Academia Brasileira de Ciencias 71, 371–384.

Castellanos, A., 2012. Depredación a ganado vacuno y mamíferos silvestres por oso andino en el Norte de Ecuador. Abstracts of the X Congreso Internacional de Manejo de Fauna Silvestre en la Amazonia y América Latina. XCIMFAUNA, Salta, Salta, Argentina 1, pp. 112.

Clapperton, C.M., 1993. Quaternary Geology and Geomorphology of South America. Elsevier, Amsterdam.

Christiansen, P., 2007. Evolutionary implications of bite mechanics and feeding ecology in bears. Journal of Zoology 272, 423–443.

Christiansen, P., Harris, J.M., 2005. Body size of Smilodon (Mammalia: Felidae). Journal of Morphology 266, 369–384.

Darimont, C.T., Paquet, P.C., Reimchen, T.E., 2009. Landscape heterogeneity and marine subsidy generate extensive intrapopulation niche diversity in a large terrestrial vertebrate. The Journal of Animal Ecology 78 (1), 126–133.

Diniz-filho, J.A.F., Sant, R.D.E., Bini, L.M., 1998. An eigenvector method for estimating phylogenetic inertia. Evolution 52 (5), 1247–1262.

Esteban, G.I., 1996. Revisión de los Mylodontinae cuaternarios (Edentata-Tardigrada) de Argentina, Bolivia y Uruguay. Sistemática, filogenia, paleobiología, paleozoografía y paleoecología. Ph.D. thesis, Universidad Nacional de Tucumán, Argentina.

Fariña, R.A., 1996. Trophic relationship among Lujanian mammals. Evolutionary Theory 11, 125–134.

Fariña, R.A., Vizcaíno, S.F., Bargo, M.S., 1998. Body mass estimations in Lujanian (late Pleistocene-early Holocene of South America) mammal megafauna. Mastozoología Neotropical 5 (2), 87–108.

Figueirido, B., Soibelzon, L.H., 2009. Inferring palaeoecology in extinct tremarctine bears (Carnivora, Ursidae) using geometric morphometrics. Lethaia 43 (2), 209–222.

Fox Dobbs, K., Nelson, A.B., Leonard, J.A., Koch, P.L., 2007. Carnivore specific stable isotope variables and variation in the foraging ecology of modern and ancient wolf populations: case studies from Isle Royale, Minnesota, and La Brea. Canadian Journal of Zoology 85, 458–471.

Fox-Dobbs, K., Leonard, J.A., Koch, P.L., 2008. Pleistocene megafauna from eastern Beringia: paleoecological and paleoenvironmental interpretations of stable carbon and nitrogen isotope and radiocarbon records. Palaeogeography, Palaeoclimatology, Palaeoecology 261 (1–2), 30–46.

Fowgill, C.J., Kubik, P.W., 2005. A glacial stage. Geografiska Annaler 87A (2), 403–408.

García-Rangel, S., 2012. Andean bear Tremarctos ornatus natural history and conservation. Mammal Review 42 (2), 85–119.

Guthrie, R.D., 2006. New carbon dates link climatic change with human colonization and Pleistocene extinctions. Nature 441, 207–209.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: palaeontological statistics software package for education and data analysis. Palaeontologia Electronica 9 (1), 1–9.

Harington, C.R., 2011. Pleistocene vertebrates of the Yukon Territory. Quaternary Science Reviews 30 (17–18), 2341–2354.

Hauthal, R., 1899. Reseña de los hallazgos en cavernas de Última Esperanza. Revista del Museo de La Plata 9, 409–420.

Heusser, C.J., 2003. Ice Age Southern Andes. In: A Chronicle of Paleoecological Events. Elsevier, Amsterdam.

Heusser, C.J., Borrero, L.A., Lanata, J.L., 1992. Late Glacial vegetation at cueva del Mylodon. Anales del Instituto de la Patagonia (Serie Ciencias Naturales) 21, 97–102.

Hoffstetter, R., 1952. Les mammifères pléistocènes de la République de l`Equateur. Mémoires de la Société géologique de France (Nouvelle Série) 31 (66), 1–391.

Johnson, W.E., Eizirik, E., Pecon-Slattery, J., Murphy, W.J., Antunes, A., Teeling, E., O'Brien, S.J., 2006. The late Miocene radiation of modern Felidae: a genetic assessment. Science 311 (5757), 73–77.

Koenker, R., Hallock, K., 2001. Quantile regression: an introduction. Journal of Economic Perspectives 15, 143–156.

Krause, J., Unger, T., Malaspinas, A., Kolokotronis, S., Stiller, M., Soibelzon, L., Spriggs, H., Dear, P.H., Briggs, A.W., Bray, S.C.E., O'Brien, S.J., Rabeder, G., Matheus, P., Cooper, A., Slatkin, M., Pääbo, S., Hofreiter, M., 2008. Mitochondrial genomes reveal an explosive radiation of extinct and extant bears near the

Miocene-Pliocene boundary. BMC Evolutionary Biology 12, 1–12. http://dx.doi.org/10.1186/1471-2148-8-220.

Labarca, E.R., Prieto, I.A., 2009. Osteometría de Vicugna vicugna Molina, 1782 en el Pleistoceno final de Patagonia meridional chilena: Implicancias paleoecológicas y biogeográficas. Revista del Museo de Antropología 2, 127–140.

Labarca, R., Prieto, A., Sierpe, V., 2008. Sobre la presencia de *Smilodon populator* Lund (Felidae Machairodontinae) el Pleistoceno tardío de Patagonia meridional. In: Libro de Actas del I Simposio de Paleontología en Chile, Santiago, Chile, vol. 1, pp. 131–135.

Latorre, C., 1998. Paleontología de mamíferos del alero Tres Arroyos I, Tierra del Fuego, XII Región, Chile. Anales del Instituto de la Patagonia (Serie Ciencias Naturales) 26, 77–90.

Lemon, R.R.H., Churcher, C.S., 1961. Pleistocene geology and paleontology of the Talara region, Northwest Peru. American Journal of Science 259, 410–429.

Lindblad-Toh, K., Wade, C.M., Mikkelsen, T.S., Karlsson, E.K., Jaffe, D.B., Kamal, M., Clamp, M., Chang, J.L., Kulbokas III, E.J., Zody, M.C., Mauceli, E., Xie, X., Breen, M., Wayne, R.K., Ostrander, E.A., Ponting, C.P., Galibert, F., Smith, D.R., de Jong, P.J., Kirkness, E., Alvarez, P., Biagi, T., Brockman, W., Butler, J., Chin, C.W., Cook, A., Cuff, J., Daly, M.J., De Caprio, D., Gnerre1, S., Grabherr, M., Kellis, M.M., Kleber, M., Bardeleben, C., Goodstadt, L., Heger, A., Hitte, C., Kim, L., Koepfli, K.P., Parker, H.G., Pollinger, J.P., Searle, S.M.J., Sutter, N.B., Thomas, R., Webber, C., Broad Institute Genome Sequencing Platform y Lander, E.S., 2005. Genome sequence, comparative analysis and haplotype structure of the domestic dog. Nature 438 (7069), 803–819.

Markgraf, V., 1985. Late Pleistocene faunal extinction in southern Patagonia. Science 228, 1110–1112.

Markgraf, V., 1988. Fell's Cave: 11,000 years of changes in paleoenvironments. In: Hyslop, J. (Ed.), Travels and Archaeology in South Chile. University of Iowa Press, Iowa.

Markgraf, V., 1991. Late Pleistocene environmental and climatic evolution in southern South America. Bamberger Geographische Schritten 11, 271–281.

Markgraf, V., 1993. Paleoenvironments and paleoclimates in Tierra del Fuego and southernmost Patagonia, South America. Palaeogeography, Palaeoclimatology, Palaeoecology 102, 53–68.

Marshall, L.G., 1976. Evolution of the Thylacosmilidae, extinct sabertooth marsupials of South America. PaleoBios 23, 1–30.

Martin, F.M., 2008. Bone crunching felids at the end of the Pleistocene in Fuego-Patagonia, Chile. Journal of Taphonomy 6 (3–4), 337–372.

Martin, F.M. Tafonomía y Paleoecología de la Transición Pleistoceno-Holoceno en Fuego-Patagonia. Interacción entre Humanos y Carnívoros y su importancia como Agentes en la Formación del Registro Fósil. Ediciones de la Universidad de Magallanes, Punta Arenas, in press.

Martin, F., Borrero, L.A., San Román, M., 2012. Prospección arqueológica de cerro Benítez, Ultima Esperanza. Informe de tareas año 2012. Informe avance segundo año proyecto FONDECYT 1100822.

Martin, F.M., Massone, M., Prieto, A., Cárdenas, P., 2009. Presencia de Rheidae en Tierra del Fuego durante la Transición Pleistoceno-Holoceno. Implicancias biogeográficas y paleoecológicas. Magallania 37, 173–177.

Martin, F.M., Prieto, A., San Román, M., Morello, F., Prevosti, F.J., Cárdenas, P., Borrero, L.A., 2004. Late Pleistocene megafauna at Cueva del Puma, Pali-Aike Lava Field, Chile. Current Research in the Pleistocene 21, 101–103.

Martin, F.M, San Román, M., Morello, F., Todisco, D., Prevosti, F.J., Borrero, L.A., 2013. Land of the ground sloths: recent research at Cueva Chica, Ultima Esperanza, Chile. Quaternary International 305, 56–66.

Martinez, J.N., Cadenillas, R., 2004. Paleoambiente de la región de Talara - La Brea (Piura, Perú) hacia el fin del Pleistoceno: datos sugeridos por las paleo-comunidades de mamíferos, Abstracts of the XII Congreso Peruano de Geología, Sociedad Geológica del Perú, Lima, Perú 1, pp. 481–484.

Massone, M., 1987. Los cazadores paleoindios de Tres Arroyos (Tierra del Fuego). Anales del Instituto de la Patagonia (Serie Ciencias Sociales) 17, 47–60.

Massone, M., 2004. Los cazadores después del hielo. Ediciones de la Dirección de Bibliotecas Archivos y Museos, Santiago.

Massone, M., Prieto, A., 2004. Evaluación de la modalidad cultural Fell 1 en Magallanes. Chungara Special Number, 303–315.

Matheus, P.E., 1995. Diet and co-ecology of Pleistocene short-faced bears and brown bears in eastern Beringia. Quaternary Research 44, 447–453.

McCulloch, R.D., Bentley, M.J., Purves, R.S., Hulton, N.R., Sugden, D.E., Clapperton, C.M., 2000. Climatic inferences from glacial and palaeoecological evidence at the last glacial termination, southern South America. Journal of Quaternary Science 15, 409–417.

McCulloch, R.D., Bentley, M.J., Tipping, R.M., Clapperton, C.M., 2005. Evidence for late-glacial ice dammed lakes in the central Strait of Magellan and Bahía Inútil, southernmost South America. Geografiska Annaler 87A, 335–362.

Menegaz, A.N., Ortiz Jaureguizar, E., 1995. Los Artiodáctilos. In: Alberdi, M.T., Leone, G., Tonni, E.P. (Eds.), Evolución biológica y climática de la región pampeana durante los últimos cinco millones de años. Un ensayo de correlación con el Mediterráneo occidental. Museo Nacional de Ciencias Naturales e Consejo Superior de Investigaciones Científicas, Madrid, pp. 311–337.

McCulloch, R., Clapperton, C., Rabassa, J., Currant, A., 1997. The glacial and post-glacial environmental history of Fuego-Patagonia. In: McEwan, C., Borrero, L.A., Prieto, P. (Eds.), Patagonia. Natural History, Prehistory, and Ethnography at the Uttermost End of the Earth. British Museum Press, London, pp. 12–31.

Miotti, L., Salemme, M., 1999. Biodiversity, taxonomic richness and specialists-generalists during Late Pleistocene/Early Holocene times in Pampa and Patagonia (Argentina, Southern South America). Quaternary International 53/54, 53–68.

Miotti, L., Vásquez, M., Hermo, D., 1999. Piedra Museo: un yamnagoo plesitocénico de los colonizadores de la meseta de Santa Cruz. El estudio de la arqueofauna. In: Belardi, J.B., Fernández, P.M., Goñi, R.A., Guráieb, A.N., De Nigris, M. (Eds.), Soplando en el viento. Actas de las III Jornadas de arqueología de la Patagonia. Universidad Nacional del Comahué, Neuquén-Buenos Aires, pp. 113–135.

Mol, J.D., Bree, P.J.H.V., Mc Donald, G.H., 2003. De Amsterdamse collectie fossielen uit de Grot van Ultima Esperanza (Patagonië, Zuid-Chili). Grondboor & Hamer 2, 26–36.

Moore, D.M., 1978. Post-glacial vegetation in the South Patagonian territory of the giant ground sloth *Mylodon*. Botanical Journal of the Linnean Society 77, 177–202.

Mowat, G., Heard, D.C., 2006. Major components of grizzly bear diet across North America. Canadian Journal of Zoology 489, 473–489.

Nami, H.G., 1985-1986. Excavación arqueológica y hallazgo de una punta cola de pescado Fell 1 en la cueva del Medio. Anales del Instituto de la Patagonia 16, 103–109.

Nami, H.G., 1987. Cueva del Medio: perspectivas arqueológicas para la Patagonia Austral. Anales del Instituto de la Patagonia (Serie Ciencias Sociales) 17, 73–106.

Nami, H.G., Menegaz, A.N., 1991. Cueva del Medio: aportes para el conocimiento de la diversidad faunística hacia el Pleistoceno-Holoceno en Patagonia Austral. Anales del Instituto de la Patagonia (Serie Ciencias Sociales) 20, 117–132.

Nami, H.G., Nakamura, T., 1995. Cronología radiocarbónica con AMS sobre muestras de huesos procedentes del sitio cueva del Medio (Ultima Esperanza, Chile). Anales del Instituto de la Patagonia 32, 125–133.

Oliveira, E.V., Prevosti, F.J., Pereira, J.C., 2005. *Protocyon troglodytes* (Lund) (Mammalia, Carnivora) in the Late Pleistocene of Rio Grande do Sul, and their palaeoecological significance. Revista Brasileira de Paleontologia 8 (3), 215–220.

Orlando, L., Metcalf, J.L., Alberdi, M.T., Telles-Antunes, M., Bonjean, D., Otte, M., Martin, F., Eisenmann, V., Mashkour, M., Morello, F., Prado, J.L., Salas-Gismondi, R., Shockey, B.J., Wrinn, P.J., Vail'ev, S.K., Ovodov, N.D., Cherry, M.I., Hopwood, B., Male, D., Austin, J.J., Hänni, C., Cooper, A., 2009. Revising the recent evolutionary history of equids using ancient DNA. Proceedings of the National Academy of Sciences 106 (51), 21754–21759.

Palmqvist, P., Perez-Claros, J.A., Janis, C.M., Figueirido, B., Torregrosa, V., Grocke, D.R., 2008. Biogeochemical and ecomorphological inferences on prey selection and resource partitioning among mammalian carnivores in an early Pleistocene community. Palaios 23 (11), 724–737.

Pardiñas, U.F.J., Tonni, E.P., Figini, A., 1998. Camet Norte: diversidad faunística próxima al último máximo glacial en el sudeste de la provincia de Buenos Aires, Argentina. Actas del X Congreso Latinoamericano de Geología y VI Congreso Nacional de Geología Económica, Segemar, Buenos Aires, Argentina 1, pp. 257–262.

Parnell, A., Jackson, A., 2012. R Package "SIAR". http://cran.r-project.org/web/packages/siar/siar.pdf.

Paunero, R.S., 2003. The presence of a Pleistocene colonizing culture in La María archaeological locality, Casa del Minero 1. In: Miotti, L., Salemme, M., Flegenheimer, N. (Eds.), Where the South Winds Blow. Ancient Evidence of Paleo South Americans. Center for the Study of the First Americans, College Station, pp. 127–132.

Phillips, D.L., 2012. Converting isotope values to diet composition: the use of mixing models. Journal of Mammalogy 93 (2), 342–352.

Ponce, J.F., Rabassa, J., Coronato, A., Borromei, A.N., 2011. Palaeogeographical evolution of the Atlantic coast of Pampa and Patagonia from the last glacial maximum to the Middle Holocene. Biological Journal of the Linnean Society 103, 363–379.

Prevosti, F.J., 2006. Grandes cánidos (Carnivora, Canidae) del Cuaternario de la Republica Argentina: Sistemática, Filogenia, Bioestratigrafía y Paleoecología. Ph.D. thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina.

Prevosti, F.J., 2010. Phylogeny of the large extinct South American canids (Mammalia, Carnivora, Canidae) using a "total evidence" approach. Cladistics 26, 456–481.

Prevosti, F.J., Palmqvist, P., 2001. Análisis ecomorfológico del cánido hipercarnívoro *Theriodictis platensis* (Mammalia, Carnivora) basado en un nuevo ejemplar del Pleistoceno de Sudamérica. Ameghiniana 38 (4), 375–384.

Prevosti, F.J., Soibelzon, L., Prieto, A., San Roman, M., Morello, F., 2003. The southernmost record of Ursidae: the occurrence of *Pararctotherium* (Tremarctinae) in the latest Pleistocene of southern Patagonia (Chile). Journal of Vertebrate Paleontology 23 (3), 709–712.

Prevosti, F.J., Vizcaíno, S., 2006. The carnivore guild of the late Pleistocene of Argentina: paleoecology and carnivore richness. Acta Paleontologica Polonica 51 (3), 407–422.

Prevosti, F.J., Forasiepi, A.M., Zimicz, N. The evolution of the Cenozoic terrestrial mammalian predator guild in South America: competition or replacement? Journal of Mammalian Evolution, in press.

Prevosti, F.J., Ubilla, M., Perea, D., 2009. Large extinct canids from the Pleistocene of Uruguay: systematic, biogeographic and palaeoecological remarks. Historical Biology 21 (1–2), 79–89.

Prieto, A.R., Stutz, S., Pastorino, S., 1999. Arqueopalinología de la cueva las Buitreras (provincia de Santa Cruz, Argentina). Præhistoria 3, 169–181.

Prieto, A., 1991. Cazadores tempranos y tardíos en Cueva del Lago Sofía 1. Anales del Instituto de la Patagonia (Serie Ciencias Sociales) 20, 75–99.

Prieto, A., Labarca, R., Sierpe, V., 2010. New evidence of the sabertooth cat *Smilodon* (Carnivora: Machairodontinae) in the late Pleistocene of southern Chilean Patagonia. Revista Chilena de Historia Natural 83 (2), 299–307.

R Development Core Team, 2012. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org/.

Redford, K.H., Eisenberg, J.F., 1992. Mammals of the Neotropics. In: The Southern Cone, vol. 2. University of Chicago Press, Illinois.

Roth, S., 1899. Descripción de los restos encontrados en la caverna de Ultima Esperanza. Revista del Museo de La Plata 9, 421–453.

Roth, S., 1904. Nuevos restos de mamíferos de la caverna Eberhardt en Ultima Esperanza. Revista del Museo de La Plata 11, 39–69.

Sacco, T., Van Valkenburgh, B., 2004. Ecomorphological indicators of feeding behaviour in the bears (Carnivora: Ursidae). Journal of Zoology 263, 41–54.

Sagredo, E.A., Moreno, P.I., Villa-Martinez, R., Kaplan, M.R., Kubik, P.W., Stern, C.R., 2011. Fluctuations of the Última Esperanza ice lobe (52°S), Chilean Patagonia, during the last glacial maximum and termination 1. Geomorphology 125, 92–108.

San Román, M., Morello, F., Prieto, A., 2000. Cueva de Los Chingues (Parque Nacional Pali-Aike), Magallanes, Chile. Historia natural y cultural I. Anales del Instituto de la Patagonia (Serie Ciencias Humanas) 28, 125–143.

Soibelzon, L.H., 2004. Revisión sistemática los tremarctine (Carnivora, Ursidae) fósiles de América del sur. Revista Museo Argentino de Ciencias Naturales 6 (1), 107–133.

Soibelzon, L.H., Tartarini, V.B., 2009. Estimación de la masa corporal de las especies de osos fósiles y actuales (Ursidae, Tremarctinae) de América del Sur. Revista del Museo Argentino de Ciencias Naturales, Nueva Serie 11 (2), 243–254.

Sorkin, B., 2006. Ecomorphology of the giant short-faced bears *Agriotherium* and *Arctodus*. Historical Biology 18 (1), 1–20.

Steele, J., Politis, G., 2009. AMS ^{14}C dating of early human occupation of southern South America. Journal of Archaeological Science 36, 419–429.

Stern, C.R., Moreno, P.I., Villa-Martínez, R., Sagredo, E.A., Prieto, A., Labarca, R., 2011. Evolution of ice-dammed proglacial lakes in Última Esperanza, Chile: implications from the late-glacial R1 eruption of Reclús volcano, Andean Austral Volcanic Zone. Andean Geology 38 (1), 82–97.

Sugden, D.E., Bentley, M.J., Fogwill, C.J., Hulton, N.R.J., McCulloch, R.D., Purves, R.S., 2005. Late-glacial glacier events in southernmost South America: a blend of northern and southern hemispheric climatic signals? Geografiska Annaler 87 (2), 273–288.

Van Valkenburgh, B., 1990. Skeletal and dental predictors of body mass in carnivores. In: Damuth, J., Macfadden, B.J. (Eds.), Body Size in Mammalian Paleobiology: Estimation and Biological Implications. Cambridge University Press, Cambridge, pp. 181–205.

Van Valkenburgh, B., 1991. Iterative evolution of hypercarnivory in canids (Mammalia: carnivore): evolutionary interactions among sympatric predators. Paleobiology 17 (4), 340–362.

Van Valkenburgh, B., Hertel, F., 1998. The decline of North American predators during the late Pleistocene. Illinois State Museum Scientific Papers 27, 357–374.

Van Valkenburgh, B., Koepfli, K.P., 1993. Cranial and dental adaptation to predation in canids. Symposia of the Zoological Society of London 65, 15–37.

Vereshchagin, N.K., Baryshnikov, G.F., 1992. The ecological structure of the "Mammoth Fauna" in Eurasia. Annales Zoologici Fennici 28, 253–259.

Villa-Martinez, R., Moreno, P.J., 2007. Pollen evidence for variations in the southern margin of the westerly winds in SW Patagonia over the last 12,600 years. Quaternary Research 68, 400–409.

Vizcaíno, S.F., Cassini, G.H., Toledo, N., Bargo, M.S., 2012. On the evolution of large size in mammalian herbivores of Cenozoic faunas of southern South America. In: Patterson, B., Costa, L.P. (Eds.), Bones, Clones and Biomes: the History and Geography of Recent Neotropical Mammals. The University of Chicago Press, Chicago, pp. 76–101.

Weinstock, J., Shapiro, B., Prieto, A., Marín, J.C., González, B.A., Thomas, M., Gilbert, P., Willerslev, E., 2009. The Late Pleistocene distribution of vicuñas (*Vicugna vicugna*) and the "extinction" of the gracile llama ("Lama gracilis"): new molecular data. Quaternary Science Reviews 28 (15–16), 1369–1373.

Wilson, P., 1984. Puma predation on guanaco in Torres del Paine National Park, Chile. Mammalia 48, 515–522.

Wilson, D.E., Mittermeier, R.A., 2009. Handbook of the Mammals of the World. In: Carnivores, vol. 1. Lynx Editions, Barcelona.

Zanón Martínez, J.I., Travaini, A., Zapata, A., Procopio, D., Santillan, M.A., 2012. The ecological role of native and introduced species in the diet of the puma *Puma concolor* in southern Patagonia. Oryx 46 (1), 106–111.

Zolitschka, B., Schäbitz, F., Lücke, A., Corbella, H., Ercolano, B., Fey, M., Haberzettl, T., Janssen, S., Maidana, N., Mayr, C., Ohlendorf, C., Oliva, G., Paez, M.M., Schleser, G.H., Soto, J., Tiberi, P., Wille, M., 2006. Crater lakes of the Pali Aike volcanic field as key sites for paleoclimatic and paleoecological reconstructions in southern Patagonia, Argentina. Journal of South American Earth Sciences 21, 294–309.