



Paleoenvironments and faunal extinctions: Analysis of the archaeological assemblages at the Paso Otero locality (Argentina) during the Late Pleistocene–Early Holocene



Gustavo Martínez^{a,*}, María A. Gutiérrez^a, Eduardo P. Tonni^b

^a INCUAPA-CONICET, Facultad de Ciencias Sociales (UNCPBA), Departamento de Arqueología, Avda. del Valle 5737, B7400JWI Olavarría, Buenos Aires, Argentina

^b División Paleontología de Vertebrados, Facultad de Ciencias Naturales y Museo (UNLP), Paseo del Bosque s/n, 1900 La Plata, Argentina

ARTICLE INFO

Article history:

Available online 31 August 2012

ABSTRACT

Paso Otero archaeological locality (Pampean region, Argentina) has provided detailed paleoenvironmental reconstructions and faunal assemblages from the Pleistocene/Holocene transition and Early Holocene. This time span is represented by Paso Otero 5 (c. 10 450–10 200 ¹⁴C BP; 12 593–11 353 cal. BP) and Paso Otero 4 (c. 9900–7700 ¹⁴C BP; 10 667–7982 cal. BP). Palaeoenvironmental studies have been carried out on the basis of data derived from geoarchaeological, sedimentary, palynofacies, pollen, diatoms and silica microremains. Unlike other areas of the Pampean region, bone assemblages from Paso Otero include high representation and diversity of taxa. In this paper, paleoenvironmental reconstructions and faunal assemblages from both sites are integrated in order to discuss the consistency of the inferences derived from the two lines of evidence, its contribution to the paleoecological scenarios, and to faunal extinctions. It is suggested that not only hunting pressure but the mere presence of humans was a factor in ecosystem disturbance and is the most parsimonious explanation for the process of extinction.

© 2012 Elsevier Ltd and INQUA. All rights reserved.

1. Introduction

Geological, paleontological, stratigraphic, chronological and paleoclimatic studies conducted in the middle basin of the Quequén Grande River have provided useful paleoenvironmental scenarios for interpreting hunter–gatherer adaptation at the local and regional scales (Tonni and Laza, 1980; Tonni and Politis, 1981; Prado et al., 1987; Bonadonna et al., 1995; Prado and Cerdeño, 1998; Zárate et al., 2000; Favier Dubois, 2006; among others). In the last two decades, archaeological projects at sites in the Paso Otero locality, chronologically situated at the Late Pleistocene and Holocene, have provided much useful information. Topics related to the adaptation and evolution of the hunter–gatherer societies that inhabited this sector of the basin have been addressed through the study of the organization of lithic technology, faunal exploitation, patterns of mobility, and settlement systems (Politis et al., 1991; Martínez, 2001, 2006; Gutiérrez et al., 2010a, 2011; Martínez and Gutiérrez, 2011; and cites therein). Other lines of research, including taphonomy, diagenesis, chronology, geoarchaeology, site formation processes, and paleoenvironmental studies, as well as

those related to the survival of extinct species into the Early Holocene, have been pursued (Johnson et al., 1998, 2012; Gutiérrez et al., 2001, 2010b, 2011; Grill et al., 2007; Gutiérrez and Kaufmann, 2007; Osterrieth et al., 2008; Martínez and Gutiérrez, 2011).

Paleoenvironmental reconstructions generated for the locality and faunal assemblages recovered from the Pleistocene/Holocene transition and Early Holocene archaeological sites are particularly important for the purposes of this paper. This time span is represented at the locality by Paso Otero 5 (PO5) (c. 10 450–10 200 ¹⁴C BP; 12 593–11 353 cal. BP) and Paso Otero 4 (PO4) archaeological sites (c. 9900–7700 ¹⁴C BP; 10 667–7982 cal. BP). The same lines of evidence were followed at both sites, which lie 1.2 km apart (Fig. 1). Thus, palaeoenvironmental reconstructions have been addressed through the generation of data derived from geoarchaeological, sedimentary, palynofacies, pollen, diatoms and silica microremains (Grill et al., 2007; Osterrieth et al., 2008; Gutiérrez et al., 2011). Bone assemblages recovered from these sites show a high representation and diversity of taxa (Martínez, 2001; Gutiérrez et al., 2011; Martínez and Gutiérrez, 2011). Unlike other areas of the Pampean region (such as the Tandilia mountain range), where few sites contain faunal remains, the archaeological contexts of the Interserrana Bonaerense area and, particularly, the middle basin of the Quequén Grande River have provided well-represented faunal assemblages (see discussion in Mazzanti and Quintana,

* Corresponding author.

E-mail address: gmartine@soc.unicen.edu.ar (G. Martínez).

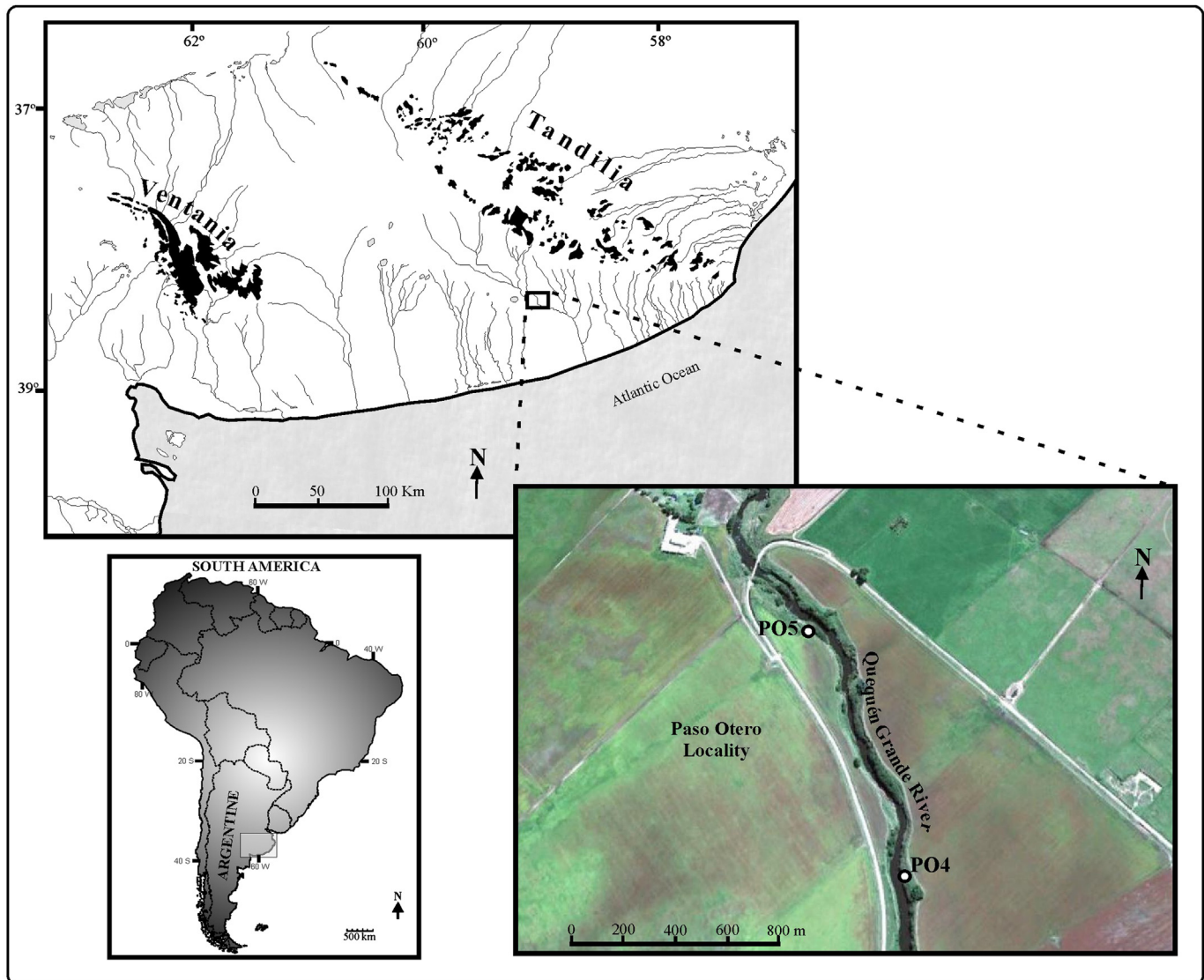


Fig. 1. Map showing the location of PO4 and PO5 within the Paso Otero locality.

2001; Politis et al., 2004; Gutiérrez and Martínez, 2008; Politis and Messineo, 2008; Salemm, in press).

Consequently, paleoenvironmental reconstructions in conjunction with the faunal assemblages recovered from the Pleistocene–Holocene transition and the Early Holocene enable: a) comparison of data from both sites to establish local paleoclimatic conditions (in the middle basin of the Quequén Grande River) and exploration of whether they accord with established regional models; b) evaluation of the faunal assemblages of both sites in order to highlight differences and similarities in terms of the taxa represented and paleoecological conditions; and c) discussion of models of faunal extinctions and survival.

2. Stratigraphic context, chronology, and the archaeological record

Unless otherwise stated, the dates in this article will be provided in ^{14}C BP. Table 1 shows the principal dates related to the period under study in this paper obtained from both sites. The total list of radiocarbon dates and discussion about their validity and which are finally considered can be consulted elsewhere (Martínez and

Gutiérrez, 2011, Table 1, p. 275 for PO5 and Gutiérrez et al., 2011, Table 1, p. 40 for PO4). The data of Table 1 are expressed in ^{14}C and calendar years (cal.) BP. The data of the latter allows comparisons among paleoclimatic reconstructions for both Northern and Southern hemispheres. The beginning of the Holocene has been set at 11 700 cal. BP (International Commission on Stratigraphy, 2009).

Both sites are located along the banks of the Quequén Grande River and share the major stratigraphic aspects of the typical sedimentary sequences of the river valleys of Buenos Aires Province (Fig. 2). The stratigraphic sequence is composed of sediments of the Luján Formation, which in turn consists of the Late Pleistocene Guerrero and the Early to Middle Holocene Río Salado Members (Tonni and Fidalgo, 1978). In the latter member, several “A” buried horizons have been detected, two of them assigned to the region-wide Puesto Callejón Viejo (c. 10 000 ^{14}C BP) and Puesto Berrendo Paleosols (c. 5000–2000 ^{14}C BP) (Gutiérrez et al., 2011; Johnson et al., 2012). The chronology of these soils, the main Holocene pedogenetic events in the Pampean region, has recently been the subject of debate. In different areas of the region the top of the Guerrero Member of the Luján Formation and the paleosol that covers it –Puesto Callejón Viejo– has been established at c.

Table 1

Radiocarbon dates of PO4 and PO5 for the Pleistocene–Holocene transition and Early Holocene. RSM–LF: Río Salado Member, Luján Formation; PCVP: Puesto Callejón Viejo Paleosol. H: Humates; R: Residues. Calibrations from Calib 6.0, IntCal09, 2 sigmas (Stuiver et al., 2005; Reimer et al., 2009). Only the selected age for the available pair of ages (Humates and Residues) for each soil sample is presented in calendar years BP.

Site/dated material	Sample/ stratigraphy	Lab. N°	¹⁴ C BP	Cal. BP ages	δ ¹³ C (‰)	References
Paso Otero 5 (Bones; <i>Megamammal</i> bone fragments)	PCVP	AA-39363	10 440 ± 100	12 028–12 593	–19.8	Martínez and Gutiérrez (2011)
	PCVP	AA-19291	10 190 ± 120	11 353–12 384	–20.6	Martínez and Gutiérrez (2011)
Paso Otero 4	RSM (LF)	AA-85157 (H)	7314 ± 73		–20.3	Gutiérrez et al. (2011)
Sediment sample “A” buried soil horizons (Lower levels)		AA-85157(R)	7729 ± 48	8421–8591	–20.3	Gutiérrez et al. (2011)
	RSM (LF)	AA-87938 (H)	8305 ± 67		–20.5	Gutiérrez et al. (2011)
		AA-87938 (R)	8913 ± 49	9800–10 206	–20.2	Gutiérrez et al. (2011)
	SPCV	AA-87939 (H)	9912 ± 53	11 217–11 602	–17.6	Gutiérrez et al. (2011)
		AA-87939 (R)	9283 ± 83		–20.7	Gutiérrez et al. (2011)

8500 ¹⁴C BP (Fucks et al., 2007). In the middle basin of the Quequén Grande River the Puesto Callejón Viejo Paleosol has yielded dates between c. 9000 and 10 000 ¹⁴C BP (Zárate et al., 2000; Gutiérrez et al., 2011; Johnson et al., 2012). Although the chronology of this soil can vary regionally, local evidence has placed it at the Pleistocene–Holocene transition.

La Postrera Formation (Tonni and Fidalgo, 1978) is not recorded in all sequences of the locality, or its presence is described in combination with other facies (e.g., fluvial) (Favier Dubois, 2006; Gutiérrez et al., 2011; Martínez and Gutiérrez, 2011; Johnson et al., 2012). The main differences among the two stratigraphic sequences (PO4 and PO5) essentially correspond to the different number of stabilization surfaces (“A” buried Horizons) recorded throughout the profiles that indicate distinct sedimentary and pedogenetic histories (Fig. 3).

Although the radiocarbon chronology of PO5 relies on both bone and soil organic matter, the chronology of PO4 is based entirely on the latter. Radiocarbon dating on bone was very difficult to obtain in all sites in the locality due to the lack of, or poor, collagen preservation (Gutiérrez et al., 2001). Organic matter dating from buried soils was carried out on bulk, humate and residue fractions, although most of the dates for the sites were obtained using the latter two methods. In a recent publication (Johnson et al., 2012), most of the radiocarbon data for the middle basin of the Quequén Grande River were presented (Paso Otero 1, 3 and 5) and the procedures for the selection of ages in the case of each soil described.

PO5 is located on the right bank of the Quequén Grande River (Fig. 2). The sequence starts with sediments belonging to the Guerrero Member of the Luján Formation (Tonni and Fidalgo, 1978),

on top of which the Puesto Callejón Viejo Paleosol is found. The archaeological component is mostly located in this buried soil, at the Pleistocene–Holocene transition, in a local unit defined as Ab6 (Fig. 3; Martínez, 2001; Martínez and Gutiérrez, 2011). The soil developed on a slowly aggrading surface, under saturated or swampy conditions in a more stable setting (Grill et al., 2007). Five landscape stabilization surfaces (buried soils) were recorded at c. 9600 ¹⁴C BP (Puesto Callejón Viejo Paleosol), c. 8800 ¹⁴C BP, c. 7800 ¹⁴C BP, c. 6600 ¹⁴C BP and c. 4200 ¹⁴C BP (probably the Puesto Berrondo Paleosol). Finally, at the top of the sequence a radiocarbon date indicates the beginning of the alluvium at c. 2500 ¹⁴C BP. The chronology of the human occupation was established through radiocarbon dating of buried soils and bones. Organic matter from the Puesto Callejón Viejo Paleosol (unit Ab6), where the archaeological component is recorded, provided an age of c. 9400 ¹⁴C BP. As discussed elsewhere (see Holliday et al., 2003; Johnson et al., 2012), organic matter fractions (bulk, humates and residues) always provide earlier dates than true ones and must be interpreted as minimal chronologies. From a broader set of radiocarbon dates obtained from bone, the accepted chronological range for the early human occupation of the site is c. 10 450–10 200 ¹⁴C BP (Martínez and Gutiérrez, 2011; see also Steele and Politis, 2009, p. 425; Table 1 and Fig. 3).

In addition to the radiocarbon data, artifactual and faunal assemblages also support the chronology assigned to the early human occupation. This data will be treated in depth below, but it is worth noting here that it is mostly represented by extinct megamammals (Table 2). PO5's lithic assemblage ($N = 86$) is composed of tools ($n = 6$) and debris ($n = 80$). The most outstanding items are two fish-tail projectile points associated with the megamammal

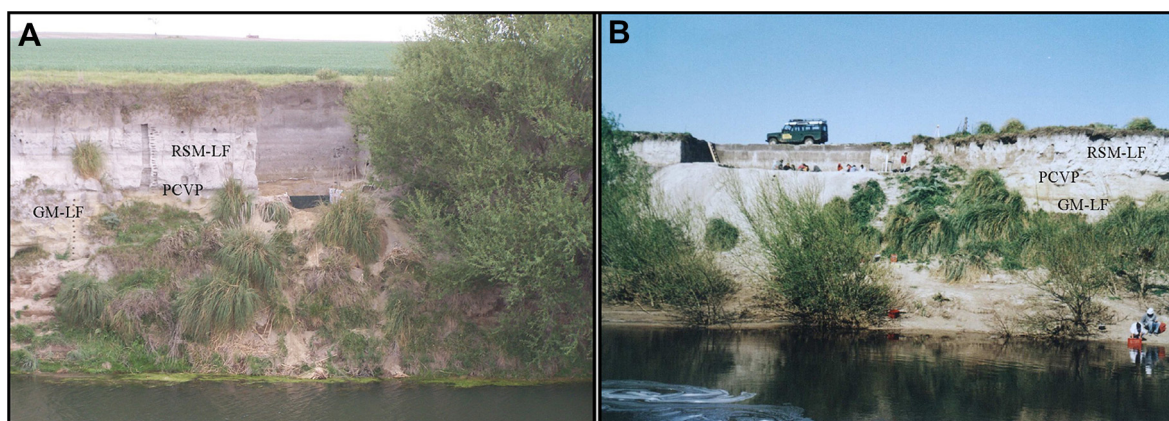


Fig. 2. Panoramic views of the excavations of PO4 (A) and PO5 (B). The Luján Formation and its Members are highlighted. GM–LF: Guerrero Member, Luján Formation; RSM–LF: Río Salado Member, Luján Formation; PCVP: Puesto Callejón Viejo Paleosol.

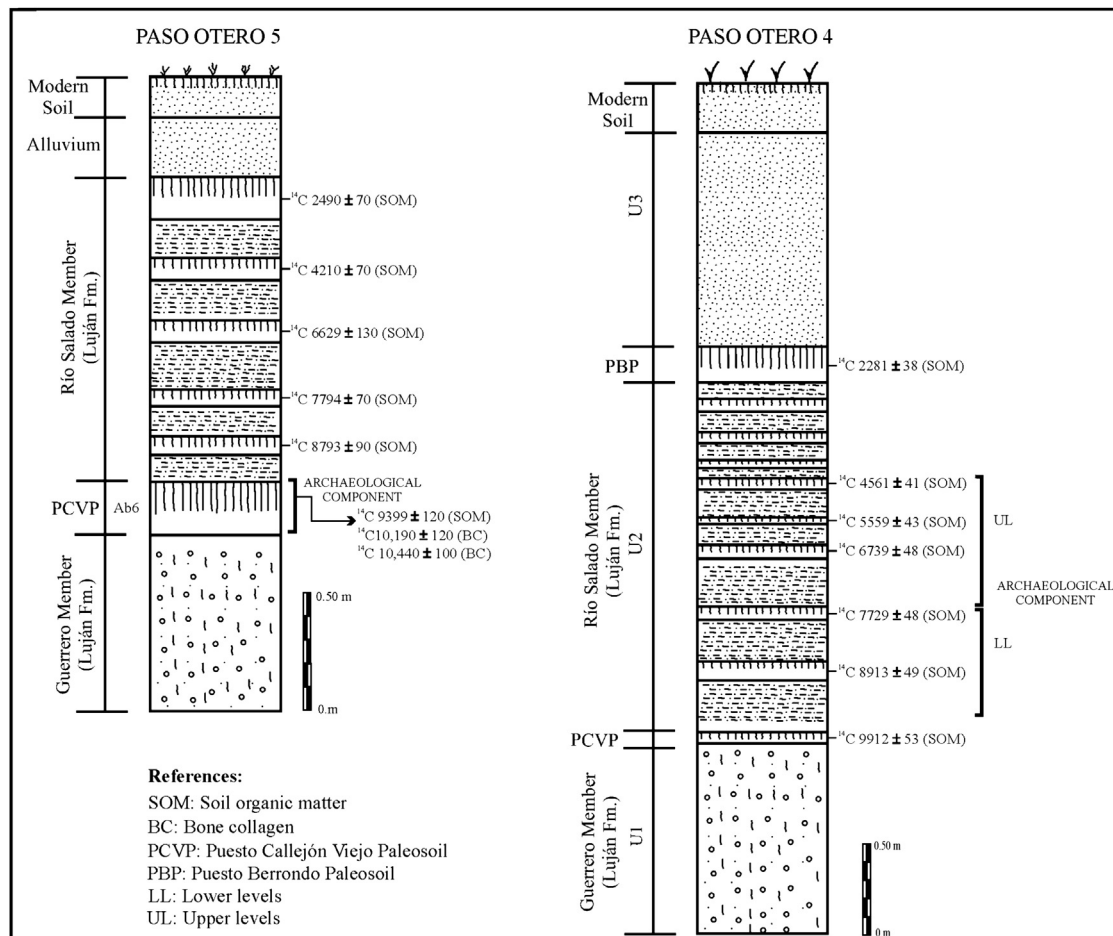


Fig. 3. Stratigraphic profiles, chronology, and archaeological components and levels of Paso Otero 5 and Paso Otero 4.

assemblage. An edge-basal stem fragment that belongs to one of the projectile points was also recovered. The rest of the artifacts consist of composite, bifacial and unifacial tools. Microdebris was also found, some refitted to the composite tool. Although most of the lithic raw material originated from the Tandilia mountain range (e.g., quartzite, quartz, chalcedony, etc.), the presence of tools such as a fish-tail projectile point made of exotic rock (silicified limestone) whose quarries are located in southern Uruguay is remarkable (Flegenheimer et al., 2003). Thus, the ranges for the acquisition of lithic raw material are from 50–70 km to 400–500 km from the site. In general terms, some of the artifacts described resemble those found in other early sites of the Pampean region (Flegenheimer et al., 2003; Mazzanti, 2003; Politis and Messineo, 2008).

Finally, the site has been referred to as a locus of specific activities, with human occupations related to hunting and/or mammal scavenging (Martínez, 2001). Prey procurement, primary processing tasks, and bone selection would have been carried out near the site, with further transportation to the site where secondary butchering and consumption would have taken place (Martínez and Gutiérrez, 2011).

PO4 is located on the left margin of the river (Fig. 2). The exposed sequence begins with the Guerrero Member of the Luján Formation (Tonni and Fidalgo, 1978), Unit 1 at the site (Fig. 3). The Puesto Callejón Viejo Paleosol separates the latter unit from the Río Salado Member or Unit 2. The sequence ends with the deposition of Unit 3 and the modern soil (Fig. 3). Ten surfaces of landscape

stabilization have been recorded throughout the stratigraphic sequence. Seven have been dated, yielding ages of c. 9900 ^{14}C BP (Puesto Callejón Viejo Paleosol), c. 8900 ^{14}C BP, c. 7700 ^{14}C BP, c. 6700 ^{14}C BP, c. 5600 ^{14}C BP, c. 4600 ^{14}C BP and c. 2300 ^{14}C BP (Puesto Berrondo Paleosol) (Fig. 3). As is the case for other sites in the locality, no radiocarbon dates from bone could be obtained due to lack of collagen; eight attempts at bone dating failed. Consequently, the chronology of the human occupation relies exclusively on the dating of soil organic matter.

The archaeological record at PO4 was collected entirely from the Río Salado Member (Unit 2) of the Luján Formation, interpreted as the result of low energy deposition occurring within interconnected lagoons throughout the landscape (Gutiérrez et al., 2011). The section of the stratigraphy that contains the archaeological record was dated to c. 8900 and 4600 ^{14}C BP. Faunal and lithic materials are continuously recorded in Unit 2, with little evidence of changes in the presence, distribution and frequencies of items throughout the sequence. However, on the basis of differential faunal representation the sequence was segregated into lower and upper levels (Gutiérrez et al., 2011). The lower levels consist of the section of the stratigraphy dated to between 8900 and 7700 ^{14}C BP (Fig. 3), and the upper levels are that part of the column dated to between c. 7700 and 4600 ^{14}C BP. Given the aims of this paper, the lower levels, which belong to the Early Holocene, will be the subject of analysis.

The lithic assemblage found in the lower levels ($N = 176$) is represented by tools ($n = 11$), debitage ($n = 158$) and ecofacts ($n = 7$).

Table 2

Presence (NISP) of species at PO4 and PO5 sites, indicating those with evidence of human consumption.

Species	Paso Otero 5 (c. 10 450 –10 200 ¹⁴ C BP)		Paso Otero 4 (c. 8900 –7700 ¹⁴ C BP)	
	NISP	Human processing	NISP	Human processing
<i>Xenarthra</i> indet.	5			
<i>Pilosa</i> indet.	1			
<i>Eutatus seguini</i>			15	●
<i>Eutatus seguini</i> (scutes)			38	
<i>Glyptodon</i> sp.	1			
<i>Scelidotherium</i> sp.	1			
<i>Glossotherium</i> sp.	2			
<i>Myiodon</i> sp.	1			
<i>Lestodon armatus</i>	2			
<i>Megatherium americanum</i>	29			
<i>Equus</i> sp.	1			
<i>Equus</i> (<i>Amerhippus</i>) <i>neogaeus</i>	2			
<i>Toxodon</i> sp.	3			
<i>Hemiauchenia</i> sp.	1	●		
<i>Litopterna</i> cf. <i>Macrauchenia</i>	2			
<i>Macrauchenia patachonica</i>	1			
Camelidae indet.	3			
<i>Lama guanicoe</i>	2		124	●
<i>Ozotoceros bezoarticus</i>			71	●
Caviidae			2	
Cricetidae			4	
<i>Ctemomys</i> sp.			5	
<i>Lagostomus maximus</i>			144	●
<i>Dolichotis patagonum</i>			2	
<i>Holochilus brasiliensis</i>			1	
Dasipodidae			418	
<i>Chaetophractus villosus</i>			116	●
<i>Chaetophractus villosus</i> (scutes)			478	
<i>Zaedyx pichiy</i> (scutes)			441	●
Canidae			29	●
<i>Dusicyon avus</i>			1	
<i>Dusicyon gimnocercus</i>	1			
Felidae			8	●
<i>Conepatus</i> sp.			2	●
<i>Lyncodon patagonicus</i>			1	
<i>Rhea americana</i>			20	●
<i>Rhea americana</i> (eggshells)			3755	
Tinamidae			9	●
Ophidia			4	
Anura			54	
Marine gastropods			7	
Total	58	1	5749	11

The tool classes include utilized flakes, slightly bevel-edged artifacts, cutting edges, notches, scrapers, and so on. Tools are simple, with maintainable designs and low morphological standardization (i.e., informal tools). The best represented raw material is quartzite (93%), whose outcrops are in the Tandilia mountain range, followed by basalt, chert and undetermined rocks. Blanks were mostly brought to the site without cortex, and most stages of tool production took place in situ, as did artifact maintenance activities. The archaeological record supports the hypothesis that PO4 was a hunter–gatherer site where activities such as the processing and consumption of a great variety of faunal species took place.

3. Paleoenvironmental trends at Paso Otero locality

The proxy data described here for inferring paleoclimatic conditions at PO4 and PO5 derive from pollen and palynofacies, silica microremains and diatoms. Details of the remaining lines of evidence (e.g., geoarchaeology, sedimentology, etc.) and their integration to the proxies described here can be consulted elsewhere (Grill et al., 2007; Osterrieth et al., 2008; Gutiérrez et al., 2011; Martínez and Gutiérrez, 2011; Johnson et al., 2012).

Palynofacial analyses at PO5 indicate that during the deposition of the sediments belonging to the upper part of the Guerrero Member (c. 12 000–10 450 ¹⁴C BP), processes of environmental disturbance and/or a plant community dominated by ruderal taxa became established toward the Final Late Pleistocene. Semi-arid, cold to temperate conditions and a strong aeolian activity that inhibited Gramineae development favored the spread of colonizing species. This scenario is in tune with studies that indicate that vegetation cover was scarce and periods of water deficit occurred under semi-arid environmental conditions (Grill et al., 2007; Osterrieth et al., 2008).

During the Pleistocene–Holocene transition (c. 10 450–9400 ¹⁴C BP) palynofacies and siliceous microremains indicate more benign and stable climatic conditions associated with paleosol development. Temporary ponds and water table fluctuations within the valley have been inferred. Accordingly, siliceous microremains show greater moisture availability, a dense vegetation cover and pulses associated with changes in river flow. The development of the Puesto Callejón Viejo Paleosol witnessed temperate and humid environmental conditions, hydromorphism and a moderate vegetation cover. In addition, grass communities indicating temperate-humid environmental conditions have been recorded (Grill et al., 2007; Osterrieth et al., 2008).

Siliceous microremains analysis also indicates that immediately after the development of the soil, during the Early Holocene, water availability was limited and remained so until c. 8800 ¹⁴C BP. After that event, a shift towards environmental stability and conditions of dense vegetation occurred, to change again at c. 7800 ¹⁴C BP to water availability restrictions and reduced grass communities as part of the vegetation cover (Osterrieth et al., 2008). This trend is not so marked in the case of the palynofacial analysis carried out on Early Holocene material, although one of the explanations for pollen destruction is the presence of wet–dry cycles (Grill et al., 2007). Local humid conditions, grass communities and temporary ponds related to flood margins have been recorded towards the Middle Holocene (c. 6600 ¹⁴C BP).

In the case of PO4, proxy data derived from pollen analyses indicate that for the Final Late Pleistocene (pre – 10 000 ¹⁴C BP) environmental disturbances occurred caused by strong aeolian activity and aridity (Gutiérrez et al., 2011). Vegetation communities were characterized by wild grasses at the expense of pastures. Siliceous microremains also show a dominance of dry conditions. The Puesto Callejón Viejo Paleosol (c. 9900 ¹⁴C BP), at the Pleistocene–Holocene transition, indicates an eroded and truncated Bt horizon. In general terms, events related to local humidity (ponds, swamps, river banks, etc.) are registered from the Early to the Late Holocene. Nevertheless, the paleoenvironmental and landscape dynamics from the Early Holocene portion of the stratigraphy (9900–7700 ¹⁴C BP) include some remarkable aspects, depending on the proxy data considered. Pollen analyses indicate the development of edaphic communities or ponds in psammophytic steppes that developed under subhumid-dry conditions. A noticeable feature is the pollen composition of a sample associated with a date of c. 8900 ¹⁴C BP that has no modern analogs. The pollen composition of this sample is difficult to interpret in a naturally developed environment; its origin is explained by disturbances produced by human activity. Diatom assemblages indicate a dry pulse under temperate-warm conditions at that time framed by moments of more humid conditions. For the Early Holocene, siliceous microremains indicate a semi-arid, warm temperate climate with occasional oscillations in water availability. Towards the Middle Holocene another pulse of aridity is registered by the pollen results (Gutiérrez et al., 2011).

From the above described paleoenvironmental reconstructions some general trends can be drawn for the sites:

- Final Late Pleistocene, upper part of the Guerrero Member (c. 12 000–10 000 ^{14}C BP): Semi-arid, cold to temperate conditions; strong aeolian activity; environmental disturbance; ruderal taxa predominate over grasses.
- Pleistocene–Holocene transition, Puesto Callejón Viejo Paleosol (c. 10 000 ^{14}C BP): more benign and stable climatic conditions; temperate and humid climates; development of paleosol; grass communities and moderate cover vegetation; fluctuations in water availability.
- Early Holocene, lower part of the Río Salado Member of Luján Formation (c. 10 000–6600 ^{14}C BP): subhumid-dry climatic conditions; edaphic communities or ponds; psammophytic steppes; wet–dry cycles and episodes of limited water availability from c. 8800 to 7700 ^{14}C BP.

As discussed elsewhere (Gutiérrez et al., 2011) the results obtained from this proxy are applicable both to the local settings (e.g., events such as droughts, water availability, etc.) and can be used to account for areal and regional palaeoclimatic trends (e.g., aridity). At the local scale, it is interesting to note the return (whether episodic or in longer lapses) to more arid conditions after the climatic amelioration indicated by the landscape stability and pedogenetic events signaled by the Puesto Callejón Viejo Paleosol. At PO1, located on the opposite bank of the Quequén Grande River to PO5, Bonadonna et al. (1995) studied the isotopic composition of freshwater gastropods. As previously noted in the case of PO4, these authors highlighted the existence of an erosive contact (unconformity) between the Puesto Callejón Viejo Paleosol and the Río Salado Member of the Luján Formation. This is interpreted as a return to drier conditions after a pulse of higher humidity and temperature (see Fig. 5 in Bonadonna et al., 1995, p. 92). Moreover, at the lower stratigraphic section of the Río Salado Member of the Luján Formation, significant isotopic variation in freshwater gastropods recorded at a level dated to c. 8700 ^{14}C BP also indicates drier conditions (Bonadonna et al., 1995). At a regional scale, this return to arid conditions during the Early Holocene has also been proposed by other authors (Tonni, 1992; Iriondo and García, 1993; Bonadonna et al., 1995; Tonni et al., 2003).

Fig. 4 represents a summary of different paleoclimatic and vegetal community's reconstructions for different areas of the Pampean region. While some of them are based on single proxies such as pollen, fauna and isotopes (Bonadonna et al., 1995; Prieto, 1996; Prado and Alberdi, 1999), others are built on multi-proxy studies including sedimentology, malacology, palynology, and

mammals (Prieto et al., 2004; Quattrocchio et al., 2008). For comparative purposes, the last column of this figure shows the trends obtained at Paso Otero locality. The scales of the reconstructions vary from single locality (e.g., Bonadonna et al., 1995) to larger areas as the Northeastern and Southern Pampas (Prieto et al., 2004; Quattrocchio et al., 2008). This certainly affects the scale of paleoclimatic reconstructions and plant communities inferred in each case. However, in general, terms, the paleoclimatic trends inferred from PO4 and PO5 are in agreement with other general models proposed for the region (Tonni, 1992; Bonadonna et al., 1995; Prieto, 1996; Tonni et al., 1999, 2003; Zárate et al., 2000; Grill et al., 2007; Quattrocchio et al., 2008; among others).

4. Faunal assemblages from PO5 and PO4 sites

At PO5, a total of 77 114 complete and fragmented bones of extinct megamammals and modern species were recorded in a 98 m² excavated surface. Among them, only 58 specimens were identifiable taxonomically (Table 2). The bone remains recovered correspond to at least 12 genera of which 10 are extinct species. The skeletal parts represented are mainly forelimb and rearlimb bones. The state of preservation of the faunal assemblage is extremely poor, presenting deep desiccation cracks and a rugged texture. Cut marks produced by lithic artifacts or any other sort of cultural or natural modifications are difficult to identify due to preservation conditions. A possible anthropic fracture was identified on a fragment of tibia of *Hemiauchenia* sp. With the exception of this taxon, it is impossible to determine if any other species at the site provides evidence of human consumption (Martínez and Gutiérrez, 2011). The number of taxonomically undetermined bones is high ($n = 77\,056$). From this sample c. 88% is smaller than 0.5 cm. These results are indicative of a significant degree of combustion and fragmentation. A striking feature of the site is the high percentage of burnt megamammal bones (c. 91%); these have been interpreted as raw material for fuel (Martínez, 2001; Joly et al., 2005).

At PO4, a total of 28 938 complete and fragmented bones were recovered from an excavated area of 14 m². From this total, 2051 specimens were identified taxonomically (Álvarez et al., in press). As was previously stated, the archaeological deposit was divided into lower (c. 8900–7700 ^{14}C BP) and upper (c. 7700–4600 ^{14}C BP) levels. The lower levels, belonging to the Early Holocene, are those considered here. The zooarchaeological assemblage is composed of a total of 10 906 specimens, including 619 bones that were taxonomically determined (Table 2; Álvarez et al., in press). Of the total,

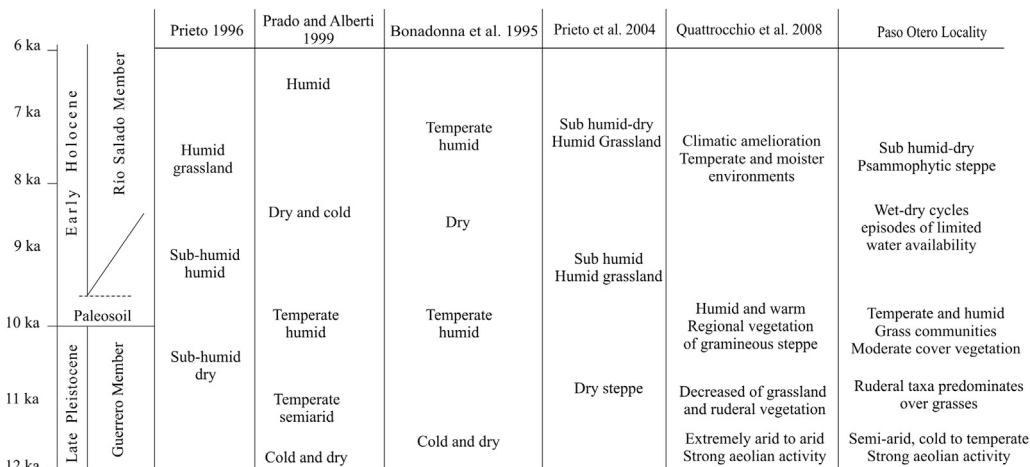


Fig. 4. Paleoclimatic and vegetation community reconstructions for different sites and areas of the Pampean region (modified from Politis and Messineo, 2008), including the Paso Otero locality.

5130 are small fragments of eggshells of the South American rhea and armadillo scutes. A large number of species ($n = 11$) present evidence of human modification, cut marks, anthropic fractures, and thermal alteration being the most frequent.

Two extinct species have been identified in PO4's Early Holocene assemblage: the extinct giant armadillo (*Eutatus seguini*) and the extinct canid (*Dusicyon avus*) (Table 2). A minimum of two giant armadillos have been identified; approximately 50% of the bones show evidence of consumption (i.e., cut marks). No evidence of human modification was found on the extinct canid. The abundance of skeletal parts and the high proportion of bones with cut marks in *E. seguini* are uncommon for Pampean archaeological sites. Moreover, the evidence of this species has been used to support the hypothesis of the survival of xenarthrans into the Holocene (Gutiérrez et al., 2010b).

5. Discussion

5.1. Paleoeological interpretation of the faunal assemblages

The megamammals and large mammals were remarkably rich in South America before the entrance of humans. During the latest Pleistocene, 36 megamammals and 47 large mammals that became extinct were present in the continent. Besides, there were different areas of endemism. Many were restricted to northern or southern areas and others to highlands or lowlands. Few reached southern South America. Consequently, although the total number of megamammals was outstanding, they were not present in all areas. Regarding the zooarchaeological record, 51 genera have been recorded in the Pampean region for the Late Pleistocene–Early Holocene period, among these, 17 (c. 33%) show evidence of exploitation (Gutiérrez and Martínez, 2008).

The contrast between PO4 and PO5 is especially remarkable in regards to the evidence of extant species. At PO5, megamammal or extinct large mammal remains dominated and only scant remains of *Lama guanicoe* and *Dusicyon gymnocercus* were recorded (Table 2). The Late Pleistocene fauna from the Pampean region was characterized by *Equus* (*Amerhippus*) *neogaeus* (Cione et al., 1999; Cione and Tonni, 2005). In addition, other common fossils include *Hippidion principale*, *Megatherium americanum*, *Glyptodon reticulatus*, *Macrauchenia patachonica*, *Toxodon platensis*, *Doedicurus clavicaudatus*, *Glossotherium robustum*, and *Scelidotherium leptocephalum* (Cione and Tonni, 2005). At PO5, six of these species were recovered; some are good climatic indicators. *E. (Amerhippus) neogaeus* is a typical horse adapted to open and arid landscapes (Prado and Alberdi, 1994). Among the xenarthrans, the most frequent is the mylodon, *G. robustum*. Both were adapted to an open biomass (Czerwonogora et al., 2011), as was the *Glyptodon* ssp. (Vizcaíno et al., 2006). *M. patachonica* and *T. platensis* inhabited similar environments. The faunal evidence recovered for PO5 suggests arid conditions that coincided at certain times with lower temperatures than at present, as indicated by the presence of Patagonian fauna (Tonni et al., 1999).

The faunal data is consistent with paleoclimatic reconstructions inferred for the end of the Pleistocene from the different paleoclimatic proxies summarized in this paper for PO5 and PO4. Bone specimens at PO5 were deposited during the period 12 360–11 900 cal. BP, which corresponds in the Southern Hemisphere to the end of the Antarctic Cold Reversal (Jouzel et al., 2007). During this period arid climatic conditions have been ascertained for the Pampas region, as well as the prevalence of erosion and aeolian deposits (Iriando, 1999; Tonni et al., 1999) and low primary productivity, to which the xenarthrans were well adapted. This adaptation was further confirmed by recent isotopic studies showing that certain xenarthrans, such as *G. robustum*, were

adapted to the consumption of C^3 plants for the period considered, which are similar to those that currently grow at approximately 40° S in the northern Patagonia (Czerwonogora et al., 2011).

In the faunal assemblage of PO5, out of a total of 10 extinct species recorded, 6 (60%) are Xenarthra, which is consistent with other paleontological and archaeological sites with similar chronologies in the Pampean region. Towards the end of the Pleistocene, a remarkable decline in native ungulates occurred (c. 10% of total), which, together with the Proboscidea, Perissodactyla and Artiodactyla, reached almost 30% of the total diversity of animals larger than 100 or 500 kg (Vizcaíno et al., 2012). In contrast, Xenarthra (two suborders, Tardigrada and Cingulata) represent over 50% of the diversity, the majority being megamammals (>1000 kg) (Vizcaíno et al., 2012). Hence, xenarthrans predominated at the end of the Late Pleistocene, a group that had certain characteristics that were more favorable compared to other taxa. Among the adaptive advantages of xenarthrans compared with epithemians of similar mass, low basal metabolic rates, less energy requirements and non-specialized diet are notable (Vizcaíno et al., 2006; see also Gutiérrez et al., 2010b and cites therein). It is possible that xenarthrans were better adapted to survive in partitioned and unstable environments such as those that characterized the Pleistocene–Holocene transition.

There is an extinct xenarthran, *E. seguini*, represented in the zooarchaeological record of PO4. Another extinct species of this assemblage that survived beyond the Early Holocene is *D. avus* (Tonni and Politis, 1981). The remaining taxa correspond to living species. These latter groups of species occur in stratigraphic contexts of the Río Salado Member of the Luján Formation at PO4 and are largely present in the Guerrero Member of this same formation in different areas of the Pampean region (Cione et al., 1999). One exception is *Ozotoceros bezoarticus*, a holarctic immigrant that is recorded in the Pampas region from the Early Holocene. It is unknown whether the presence of this species is directly linked to paleoenvironmental aspects, as part of a process of turnover among cervids. Thus, while species of the genus *Paraceros* and *Morenelaphus*, present since at least the Middle Pleistocene, became extinct, others such as *Blastoceros dichotomus* and *O. bezoarticus* entered the Pampean region during the Holocene (Cione et al., 1999).

Considering mammals with living representatives inhabiting the Pampas, PO4 produced a total of 11 species. Of these, four are currently not found in the area (*L. guanicoe*, *Zaedyus pichiy*, *Lyncodon patagonicus*, and *Dolichotis patagonum*) due to environmental climatic factors. Additionally, the regional extinction of *O. bezoarticus* may have occurred as a result of intensive hunting pressure, especially during the second half of the nineteenth century (González et al., 1994). Prior to the sixteenth century, the camelid *L. guanicoe* had a wide distribution in the Pampean region during the arid and semi-arid phases of the Late Pleistocene and Holocene (Politis and Pedrotta, 2006; and references therein). Currently this species is found in the mountain area of Ventania and in the transition between Pampa and Patagonia regions (Politis and Pedrotta, 2006). *Chaetophractus villosus* and *Z. pichiy* are now sympatric species south of 40° S, currently located in the transition between the Eastern Pampa and Patagonia regions. Today, *Z. pichiy* lives "... in xeric shrublands and Grasslands, as well as Patagonian steppe habitats" (Abba and Superina, 2010, p. 178). The mustelid *L. patagonicus* does not currently inhabit the area. The closest geographic record of this species is c. 200 km NW of the Paso Otero locality (36° 47' S, 59° 51' W, see Prevosti and Pardiñas, 2001). However, this record corresponds to the nineteenth century when arid and semi-arid climatic conditions were recorded in the Pampean region (Tonni, 2006). Currently, *L. patagonicus* is recorded south of 40° S in Buenos Aires province, at the transition of the

Eastern Pampas and Patagonia regions (Prevosti and Pardiñas, 2001). Today, *D. patagonum* lives west of 64° W in the Pampean region (Campos et al., 2001).

The distribution and habitat of species that are no longer found in the area of Paso Otero locality appear to be adapted to Patagonian or central arid environments. Together with the species that still inhabit the area, as a group they are better adapted to more arid conditions than today. The evidence of *Holochilus*, a Brazilian cricetids, two species of which are now found in the province of Buenos Aires (*Holochilus brasiliensis* and *Holochilus chacarius*, see Voglino et al., 2004), accords well. Recent records of *H. brasiliensis* demonstrate the southern distribution of this eurytopic rodent is in semiarid to arid conditions, such as those that occur at c. 40° S, and includes other eurytopic and stenotic cricetids and rodents that characteristically inhabit arid environments (Formoso et al., 2010). This species has been recorded in these latitudes during the Late Holocene (Prates, 2008; Stoessel et al., 2008; Fernández et al., 2011).

The Early Holocene faunal assemblage from PO4 is composed of species adapted to arid to semi-arid environments. After the brief climatic amelioration recorded for the Pleistocene–Holocene transition a return to arid conditions has been proposed (Tonni, 1992; Iriondo and García, 1993; Bonadonna et al., 1995; Tonni et al., 2003). This climatic pattern coincides with the evidence provided by various paleoenvironmental proxies at PO4 and PO5.

5.2. Faunal extinctions and the role of hunter–gatherers

The issue of continuity and change in relation to both paleoenvironmental changes and faunal communities has been addressed by various disciplines (i.e., paleontology, biology, archaeology, etc.) during the past several years around the world. Particularly, faunal extinctions have been the subject of a stimulating debate. Among the principal causes that have been proposed for the extinction and/or survival of mammals, the most commonly mentioned are the interaction with hunter–gatherers and climate change, or a combination of both. Other models also invoke other causes such as hypervirulent diseases and synergetic processes trigger by human and natural interactions (e.g., fires, vegetation changes and habitat transformation). The degree of influence of these factors and the timing of the extinction process (i.e., gradual or catastrophic) varies according to the proposed models (Martin, 1984; MacPhee and Marx, 1997; Alroy, 2001; Grayson, 2001; Haynes, 2002; Johnson, 2002; Burney and Flannery, 2005; Miller et al., 2005; Steadman et al., 2005; Fiedel, 2009; Barnosky and Lindsey, 2010; Crowley, 2010; among many others).

A recent stimulating debate about the causes of faunal extinction in North America has been fuelled by many scholars (Haynes, 2002; Grayson and Meltzer, 2003, 2004; Grayson, 2007; Fiedel, 2009; among many others). A diversity of fauna, mostly large mammals, became extinct between 12 000–10 000 BP (see discussion in Grayson, 2007; Barnosky and Lindsey, 2010). Conversely, the survival of megamammals and large mammals until c. 7000 ¹⁴C BP in South America indicates extinctions occurred through an extended period (c. 6000–4000 ¹⁴C BP) in relation to the timing of human dispersal in the southern cone of South America (see discussion in Steele and Politis, 2009; Barnosky and Lindsey, 2010; and references therein).

The process of extinction in the South America has been tackled by several authors. Prado et al. (2001) have proposed that maximum species diversity occurred in c. 14 000 ¹⁴C BP, with a steady decline since. These authors suggest that the extinction of large mammals was a process that primarily began as a result of climatic change (that is, before the arrival of humans) but was accelerated by co-existence with hunter–gatherers. Politis and

Messineo (2008) argued that extinctions in South America were the result of a combination of climatic/environmental changes and anthropogenic causes that present strong regional variations (see also Borrero, 2006, 2009). Politis et al. (1995) proposed that humans played a secondary role in the extinction of the native fauna of South America and immigrant species (e.g., horse, mastodon, etc.) were most affected. Cione et al. (2009) indicated that extinctions would have focused on taxa of South American origin. It has been suggested that without the arrival of humans on the continent the wide variety of large mammals and megamammals present in South America during the Pleistocene could have recovered as recorded for each of the previous interglacial periods (Cione et al., 2009). This argument is the basis of the Broken Zig-Zag Model, which originally proposed “... that megamammal and large mammal extinction in South America during the Late Pleistocene–Earliest Holocene was caused by human foragers” (Cione et al., 2003, p. 10). In a later work, Cione et al. (2009, p. 126) argued that “humans certainly did not exterminate all the extinct taxa (e.g., the large carnivores), but killed off many and provoked changes that occasioned the disappearance of the remaining ones”.

This brief summary of the proposals that explain the extinction of Pleistocene fauna shows a large variety of situations and inter-related factors. In any case, the factor common to all is human presence on the continent. The arrival of humans in the southern cone of South America c. 13 000 cal. BP (Steele and Politis, 2009) can be considered the unique novel factor in the paleoecological scenario during the present interglacial period (Cione et al., 2003).

The archaeological and paleontological record often presents important temporal and spatial gaps (Crowley, 2010). In this regard, the Paso Otero locality is an important case study considering the brief temporal gap represented between the two studied sites. The assemblages from PO5 and PO4 highlight the change in faunal stocks that involves a remarkable process of extinction and replacement over a relatively short period of time (c. 2500 cal. BP). The extinction process marked the end of the megamammal trophic level, which had been part of the Pampean terrestrial ecosystem since at least the Upper Miocene–Pliocene (Montehermosense, with *Trigodon gaudryi* among others), and perhaps even the Early Upper Miocene (Chasicuense, with *Chasicotherium rothi*). Also, along a brief time span (c. 12 500–8500 cal. BP) important and fluctuating climatic changes (e.g., arid-semiarid and cold – temperate and humid – dry and return to arid conditions – temperate and humid conditions/hypsithermal) occurred as it was shown in a local and regional scale (Fig. 4).

In this new socio-environmental scenario, the archaeological record potentially informed about the role that humans played in mammal extinctions. For the Late Pleistocene–Early Holocene (c. 12 000–7000 ¹⁴C BP) subsistence of human populations has been characterized as a generalized regional economy (Miotti and Salemme, 1999; Mazzanti and Quintana, 2001; Martínez and Gutiérrez, 2004). It has been argued that diet was focused on large mammals (principally artiodactyls) followed by small mammals and birds, while megamammals occupied a marginal position (Gutiérrez and Martínez, 2008). However, based on the zooarchaeological evidence from the few sites with the earliest human occupations (c. 12 000 to 10 000 ¹⁴C BP) in the Interserrana Area (e.g., Arroyo Seco 2 and Paso Otero 5; Martínez and Gutiérrez, 2011; Politis et al., in press) it is still difficult to know what would have been the role of the various fauna in human subsistence. As such, for the critical period during which extinctions occurred, the record of modern species is as scant as is that of extinct ones in terms of both presence and evidence of consumption. In this sense, for this period no records of mass killing sites in the Pampas have been registered. The MNI of extinct taxa recorded at each site are very low (≤ 2) and the intra site variability does not suggest any

function related to massive kills (Politis et al., 1995; Cione et al., 2003; Borrero, 2006; Gutiérrez and Martínez, 2008). Furthermore, clear evidence of butchering on Pleistocene fauna bone surfaces is not always recognized. Context of scavenging have been proposed (Politis and Gutiérrez, 1998; Martínez and Gutiérrez, 2004; Politics and Messineo, 2008; Borrero and Martin, 2012) although they are difficult to infer.

The scarcity of early sites and anthropic evidences of predation is one expected result of the *Blitzkrieg* model, due to the fact that a rapid killing of faunas would leave very little evidence of human-prey interaction given the short period of coexistence in certain places (see discussion in Johnson, 2002, p. 2225; Burney and Flannery, 2005, p. 398). In the Pampean case, the evidence of sites and butchery marks are not abundant despite the survival of some Pleistocene faunas would give more time for the coexistence and interaction between humans and prey. Clearly, the hypothesis of *Blitzkrieg* and a process of overkill are not supported by the data (see also Politics and Messineo, 2008; Borrero, 2009; Cione et al., 2009; Barnosky and Lindsey, 2010, among others). Regarding the climatic changes as a factor that promote extinctions, explanations are still inadequate as unique major global processes. Regardless of the environmental changes occurring at the Pleistocene–Holocene boundary, other severe climate changes have occurred over the last 50 000 years and there is not a single climatic shift that may explain the uneven processes of extinction and survival of faunas in different parts the globe (Cione et al., 2003, 2009; Burney and Flannery, 2005; Miller et al., 2005; Hubbe et al., 2007; Gutiérrez and Martínez, 2008; Politics and Messineo, 2008).

The intensity of human colonization and how it impacted faunas and ecosystems still remain to be discussed. Humans can produced direct effects on faunas, such as over-hunting, but they also can induce indirect effects (Norton et al., 2010). Human impacts other than hunting can be also considered: ecosystem reorganization by firing, diseases, reductions and transformation of habitats, competition between humans and animals for the same resources, among others (Johnson, 2002; Burney and Flannery, 2005; Miller et al., 2005; Crowley, 2010). Consequences of this indirect human impact are several. In the Australian case, systematic burning by Pleistocene hunters changed the biomass, reduced plant diversity, and produced a dramatic change at the base of the food web (Miller et al., 2005). In Madagascar, human predation during Late Holocene had an uneven effect on faunas considering both the fauna size and the eco-region of the island. Nevertheless, Crowley (2010, p. 2601) indicates that “...humans affected the ecologies of the endemic vertebrate communities before the establishment of substantial human settlements, vegetation transformation, or increase in fire frequency”. According to Burney and Flannery (2005, p. 398), “low density human populations do things to the environment other than killing animals”, and these human activities are traceable through the study of other lines of evidence such as pollen. The pollen assemblage recorded in levels of Paso Otero 4 chronologically located at c. 8900 BP (Early Holocene) has no modern analogs, and the natural environments can not be taken into account for providing explanations about the association of some plant species. This pattern has been interpreted as the result of disturbances by human-induced activities (Gutiérrez et al., 2011, p. 44).

Barnosky and Lindsey (2010) suggested that ecological pressure induced by humans entering new ecosystems combined with abrupt climatic changes was critical for megafauna. Thus, these authors proposed that a synergetic direct and indirect human impacts and climatic changes accelerate faunal extinctions.

Declines in faunas are also the result of a combination of hunting, climatic change, and habitat reduction and transformation. This indirect consequences of hunter–gatherers populations are also mentioned by Johnson (2002, pp. 2225–2226): “... an explanation

for the Late Quaternary megafauna extinctions is environmental change, driven either by climatic change or by human impact on the environment”. This author also mentioned that, “... hunting need not have accompanied the extinctions, but it may have increased the risk of extinction for species already stressed by environmental change”. Interaction between humans and animals could cause the transfer of diseases (MacPhee and Marx, 1997) and it has been proposed in the context of competition for the same places for dwelling (Grayson, 2001; Borrero and Martin, 2012). Recently, Cajal et al. (2010) have proposed for South America that the extinction of some large mammals (e.g., *Lama gracilis*) can also be attributed to anthropic action that not only includes the hunt burden but also other factors such as environmental and ethological changes caused by the presence of humans. In this vein, Gutiérrez and Martínez (2008, p. 63) suggest that the combination of diet, habitat preferences, body mass and physiology has a role in the pattern of extinctions and survival. Johnson (2002) also proposed that the large size of extinct species was not necessarily related to risk of extinction, but species with slow reproductive rates. As has been discussed elsewhere (Gutiérrez and Martínez, 2008), the human impact on large mammal and megamammal populations is generally considered as negative in terms of survival. However, human behaviors mediated by food preferences and hunting strategies could also have promoted the survivorship of some species. In this context, the few remains of *L. guanicoe* from the Late Pleistocene may indicate either that this camelid was sparsely represented in Lujanian times, or that their capture represented a low “appetite index” (*sensu* Valverde, 1964).

6. Conclusion

To sum up, the zooarchaeological record of the Pampean region for the timing of the earliest human settlement do not support the models related to overkill. Thus, hunting pressure must have been one more of the factors at play, but not the only one.

No doubt climatic change played a role and contributed to the process of extinction, but changes should be tied to particular natural disappearance of these faunas and the characteristics of differential survival according to particular taxa inhabiting specific areas into regions. Human presence and its impact in fauna and landscapes is also variable depending of particular colonization processes, and how prolonged or intermittent occupational histories of region have been. The evidence provided by PO4 and PO5 sites, in the context of other Pampean sites, supports the hypothesis that not simply hunting pressure but the mere presence of humans was a factor in ecosystem disturbance, and is thus the most parsimonious explanation for the process of extinction.

Acknowledgments

Financial support for this investigation comes from National Geographic Society (Archaeology, taphonomy, and paleoenvironment for the last 12 000 years BP in the middle basin of the Río Quequén Grande, Pampean region, Argentina; Grant 8329-07) and Agencia Nacional de Promoción Científica y Técnica (Arqueología y tafonomía actualística en la llanura interserrana y sectores periserranos adyacentes; PICT 08-814). The authors thanks to Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), INCUAPA (Department of Archaeology, Facultad de Ciencias Sociales, Universidad Nacional del Centro de la Provincia de Buenos Aires), and La Dulce Seguros de Granizo (Nicanor Olivera, Buenos Aires). The authors also want to thank Luis Borrero, María Clara Álvarez, María Paula Barros, Ana Paula Alcaraz, Pablo Bayala, and Cristian Kaufmann for providing data, bibliography, and technical support with figures. Benjamin Alberti revised and

improved the English. However, the content and interpretations are full responsibility of the authors.

References

- Abba, A.M., Superina, M., 2010. The 2009/2010 armadillo Red List assessment. *Edentata* 11 (2), 135–184.
- Alroy, J., 2001. A multispecies overkill simulation of the end-Pleistocene megafaunal mass extinction. *Science* 292, 1893–1896.
- Álvarez, M.C., Alcaraz, A.P., Gutiérrez, M.A., Martínez, G. Análisis zooarqueológico del sitio Paso Otero 4 (Partido de Necochea). Aportes a la discusión de modelos de subsistencia para la región pampeana. Intersecciones en Antropología, in press.
- Barnosky, A.D., Lindsey, E.L., 2010. Timing of Quaternary megafaunal extinction in South America in relation to human arrival and climate change. *Quaternary International* 217, 10–29.
- Bonadonna, F., Leone, G., Zanchetta, G., 1995. Composición isotópica de los fósiles de gasterópodos continentales de la Provincia de Buenos Aires. Indicaciones paleoclimáticas. 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*. Monografías del Museo Nacional de Ciencias Naturales. CSIC, Madrid, pp. 77–104.
- Borrero, L.A., 2006. Paleoindians without mammoths and archaeologists without projectile points? The archaeology of the first inhabitants of the Americas. In: Morrow, J.E., Gnecco, C. (Eds.), *Paleoindian Archaeology. A Hemispheric Perspective*. University Press of Florida, Gainesville, pp. 9–20.
- Borrero, L.A., 2009. The elusive evidence: the archeological record of the South American extinct megamammals. In: Haynes, G. (Ed.), *American Megafaunal Extinctions at the End of the Pleistocene*. Springer Science + Business Media B.V., pp. 145–168.
- Borrero, L.A., Martin, F.M., 2012. Ground sloths and humans in southern Fuego-Patagonia: taphonomy and archaeology. *World Archaeology* 44 (1), 102–117.
- Burney, D.A., Flannery, T.F., 2005. Fifty millennia of catastrophic extinctions after human contact. *Trends in Ecology & Evolution* 20, 395–401.
- Cajal, J., Tonni, E.P., Tartarini, V., 2010. The extinction of some South American camelids: the case of *Lama (Vicugna) gracilis*. *Mastozoología Neotropical* 17 (1), 129–134.
- Campos, C.M., Tognelli, M.F., Ojeda, R.A., 2001. Dolichotis patagonum. *Mammalian Species* 652, 1–5.
- Cione, A.L., Tonni, E.P., 2005. Bioestratigrafía basada en mamíferos del Cenozoico superior de la provincia de Buenos Aires, Argentina. In: de Barrio, R.E., Etcheverry, R.O., Caballé, M.F., Llambías, E. (Eds.), *Geología y Recursos Minerales de la Provincia de Buenos Aires*, Relatorio del XVI Congreso Geológico Argentino, La Plata, pp. 183–200 (Chapter 11).
- Cione, A.L., Tonni, E.P., Soibelzon, L., 2003. The Broken Zig-Zag: Late Cenozoic large mammal and tortoise extinction in South America. *Revista del Museo Argentino de Ciencias Naturales* 5 (1), 1–19.
- Cione, A.L., Tonni, E.P., Soibelzon, L., 2009. Did humans cause the Late Pleistocene–Early Holocene mammalian extinctions in South America in a context of shrinking open areas? In: Haynes, G. (Ed.), *American Megafaunal Extinctions at the End of the Pleistocene*. Springer Science + Business Media B.V., pp. 125–144.
- Cione, A.L., Tonni, E.P., Bond, M., Carlini, A., Pardiñas, U., Scillato Yané, G., Verzi, D., Vucetich, M.G., 1999. Occurrence charts of Pleistocene mammals in the Pampean area, eastern Argentina. In: Tonni, E.P., Cione, A.L. (Eds.), *Quaternary Vertebrate Palaeontology in South America*. Quaternary in South America and Antarctic Peninsula, vol. 12, pp. 53–60.
- Crowley, B.E., 2010. A refined chronology of prehistoric Madagascar and the demise of the megafauna. *Quaternary Science Reviews* 29, 2591–2603.
- Czerwogora, A., Fariña, R., Tonni, E.P., 2011. Diet and isotopes of Late Pleistocene ground sloths: first results for *Lestodon* and *Glossotherium* (*Xenarthra*, *Tardi-grada*). *Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen* 262 (3), 257–266.
- Favier Dubois, C., 2006. Dinámica fluvial, paleoambientes y ocupaciones humanas en la localidad Paso Otero, Río Quequén Grande, Provincia de Buenos Aires. *Intersecciones en Antropología* 7, 109–127.
- Fernández, F.J., del Papa, L.M., Moreira, G.J., Prates, L., De Santis, L.J.M., 2011. Small mammal remains recovered from two archaeological sites in the middle and lower Negro River valley (Late Holocene, Argentina): taphonomic issues and paleoenvironmental implications. *Quaternary International* 245, 136–147.
- Fiedel, S., 2009. Sudden deaths: the chronology of terminal Pleistocene megafaunal extinction. In: Haynes, G. (Ed.), *American Megafaunal Extinctions at the End of the Pleistocene*. Springer Science + Business Media B.V., pp. 21–37.
- Flegenheimer, N., Bayón, C., Valente, M., Baeza, J., Femenías, J., 2003. Long distance tool stone transport in the Argentine Pampas. *Quaternary International* 109–110, 49–64.
- Formoso, A.E., Udrizsar Sauthier, D.E., Pardiñas, U.F.J., 2010. Mammalia, Rodentia, Sigmodontinae, *Holochilus brasiliensis* (Desmarest, 1819): distribution extension. *Check List* 6 (2), 195–197.
- Fucks, E., Huarte, R., Carbonari, J., Figini, A., 2007. Geocronología, paleoambientes y paleosuelos Holocenos en la Región Pampeana. *Revista de la Asociación Geológica Argentina* 62 (3), 425–433.
- González, S., Merino, M., Giménez Dixon, M., Ellis, S., Seal, U.S., 1994. Population and Habitat Viability Assessment for the Pampas Deer (*Ozotoceros bezoarticus*). Workshop Report Captive Breeding Specialist Group, Apple Valley, Minnesota.
- Grayson, D.K., 2001. The archaeological record of human impacts on animal populations. *Journal of World Prehistory* 15 (1), 1–68.
- Grayson, D.K., 2007. Deciphering North American Pleistocene extinctions. *Journal of Anthropological Research* 63, 185–213.
- Grayson, D.K., Meltzer, D.J., 2003. A requiem for North American overkill. *Journal of Archaeological Science* 30, 585–593.
- Grayson, D.K., Meltzer, D.J., 2004. North American overkill continued? *Journal of Archaeological Science* 31, 133–136.
- Grill, S., Borromei, A., Martínez, G., Gutiérrez, M.A., Cornou, M.E., Olivera, D., 2007. Palynofacial analysis in alkaline soils – Paso Otero 5 archaeological site (Necochea District, Buenos Aires province, Argentina). *Journal of South American Earth Sciences* 24, 34–47.
- Gutiérrez, M.A., Kaufmann, C.A., 2007. Methodological criteria for the identification of formation processes in guanaco (*Lama guanicoe*) bone assemblages in fluvial-lacustrine environments. *Journal of Taphonomy* 5 (4), 151–176.
- Gutiérrez, M.A., Martínez, G., Nielsen-Marsh, C.M., 2001. Alteración diagenética y preservación diferencial de los conjuntos óseos de la localidad arqueológica Paso Otero (Provincia de Buenos Aires, Argentina). *Estudios Geológicos* 56, 291–299.
- Gutiérrez, M.A., Martínez, G., Luchsinger, H., Álvarez, M.C., Barros, M.P., 2010a. Investigaciones arqueológicas y geoarqueológicas preliminares en el sitio Paso Otero 4 (partido de Necochea). In: Berón, M., Luna, L., Bonomo, M., Montalvo, C., Aranda, C., Carrera Aizpitarte, M. (Eds.), *Mamul Mapu: pasado y presente. Perspectivas de la arqueología pampeana a comienzos del tercer milenio*. Libros del Espinillo, Buenos Aires, pp. 69–84.
- Gutiérrez, M.A., Martínez, G., Bargo, M.S., Vizcaíno, S., 2010b. Supervivencia diferencial de megafauna en la región pampeana en el Holoceno temprano y su relación con aspectos paleobiológicos. In: Gutiérrez, M.A., De Nigris, M., Fernández, P.M., Giardina, M., Gil, A.F., Izeta, A., Neme, G., Yacobaccio, H.D. (Eds.), *Zooarqueología a principios del siglo XXI: aportes teóricos, metodológicos y casos de estudio*. Libros del Espinillo, Buenos Aires, pp. 231–241.
- Gutiérrez, M.A., Martínez, G., Luchsinger, H., Grill, S., Zucol, A., Hassan, G., Barros, M.P., Kaufmann, C.A., Álvarez, C., 2011. Paleoenvironments in the Paso Otero locality during Late Pleistocene–Holocene (Pampean region, Argentina): an interdisciplinary approach. *Quaternary International* 245, 37–47.
- Gutiérrez, M.A., Martínez, G., 2008. Trends in the faunal human exploitation during the Late Pleistocene and Early Holocene in the Pampean region (Argentina). *Quaternary International* 191, 53–68.
- Haynes, G., 2002. The catastrophic extinction of North American mammoths and mastodons. *World Archaeology* 33 (3), 391–416.
- Holliday, V.T., Martínez, G.A., Johnson, E., Buchanan, B., 2003. Geoarchaeology of Paso Otero 5 (Pampas of Argentina). In: Miotti, L., Salemme, M., Flegenheimer, N. (Eds.), *Where the South Winds Blow. Ancient Evidence of Paleo South Americans*. Texas A&M University Press, College Station, pp. 37–43.
- Hubbe, A., Hubbe, M., Neves, W., 2007. Early Holocene survival of megafauna in South America. *Journal of Biogeography* 34, 1642–1646.
- International Commission on Stratigraphy, 2009. International Stratigraphic Chart. International Union of Geological Sciences.
- Iriondo, M., 1999. Climatic changes in the South American plains: records of a continent-scale oscillation. *Quaternary International* 57–58, 93–112.
- Iriondo, M., García, N., 1993. Climatic variations in the Argentine plains during the last 18,000 years. *Palaeogeography, Palaeoclimatology, Palaeoecology* 101, 209–220.
- Johnson, C.N., 2002. Determinants of loss of mammal species during the Late Quaternary 'megafauna' extinctions: life history and ecology, but not body size. *The Royal Society* 269, 2221–2227.
- Johnson, E., Holliday, V.T., Martínez, G., Gutiérrez, M.A., Politis, G., 2012. Geochronology and Landscape Development Along the Middle Río Quequén Grande at the Paso Otero Locality, Pampa Interserrana, Argentina. *Geoarchaeology: An International Journal* 27, 300–323.
- Johnson, E., Politis, G., Martínez, G., Hartwell, W.T., Gutiérrez, M.A., Haas, H., 1998. Radiocarbon chronology of Paso Otero 1 in the Pampean region of Argentina. *Quaternary of South America and Antarctic Peninsula* 16, 15–25.
- Joly, D., March, R., Martínez, G.A., 2005. Les os brûlés de Paso Otero 5: un témoignage possible de l'utilisation de l'os comme combustible par des chasseurs-cueilleurs de la fin du Pléistocène en Argentine. *Archéosciences, Revue d'archéométrie* 29, 83–93.
- Jouzel, J., Masson-Delmotte, V., Cattani, O., Dreyfus, G., Falourd, S., Hoffmann, G., Minster, B., Nouet, J., Barnola, J.M., Chappellaz, J., Fischer, H., Gallet, J.C., Johnsen, S., Leuenberger, M., Loulergue, L., Luethi, D., Oerter, H., Parrenin, F., Raisbeck, G., Raynaud, D., Schilt, A., Schwander, J., Selmo, E., Souchez, R., Spahni, R., Stauffer, B., Steffensen, J.P., Stenni, B., Stocker, T.F., Tison, J.L., Werner, M., Wolff, E.W., 2007. Orbital and millennial Antarctic climate variability over the past 800,000 years. *Science* 317 (5839), 793–796.
- MacPhee, R.D.E., Marx, P.A., 1997. The 40,000-year plague: humans, hypervirulent diseases, and first-contact extinctions. In: Goodman, S.M., Patterson, B.D. (Eds.), *Natural Change and Human Impact in Madagascar*. Smithsonian Press, Washington, DC, pp. 169–217.
- Martin, P.S., 1984. Prehistoric overkill: the global model. In: Martin, P.S., Klein, R.G. (Eds.), *Quaternary Extinctions: a Prehistoric Revolution*. University of Arizona Press, Tucson, pp. 354–403.
- Martínez, G., 2001. 'Fish-Tail' projectile points and megamammals: new evidence from Paso Otero 5 (Argentina). *Antiquity* 75, 523–528.

- Martínez, G., 2006. Arqueología del curso medio del río Quequén Grande: estado actual y aportes a la arqueología de la región pampeana. *Relaciones de la Sociedad Argentina de Antropología* 31, 249–275.
- Martínez, G., Gutiérrez, M.A., 2004. Tendencias en la Explotación Humana de la Fauna durante el Pleistoceno Final-Holoceno en la Región Pampeana (Argentina). In: Mengoni Goñalons, G. (Ed.), *Zooarchaeology of South America*. British Archaeological Research International Series 1298, Oxford, UK, pp. 81–98.
- Martínez, G., Gutiérrez, M.A., 2011. Paso Otero 5: a summary of the interdisciplinary lines of evidence for reconstructing early human occupation and paleoenvironment in the Pampean region, Argentina. In: Vialou, D. (Ed.), *Peuplements et Préhistoire de l'Amérique*. Muséum National d'Histoire Naturelle. Département de Préhistoire, U.M.R., Paris, pp. 271–284.
- Mazzanti, D., 2003. Human settlements in caves and rockshelters during the Pleistocene–Holocene transition in the Eastern Tandilia Range, Pampean region, Argentina. In: Miotti, L., Salemme, M., Flegenheimer, N. (Eds.), *Where the South Winds Blow*. Ancient Evidence of Paleo South Americans. Texas A&M University Press, College Station, pp. 57–61.
- Mazzanti, D., Quintana, C. (Eds.), 2001. Cueva Tixi: cazadores y recolectores de las sierras de Tandilia oriental. *Geología, Paleontología y Zooarqueología*. Facultad de Humanidades (UNMP), Publicación Especial 1, Mar del Plata.
- Miller, G.H., Fogel, M.L., Magee, J.W., Gagan, M.K., Clarke, S.J., Johnson, B.J., 2005. Ecosystem collapse in Pleistocene Australia and a human role in megafaunal extinction. *Science* 309, 287–290.
- 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.
- Norton, C.J., Kondo, Y., Ono, A., Zhang, Y., Diab, M.C., 2010. The nature of megafaunal extinctions during the MIS 3–2 transition in Japan. *Quaternary International* 211, 113–122.
- Osterrieth, M., Martínez, G., Gutiérrez, M.A., Alvarez, M.F., 2008. Biomorfos de sílice en la secuencia pedosedimentaria del sitio arqueológico Paso Otero 5, Buenos Aires, Argentina. In: Korstanje, M.A., Babor, M. del P. (Eds.), *Matrices interdisciplinarias en estudios fitolíticos y de otros microfósiles*. British Archaeological Research International Series S1870, Oxford, pp. 77–90.
- Politis, G., Gutiérrez, M.A., 1998. Gliptodontes y cazadores-recolectores de la Región Pampeana (Argentina). *Latin American Antiquity* 9 (2), 111–134.
- Politis, G., Messineo, P.G., 2008. The Campo Laborde site: new evidence for the Holocene survival of Pleistocene megafauna in the Argentine Pampas. *Quaternary International* 191, 98–114.
- Politis, G., Pedrotta, V., 2006. Recursos faunísticos y estrategias de subsistencia en el este de la región pampeana durante el Holoceno tardío: el caso del guanaco (*Lama guanicoe*). *Relaciones de la Sociedad Argentina de Antropología XXXI*, 301–336.
- Politis, G., Gutiérrez, M.A., Scabuzzo, C. (Eds.), Estado actual de las investigaciones en el sitio Arroyo Seco 2 (Partido de Tres Arroyos, provincia de Buenos Aires, Argentina). Serie Monográfica del INCUAPA N° 5. FACS-UNCPBA, Olavarría, in press.
- Politis, G., Gutiérrez, M.A., Martínez, G., 1991. Informe preliminar de las investigaciones en el sitio Paso Otero 1 (Pdo. de Necochea, Pcia. de Buenos Aires). *Boletín del Centro de Registro Arqueológico y Paleontológico* 2, 80–90.
- Politis, G., Messineo, P., Kaufmann, C., 2004. El poblamiento temprano de las llanuras pampeanas de Argentina y Uruguay. *Complutum* 15, 207–224.
- Politis, G., Prado, J.L., Beukens, R., 1995. The human impact in Pleistocene–Holocene extinctions in South America: the Pampean case. In: Johnson, E. (Ed.), *Ancient People and Landscapes*. Museum of Texas Tech University, Lubbock, TX, pp. 187–205.
- Prado, J.L., Alberdi, M.T., 1994. A quantitative review of the horse *Equus* from South America. *Paleontology* 37, 459–481.
- Prado, J.L., Alberdi, M.T., 1999. The mammalian record and climatic change over the last 30,000 years in the Pampean region, Argentina. *Quaternary International* 57–58, 165–174.
- Prado, J.L., Cerdeño, E., 1998. Los mamíferos Pliocenos de la Fauna local Quequén Grande (Provincia de Buenos Aires, Argentina). *Estudios Geológicos* 54 (1–2), 75–83.
- Prado, J.L., Alberdi, M.T., Azanza, B., Sánchez, B., 2001. Climate and changes in mammal diversity during the Late Pleistocene–Holocene in the Pampean region (Argentina). *Acta Paleontológica Polonica* 46 (2), 261–276.
- Prado, J.L., Menegaz, A.N., Tonni, E.P., Salemme, M., 1987. Los mamíferos de la Fauna local Paso Otero (Pleistoceno tardío), Provincia de Buenos Aires. Aspectos paleoambientales y bioestratigráficos. *Ameghiniana* 24, 217–233.
- Prates, L., 2008. Los indígenas del río Negro. Un enfoque arqueológico. *Sociedad Argentina de Antropología*, Buenos Aires.
- Prevosti, F.J., Pardiñas, U.F.J., 2001. Variaciones corológicas de *Lyncodon patagonicus* (Carnívora, Mustelidae) durante el Cuaternario. *Mastozoología Neotropical* 8 (1), 21–39.
- Prieto, A.R., 1996. Late Quaternary vegetational and climatic changes in the Pampa grassland of Argentina. *Quaternary Research* 45 (1), 73–88.
- Prieto, A.R., Blasi, A.M., De Francesco, C.G., Fernández, C., 2004. Environmental history since 11,000 ¹⁴C yr B.P. of the northeastern Pampas, Argentina, from alluvial sequences of the Luján River. *Quaternary Research* 62, 146–161.
- Quattrocchio, M.E., Borromei, A.M., Deschamps, C., Grill, S.C., Zavala, C.A., 2008. Landscape evolution and climate changes in the Late Pleistocene–Holocene southern Pampa (Argentina): evidence from palynology, mammals and sedimentology. *Quaternary International* 181, 123–138.
- Reimer, P.J., Baillie, M.G.L., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., Buck, C.E., Burr, G.S., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hajdas, I., Heaton, T.J., Hogg, A.G., Hughes, K.A., Kaiser, K.F., Kromer, B., McCormac, F.G., Manning, S.W., Reimer, R.W., Richards, D.A., Southon, J.R., Talamo, S., Turney, C.S.M., van der Plicht, J., Weyhenmeyer, C.E., 2009. IntCal09 and Marine09 radiocarbon age calibration curves, 0–50,000 years cal BP. *Radiocarbon* 51 (4), 1111–1150.
- Salemme, M. Zooarqueología y paleoambientes en la Región Pampeana. In: Politis, G., Gutiérrez, M.A., Scabuzzo, C. (Eds.), Estado actual de las investigaciones en el sitio Arroyo Seco 2 (Partido de Tres Arroyos, provincia de Buenos Aires, Argentina). Serie Monográfica del INCUAPA N° 5. FACS-UNCPBA, Olavarría, in press.
- Steadman, D.W., Martin, P.S., MacPhee, R.D.E., Jull, A.J.T., McDonald, H.G., Woods, C.A., Iturralde-Vinent, M., Hodgins, G.W.L., 2005. Asynchronous extinction of Late Quaternary sloths on continents and islands. *Proceedings of the National Academy of Science* 102 (33), 11763–11768.
- Steele, J., Politis, G., 2009. AMS ¹⁴C dating of early human occupation of southern South America. *Journal of Archaeological Science* 36, 419–429.
- Stoessel, L., Bogan, S., Martínez, G., Agnolin, F., 2008. Implicaciones paleoambientales de la presencia del género *Ceratophrys* (anura, ceratophryinae) en contextos arqueológicos de la transición pampeano-patagónica en el Holoceno tardío (curso inferior del río Colorado, Argentina). *Magallania* 36 (2), 195–203.
- Stuiver, M., Reimer, P.J., Reimer, R.W., 2005. CALIB 6.0 (WWW Program and Documentation).
- Tonni, E.P., 1992. Mamíferos y Clima del Holoceno en la Provincia de Buenos Aires. In: Iriondo, M. (Ed.), *Holoceno en la Argentina*, vol. 1. CADINQUA, pp. 64–78.
- Tonni, E.P., 2006. Cambio climático en el Holoceno tardío de la Argentina. Una síntesis con énfasis en los últimos 1000 años. *Folia Histórica del Nordeste* 16, 187–195.
- Tonni, E.P., Fidalgo, F., 1978. Consideraciones sobre los cambios climáticos durante el Pleistoceno tardío-Reciente en la provincia de Buenos Aires. Aspectos ecológicos y zoogeográficos relacionados. *Ameghiniana* 15, 235–253.
- Tonni, E.P., Laza, J.H., 1980. Las aves de la Fauna local Paso Otero (Pleistoceno tardío) de la provincia de Buenos Aires. Su significación ecológica, climática y zoogeográfica. *Ameghiniana* 17, 313–322.
- Tonni, E.P., Politis, G., 1981. Un gran cánido del Holoceno de la provincia de Buenos Aires y el registro prehispánico de *Canis* (*Canis*) *familiaris* en las áreas Pampeana y Patagónica. *Ameghiniana* 18, 251–265.
- Tonni, E.P., Cione, A.L., Figini, A.J., 1999. Predominance of arid climates indicated by mammals in the pampas of Argentina during the Late Pleistocene and Holocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 147, 257–281.
- Tonni, E.P., Huarte, R.A., Carbonari, J.E., Figini, A.J., 2003. New radiocarbon chronology for the Guerrero Member of the Luján Formation (Buenos Aires, Argentina): palaeoclimatic significance. *Quaternary International* 109–110, 45–48.
- Valverde, J.A., 1964. Remarques sur la structure et l'évolution des communautés de vertébrés terrestres. 1. Structure d'une communauté. 11: Rapports entre prédateur et proies. *La Terre et la Vie* 2, 121–164.
- Vizcaíno, S.F., Bargo, M.S., Cassini, G.H., 2006. Dental occlusal surface area in relation to body mass, food habits and other biological features in fossil xenarthrans. *Ameghiniana* 43, 11–27.
- 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. (Eds.), *Bones, Clones, and Biomes. The History and Geography of Recent Neotropical Mammals*. The University of Chicago Press, Chicago, pp. 76–101.
- Vogliano, D., Pardiñas, U.F.J., Teta, P., 2004. *Holochilus chacarius chacarius* (Rodentia, Cricetidae) en la provincia de Buenos Aires, Argentina. *Mastozoología Neotropical* 11 (2), 243–247.
- Zárate, M., Kemp, R.A., Espinosa, M., Ferrero, L., 2000. Pedosedimentary and palaeoenvironmental significance of a Holocene alluvial sequence in the southern Pampas, Argentina. *The Holocene* 10 (4), 481–488.