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Biodiversity, taxonomic richness and specialists-generalists during Late Pleistocene/Early Holocene times in Pampa and Patagonia (Argentina, Southern South America)

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Abstract

Human subsistence systems in the Pampa and Patagonia regions evolved from generalists during the Late Pleistocene/Early Holocene to specialists during the Middle Holocene, according to diversity and relative taxonomic richness counts. The general hypothesis is summarized as follows: 1) at the end of the Pleistocene and beginning of the Holocene (interval between 13.0 and 8.5 ka), the Pampean and Patagonian landscape was different from the present one, with a mammal biodiversity larger than in the Middle Holocene; 2) during the Middle Holocene, the highest mammal taxonomic richness corresponds to one species, *Lama guanicoe*. Although available biomass was the same for the hunter-gatherers, it was due to the larger abundance of individuals of that single species; 3) the emerged continental surface during the Late Pleistocene/Early Holocene was more extensive than during the Middle Holocene. In ecological terms, this greater land mass is reflected in an equally larger biodiversity, even assuming that populations of Pleistocenic megafauna were diminishing in number since ca. 13,500 years BP.

Based on the analysis of our own information and published data, we state that the human groups which colonized the Pampean and Patagonian regions towards the end of the Pleistocene and beginning of the Holocene used generalist strategies encompassing a wide range of faunal resources (birds and mammals, especially of terrestrial habitats). Plasticity of hunter-gatherer societies, plus a complex technology, a higher social mobility and unfilled territories, allowed them to rapidly replace one resource for another in conditions of environmental stress. This lifestyle resulted in the occupation of different ecological zones (niches) and the evolution to specialized systems, based on one or a few mammal species, once the colonization and support in the different environments were successful and the resources of the Late Pleistocene/Early Holocene disappeared. © 1998 INQUA/Elsevier Science Ltd. All rights reserved.

1. Introduction

Palaeoenvironmental studies in the Pampa and Patagonia regions (Argentina, South America) have increased in the last 20 years due to multidisciplinary investigations in archaeology and other Quaternary sciences. Results are being incorporated in the theoretical and empirical *corpus* of the past over the ecosystems, the hydrologic and glacial regimes, and sea level oscillations. These data, which have been integrated with the archaeological record, suggest that changes took place both in the palaeoenvironments and in the hunter-gatherer ways of colonization. Some of our own ideas which had been formulated earlier (Tonni et al., 1982, 1985, 1988; Fidalgo et al., 1986; Salemme, 1987; Salemme and Miotti, 1987,

1995; Miotti et al., 1988; Menegaz et al., 1989a), are herein reinforced and/or modified.

Archaeological sites from the Pampa and Patagonia regions, in which lithic materials have been found associated with extinct fauna, have been known since the last century (e.g., Ameghino, 1880; Roth, 1899; Nordenskjöld, 1900; Outes, 1905). Based on this evidence, two main ideas frequently have been formulated: a) the coexistence of Pleistocenic megafauna and hunter-gatherers; and b) the exploitation of these megamammals as a complementary resource in different areas of the Pampa and Patagonia. These findings have brought together the following interdependent subjects: 1) the relationship between man and fauna; 2) the megafauna extinction, explained by means of primary and concurrent factors,

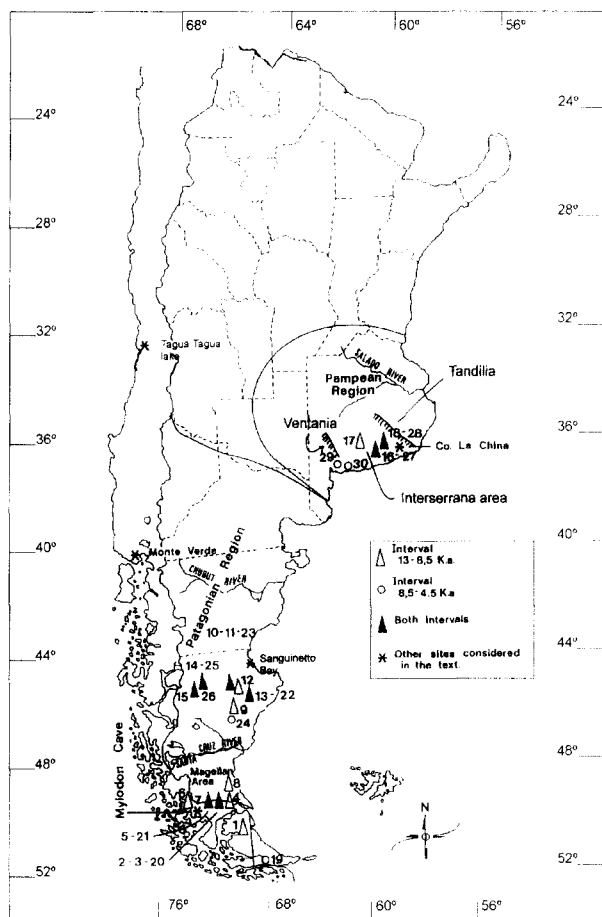


Fig. 1. Map displaying the geographical distribution of archaeological sites or components included in the Pampean and Patagonian Regions. 1. Tres Arroyos Rockshelter, Levels Va, Vb (Massone, 1987); 2. Fell Cave Period I; 3. Fell Cave Period II; 4. Pali Aike Cave Period I; 5. Cerro Sota Cave Lower Levels (Bird, 1993); 6. Cueva del Medio Component I, equivalent to Bird's Period I; 7. Cueva del Medio Component II equivalent to Bird's Period III (Nami, 1987); 8. Las Buitreras Cave Layers VII, VIII (Bórmida, 1976); 9. El Ceibo Cave 7, Layer 12 (Cardich et al., 1981, 1982); 10. Los Toldos Cave 3, Industry Level 11; 11. Los Toldos Cave 3, Toldense Industry (Cardich et al., 1973); 12. Los Toldos Cave 2, Layer B (Menghin, 1952; Mengoni Goñalons, 1976–1980); 13. Piedra Museo AEP1 Rockshelter, Lower Component (Miotti, 1992); 14. Arroyo Feo Cave, Layer 11 (Silveira, 1979); 15. Manos Pintadas Cave, Rio Pinturas I (Mengoni Goñalons and Silveira, 1976; Gradin, 1980); 16. Arroyo Seco Site 2, Lower Component (Fidalgo et al., 1986); 17. La Moderna Lower Component (Politis, 1985); 18. Tixi Cave, Earliest Occupation (Mazzanti, 1994); 19. Tunnel I, First Component (Piana, 1984); 20. Fell Cave Period III; 21. Cerro Sota Cave Upper Level; 22. Piedra Museo AEP1, Upper Component; 23. Los Toldos Cave 3, Casapedrense Industry; 24. La Martita Lower Component (Aguerre, 1987); 25. Arroyo Feo Cave, Layer 8/9; 26. Alero Cárdenas (Gradin and Aguerre, 1994); 27. Arroyo Seco Site 2, Middle Component; 28. Tixi Cave, Middle Occupation; 29. La Toma Lower Component (Salemme, 1990); 30. La Olla (Politis et al., 1994).

such as environmental changes, over-exploitation, inter-specific competition (Guilday, 1967; Martin, 1984); and 3) the chronological position and radiocarbon datings of these events, not only with regard to the peopling and

the extinctions but also the characterization of the Pleistocene–Holocene transition.

The recurrences and divergences of several taxa that traditionally have been considered extinct at the end of the Pleistocene are analyzed in this paper. Several hypotheses about these subjects are formulated, using the data coming from archaeological sites in the Pampean and Patagonian regions (Fig. 1). These sites have been grouped into two time-periods: 1) Late Pleistocene/Early Holocene, 13.0 ka to 8.5 ka BP; and 2) Middle Holocene, 8.5 to 4.5 ka BP.

The Holocene has been divided into three stages (Early, Middle and Late) based on other indicators (Mangerud et al., 1982; Rabassa, 1987). However, only the Early and Middle intervals are considered, as these intervals are where the fluctuations in biodiversity and taxonomic richness occurred. Furthermore, the end of the early Holocene is placed at ca. 8.5 ka BP, in agreement with the presence of the last individuals of extinct mammals in the Pampa and Patagonia regions ("massive extinction process" Marshall et al., 1984; Tonni, 1992). However Politis et al. (1995) argue that the extinct megamammals coexisted at least until ca. 7 ka BP.

The Middle Holocene coincides with the moment of highest sea level curves (Rabassa, 1987; Rabassa et al., 1989; Gordillo et al., 1994); from the palynological information, two phases point towards an increase of temperature and aridity, but the oldest one was probably drier than the youngest (Heusser and Streeter, 1980; Markgraf, 1986).

The aim of this paper is to demonstrate the evolutionary tendency of the hunter-gatherer economic systems in the Pampean and Patagonian regions, from the first interval or *Hunter-gatherer Colonization Phase* (13–8.5 ka BP) and the second interval or *Hunter-gatherer Territorial Consolidation Phase* (8.5–4.5 ka BP), taking into account the impact produced by the extinction of the megamammals towards the end of the first interval.

2. Data and methods

2.1. Physiographic setting and environmental characteristics

The Pampa and Patagonia are major, distinct, natural physiographic regions (Difrieri, 1958; Ringuet, 1961; Cabrera, 1971). Pampa, west-bounded by the 600 mm isohyet, is an extensive grassland (lat. 34°–38°S) with rich soils, low elevations, and temperate climate. The sites are located in the hilly areas of the Ventania and Tandilia ranges and the Interserrana (flat plains between the ranges) area (Fig. 1). Patagonia (lat. 38°–55°S), east of the southern Andes, is a high, semi-arid plateau, where cold winds blow constantly. Soils are shallow and unfertile, trees are scarce or absent, and most of the area is an

extended dry steppe. The sites pertinent to this discussion are located south of lat. 47°S (Fig. 1).

2.2. Site distribution and chronology

The faunal samples considered come from multicomponent open-air and cave sites, which were selected based on the following characteristics: 1) faunal association, including extinct species; 2) radiocarbon data; and 3) technological and faunal associations that lead to cross-dated archaeological contexts through relative chronologies. On the basis of these criteria, the sites were clustered into two chronological groups between 13–8.5 ka BP and 8.5–4.5 ka BP (Fig. 1 and Table 1).

Two very well known sites in the archaeological literature have been included in this paper only to be considered in the final discussion, Mylodon Cave and Cerro La China 1 rockshelter (Fig. 1). Although Mylodon Cave was excavated repeatedly, obtaining huge archaeological samples and numerous radiocarbon dates, it presents serious taphonomic problems relating to site formation such as anthropic disturbance, aqueous reworking, trampling, scavenging, diagenesis, and root activity (see Borrero, 1986; Borrero et al., 1988). An interesting lithic assemblage has been recovered from Cerro La China 1 Rockshelter (Flegenheimer, 1987). However, post-depositional processes such as pedogenesis, erosion, slope creep, burrowing, and anthropic disturbance (Flegenheimer and Zárate, 1993: 96), are probably, the main reasons for the absence of a bone assemblage in the Lower Level. The only faunal finding associated is a scute of *Eutatus sequini*. However, evidence of human modification is lacking.

2.3. Review of the nomenclature

The information obtained from faunal remains studied by us, as well as the available literature, are presented in Fig. 2a. Only identifiable specimens and/or elements (Salemme et al., 1991) are employed in this analysis. Names of each taxon correspond to the nomenclature based on available systematic revisions, and most recent usage in the literature. The original papers for each site must be reviewed for comparison with the nomenclature used in this paper.

Several taxa require particular attention. The South-American forms of equids are in two genera: *Equus*, subgenus (*Amerhippus*) and *Hippidion* (Alberdi, 1987). *Hippidion* has at least two morphotypes: the robust and large Pampean specimens, and the smaller Patagonian specimens. Equids have been re-examined at the genus and specific levels (Alberdi et al., 1987; Alberdi and Prado, 1992, 1993; Prado and Alberdi, 1994).

The remains of a small sized camelid from Los Toldos Caves 2 and 3 and El Ceibo Cave 7 were identified as *Lama* (*Vicugna*) *gracilis* (Menegaz et al., 1989a). New

findings of bones were assigned to this species at the site AEP1 (Miotti, 1992; 1996). Remains of camelids corresponding to the upper range known for the Family were assigned to *Lama* sp. This range interval includes the species *Hemiauchenia paradoxa* ("Paleolama wedelli"), *Lama oweni*, and *Lama guanicoe* (Menegaz et al., 1986b). Therefore, remains coming from Arroyo Seco site 2 initially identified as *Paleolama* cf. *wedelli* (Fidalgo et al., 1986) correspond, according to the latest review, to *Hemiauchenia paradoxa* (*sensu* Webb, 1974).

Bones of Felidae recovered in the sites Mylodon Cave, Cerro Sota and Cueva del Medio are included under the name "*Felis listai*". The remains from Mylodon Cave identified by Roth (1902) as this species were renamed as *Panthera onça mesembrina* by Cabrera (1934); therefore, the validity of this taxon is doubtful after later revisions (Hershkovitz, 1949). New findings from Cueva del Medio include bones even bigger in size than those studied by Cabrera (1934), although the cultural association is doubtful (Borrero et al., 1988; Nami and Menegaz, 1992). Based on the last reviews, the name *Panthera onça mesembrina* (Berman, 1994) is used.

Remains of Mylodon coming from Southern Patagonia have been assigned to *Mylodon* (?) *listai*, following the criteria proposed by Scillato Yané (1976) in the study of Las Buitreras materials. This Patagonian form has a characteristic smaller size than the Pampean forms known as *Mylodon darwinii*. Scillato Yané (1976) suggested the use of the name *Mylodon* (?) *listai* until a new revision of the group is made.

The nomenclature used by each for canids has been maintained. The Canidae family requires a detailed systematic revision beyond the scope of this study.

2.4. Assumptions

It is assumed that the presence of a taxa in different archaeological sites repeatedly enhances the hypothesis of being a potentially economic resource in the area. In that sense, the exploitation of faunal resources by hunter-gatherers during the Late Pleistocene and Early Holocene has been analyzed in two levels: 1) *regional level*, based on the recurrences of taxa in the archaeological record (Table 2). Thus, the palaeodistribution of the taxa is a criterion for the interpretation of the potential availability in both regions; 2) *contextual level*, based on anthropogenic evidence: modifications and marks on bone remains (e.g., like cutmarks, burnt bones, bony instruments); the frequency of certain skeletal elements; and associated lithic assemblages (Table 1). The last consideration has been used as a good criterion for the interpretation of site function. The isolated record of bones assigned to an extinct taxa in certain archaeological contexts only testifies to its presence and, likely, its contemporaneity, but it does not necessarily imply its use by the hunter-gatherers living in these regions.

Table 1
Contextual analysis of the studied sites

Contextual attributes	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	Inferred Functions		
1. Tres Arroyos	*																																								Multiple activities site
2. Fell Cave I	*																																							Multiple activities site	
3. Fell Cave II	*																																							Multiple activities site	
4. Pali Aike	*																																							Trapped and kill site	
5. Cerro Sota	*																																							Kill sites and burials	
6. C. del Medio I	*																																						Multiple activities site		
7. C. del Medio III	*																																						Multiple activities site		
Mythodon Cave	*																																						Trapped, kill site and butchering		
8. Las Bumeras	*																																						Trapped, kill site and consumption		
9. El Ceibo 7	*																																						Special activities, workshop-skin and consumption		
10. LT3 Level 11	*																																						Multiple activities site		
11. LT3 Toldense	*																																						Multiple activities site		
12. LT 2 B	*																																						Multiple activities site		
13. AEP1 - Lower Comp	*																																							Kill site and butchering	
14. Arroyo Feo II	*																																						Multiple activities site		
15. Manos Pintadas	*																																						Multiple activities site		
16. AS 2 Lower Comp.	*																																						Multiple activities site and burials		
17. La Moderna Lower Comp.	*																																						Multiple activities site		
18. Tivi Cave Lower Comp.	*																																						Kill site and lithic workshop		
19. Tunnel 1 Lower Comp.	*																																					Lithic workshop			
20. Fell Cave III	*																																					Exploration camp site			
21. Cerro Sota Upper Comp.	*																																						Multiple activities site		
22. AEP1-Upper Comp.	*																																						Multiple activities site		
23. LT3 Casapdrese	*																																						Multiple activities site		
24. La Marrita Lower Comp.	*																																						Multiple activities site		
25. Arroyo Feo 8 9	*																																						Multiple activities site		
26. Alero Cardenas	*																																						Multiple activities site		
27. AS 2 Middle Comp.	*																																						Multiple activities site		
28. Tivi Cave Middle Holoc.	*																																								
29. La Loma Lower Comp.	*																																								
30. La Olla	*																																								

* Presence. ● Paleolagoan. ? Ignored. † Only one finding.

Codes of Attributes: 1. Cave or rockshelter; 2. Open air site; 3. River terrace; 4. Creek cliffs; 5. Site nearby lagoons or ponds; 6. Topographic traps; 7. Bone concentrations; 8. Articulated long bones; 9. Articulated ribs vertebrae; 10. Fragments of limb bones; 11. Fragments of skull; 12. Tusk or antlers; 13. Mandibles; 14. Complete articulated skeleton; 15. Green-bone splits; 16. Vertebrae; 17. Ribs; 18. Pelvis and/or scapula; 19. Autopodial bones; 20. Utilized flakes and knives; 21. Projectile points; 22. Scrapers; 23. Blades or knives; 24. Awl; 25. Artifacts with natural edge; 26. Flakes and debris; 27. Tools without edges; 28. Weapons; 29. More % bones than lithic; 30. Lower % bones than lithic; 31. Similar % bones lithic; 32. None or few cortical flakes; 33. Utilized bone bone tools; 34. Hearth charcoal burnt bones; 35. More than 4 animal species; 36. Nodules and/or hammerstone; 37. Cores; 38. Bones with cutmarks.

† Special activities
‡ Butchering and vegetal gathering

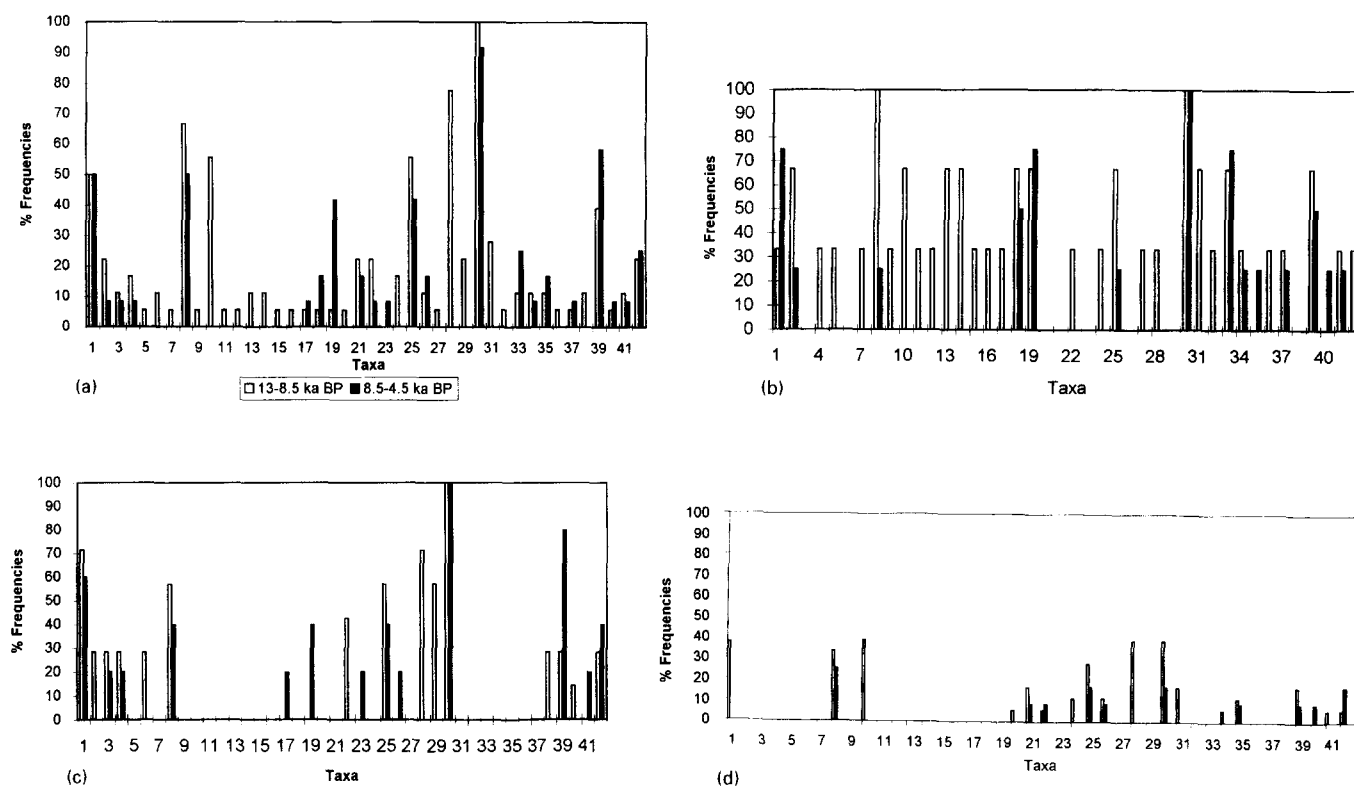


Fig. 2. Diversity and richness of taxa for both intervals: a. Total frequencies in Pampean and Patagonian regions. b. Frequencies in Pampean region. c. Frequencies in Central Plateau, Patagonian region. d. Frequencies in Magellan area and Tierra del Fuego, Patagonian region.

In this case, the bones are a means to interpret the palaeoenvironmental evolution more than cultural indicators.

2.5. Quantitative measures

In previous papers, the idea of economic and environmental changes (Miotti et al., 1988; Menegaz et al., 1989a) was presented while the hypothesis of a decrease in faunal diversity from Late Pleistocene to Holocene times in Southern Patagonia was formulated (Miotti, 1989, 1993a, 1996).

Data available allow presence, frequencies, NISP, MNI and NSpecies determinations for most of or all of the taxa. These numbers were processed using diversity (dI) and richness (H') indexes (Grayson, 1984; Cruz Uribe, 1988). Other possible relationships include correlation between diversity measures and sample size, taphonomic differences, technical methodology bias, and trend to the rarefaction of the samples and their distribution. However, many reasons exist why the definition of diversity indexes is a useful tool to interpret and infer the evolution of economic systems and environments and the relationship between hunter-gatherers and their prey. While Grayson (1984) considers the diversity and richness indexes as methodological biases as they are correlated

with sample size, these measures are otherwise employed for inferring changes in the tendencies of economic systems (Wing, 1963; Klein, 1980; Cruz Uribe, 1988).

Even though we agree with the claims of these authors, we think the use of those indexes are a better approach than the qualitative analysis only. According to Lyman (1994), it is necessary to state clearly which and how the units and indexes are employed; since "... the application of diversity indices in archaeology is highly prone to sample size effects". (Grayson, 1984: 166). This was demonstrated in Salemme and Miotti (1995), and will be discussed below.

3. Palaeoenvironmental contexts and economy

The following comments are based on these considerations and the zooarchaeological data presented (Table 2; Figs 2a–d; 3a). First, none of the archaeological sites are in sediments deposited during the Last Glacial Maximum (LGM: 21–16 ka). All the studied contexts come from Late Glacial (16–10 ka) and Early Holocene deposits. In the first interval, the Pleistocene fauna recovered from correlative Late Glacial and Postglacial sediments in archaeological contexts show difference in diversity and frequency as regards the fauna recorded in

the “Lujanense” Land Mammal Unit (Tonni et al., 1985). The contexts belonging to the first interval show a tendency towards a major diversity of megaherbivores and large and medium size mammals (both herbivores and carnivores) than that recorded in the assemblages of the second interval that only show living fauna (Figs 2a and 3a).

Second, birds have not received enough attention in archaeological contexts, although the Aves class is a significant taxon (Table 2 and Fig. 2a). Several taxa of birds are frequent in different sites. In the first interval, birds of middle and small size represents 65% while in the second interval, this class decreased to 37%. Taxa (8) in Table 2

represents all of those genera that could not be assigned to a lower systematic level, such as Anatidae (ducks) and birds of prey.

Third, between 13.0 and 8.5 ka BP, equids, camelids, giant sloths and flightless birds are frequent in both Patagonian and Pampean contexts. However, three different faunistic associations are detected at the regional level: a) *Hippidion* sp. — *Myiodon* (?) *listai*-*Lama oweni* in the Andean Cordillera and southern extra-andean Patagonia; b) *Lama gracilis* — *Hippidion* sp. — *Rhea* cf. *americana* or similar species in extra-andean Patagonia and c) *Equus* (*Amerhippus*) — *Hippidion* sp. — *Megatherium americanum* — *Rhea americana* in the Pampean

Table 2
List of taxa recorded at the sites

Sites	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Taxa															
1. Rheidae					x		x		x		x		x	x	x
2. <i>Rhea americana</i>											x			x	
3. <i>Pterocnemia pennata</i>									x				x		
4. <i>Eudromia elegans</i>										x			x		
5. <i>Nothura maculosa</i>															
6. <i>Fulica</i> sp.														x	x
7. <i>Speotyto cunicularia</i>															
8. Aves	x	x	x	x	x	x		x	x	x	x			x	
9. <i>Megatherium</i>															
10. <i>Myiodon</i> sp.	x	x		x	x	x	x	x							
11. <i>Toxodon</i> sp.															
12. <i>Glossotherium</i> sp.															
13. <i>Eutatus</i>															
14. <i>Glyptodon</i> sp.															
15. <i>Doedicurus</i> sp.															
16. <i>Sclerocalyptus</i>															
17. <i>Tolypeutes</i>															
18. <i>Chaetophractus villosus</i>															
19. <i>Zaedyus pichiy</i>															
20. <i>Pantera onça mesembrina</i>															
21. <i>Felis</i> sp.		x	x												
22. <i>Felis concolor</i>					x				x		x				x
23. <i>Lutra</i> sp.															
24. <i>Canis (D.) arus</i>	x							x							
25. Canidae		x	x	x	x	x					x		x	x	x
26. <i>Canis (C.) familiaris</i>		x	x												
27. <i>Equus (Amerhippus)</i>															
28. <i>Hippidion</i> sp.	x	x		x	x	x	x	x	x	x	x	x	x		
29. <i>Lama (V.) gracilis</i>									x	x		x	x		
30. <i>Lama guanicoe</i>		x	x	x	x	x	x	x	x	x	x	x	x	x	x
31. <i>Lama</i> sp.	x					x	x								
32. <i>Macrauchenia</i>															
33. <i>Ozotoceros bezoarticus</i>															
34. Cervidae						x									
35. Pinnipedia							x	x							
36. <i>Dolichotis patagonum</i>															
37. <i>Lagostomus maximus</i>															
38. <i>Lagidium</i> sp.														x	x
39. <i>Ctenomys</i> sp.	x	x			x								x	x	
40. Pisces															x
41. <i>Adelomedon brasiliensis</i>	x														
42. Volutidae							x					x		x	

Table 2 (Continued)

Sites	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Taxa															
1. Rheidae	×						×		×			×		×	×
2. <i>Rhea americana</i>	×	×												×	
3. <i>Pterocnemia pennata</i>							×								
4. <i>Eudromia elegans</i>	×						×								
5. <i>Nothura maculosa</i>	×														
6. <i>Fulica</i> sp.															
7. <i>Speotyto cunicularia</i>	×														
8. Aves		×		×	×	×	×	×				×			
9. <i>Megatherium</i>	×														
10. <i>Myiodon</i> sp.	×	×													
11. <i>Toxodon</i> sp.	×														
12. <i>Glossotherium</i> sp.	×														
13. <i>Eutatus</i>	×		×												
14. <i>Glyptodon</i> sp.	×	×													
15. <i>Doedicurus</i> sp.		×													
16. <i>Sclerocalyptus</i>		×													
17. <i>Tolypeutes</i>		×									×				
18. <i>Chaetophractus villosus</i>	×		×									×		×	
19. <i>Zaedyus pichiy</i>	×		×					×				×	×	×	
20. <i>Pantera onça mesembrina</i>															
21. <i>Felis</i> sp.					×										
22. <i>Felis concolor</i>			×			×									
23. <i>Lutra</i> sp.							×								
24. <i>Canis (D.) avus</i>			×												
25. Canidae	×		×		×	×		×			×		×		
26. <i>Canis (C.) familiaris</i>					×			×							
27. <i>Equus (Amerhippus)</i>	×														
28. <i>Hippidion</i> sp.	×														
29. <i>Lama (V.) gracilis</i>															
30. <i>Lama guanicoe</i>	×	×	×		×	×	×	×	×	×	×	×	×	×	×
31. <i>Lama</i> sp.	×		×												
32. <i>Macrauchenia</i>	×														
33. <i>Ozotoceros bezoarticus</i>	×		×									×	×	×	
34. Cervidae	×														×
35. Pinnipedia				×											×
36. <i>Dolichotis patagonum</i>	×												×		
37. <i>Lagostomus maximus</i>	×														
38. <i>Lagidium</i> sp.															
39. <i>Ctenomys</i> sp.	×		×		×	×	×	×	×		×		×	×	
40. Pisces				×											
41. <i>Adelomedon brasiliensis</i>	×														×
42. Volutidae	×			×		×	×	×						×	

region. Likewise, in these associations, another species is always present: *Lama guanicoe* (Figs 2b–d).

Fourth, *Hippidion* sp. and *Lama gracilis* (morphotypes of small size) are present exclusively in Late Glacial and Early Holocene Patagonian deposits. In the Pampean region, *Lama gracilis* is found only within deposits that are correlated with the LGM; it is still unknown in archaeological contexts. In the case of *Hippidion*, different species occurred in the Pampa and Patagonia, *H. principale* and *H. saldiasi*, respectively (Alberdi and Prado, 1992). The latter species "... is stratigraphically and geographically restricted to the period between 13,000 and 8500 BP in Patagonian Region". (Alberdi and Prado, 1993: 19).

From these observations, the following remarks concern the regional zooarchaeological analysis for the first interval:

1. From a regional viewpoint in both regions, the recurrence at a suprageneric level of giant sloth, camelids, equids, and flightless birds is seen.

2. From a microregional viewpoint, the recurrence at generic and specific levels of edentates, camelids, equids, and birds is seen.

2a. Giant edentates (armadillos and sloths) have been found only in Pampean archaeological assemblages. Bones of *Glyptodon reticulatus*, *Myiodon* sp., and "*Megatherium australis*" (Menegaz et al., 1989a) were found in Patagonian sites closed to Bahia Sanguineto, although

the association with cultural materials is not reliable (Ameghino, 1902; Outes, 1905). Although these materials never have been considered a result of human occupation related to the exploitation of megamammals, this question should be raised in order to investigate whether or not in southern Extra-andean Patagonia the edentates were available and resources exploited by early hunter-gatherers.

2b. A characteristic association formed by the extinct taxa *Hippidion saldiasi*, *Mylodon* (?) *listai*, *Canis* (*Dusicyon*) *avus*, *Panthera onca mesembrina*, *Canis familiaris* and, likely *Lama oweni*, is present in the archaeological sites of the Magellan area. In the case of Cueva del Medio, the association of felid remains with the human industry is unlikely.

In Fell and Pali Aike caves, the association of canids points out an important issue not yet resolved. Some remains of this family correspond to the domestic species *Canis familiaris*. The wild canids seem to have been important resources (economic or symbolic), but also appear as relevant indicators of exchange in social communication. It is assumed that during the first interval, the societies of the Magellan area had colonized it and maintained a wide network of communication with their neighbours on the Central Plateau of the Santa Cruz province. However, the artifacts of different contexts from both microregions support this assumption (Bird, 1993; Nami, 1987; Cardich, 1987; Massone, 1987; Miotti, 1993a, b).

This strategy would be useful in an environment socially unfilled, where the territories were still wide, but the social groups of colonizers had exclusive systems (Gamble, 1993).

2c. *Lama (Vicugna) gracilis* is present only in the archaeological contexts of the Patagonian Plateau. In the Pampean region, this species has been recovered only from palaeontological sites (Menegaz et al., 1989b), corresponding to the LGM period which is not synchronous with the earliest human occupations in the area. Therefore, the species was not available in the Pampean area when the pioneer hunter-gatherer groups arrived but was available during the first interval in the Central Plateau.

2d. *Lama guanicoe* (guanaco) is the only recurrent species in all the studied contexts for the first interval (Fig. 2b–d). In the second interval, guanaco is absent at Túnel I, First Component. While this occupation was interpreted by Piana (1984) as a brief stay of a hunter-gatherer crew who arrived at the Beagle Channel coast looking for guanaco, the faunal remains suggest the consumption of scarce marine resources.

2e. Remains of *Lama oweni*, a large-sized camelid, were recorded only in the Magellan area around 10,000 years BP. In the archaeological levels of Los Toldos (sites 10, 11, Table 2), both remains of a remarkable large size were found and they originally identified as *Lama guanicoe* (Miotti, 1986, 1989).

2f. The taxa of birds (4) to (7) in Table 2 indicate the same tendency to decrease: they are more abundant in the first interval than in the second one (Fig. 2a). This effect is remarkable because *Eudromia*, *Nothura* and *Fulica* (partridges and like-hens) are potential food resources. Bones of small birds like partridges and owls have been employed as funerary offerings, such as at Arroyo Seco 2, where *Speotyto cunicularia* and *Nothura maculosa* were associated with human burials (Fidalgo et al., 1986).

The Rheidae family forms a higher proportion in the first interval than in the second one (Fig. 2a). Specimens of Rheidae (egg shells and bones) were found in Pampean and Patagonian contexts and assigned to *Pterocnemia pennata* and *Rhea americana*. In the first period, both species would have been available resources in southern Patagonia. *Rhea americana* was present in Patagonia to 9.0 ka BP. However, after that time *Pterocnemia pennata* filled the ecological niche of *R. americana*, due to the displacement of this latter species towards the north (Cardich and Miotti, 1983; Tambussi and Tonni, 1985; Salemme and Miotti, 1987); this displacement occurred during the second interval (Fig. 2c). *Pterocnemia* is absent in Pampean archaeological sites and from the Pampa today. Both flightless species have been exploited by hunter-gatherers for consumption, bone raw material and feathers.

3. A living species of Cervidae, *Ozotoceros bezoarticus*, was recorded only in Pampean palaeontological and archaeological contexts, all of them Holocene in age (Fig. 2b); "its presence in pre-Holocene sediments is still rather uncertain" (Menegaz and Tonni, 1985: 46). No findings of this species have been reported from Patagonia, neither in Late Pleistocene nor Holocene contexts.

4. The Canidae family has been recorded in different contexts, in a few cases identified at a genus level. Some of the records correspond to *Canis* (*Dusicyon*) *avus*, a big canid species that existed during the Late Pleistocene to the Late Holocene (after 4.5 ka BP) in sites of both regions (Patagonia, in Punta Bustamante (Miotti, 1989) and Pampa, in Zanjón Seco 2 (Tonni and Politis, 1981)). These records are reliable indicators of cold, arid micro-regional and regional environments (Berman and Tonni, 1985; Miotti and Berman, 1988).

5. Pinnipedia occurs in two sites of both regions but only in the second interval, La Olla and Túnel I. A marine mammal bone comes from the first component of Las Buitreras Cave, but its association is not reliable (Scillato Yané, 1976; Caviglia et al., 1986; Mengoni Goñalons, 1986). In both coastal sites, marine mammal remains are associated with land mammals and birds. In La Olla and Túnel I, marine mammals were the basic economic resources: meat, fat, skins and bones were utilized.

6. Valves of marine mollusks (bivalves and snails) in continental sites (some of them caves) undoubtedly are

products of anthropic action. Their occurrences have a similar frequency in contexts of both intervals and macro-regions (Fig. 2a). For the first interval, the specimens of Volutidae are more abundant than in the second one. These specimens could be the result of exchange with coastal groups or due to the mobility of hunter-gatherers. In any case, they were used as funeral offerings in the inland sites, as evidenced by a human burial from Arroyo Seco 2, where a specimen of *Amiantis* sp. was found.

Marine mollusk remains are occasional in almost all contexts; hence, they would not be potential dietary resources, with the exception of Túnel I. This site is a shell midden where most of the valves (*Mytilus* sp. and *Aulacomya* sp.) are the result of consumption. The idea of exchange and ceremonial goods should be investigated and these resources re-analyzed as items of social communication between marine littoral and inland as a way of information flow about environments, societies, territories, and availability of different resources.

4. Discussion

The *regional analysis* indicates the recurrence of several taxa in Pampean and Patagonian archaeological sites inhabited between 13.0 and 8.5 ka BP (Table 2). This recurrence probably is due to similar adaptive strategies: forager (Binford, 1980; Stanford, 1991) or generalist (Smith, 1975) in the management of faunal resources. The availability of certain species implies equivalent environmental conditions.

According to the *contextual analysis*, several characteristics (e.g., certain skeletal parts, concentrations of bones, bones anatomically connected, spatial distribution) are used to explain the activities at the sites and classify them as kill site, butchering site, and sites of qualified activities and multiple activities (see Table 1).

The studied assemblages represent the hierarchical use of space developed by the groups of hunter-gatherers who colonized Pampa and Patagonia during the first interval. These people, primarily hunters, may have supplemented their subsistence through gathering. However, at Monte Verde (Fig. 1), hunting resources were minimum in the economy with the emphasis on the vegetable resources of the woodland (Dillehay, 1986).

Little can be stated about the utilization of smaller mammals and plants in the localities of Pampa and Patagonia. One of the reasons is related to the data about the first colonizers (First interval). These data are limited to a few sites or site components and careful evaluation indicates great archaeological variability in terms of tasks and function (Table 1). Another reason is that not all sites were excavated and studied under the same methodology and objectives. Several areas are lacking research with emphasis in geoarchaeology,

pedology, quantitative zooarchaeology, phytolith studies, palaeoecology, palynology, and radiocarbon dating.

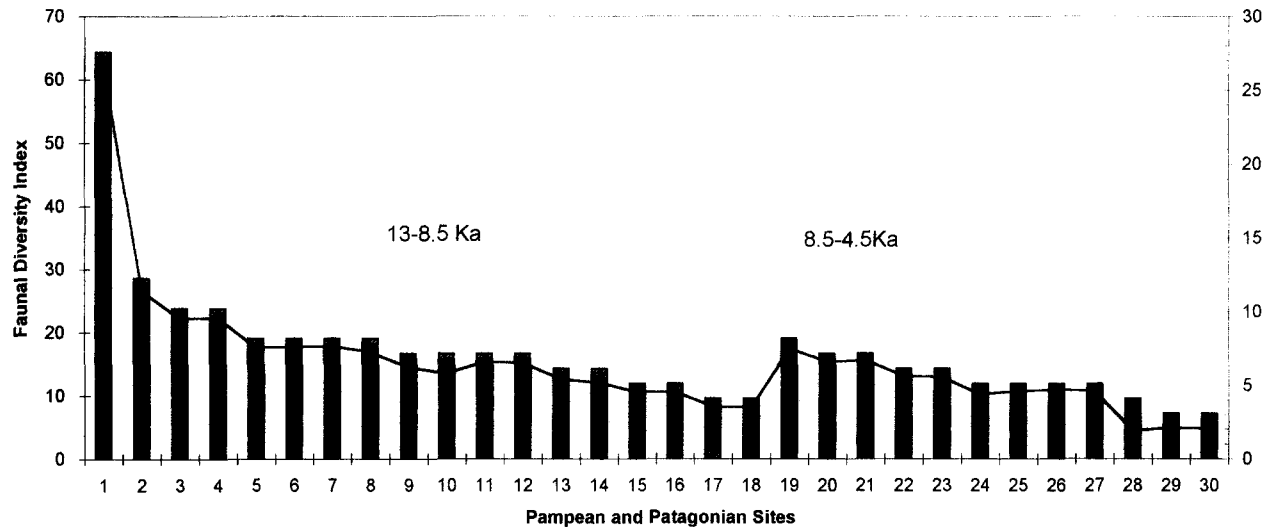
For the second interval, the contextual analysis suggests that both regions were fully occupied, although it is not clear if the social groups were “culturally” different from those of the first interval or whether they are the result of local evolution. However, the subsistence strategies seem to be different and more specific than in the previous period, as inferred from the decrease of faunal diversity after 8.5 ka BP (Fig. 3a, b).

The exploitation of the species *Lama guanicoe* is unquestionable during the two intervals (see taxon 30 in Fig. 2a). Researchers of each site have formulated the utility of guanaco as the main economic resource due to this species is the best represented and its flexibility in terms of hunting strategies, i.e., individual or communal hunts. Ethnohistorical information obtained from Patagonia indicates that the guanaco was a food resource even in critical seasons, when its meat could be eaten as “charqui” (dry and salty meat), prepared during spring/summer for periods of scarcity and stored for a long time (Miotti, 1989, and the bibliography cited there).

During the first interval in Patagonia, besides the guanaco, an extinct species of small camelid (*Lama (Vicugna) gracilis*) was exploited as well. Larger-sized camelids (*Lama oweni*) could have been a potential resource (Fig. 2c). The recent revision of this taxa (Menegaz et al., 1989b), assigned to an extinct species, negated the hypothesis of guanaco individuals of exceptional size. On the other hand, in the Pampean region, only the guanaco seems to have been exploited. *Lama (Vicugna) gracilis* has not been found in an archaeological context and the remains of the large and extinct species *Hemiauchenia paradoxa* found in Arroyo Seco Site 2 are not culturally modified. Nevertheless, this extinct camelid co-inhabited the Pampa and was a potential resource available for Pampean hunter-gatherers (Fig. 2b).

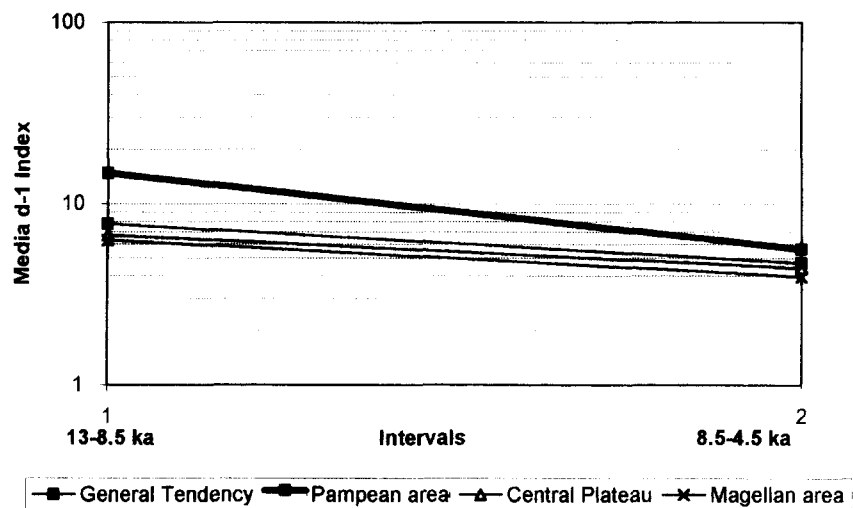
The evidence suggests that other species of the extinct megaherbivore fauna would have been a part of the hunters economy in Pampa and Patagonia during the Late Pleistocene and Early Holocene. Miotti et al. (1988) have stated that in spite of the scarce record of these megamammals in each site, some species were used as economic resources, primarily as food. Taking into account new zooarchaeological findings and more refined analyses developed in both regions, this hypothesis needs to be tested. In addition, in the first interval, another hypothesis to test is that the people used a wider range of faunistic resources than during the second interval (Fig. 2a–d).

The use of Pleistocene megamammals by the earliest hunters is in a differential and selected way in the regions under study. The most evolved animals seem to have been the equids and the giant sloths in Pampa and Patagonia as well, although there are differences in the



(a) Histogram: %Nspecies Index Line: d-1 Index

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(b)

Fig. 3. Faunal diversity during the first and second intervals: a. Expressed at percental species in each site (% Nsp.) and Simpson Index (d-1). b. General and regional faunal tendency as media of d-1.

genus and/or species. *Mylodon (?) listai* is the more representative species in Southern Patagonia, whereas *Mylodon* sp. was present in the Pampas, where it may have been another, bigger species.

South of the Río Santa Cruz, *Mylodon (?) listai* would have been used for consumption (Fig. 2d). In the Pampean sites (Arroyo Seco 2 and La Moderna) the data do not indicate consumption of mylodons. However, in the Pampean region, a larger edentat (*Megatherium americanum*) seems to have been consumed at Arroyo Seco Site 2, as indicated by cutmarks recorded on several bones (Politis, 1984; Fig. 2b). Small dermal bones from the hides

of mylodons have been found in the Pampean sites, associated with the archaeological context. But this evidence is not strong enough to formulate the use of the skins of those animals, because the characteristics of the dermal bones themselves (round, small, light) made them easy to roll. The association of these bones could be a result of natural deposition.

In summary, it is difficult to establish with the available evidence, whether the mylodons were hunted or not by the hunters at the end of the Pleistocene and beginning of the Holocene. However, the hypothesis of "scavenging" is highly probable, based on various Patagonian

sites. Isolated findings of extinct fauna only testify to its presence, and possibly its contemporaneity with ancient people, but its use cannot always be proved.

Glyptodons were only found in Patagonian palaeontological sites, but in the Pampean contexts they were associated with cultural remains. Four species of *Glyptodon* were recorded from those sites and at least two of them used as economic resources: a) *Doedicurus clavicaudatus* in La Moderna, employed for consumption; b) *Glyptodon* sp., represented in Arroyo Seco 2 by a scute associated with a human skeleton, as a funerary good, and c) *Sclerocalyptus* sp. (found in La Moderna) and *Eutatus sequini* (recorded in Cerro La China 1 and Arroyo Seco 2), which do not show evidence of anthropic action (Flegenheimer, 1980; Politis, 1985; Fig. 2b).

The *Glyptodon* scute could have been collected without implying necessarily that the animal was hunted. However, palaeontological associations and radiocarbon dates from Arroyo Seco and other Pampean sites indicate that several species of *Glyptodon* were living around 10 ka BP in the Pampas (Politis et al., 1987; Politis, 1989). These edentates were a potential regional resource.

Evidence of consumption of equids has been verified through cutmarks present on bones both in Patagonia and Pampa, although they belong to different genera and species. Pampean hunters killed larger-sized equids, *Equus* (*Amerhippus*) and *Hippidion* cf. *principale*, whereas Patagonian hunters used the smaller species, *Hippidion saldiassi*. The selection of one or the other is explained by the availability of the species in each region (Fig. 2b, d).

The presence of carnivores in the archaeological record is due to anthropic and/or natural agents. *Canis* (*Dusicyon*) *avus* is associated with Pleistocene megaherbivores, although at a low proportion in a few sites. This species seems to have been exploited for its pelt and/or as a food source, based on a probable cutmark in a hemimandible of that canid (Mengoni Goñalons, 1988) Tres Arroyos I. Although extinct now, *Canis* (*Dusicyon*) *avus* seems to have survived during the Holocene, both in Pampa and Patagonia (Tonni and Politis, 1981; Berman and Tonni, 1985; Mansur, 1987; Miotti and Berman, 1988; Miotti, 1989).

Numerous canines from unidentified canids were found in the Lower Component of Arroyo Seco Site 2 (Fidalgo et al., 1986; Politis et al., 1987; Politis, 1989). They were arranged as funerary goods, forming a necklace and bracelets on a human skeleton. Only two bones identified as Canidae come from this component away from the burials. Canids at Arroyo Seco 2 were important economically, not only as a food resource.

Evidence of anthropic action with felids is not present in any of the analyzed components. Moreover, its record in archaeological contexts suggests that the association is due to natural causes. It implies its contemporaneity with humans, as in Cueva del Medio, where remains of

Smilodon seems not to be synchronous with the first human occupation in the site. Nami (1987) has published a ^{14}C date of 12.3 ka BP on a charcoal sample associated with these remains. However, this date is much older than the ones obtained for the first component (around 10.5 ka). Nami (1987) points out that this date indicates a high antiquity for the region. In the Central Plateau of Santa Cruz province, an age of 12.6 ka BP dates the Level 11 Industry in Los Toldos Cave 3 (Cardich et al., 1973). Cardich (1979), based on the analysis of rock art from El Ceibo Cave 6B, assigned one of the pictures to a giant subspecies of jaguar, that could have inhabited Patagonia from 13 to 10 ka BP. Craneal remains and pieces of skin obtained by Hauthal in 1885 from the area of Ultima Esperanza (Chile) were determined by Cabrera (1934) as *Panthera onça mesembrina*. The palaeontological and palaeoenvironmental data presented by Cardich (1979) are highly significant in terms of relating the rock art with the information coming from Ultima Esperanza and Cueva del Medio.

Generally, the preservation of bird bones is rather difficult because of the bone structure itself. However, several remains of small birds have been found related to human burials (Fidalgo et al., 1986). Likewise, based on the tendencies obtained from the different studied regions (Fig. 3b), in the faunal analysis referred to the earliest occupations, each author has emphasized the megamammal remains and ignored those of the minor fauna. This bias has emphasized even more the apparent relevance that the megaherbivores would have had in the prehistoric economy. The information from present hunter-gatherers details the importance of birds in social life, as food as well as exchange goods. Feathers are employed in dress, religious ceremonies, or totemic clan activities.

In the last excavations in continental Patagonia, larger quantities of middle-sized birds (e.g. partridges) have been recorded in several archaeological components corresponding to the first interval (Miotti, 1995, 1996). Large flightless birds from the Rheidae family constitute a particular case. The presence of the two species (*Rhea americana* and *Pterocnemia pennata*) at different times in Patagonia have been used as a palaeoclimatological indicator. Regarding the utility of those rheids as a food resource, the ethnohistorical and ethnographical data suggest that the Pampean and Patagonian hunters' had a preference for the meat and fat of the "ñandú" (Miotti, 1989). However, and paradoxically, the bone records of these species are scarce; usually, shell-eggs that can be identified only in the family level (Rheidae) are what is recovered. The exception is the Lower Component of AEP1, where the NISP of *Pterocnemia* is 30 and *Rhea* climbs to 15 (Miotti et al., 1994). A plausible explanation may be the type of sites analyzed here (Table 1) as the European voyagers mentioned that usually the hunting and consumption of "ñandúes" took place in the sites

where guanacos were killed (Miotti, 1989). But in this study, no evidence is available to assign any of the sites to a guanaco kill site.

Conclusions

Regional differences and similarities are the result of the presence or absence of one taxa or a group of taxa in the different components of archaeological sites which are interpreted through the following hypotheses:

H1. Differences and similarities are the result of regional palaeoecological characteristics.

H2. Differences and similarities are the result of anthropic action (resource management: selectivity, technology, taboos).

2.1. Economic resource (food, clothes, housing, tools).

2.2. Constant flow of communication (environmental and social information).

2.3. Symbolic objects (i.e. funerary goods, art, religion).

Most of the taxonomic differences at the specific level are interpreted according to H1. The taxonomic similarities in the supraspecific and specific levels are interpreted following the statements in the frame of H2.

The contexts of first inhabitants (First interval: 13–8.5 ka BP), suggest that those societies explored and colonized the ample territories of Pampa and Patagonia. This *Colonization Phase* shows a greater faunal diversity than those contexts from the *Consolidation Phase* (second interval: 8.5–4.5 ka BP), based on birds, megamammals and large mammals that were considered the best potential economic resource.

Before 8.5 ka in both ecological areas of Southern Patagonia, the diversity of megaherbivores (i.e. *Mylodon* sp., *Hippidion* sp.), large-sized herbivores (i.e. *Lama guanicoe*, probably *L. oweni* and *Rheids*), and medium-sized herbivores (i.e. *Lama gracilis*), is greater than the variety recorded during the Middle Holocene. These differences are interpreted as a result of a transitional period of more temperate environmental conditions than during the rest of the Holocene. This difference is more marked in the central Santa Cruz plateau, where besides the grazer megamammals, *Rhea americana* was also recorded. The presence of this species in such high latitudes has been explained as a palaeoclimatological indicator (Tambussi and Tonni, 1985). Likewise, the palynological (Markgraf, 1986; Heusser, 1983; Heusser and Rabassa, 1987), palaeontological and geological data (Tonni and Fidalgo, 1978; Rabassa, 1987; Rabassa et al., 1989; Codignotto et al., 1990; Isla, 1989; Quattrocchio et al., 1993) enhance the hypothesis of a climate amelioration in both studied regions for, at least, the period between 10.2 and 9.0 ka. This amelioration allowed the expansion of the forest ecosystems in the Andean Cordillera and Southern Tierra del Fuego.

In agreement with H2, the economy of colonizer hunter-gatherers was that of generalist in *Pampa* (Inter-serrana area) and *Patagonia* (Central Plateau of Santa Cruz province and Magellan zone). They developed adequate strategies to exploit a wide range of animals, according to the ecological and environmental conditions, as demonstrated through the faunal remains. Even though the technology is not very similar in both regions, the functions of the instruments are recurrent, as scrapers, projectile points and to a lesser extent, bola stones.

The guanaco was, in all cases, the main resource; characteristics of this species permitted flexible hunting techniques. The extinct megamammals probably required alternatives in the chase practices and other factors may have had a certain influence in their management (e.g. size, mobility territories, refuge places). It is highly significant that the proportion of Pleistocene megamammals (except for the equids) are lower than that of the guanaco. If they were used in the hunter diet, the reason for the scarcity of extinct megamammal remains in the archaeological record has not been addressed adequately. Some of the answers could be explained in this way:

a. The numerical retreat in the population of Pleistocene species would suggest the absence of large communities of these species near the sites;

b. inadequate hunting techniques or an unawareness of these techniques;

c. occasional supply of dead animals (scavenging);

d. cultural taboos;

Possibilities b, c, and d probably cannot be proven, due to the lack of supporting evidence, but all of them should be investigated.

Even though the human population could be low and the environment was not saturated (Miotti, 1989, 1993a), the high frequency of sites with abundant guanaco remains suggest an excellent knowledge in the management of this camelid and difficulties of handling at least the largest megamammals, for example: habits, the size of the preys, among others. Then we assume the alternative "a" could be the more reliable.

Likewise, it is suggested that horses could be managed with similar hunting techniques to that of the guanaco, although they were species of larger size but similar behaviour, as they are herd animals. *Hippidion* could have been, at least in Patagonia, profitted like the camelids (Nami and Menegaz, 1991).

1) Although people were contemporaneous with different species of the "Pleistocene megafauna", they were not a limiting factor in their extinction (Politis et al., 1995). The Pampean and Patagonian hunter-gatherers during the *Colonization Phase* had a generalist economy, mainly with emphasis on the chase of guanaco (*Lama guanicoe*) and, secondarily on the extinct horses and birds, as indicated in the earliest occupations. Colonizers

would have taken advantage of other extinct megamammals as a complementary resource (*Mylodon*, *Megatherium*, *Glyptodon*; as it is formulated in H2-2.1).

2) The survival of extinct megafauna that flourished in Late Pleistocene times is confirmed at least until 9.5 ka in Patagonia and 8.5 ka in the Pampean region (Menegaz et al., 1989a; Salemme, 1990; Miotti, 1993; Politis et al., 1995). The frequency and diversity, however, decreased significantly from that detected in Late Glacial deposits. The extinct canid *Canis (D.) avus* seems to have survived until the Late Holocene in both regions.

3) The studied contexts come from Late Glacial and Early Holocene deposits. The interval taken (13–8.5 ka) has been treated as a unit, according to the faunal associations and environmental conditions. Those sites referred to the Late Pleistocene or to the Early Holocene depend on factors and criteria used in the definition of that boundary. The Pleistocene–Holocene boundary must be considered regionally as a transitional interval more than a boundary. In this period, dramatic changes occurred and the faunal components indicate environmental stress (Broecker and Denton, 1990). At the end of this interval, 21 species of megamammals and large mammals disappeared in both regions. Likewise, it was the time of the colonization of Southern South America. The taxonomic diversity and richness in both regions was still larger than during the next interval (Middle Holocene). Therefore, generalist economic strategies for the colonizers are suggested.

4) Since 8.5 ka, the hunters changed with the disappearance of those species and turned to an adaptive process towards more arid environmental conditions, where the availability of faunal resources offered a smaller variety. The guanaco became the dominant game animal in both Patagonia and Pampa Regions, but birds also were important resources. Between 8.5–4.5 ka, two events occurred that affected the hunter-gatherer economies:

4a) Relative sea-level has risen to positions similar to the present ca. 8 ka (Isla, 1989; Gordillo et al., 1992); thus, the available terrestrial surface would have diminished compared with LGM times and climate had improved, as showed by sea-level rise. This change might explain in part the impoverishment of the palaeoecosystems, although this impoverishment was balanced by the increase in the number of individuals, specially of two species (guanaco and ñandú) of interest for human beings.

4b) The physical territory was saturated by societies which had increased everywhere in the Patagonian and Pampean territories. Environmental changes needed a more specialized economic strategy. The more important species were *Lama guanicoe* and *Rhea* or *Pterocnemia* (ecological niche equivalents in each region).

A sensible reduction in the taxonomic diversity implies the development of more specialized economic strategies

focused on just a few taxa. The hilly and interrange areas of the Pampean region show a greater diversity compared with both microregions in Patagonia (Fig. 2b–d). This diversity suggests that in both intervals, the Pampas would have been potentially richer than the southernmost regions.

A greater diversity occurs in the extra-andean Patagonia than in the Andean Cordillera and the Fuegian-Magellan area (presently, steppe and open forest; Fig. 2c, d). Furthermore, differences exist in the ecological equivalents of horses and camelids. Those from the first interval in the Central Plateau correspond to smaller species of gramineous steppe whereas in the Magellan area, the individuals are larger. Probably, differences in the vegetation and a more rigorous climate existed, as it does today, between the two microregions. Rheids of large size recorded in the Central Plateau testify to a more favourable environment for the first interval whereas their absence indicates a more eremic conditions for the second.

Finally, both proposed hypotheses are not exclusive but, on the contrary, one explanation (H1) involves the other (H2), and vice versa. The presence of certain species in a certain area are those animals available as a faunal resource that the *generalists* of the *Colonization Phase* (First Interval), and later on, the *specialists* during the *Territorial Consolidation Phase* (Second Interval) could have considered in managing their subsistence economies.

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