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## HUMAN PREDATION AND NATURAL HISTORY OF HUEMUL (CERVIDAE; *HIPPOCAMELUS BISULCUS* MOLINA) IN PATAGONIA: A ZOOARCHAEOLOGICAL ANALYSIS

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We use published zooarchaeological evidence to discuss the various hypotheses concerning the past distribution of huemuls in Patagonia, southern South America. We then use these data to evaluate the interactions between this cervid and hunter-gatherers during the Holocene. The zooarchaeological record shows that huemul mainly inhabited forested and forest-steppe ecotonal environments during the Holocene. Huemul were hunted in exceptional circumstances during the early occupation of Patagonia. Its presence in the zooarchaeological record of South Patagonia increases after 9500 BP and is more frequent after 2200 BP. However, the taxonomic contribution of the species' bone remains to the archaeological record is always low. The few assemblages where there are a high number of huemul bones would have been the result of opportunistic hunting episodes. This in turn suggests that hunting of huemul had little or no influence on the animal's regional distribution over time. However, the progressively greater human presence in some forested areas towards the end of the Holocene could have affected huemul populations at the local scale. The zooarchaeological information presented in this paper illustrates interspecific and long-term relationships and, hence, could serve as essential information in future management strategies for huemul in Argentina and Chile.

**Keywords:** zooarchaeology, *Hippocamelus bisulcus*, Patagonia, chorology, conservation biology

En este trabajo se utiliza la evidencia zooarqueológica publicada con el fin de discutir las hipótesis propuestas en la bibliografía sobre la distribución pasada del huemul en Patagonia, sur de Sudamérica. Se evalúa si las interacciones entre este cérvido y las poblaciones de cazadores recolectores del Holoceno incidieron de alguna manera sobre los primeros. Los resultados muestran que el huemul no fue incluido como presa desde los primeros momentos de ocupación de un área. Su representación zooarqueológica aumenta en los depósitos de Patagonia Sur a partir de 9.500 y son sensiblemente más abundantes para 2.200 años AP. Sin embargo, la contribución taxonómica de la especie al registro zooarqueológico es siempre baja. El registro zooarqueológico es concordante con una distribución pasada en la que los ambientes boscosos y el ecotono bosque-estepa serían los dominantes para esta especie. Los escasos registros en los que hay mayor frecuencia de restos de la especie corresponderían a eventos de caza oportunista, por lo que se sugiere que la predación de los cazadores recolectores habría tenido escasa o nula influencia sobre la distribución de la especie a una escala regional. La información zooarqueológica presentada ilustra las relaciones interespecíficas en el largo plazo y, por lo tanto, constituye una herramienta esencial para enriquecer las estrategias de manejo futuras para la especie en Argentina y Chile.

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## Introduction

Understanding animal natural history is essential for making sound management and conservation decisions (Frazier 2007; Lyman and Cannon 2004; Wolverton and Lyman 2012). As a result, archaeologists, historians, biologists, and ecologists strive to estimate past species distribution, changes in habitat, and the role of human populations in relation to these attributes. The zooarchaeological record can tease out long-term trends in these patterns that cover timescales beyond the reach of ecological studies or can reveal more specific events than those recorded in historical sources. This makes zooarchaeological studies a valuable asset for biological conservation (e.g., Braje and Rick 2011; Frazier 2007, 2010; Kay and Simmons 2002; Lyman and Cannon 2004; Rick and Erlandson 2008; Wolverton and Lyman 2012).

During the last decade, zooarchaeologists working in Patagonia have contributed to this large literature on conservation zooarchaeology. Specially, they have studied the impact of human populations on regional fauna, the distribution of particular species, and their morphological changes through time (Cruz 2001; Cruz et al. 2015; L'Heureux 2008; Scartascini and Volpedo 2013; Zangrando and Martinoli 2011). One such animal that has been the focus of biological and conservation studies in Patagonia is the cervid, huemul (*Hippocamelus bisulcus*, Molina) (e.g., Flueck and Smith-Flueck 2012; Vila et al. 2005). Huemul is endemic to the sub-Antarctic forests of Argentina and Chile (Cabrera 1957; Díaz 1993, 2000; Serret 2001; Vila et al. 2006). Since the arrival of Europeans in South America, its historical range has been reduced by half (Vila et al. 2005, 2006) due to habitat destruction and increased hunting pressure (Serret 2001; Smith-Flueck 2000). As a result, in 1996, several organizations placed huemul on the endangered list, including the *International Union for the Conservation of Nature* (IUCN 2014), the *Regional Patagonian Assessing Council for Wild Fauna* (CARPFS 1995), the *Red Book of Endangered Mammals of Argentina* (Díaz and Ojeda 2000), and the *Red Book of Terrestrial Vertebrates of Chile* (Glade 1988). It is the only South American cervid that is considered to be endangered and its numbers are waning (IUCN 2014). In Argentina, Federal Law 24.702/96 declared them a "natural treasure"; this represents the highest degree of legal protection that a species can have. This cervid is also listed in the *Convention on International Trade in Endangered Species of Wild Fauna and Flora* (Appendix 1, CITES 2013) and the *Convention on Conservation of Migratory Species of Wild Animals* (Appendix 1, CMS 2012), since it normally moves between Argentina and Chile. The endangered status of the huemul has triggered a strong interest in understanding its biology and especially its interaction with humans as a way to improve huemul management decisions and its conservation (e.g., Aldridge 1988; Frid 1994; Marín et al. 2013; Povilitis 1978; Smith-Flueck and Flueck 2001).

The conservation and management plans for the huemul in Argentina (2002) and Chile (2008-2012) explicitly recognize the importance of understanding the historical distribution of the huemul. In particular, the plans note the importance of comparing this historical information to modern huemul distributions and the location of their present-day optimal habitat. As is stated in the conservation and management plan in Argentina (Plan Nacional 2002), overlap between these data

could potentially allow us to identify areas suitable for huemuls and thereby determine and evaluate the possible causes behind the local extinction of sub-populations. Furthermore, this long-term analysis will also provide data useful for huemul rescue, translocation, and re-introduction (Plan Nacional 2002).

Fifteen years of zooarchaeological investigations in Patagonia have revealed a range of information about huemul ecology and human use throughout the Holocene. In general, it has been demonstrated that Patagonian hunter-gatherers relied on a limited number of medium-large ungulate species, including the huemul, in the context of an overall low diversity of medium-large ungulates (Redford and Eisenberg 1992). During the Holocene, the guanaco (*Lama guanicoe* Müller), an ungulate of the camelid family (averaging 80-100 kg), and pinnipeds (averaging 50-300 kg; *Otaria flavescens* Shaw and *Arctocephalus australis* Zimmermann) were the main prey for Patagonian hunters (Borrero 1999, 2013; Muñoz 2011). Other prey included the lesser rhea (*Rhea pennata* D'Orbigny), a flightless bird of the Ratites family (averaging 17-27 kg).

Typically, zooarchaeological analyses have focused on the local level, with the goal of understanding the hunting of huemul (e.g., De Nigris 2004a, 2004b; Fernández 2008, 2010; Legoupil 2000; Mena 1992; San Román et al. 2002). Some specific methodological tools have also been developed as an aid to understanding the dietary contribution of huemul as represented in the zooarchaeological record (Belardi and Gómez Otero 1998). A number of studies discuss the huemul zooarchaeological evidence within a conservation framework, with contributions from taphonomy (Fernández and Forlano 2009) and isotope ecology (Barberena et al. 2011; Méndez et al. 2014; Tessone et al. 2014). Finally, several hypotheses dealing with huemul historical distribution have been offered by researchers (Díaz 2000; Flueck and Smith-Flueck 2012; Serret 2001; Vila et al. 2005), with the aim of improving management decisions.

In this article, we analyze previously published information on huemul remains found in archaeological and paleontological contexts across Patagonia. This analysis is directed toward evaluating competing hypotheses about huemul past distribution. In particular, we analyze spatial and temporal fluctuations in this cervid's distribution and explore huemul/hunter-gatherer interactions during the Holocene. Our results indicate that huemul contribution to human subsistence in Patagonia was minimal during that time period, that there is no hunting pressure and/or overkill evidence and, therefore, hunter-gatherer predation did not impinge on the species' past distribution. By providing a long-term and spatially explicit record of huemul distribution, this analysis has the potential to contribute to information essential to modern huemul management, as it is required by national conservation agencies of Argentina and Chile (Plan Nacional 2002; Plan Nacional 2008-2012).

## The Huemul

The South American deer genus *Hippocamelus* is comprised of two species, the taruca, sometimes called the North Andean huemul (*Hippocamelus antisensis* D'Orbigny), and the South Andean huemul, or simply, the huemul. The huemul is a medium-sized deer with short legs and a stocky build (Figure 1). Males have small antlers, usually only two points per unit, which are cast annually. Males



Figure 1. Female (top) and male (bottom) *Hippocamelus bisulcus* (Photo: Eduardo Ramilo; Composition: Ana Forlano; Location: Female, Los Glaciares National Park, Argentina, Male, Lago Cochrane National Reserve, Chile).

reach a height of 80-90 cm at the shoulders, and weigh up to 90 kg. Females are more slender and lighter in weight (up to 80 kg) than males. The huemul undertakes altitudinal displacements according to the annual seasons. It is normally a browser, although it can also graze. Huemuls are found generally alone or in groups of two or three individuals. Solitary individuals are more frequently observed than groups of two (male and female couples or a female with a fawn) and three individuals. Nevertheless, on some occasions they are in groups of up to seven. Smaller groups tend to occupy the denser forested areas (Povilitis 1978; Redford and Eisenberg 1992; Vila et al. 2010).

Nowadays this cervid has a wide latitudinal distribution extending along the length of the Patagonian Andes. Huemuls inhabit the forest and forest-steppe ecotone and the forested coasts of the Pacific Ocean (Vila et al. 2006). In Chile, they are found as an isolated population located in the Nevados de Chillán (approximately at 36° 50' S), and then more or less continually between 40° S and the Magellan Strait (53° 50' S). In Argentina, the northern limit of the species is located in the Neuquén Province (40° 9' S), while to the south they are found in the Santa Cruz Province (50° 73' S) (Vila et al. 2006:265). The easternmost limit of the huemul is Cerro Alegre in the Río Negro Province (71° 22' W) (APN-SIB 2014). Huemul populations number between 1000 and 2000 individuals spread across 101 fragmented subpopulations (Vila et al. 2006) with an average density of 1.25 deer/km<sup>2</sup> (Díaz and Smith-Flueck 2000).

### **Hypotheses about Huemul Historical Distribution**

Several researchers have proposed hypotheses about huemul historical distribution based on historical data compiled from reports, chronicles, and narratives by travellers, explorers, and naturalists who visited the Patagonian coasts and hinterland from the mid-sixteenth century onward. Díaz (1990, 1993, 2000) undertook an exhaustive recompilation of this historical information, augmenting it with archaeological data. She proposed two scenarios for the huemul's historical distribution that, with slight variations, have been discussed for the last 25 years. The first one stated that huemuls were originally found throughout all of Patagonia before retreating to the Andean area under pressure from a number of factors that acted in isolation or in combination with other pressures (ecological changes, predation, and the establishment of ranching). The second scenario points out that huemuls inhabited the Andean forests and only occasionally came down to the Atlantic coast, traversing areas inhospitable for the species through river valley corridors (Díaz 1993, 2000). Díaz stated that given the information at hand when this review was done it was not possible to choose between these two scenarios (Díaz 1990, 1993, 2000).

Based on more recent historical data and also oral testimonies and archaeological data, Serret (2001) argues for a more restricted modern distribution than that in the past. He suggests that prior to European colonization of Argentina, the transitional environment between forest and steppe was an optimal habitat for huemuls and that it was there that the largest populations of these animals existed. He posits that their displacement towards the forest occurred as a consequence of the advance of ranching and urbanization.

Vila et al. (2005) also suggested two scenarios for past huemul distribution based on National Parks Administration (Argentina) records, toponyms, and data from more than 70 archaeological sites. The first scenario includes arid Patagonia among the places where huemuls lived, although the authors contend that this may overestimate their range. The second scenario includes the forest and ecotonal areas and suggests the possibility of huemuls entering the arid regions of Argentina via ravines and hydrographic basins. Finally, the most recent proposal about huemul historical distribution (Flueck and Smith-Flueck 2012) suggests huemuls originally occupied the steppe, and from there were displaced towards the forest by the arrival of humans during the Pleistocene-Holocene transition. According to these authors, hunting pressure on the species was so high that it led to the huemul's virtual extinction from the steppe well before the arrival of European colonists.

### Methods

We collated a zooarchaeological database of published information on huemul remains from Argentina and Chile up to 2012. A comprehensive search was conducted on published journal articles and books as well as other bibliographic resources available in Argentina and Chile. Given that the lowest levels of some of the archaeological sites included paleontological material, the database includes a few huemul remains from contexts with no associated human activity. The database includes information on site location, chronology, modern-day environment, and the relative and absolute abundance of huemul remains (NISP [Number of Identified Specimens], and MNI [Minimum Number of Individuals]). We also included entries for Cervidae when the authors stated that these remains were probably huemul.

The database includes all vertebrate remains except rodents. We excluded rodents because these bones are not usually the product of human consumption and because they are not included in many of the published faunal lists. In addition, the incorporation of rodents into the comparative analysis would artificially diminish the relationship between huemuls and the other represented species. We also excluded larger taxonomic categories such as mammals, even when the authors divided them by size (e.g., small, medium, and large mammals), because our aim is to compare the huemul's importance in relation to other species. Finally, given that the samples come from different types of archaeological sites, we considered each stratigraphic unit or deposit with huemul remains as an individual assemblage. In this way, every unit was analyzed independently, even if they came from the same site.

The results of our study are presented in two regional blocks that divided Patagonia in two across the 45° S parallel; this cut coincides with the Northern Patagonian Ice Field in Chile. This partition is justified by the fact that there are different precipitation regimes north and south of this line. The north has Mediterranean characteristics with seasonal rains, while the south has an isohydric regime (Veblen et al. 1996), in which precipitation is distributed across the whole year.

Table 1. Chronological periods used in the analysis of huemul remains compiled data (all uncalibrated dates).

| Period            | Acronym | Chronology (years BP) |
|-------------------|---------|-----------------------|
| Early Holocene 1  | EH1     | 11,700-9950           |
| Early Holocene 2  | EH2     | 9949-8200             |
| Middle Holocene 1 | MH1     | 8199-6200             |
| Middle Holocene 2 | MH2     | 6199-4200             |
| Late Holocene 1   | LH1     | 4199-2200             |
| Late Holocene 2   | LH2     | 2199 to the present   |

The modern environmental context of the archaeological sites includes three different ecosystems: forest, steppe, and forest-steppe ecotone. Although it would have been preferable to include paleo-environmental information, few of the articles provided these data. Since paleo-environmental studies suggest that the forest-steppe ecotone fluctuations that took place since the end of the Pleistocene in Patagonia have to be studied at the local or basin level (e.g., Iglesias et al. 2012), we avoid the use of general paleo-environmental reconstructions. In those cases for which the article does not provide data concerning the modern environment, we located the site on Google Earth to determine current landscape conditions.

We divided the Holocene following Walker et al. (2012), with the addition of subdivisions that permitted a better understanding of possible temporal variations (Table 1). When the published chronology of a given deposit covers more than one of these divisions (e.g., "Holocene" or "6900 to present") then it was excluded for the purposes of the chronological analysis although it was considered in the analysis of taxonomic abundance. Within sites, an undated context between two dated contexts was assigned to the interface between the former and latter periods. This was done on four contexts from the Cerro Casa de Piedra 7 site. In four other contexts (Punta Eugenia 2, Caleta Alonso, Martín Pescador 2, Puesto La Sal) the chronological marker was based on the height of the site above sea level, following the criteria established by the authors (San Román et al. 2002).

## Results

### Spatial Distribution of Deposits with Huemul Remains

According to the analysis of the published data, huemul remains in the archaeological sites are distributed between 38° 53' S and 53° 37' S, covering approximately 1640 km (Figures 2 and 3). We identified a total of 74 archaeological sites with huemul remains, which can be divided into 113 different contexts. Of these, 18 sites (26 contexts) correspond to Northern Patagonia (NISP = 306; Figure 2; Table 2). There is spatial continuity in huemul records from 40° 19' S through to 43° S (Figure 2). These sites are located in the Patagonian Andean forest or in its steppe ecotone. In some of these sites, the huemul was the most highly represented species (e.g., Cerro Pintado and Paredón Lanfré). South of the 43° S parallel there was an approximately 200 km gap in the records until approximately 44° 42' S, representing a virtual vacuum



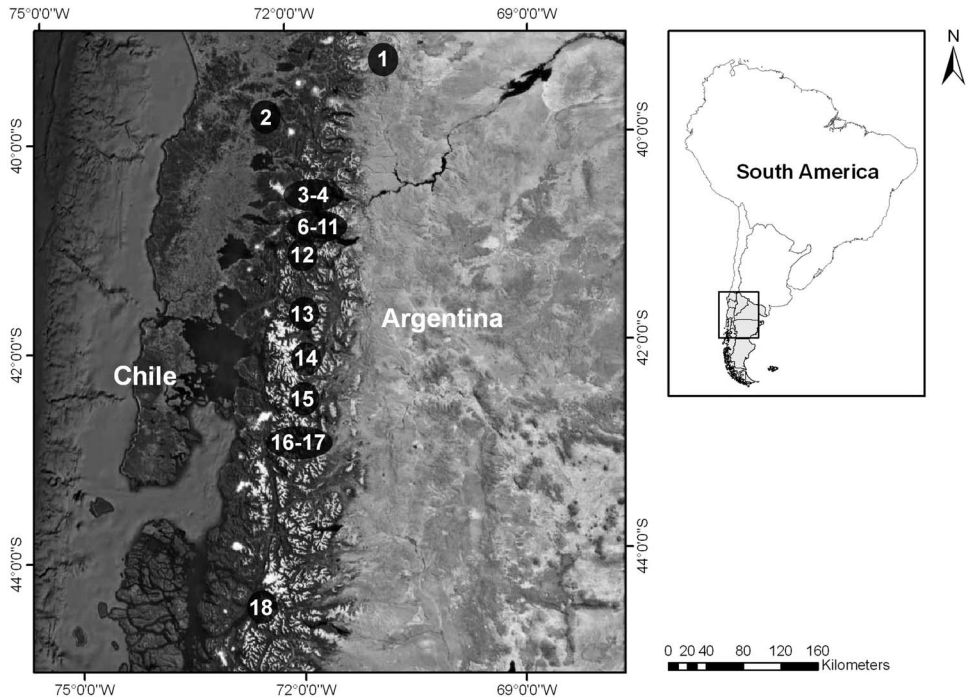


Figure 2. Huemul remains in Northern Patagonia. Site distribution data taken from Table 2.

from a zooarchaeological perspective. In Southern Patagonia the number of huemul contexts is 87 from 56 sites (total NISP = 2510; Table 3). Between  $48^{\circ}$  S and  $51^{\circ} 30'$  S, huemul remains are again absent in archaeological contexts – with the exception of the P35 site, an outlier on the Atlantic coast – which coincided with the Southern Patagonian Ice Field (Figure 3).

Archaeological sites with huemul remains in Northern Patagonia were located exclusively in what is now forest or the forest-steppe ecotone (72% and 28% respectively; Figure 4). In Southern Patagonia, about half of the sites are located in the forest (52%) and 21% are on the forest-steppe ecotone. Two-thirds of the sites located in the forest were alongside or close to the seacoast (24 of 37 sites). There were also 15 sites located in the steppe (27%; Figure 4). Some of these latter sites were relatively close to the present-day forest-steppe ecotone (Figure 3, Map numbers 25, 26, 27, 31, 32, 41, 44, 60, and 65) and some were more than 100 km from the edge of the modern forest (Figure 3, Map numbers 23, 28, 35, 62, 63, and 64).

There are clear differences in the spatial distribution and frequency of huemul specimens between Northern and Southern Patagonia (Tables 2 and 3). Southern Patagonia has more assemblages, a higher total of NISP, and is represented in more diverse environments. Nevertheless, the differences in archaeological visibility, site sampling strategies, bone preservation, and environment between the two regions make it difficult to explain this pattern only in terms of hunter-gatherer behavior.

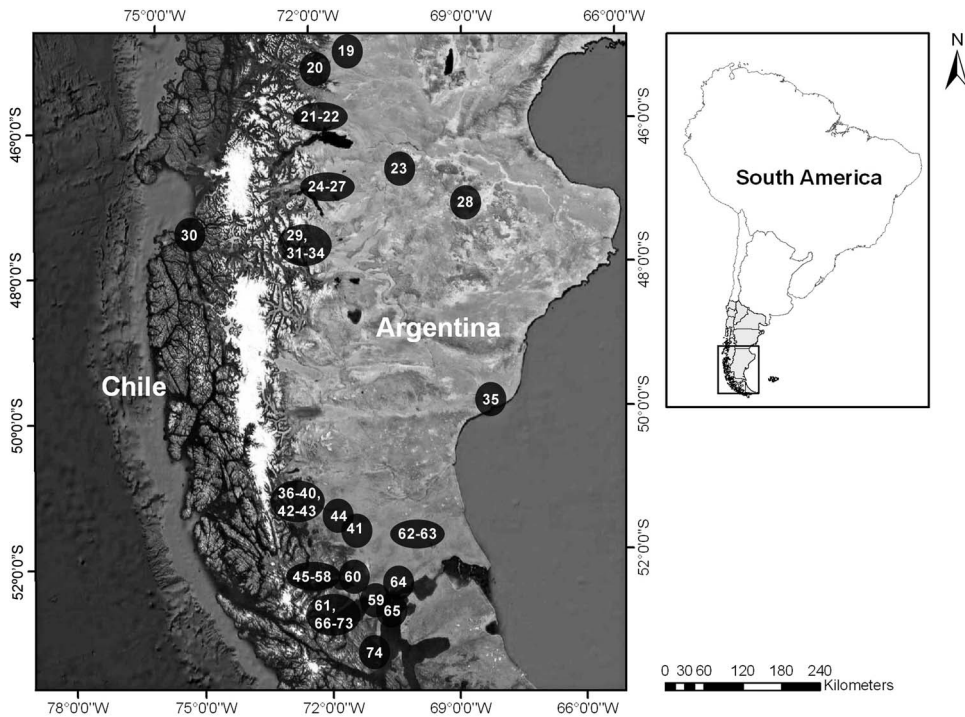


Figure 3. Huemul remains in Southern Patagonia. Site distribution data taken from Table 3.

### Chronological Distribution of Huemul Remains

Huemul remains are recorded from the Pleistocene-Holocene transition to historic times (Figure 5). In Northern Patagonia, the human exploitation of the huemul dates back to the beginning of the Holocene at El Trébol site (Table 2, code 12.3), while in Southern Patagonia, huemul remains are recorded before human presence, as the bones recovered in carnivore dens of Late Pleistocene and EH1 age show (Borrero et al. 1997; Labarca et al. 2008; Martín 2013; Nami and Menegaz 1991). The first evidence of huemul and human presence in Southern Patagonia corresponds to the EH2 chronological period, and was recorded at the Cerro Casa de Piedra 7 (De Nigris et al. 2010) and Cueva Baño Nuevo 1 (Velásquez and Mena 2006) archaeological sites, both located in modern forest-steppe ecotone. In this region there are remains from MH1, a time interlude for which there are no huemul remains in Northern Patagonia. The escalation in the number of sites with huemul remains during the LH2 follows the general increase in the number of archaeological sites during this period (Borrero 1994-95). In Northern Patagonia, this increase was also associated with comparatively more frequent use of the forest, a trend observed for the last 1700 yrs BP (Fernández et al. 2013).

### Taxonomic Abundance

The quantitative data of huemul remains recovered from the archaeological contexts is incomplete. In Northern Patagonia, almost a third of the records do

not present quantitative data, while in Southern Patagonia, 14% of the records are not quantified. This initial bias, which derives from the archaeological research trajectories developed in each area, influences the comparative analyses between both of these regions of Patagonia.

Nevertheless, on the basis of the quantitative data available, it is possible to establish that the taxonomic contribution of huemul remains in the zooarchaeological record of Northern and Southern Patagonia is low. The majority of the contexts contains few huemul specimens ( $N < 40$ ), and thus represents a small proportion of the total NISP (Tables 2 and 3). In Northern Patagonia (Figure 6), more than half of the records ( $N = 11$ ) display a huemul %NISP of less than 17%. Small sample sizes account for huemul remains exceeding 17% of the assemblage composition (general NISP  $< 100$ ,  $N = 6$ ). In Southern Patagonia, huemul contribution to the total NISP is less than 20% in the majority of the records (Figure 7). A similar pattern is seen in the MNI from both areas (Tables 2 and 3). Exceptional bone assemblages dominated by huemul remains (Table 2, code 15.2 and Table 3, codes 21.1 and 21.2) were interpreted as reflecting the differential availability of ungulates (Fernández 2008; Mena 1992; Velásquez and Trejo 2005).

### Discussion

The regional zooarchaeological analysis addressed here allows us to reconsider the extant hypotheses about huemul past distribution. Analysis of the Patagonian zooarchaeological record across the whole of the Holocene shows that the huemul distribution did not include the arid steppe, supporting the second scenario proposed by Vila et al. (2005). The location of archaeological contexts with huemul remains highlights the importance of the forest and ecotones in the past distribution of huemuls. For example, huemul remains are present across the whole sequence of human occupation of the CCP7 site (Map number 34), except for the very beginning of this occupation (c. 10,000 yrs BP), when pollen records indicate a grassy steppe environment (Mancini 2007). This zooarchaeological pattern is consistent with the modern distribution of huemuls (Peri et al. 2013; Vila et al. 2006) and with the isotopic signals that indicate its use of open forest ecotones (Barberena et al. 2011; Méndez et al. 2014; Tessone et al. 2014). We suggest that the few huemul remains discovered far from the forest in Southern Patagonia can be explained by human transportation of antlers and skulls. The antler recovered on the Atlantic coast, at the mouth of the Santa Cruz River, at the P35 archaeological site (Cruz et al. 2010), is a good example of this. Its isotopic signal of  $\delta^{15}\text{N} +0.34$  is similar to those registered for the open forest huemuls (Tessone et al. 2014).

Aside from these cases of human transport, one could argue that the huemul remains that might have been left on the steppe were not preserved (Flueck and Smith-Flueck 2012). However, this seems not to be the case, because huemul bone characteristics (size, morphology and mineral density) are similar to those of guanacos, and this species is represented by hundreds of specimens in nearly all the archaeological sites in Patagonia, both in Argentina and Chile (Emperaire et al. 1963; De Nigris 2004a; Fernández 2010). Therefore, the absence of huemul

Table 2. Huemul remains found in Northern Patagonia archaeological sites.

| Map number | Unit (Site-Level) | Archaeological site | Provenience   | Modern environment | Chronology (years BP)                             | Huemul NISP | Huemul MNI | General NISP | Reference                |
|------------|-------------------|---------------------|---------------|--------------------|---|-------------|------------|--------------|--------------------------|
| 1          | 1                 | Alero IV del Tromen | Neuquén, AR   | Ecotone            | 3890±200<br>4180±530<br>4460±130                  | 1           | 1          | 219          | Perrota and Pereda 1987  |
| 2          | 2                 | Marifilo 1          | X Región, CH  | Forest             | 1410±50 AD  | 5           | 1          | 183          | Velásquez and Adán 2004  |
| 3          | 3                 | Cueva Parque Diana  | Neuquén, AR   | Forest             | 730±80  | 6           | 2          | 16           | Pérez and Batres 2008    |
| 4          | 4.1               | Lago Meliquina      | Neuquén, AR   | Forest             | 730±80  | 5           | 2          | 10           | Pérez and Batres 2008    |
| 4          | 4.2               | Lago Meliquina      | Neuquén, AR   | Forest             | 750±50  | 9           | 2          | 16           | Pérez and Batres 2008    |
| 5          | 5.1               | Alero Larivière     | Neuquén, AR   | Forest             | 920±60  | Present     | ND         | ND           | Silveira 1999            |
| 5          | 5.2               | Alero Larivière     | Neuquén, AR   | Forest             | 2760±80   | Present     | ND         | ND           | Silveira 1999            |
| 6          | 6                 | Alero Las Mellizas  | Neuquén, AR   | Forest             | 780±50  | Present     | ND         | ND           | Silveira 1982            |
| 7          | 7.1               | Alero Los Cipreses  | Neuquén, AR   | Forest             | 590±90  | Present     | ND         | 22           | Silveira 1996            |
| 7          | 7.2               | Alero Los Cipreses  | Neuquén, AR   | Forest             | 2890±100<br>3490±80                               | Present     | ND         | 104          | Silveira 1996            |
| 8          | 8                 | Alero Cicuta        | Neuquén, AR   | Ecotone            | 840±90<br>1510±90                                 | 1           | 1          | 13           | Silveira 1999            |
| 9          | 9.1               | Traul I             | Neuquén, AR   | Ecotone            | 1080±50<br>1370±55                                | 9           | 1          | 278          | Cordero 2010             |
| 9          | 9.2               | Traul I             | Neuquén, AR   | Ecotone            | 2230±40<br>2720±40                                | 2           | 1          | 1606         | Cordero 2010             |
| 10         | 10                | Valle Encantado 1   | Río Negro, AR | Ecotone            | 6030±115<br>6240±60                               | Present     | ND         | ND           | Hajduk and Albormoz 1999 |
| 11         | 11.1              | Cuyín Manzano       | Neuquén, AR   | Forest             | ND  | Present     | ND         | ND           | Ceballos 1982            |
| 11         | 11.2              | Cuyín Manzano       | Neuquén, AR   | Forest             | Historical times                                  | Present     | ND         | ND           | Ceballos 1982            |
| 12         | 12.1              | Alero El Trébol     | Río Negro, AR | Forest             | ND  | 39          | ND         | 308          | Lezcano et al. 2010      |
| 12         | 12.2              | Alero El Trébol     | Río Negro, AR | Forest             | 5620±80<br>5731±70                                | 19          | 1          | 299          | Lezcano et al. 2010      |
| 12         | 12.3              | Alero El Trébol     | Río Negro, AR | Forest             | 5863±83<br>10,570±130<br>10,600±100<br>10,640±120 | 12          | 2          | 317          | Hajduk et al. 2012       |
| 13         | 13                | Paredón Lanfré      | Río Negro, AR | Forest             | 330±50 to<br>1570±60                              | 22          | 1          | 135          | Unpublished data         |

Table 2. Continued.

| Map number | Unit (Site,Level) | Archaeological site       | Provenience   | Modern environment | Chronology (years BP)   | Huemul NISP | Huemul MNI | General NISP | Reference                   |
|------------|-------------------|---------------------------|---------------|--------------------|-------------------------|-------------|------------|--------------|-----------------------------|
| 14         | 14                | Risco de Azócar 1         | Chubut, AR    | Forest             | 820±60 to 1690±60       | 20          | 1          | 93           | Podestá et al. 2007         |
| 15         | 15.1              | Cerro Pintado             | Chubut, AR    | Forest             | 680±60 to 1870±80       | 3           | 1          | 31           | Fernández 2008              |
| 15         | 15.2              | Cerro Pintado             | Chubut, AR    | Forest             | 680±60 to 1870±80       | 108         | 3          | 133          | Fernández 2008              |
| 16         | 16                | Sendero de Interpretación | Chubut, AR    | Forest             | 400±40 to 1670±80       | 5           | 1          | 73           | Arrigoni and Fernández 2004 |
| 17         | 17                | Alero del Shamán          | Chubut, AR    | Forest             | 1460±40 to 3040±90      | 13          | 1          | 56           | Fernández 2011              |
| 18         | 18                | Alero El Toro             | XI Región, CH | Forest             | 2460±40 2480±40 2560±90 | 27          | 2          | 42           | Mena et al. 2004            |

Notes: AR = Argentina; CH = Chile; ND = no data available; AD = Anno Domini.

Table 3. Huemul remains found in Southern Patagonia archaeological sites.

| Map number | Unit (Site-Level) | Archaeological site         | Provenience    | Modern environment | Chronology (years BP) | Huemul NISP | Huemul MNI | General NISP | Reference                             |
|------------|-------------------|-----------------------------|----------------|--------------------|-----------------------|-------------|------------|--------------|---------------------------------------|
| 19         | 19.1              | Cueva Baño Nuevo 1          | XI Región, CH  | Forest             | 3000 to 5000          | Present     | 1          | 137          | Velásquez and Mena 2006               |
| 19         | 19.2              | Cueva Baño Nuevo 1          | XI Región, CH  | Forest             | 5000 to 8000          | Present     | 1          | 85           | Velásquez and Mena 2006               |
| 19         | 19.3              | Cueva Baño Nuevo 1          | XI Región, CH  | Forest             | 8000 to 9500          | Present     | 1          | 31           | Velásquez and Mena 2006               |
| 20         | 20                | Lomo del Dragón Bajo        | XI Región, CH  | Forest             | 6980±30               | 1           | 1          | 1            | Méndez et al. 2013                    |
| 21         | 21.1              | Alero Fontana               | XI Región, CH  | Forest             | 2110±60               | 205         | 1          | 261          | Mena 1992; Velásquez and Trejo 2005   |
| 21         | 21.2              | Alero Fontana               | XI Región, CH  | Forest             | 4830±60               | 1429        | 15         | 1462         | Mena 1992; Velásquez and Trejo 2005   |
|            |                   |                             |                |                    | 340±50                |             |            |              |                                       |
|            |                   |                             |                |                    | 460±90                |             |            |              |                                       |
|            |                   |                             |                |                    | 500±110               |             |            |              |                                       |
|            |                   |                             |                |                    | 690±100               |             |            |              |                                       |
| 22         | 22.1              | Alero Las Guanacas          | XI Región, CH  | Ecotone            | 13,275±30             | 5           | 1          | 540          | Labarca et al. 2008                   |
| 22         | 22.2              | Alero Las Guanacas          | XI Región, CH  | Ecotone            | 5340±190              | 32          | 3          | 488          | Fuentes Mucherl and Mena Larraín 2010 |
| 22         | 22.3              | Alero Las Guanacas          | XI Región, CH  | Ecotone            | 450±70                | 38          | 6          | 211          | Fuentes Mucherl and Mena Larraín 2010 |
| 23         | 23                | Cueva Grande del Arroyo Feo | Santa Cruz, AR | Steppe             | 1660±50               | 1           | 1          | 1002         | Silveira 1979                         |
| 24         | 24                | Alero Gianella              | XI Región, CH  | Ecotone            | ND                    | 9           | 1          | 747          | Fuentes Mucherl et al. 2012           |
| 25         | 25.1              | Entrada Baker               | XI Región, CH  | Steppe             | 2120±40               | Present     | 1          | 439          | Mena and Jackson 1991                 |
| 25         | 25.2              | Entrada Baker               | XI Región, CH  | Steppe             | 2580±50               | Present     | 1          | 880          | Mena and Jackson 1991                 |
| 26         | 26                | Cerro Cuadrado              | Santa Cruz, AR | Steppe             | 230±70                | 2           | 1          | 216          | De Nigris and Tecce 2013              |
| 27         | 27                | Estancia Pueyrredón 2       | Santa Cruz, AR | Steppe             | 390±50                | 1           | 1          | 354          | De Nigris and Tecce 2013              |
| 28         | 28                | Los Toldos Cueva 3          | Santa Cruz, AR | Steppe             | 2080±20               | 1           | 1          | 13           | Cardich and Miotti 1983               |
| 29         | 29                | Alero Gorra de Vasco        | Santa Cruz, AR | Ecotone            | 4900±30               | 3           | 1          | 269          | Rindel 2008                           |
| 30         | 30.1              | Stuven 1                    | XI Región, CH  | Forest             | 360±60                | 7           | ND         | 603          | Legoupil et al. 2007                  |
| 30         | 30.2              | Stuven 1                    | XI Región, CH  | Forest             | ND                    | 9           | ND         | 992          | Legoupil et al. 2007                  |
| 30         | 30.3              | Stuven 1                    | XI Región, CH  | Forest             | ND                    | 3           | ND         | 814          | Legoupil et al. 2007                  |
| 30         | 30.4              | Stuven 1                    | XI Región, CH  | Forest             | ND                    | 1           | 1          | 329          | Legoupil et al. 2007                  |

Table 3. Continued.

| Map number | Unit (Site-Level) | Archaeological site             | Provenience    | Modern environment | Chronology (years BP)                                    | Huemul NISP | Huemul MNI | General NISP | Reference            |
|------------|-------------------|---------------------------------|----------------|--------------------|--|-------------|------------|--------------|----------------------|
| 30         | 30.5              | Stuven 1                        | XI Región, CH  | Forest             | 2225±45 to 1970±60                                       | 1           | 1          | 88           | Legoupil et al. 2007 |
| 31         | 31                | Alero Dirección Obligatoria     | Santa Cruz, AR | Steppe             | 240±50<br>390±110<br>770±60                              | 1           | 1          | 550          | Rindel 2008          |
| 32         | 32.1              | Alero Destacamento Guardaparque | Santa Cruz, AR | Steppe             | 5570±230<br>6700±80                                      | 5           | 1          | 434          | Rindel 2008          |
| 32         | 32.2              | Alero Destacamento Guardaparque | Santa Cruz, AR | Steppe             | 2830±60<br>3340±70                                       | 4           | 1          | 424          | Rindel 2008          |
| 33         | 33.1              | Cerro Casa de Piedra Cueva 5    | Santa Cruz, AR | Ecotone            | 2550±50<br>2805±105                                      | 8           | 1          | 280          | De Nigris 2007       |
| 33         | 33.2              | Cerro Casa de Piedra Cueva 5    | Santa Cruz, AR | Ecotone            | 2740±105   | 48          | 2          | 1026         | De Nigris 2007       |
| 33         | 33.3              | Cerro Casa de Piedra Cueva 5    | Santa Cruz, AR | Ecotone            | 4330±120<br>4735±160<br>4850±110<br>4930±160<br>6540±110 | 27          | 1          | 712          | De Nigris 2007       |
| 33         | 33.4              | Cerro Casa de Piedra Cueva 5    | Santa Cruz, AR | Ecotone            |  | 40          | 2          | 370          | De Nigris 2007       |
| 34         | 34.1              | Cerro Casa de Piedra Cueva 7    | Santa Cruz, AR | Ecotone            | 3480±70<br>3460±71                                       | 33          | 2          | 786          | De Nigris 2004a      |
| 34         | 34.2              | Cerro Casa de Piedra Cueva 7    | Santa Cruz, AR | Ecotone            | 4270±90  | 31          | 2          | 465          | De Nigris 2004a      |
| 34         | 34.3              | Cerro Casa de Piedra Cueva 7    | Santa Cruz, AR | Ecotone            | ND   | 6           | 1          | 649          | De Nigris 2004a      |
| 34         | 34.4              | Cerro Casa de Piedra Cueva 7    | Santa Cruz, AR | Ecotone            | 5120±80<br>5320±90<br>3970±80                            | 71          | 1          | 1870         | De Nigris 2004a      |
| 34         | 34.5              | Cerro Casa de Piedra Cueva 7    | Santa Cruz, AR | Ecotone            | 6150±105   | 13          | 1          | 504          | De Nigris 2004a      |
| 34         | 34.6              | Cerro Casa de Piedra Cueva 7    | Santa Cruz, AR | Ecotone            | 5310±100   | 30          | 1          | 758          | De Nigris 2004a      |
| 34         | 34.7              | Cerro Casa de Piedra Cueva 7    | Santa Cruz, AR | Ecotone            | 5610±110<br>3920±80                                      | 9           | 1          | 301          | De Nigris 2004a      |

Table 3. Continued.

| Map number | Unit (Site:Level) | Archaeological site          | Provenience    | Modern environment | Chronology (years BP)           | Huemul NISP | Huemul MNI | General NISP | Reference                   |
|------------|-------------------|------------------------------|----------------|--------------------|---------------------------------|-------------|------------|--------------|-----------------------------|
| 34         | 34.8              | Cerro Casa de Piedra Cueva 7 | Santa Cruz, AR | Ecotone            | 7060±105                        | 13          | 1          | 309          | De Nigris 2004a             |
| 34         | 34.9              | Cerro Casa de Piedra Cueva 7 | Santa Cruz, AR | Ecotone            | ND                              | 4           | 1          | 196          | De Nigris 2004a             |
| 34         | 34.10             | Cerro Casa de Piedra Cueva 7 | Santa Cruz, AR | Ecotone            | 8380±120                        | 27          | 2          | 617          | De Nigris 2004a             |
| 34         | 34.11             | Cerro Casa de Piedra Cueva 7 | Santa Cruz, AR | Ecotone            | ND                              | 55          | 2          | 946          | De Nigris 2004a             |
| 34         | 34.12             | Cerro Casa de Piedra Cueva 7 | Santa Cruz, AR | Ecotone            | 8300±115                        | 26          | 1          | 722          | De Nigris 2004a             |
| 34         | 34.13             | Cerro Casa de Piedra Cueva 7 | Santa Cruz, AR | Ecotone            | ND                              | 33          | 2          | 835          | De Nigris 2004a             |
| 34         | 34.14             | Cerro Casa de Piedra Cueva 7 | Santa Cruz, AR | Ecotone            | ND                              | 5           | 1          | 294          | De Nigris 2004a             |
| 34         | 34.15             | Cerro Casa de Piedra Cueva 7 | Santa Cruz, AR | Ecotone            | 9730±100                        | 14          | 1          | 856          | De Nigris et al. 2010       |
| 34         | 34.16             | Cerro Casa de Piedra Cueva 7 | Santa Cruz, AR | Ecotone            | 8920±200                        | 10          | 1          | 684          | De Nigris et al. 2010       |
| 34         | 34.17             | Cerro Casa de Piedra Cueva 7 | Santa Cruz, AR | Ecotone            | 9100±150<br>9640±190<br>9390±40 | 4           | 1          | 653          | De Nigris et al. 2010       |
| 35         | 35                | P35                          | Santa Cruz, AR | Steppe             | 1150±30                         | 1           | ND         | ND           | Cruz et al. 2010            |
| 36         | 36                | Dos Herraduras 1             | XII Región, CH | Ecotone            | 2870±62<br>2915±115             | Present     | ND         | ND           | Borrero 1980                |
| 37         | 37                | Dos Herraduras 2             | XII Región, CH | Ecotone            | 2870±62                         | Present     | ND         | ND           | Borrero and Massone 1994    |
| 38         | 38                | Dos Herraduras 3             | XII Región, CH | Ecotone            | 2530±70<br>2575±115             | 2           | ND         | 33           | Muñoz 1997                  |
| 39         | 39                | Cueva del Milodón            | XII Región, CH | Ecotone            | 2556±45                         | Present     | ND         | ND           | Borrero 1980                |
| 40         | 40                | Alero Quemado                | XII Región, CH | Ecotone            | ND                              | 85          | 3          | 258          | Sierpe et al. 2009          |
| 41         | 41                | Little Hill                  | Santa Cruz, AR | Steppe             | ND                              | 1           | 1          | 1            | Carballo Marina et al. 2008 |



Table 3. Continued.

| Map number | Unit (Site,Level) | Archaeological site       | Provenience    | Modern environment | Chronology (years BP)               | Huemul NISP | Huemul MNI | General NISP | Reference                 |
|------------|-------------------|---------------------------|----------------|--------------------|-------------------------------------|-------------|------------|--------------|---------------------------|
| 42         | 42                | Cueva Lago Sofía 4        | XII Región, CH | Ecotone            | 11,590±100 to 13,400±90             | 8           | ND         | 710          | Borrero et al. 1997       |
| 43         | 43                | Cueva del Medio           | XII Región, CH | Ecotone            | Late Pleistocene (before 12,400 BP) | 2           | 1          | 14           | Nami and Menegaz 1991     |
| 44         | 44                | Laguna Cóndor             | Santa Cruz, AR | Steppe             | ND                                  | Present     | ND         | ND           | Borrero and Borrazzo 2011 |
| 45         | 45                | Skyring 3                 | XII Región, CH | Forest             | 1290±100                            | 4           | ND         | 2596         | Legoupil 2000             |
| 46         | 46                | Skyring 6                 | XII Región, CH | Forest             | ND                                  | 1           | 1          | 46           | Legoupil 2000             |
| 47         | 47                | Skyring 14                | XII Región, CH | Forest             | 1215±70                             | 4           | ND         | 653          | Legoupil 2000             |
| 48         | 48                | Skyring 15                | XII Región, CH | Forest             | ND                                  | 1           | ND         | 129          | Legoupil 2000             |
| 49         | 49                | Skyring 16                | XII Región, CH | Forest             | ND                                  | 4           | ND         | 129          | Legoupil 2000             |
| 50         | 50                | Skyring 24                | XII Región, CH | Forest             | ND                                  | 8           | ND         | 212          | Legoupil 2000             |
| 51         | 51                | Skyring 25                | XII Región, CH | Forest             | ND                                  | 2           | ND         | 80           | Legoupil 2000             |
| 52         | 52                | Skyring 26                | XII Región, CH | Forest             | 3970±60                             | 2           | ND         | 4            | Legoupil 2000             |
| 53         | 53                | Skyring 28                | XII Región, CH | Forest             | ND                                  | 1           | ND         | 4            | Legoupil 2000             |
| 54         | 54                | Skyring 32                | XII Región, CH | Forest             | ND                                  | 2           | ND         | 34           | Legoupil 2000             |
| 55         | 55                | Skyring 34                | XII Región, CH | Forest             | ND                                  | 2           | ND         | 64           | Legoupil 2000             |
| 56         | 56                | Skyring 35                | XII Región, CH | Forest             | ND                                  | 2           | ND         | 7            | Legoupil 2000             |
| 57         | 57                | Skyring 42                | XII Región, CH | Forest             | ND                                  | 1           | ND         | 6            | Legoupil 2000             |
| 58         | 58                | Skyring 49a               | XII Región, CH | Forest             | 1040±50                             | 17          | ND         | 133          | Legoupil 2000             |
| 59         | 59                | Bahía Laredo - Cabo Negro | XII Región, CH | Forest             | ND                                  | Present     | ND         | ND           | Prieto 1988               |
| 60         | 60                | Río Verde 1               | XII Región, CH | Steppe             | 280±60                              | 2           | ND         | 627          | San Román et al. 2002     |
| 61         | 61                | Punta Eugenia 2           | XII Región, CH | Forest             | ND                                  | 4           | ND         | 62           | San Román et al. 2002     |
| 62         | 62.1              | Cueva Fell                | XII Región, CH | Steppe             | 6560±115<br>6740±130<br>8180±135    | 1           | 1          | 292          | Empeiraire et al. 1963    |
| 62         | 62.2              | Cueva Fell                | XII Región, CH | Steppe             | ND                                  | 2           | 1          | 188          | Empeiraire et al. 1963    |
| 63         | 63                | Cueva de los Chingues     | XII Región, CH | Steppe             | 11,210±50                           | Present     | ND         | ND           | Martin 2013               |
| 64         | 64                | San Gregorio 10           | XII Región, CH | Steppe             | ND                                  | 1           | 1          | ND           | Massone 1984              |

Table 3. Continued.

| Map number | Unit (Site.Level) | Archaeological site | Provenience    | Modern environment | Chronology (years BP) | Huemul NISP | Huemul MINI | General NISP | Reference                |
|------------|-------------------|---------------------|----------------|--------------------|-----------------------|-------------|-------------|--------------|--------------------------|
| 65         | 65                | Isla Isabel         | XII Región, CH | Steppe             | ND                    | Present     | ND          | ND           | Borero and Borrazzo 2011 |
| 66         | 66                | Caleta Alonso 2     | XII Región, CH | Forest             | ND                    | 1           | 1           | 98           | San Román et al. 2002    |
| 67         | 67                | Caleta Eros 2       | XII Región, CH | Forest             | ND                    | 10          | ND          | 24           | San Román et al. 2002    |
| 68         | 68                | Pizzulic 2          | XII Región, CH | Forest             | 5945±45 to 6200±40    | 4           | ND          | 3515         | San Román Bortés 2013    |
| 69         | 69                | Pizzulic 4          | XII Región, CH | Forest             | 985±45 to 1340±30     | 1           | ND          | 270          | San Román Bortés 2013    |
| 70         | 70                | Bahía Colorada      | XII Región, CH | Forest             | 5500                  | 1           | 1           | 6072         | Legoupil 1997            |
| 71         | 71                | Martín Pescador 2   | XII Región, CH | Forest             | ND                    | 6           | ND          | 100          | San Román et al. 2002    |
| 72         | 72                | Río Caleta 2        | XII Región, CH | Forest             | 110±40                | 28          | ND          | 34           | San Román et al. 2002    |
| 73         | 73                | Puesto La Sal       | XII Región, CH | Forest             | ND                    | 1           | 1           | 1            | San Román et al. 2002    |
| 74         | 74                | Punta Santa Ana 3   | XII Región, CH | Forest             | ND                    | 33          | ND          | 4226         | Morello et al. 2012      |

Notes: AR = Argentina; CH = Chile; ND = no data available.

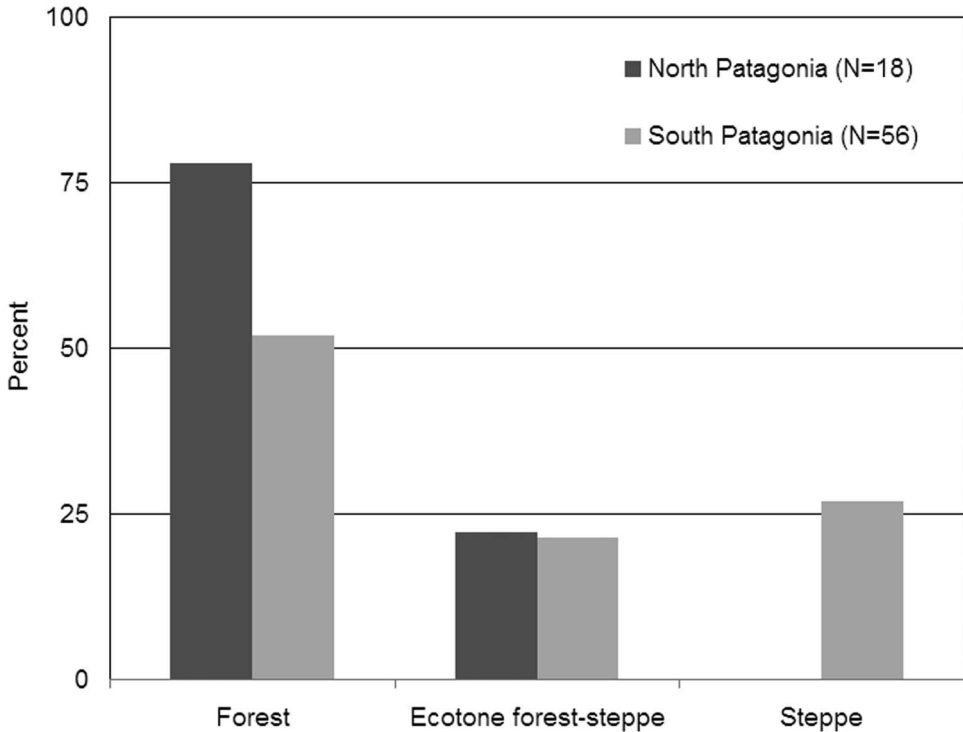


Figure 4. Frequency of archaeological sites with huemul remains according to present-day environment.

remains in steppe archaeological deposits can only be attributed to the absence of huemuls from arid Patagonia in the past.

Data compiled here indicate that Holocene hunter-gatherers did not have an impact on the past distribution of huemuls. The zooarchaeological data show that huemuls were not prey for humans at the beginning of the human colonization of Patagonia. The site of Marifilo 1, located in the Valdivian forest, on the shores of Calafquén Lake, has a record of human occupation from ca. 10,200 yrs BP. At this site huemul remains are only recorded in Late Holocene levels, dated between ca. 800-1500 yrs BP (Table 2, code 2). Similarly, at Última Esperanza, huemul remains are clearly identified in the Late Holocene level of the Dos Herraduras 3 (Table 3, code 38) archaeological site (Muñoz 1997), even though human occupation of the area dates back to the Pleistocene-Holocene transition and includes the consumption of a great diversity of faunal resources of different sizes and behaviors (Nami 1987). Until now, the lower level of the El Trébol site (Table 2, code 12.3) is the only exception to this pattern. In other words, although the paleontological records show that huemuls were present at the time of initial human colonization, the zooarchaeological record demonstrates that in some areas it was only hunted during the Late Holocene. On this basis, and contrary to Flueck and Smith-Flueck (2012), we confirm that there was no over-hunting of

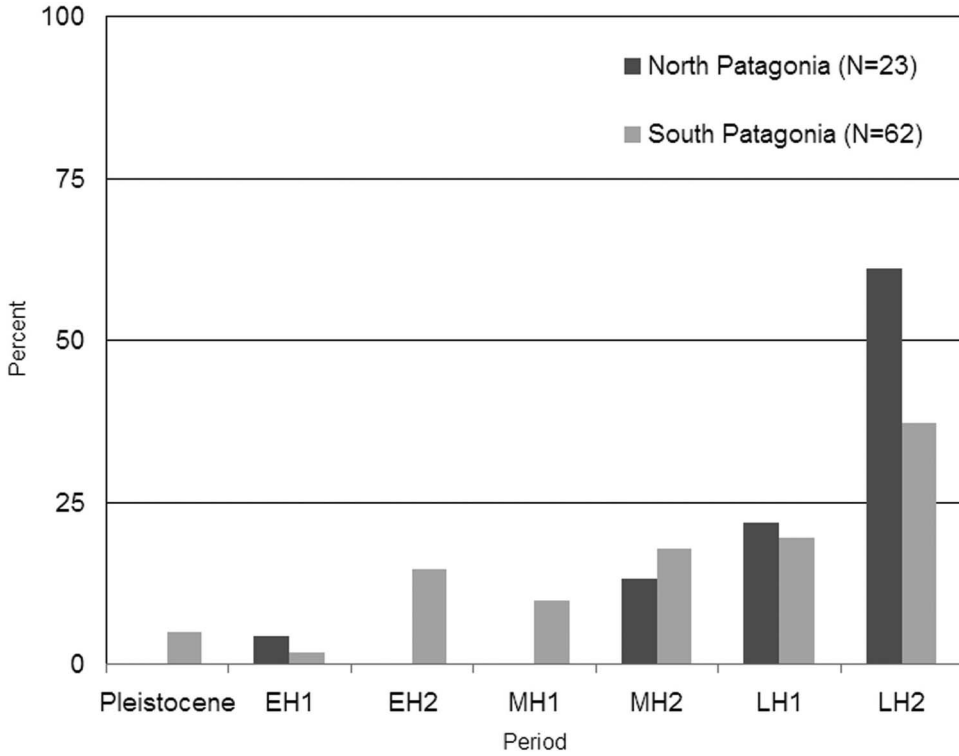


Figure 5. Comparison of percent abundance of huemul remains through time in North and South Patagonia sites. Time spans acronyms from Table 1. Chronological contexts from Tables 2 and 3.

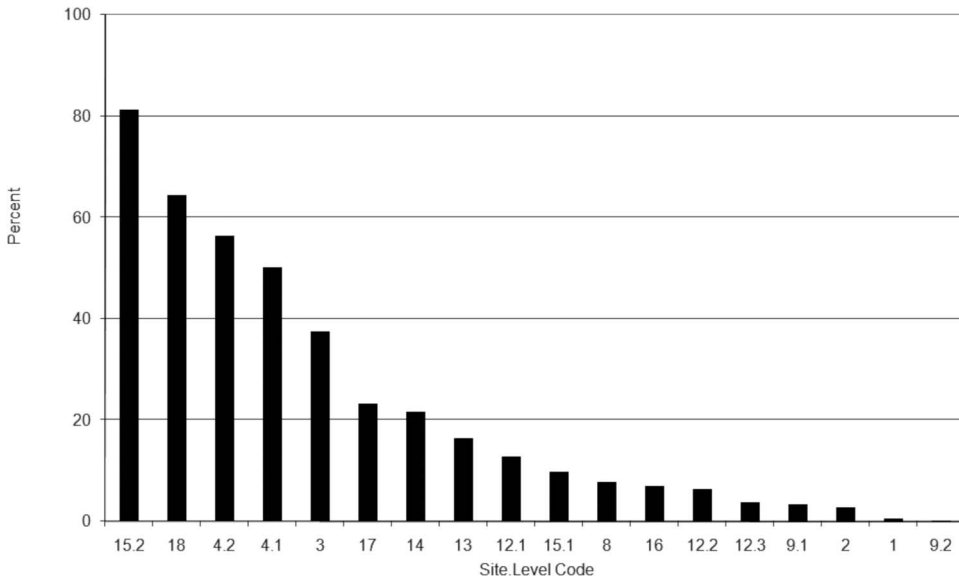


Figure 6. Percent of NISP huemul remains relative to the general NISP for Northern Patagonia zooarchaeological deposits (N=18). Records with huemul remains (x-axis) and general NISP taken from Table 2.

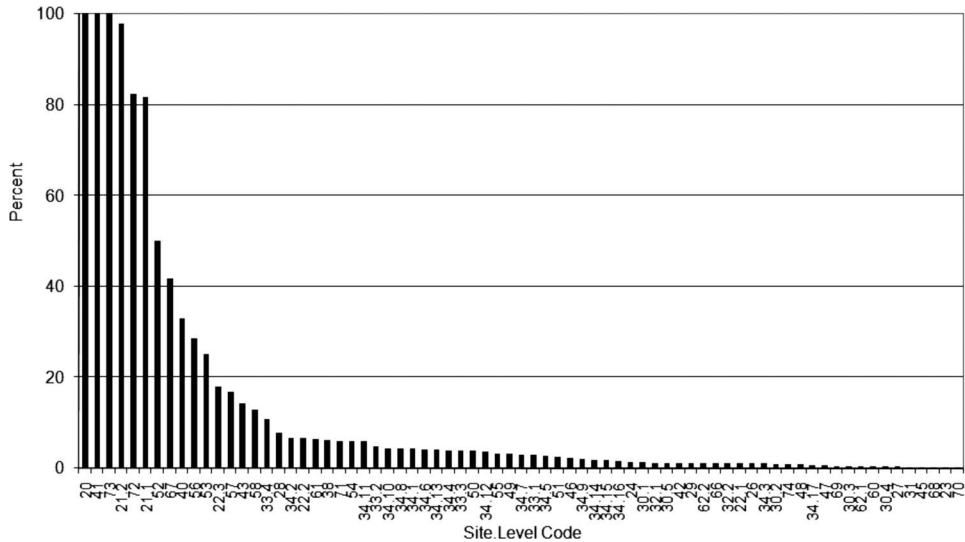


Figure 7. Percent of NISP huemul remains relative to the general NISP for Southern Patagonia zooarchaeological deposits (N=73). Records with huemul remains (x-axis) and general NISP taken from Table 3.

huemul by hunter-gatherer populations in arid steppe Patagonia. Although huemul records are more abundant during the LH2 (2200 yrs BP) in both areas of Patagonia, their place in human subsistence seems to have always been marginal.

Furthermore, the few records displaying a higher number of huemul remains could be explained by means of opportunistic hunting events, as is the case at Alero Fontana, located in the forest along the shore of a small lake (Mena 1992). Bodies of water are important in the anti-predator behavior of the huemul (Fernández and Forlano 2009), so this site was the ideal locus for hunting and processing this animal.

To conclude, predation by hunter-gatherers would have had little or no influence on the distribution of this species on a regional scale. Nevertheless, it is possible that the increasing human presence in certain forested areas during the last 2000 years might have affected huemul populations at a local scale. As Serret (2001) and Smith-Flueck (2000) state, it is only from the end of the nineteenth century that human populations started exerting increasing pressure on huemul numbers, both through hunting and modification of their habitat.

### Conclusions

This paper demonstrates that the zooarchaeological record of Patagonia is a valuable tool for understanding the natural history of the huemul. As stated previously, the endangered status of huemuls has prompted a strong interest in its interaction with humans to improve huemul management decisions and conservation (e.g., Aldridge 1988; Frid 1994; Marín et al. 2013; Povilitis 1978; Smith-Flueck and Flueck 2001). The zooarchaeological record analyzed here

helps not only to explore the variation of the species' historical distribution, but also to explore more specific aspects, such as the evolution of interspecific relationships and the resulting possible impacts on animal populations. As Lyman (2012) clearly states, models built upon these kinds of data are the key foundations to propose more realistic ecological restoration benchmarks. Analyses such as the one presented in this paper will support huemul management decisions, particularly those related with environmental variability, isolation of local populations, extinctions, and re-introductions. In other words, the resulting knowledge is not only of benefit for archaeologists studying long term human-animal interactions, but also to those who are dedicated to this species' management and conservation in Argentina and Chile (Plan Nacional 2002; Plan Nacional 2008-2012). The diachronic and spatial evidence serves to show that the distribution of the huemul throughout the Holocene was similar to that reconstructed for the historical periods that are associated with the Patagonian Andean Forest and the forest-steppe ecotone.

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