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Patterns of Resource Use and Isotopic Niche Overlap Among Guanaco (*Lama guanicoe*), Pampas Deer (*Ozotoceros bezoarticus*) and Marsh Deer (*Blastocerus dichotomus*) in the Pampas. Ecological, Paleoenvironmental and Archaeological Implications

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ABSTRACT

In this paper, we analyze the isotopic niche and resource use of the guanaco (*Lama guanicoe*), pampas deer (*Ozotoceros bezoarticus*) and marsh deer (*Blastocerus dichotomus*) on the temperate plain of the northern Pampa region in the southeast of South America. The measured stable isotope compositions in bone tissue are $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{18}\text{O}$. All the analyzed samples were recovered from different archaeological sites from the late Holocene. According to the results, the guanaco was strictly confined to the Pampa plain environment, developing a broad niche based on C_3 plants and a variable contribution of C_4 grasses within a grazing trend. The pampas deer preferentially used the Pampa plain, but also the prairies on the borders of the wetland, showing eurioic characteristics and a narrower niche based on C_3 plants. In turn, the marsh deer was strictly confined to wetland environments, developing a C_3 diet-base, within a narrow isotopic niche and stenoic characteristics. The three mammals showed a wide range of intraspecific variability, which was a key factor in their adaptability to spatial and temporal changes in the vegetation coverage. In fact, the temporal trends of their isotopic values were concurrent with the major climatic variations of the Holocene. Differences in the correlations between the values of both carbon sources in both deer species compared with the guanaco suggest a distinct chemical composition of their diet and/or differences in the allocation of nutrients. The isotopic values of nitrogen and spacing of the carbon sources in guanaco (pseudoruminant) and both deer species (ruminants) show no significant differences between them, thus establishing the values for local large herbivores. Significant correlations between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were found in the guanaco and marsh deer. The regional and extra-regional variability in the guanaco's $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{15}\text{N}$ probably reflect the clinal variations in the vegetation coverage and the amount of rainfall. The collagen isotope values in the guanaco throughout the entire Holocene show that the humid Pampa would have shifted between being a more recurrent mesic and temperate plain with minor phases of dry-mesic conditions like during the Little Ice Age, and a humid and warm one at the peaks of the Holocene Thermal Maximum and the Medieval Climatic Anomaly. The guanaco and the pampas deer adapted to all the climatic changes that happened on the humid Pampa until the biological invasions of large European mammals changed the herbivores' guild composition of this vast plain, pushing them into peripheral habitats due to competition. The within-species variability in isotopic signals through time and space make it necessary to carry out adequate sampling before reconstructing the diets of local past populations.

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Introduction

The main focus of this paper is to analyze the resource consumption, habitat use and isotopic niche of the guanaco (*Lama guanicoe*), the pampas deer (*Ozotoceros bezoarticus*) and the marsh deer (*Blastocerus dichotomus*) in the northern Pampa region, Argentina. Secondly, the purpose is to provide data to discuss the regional climatic variability and some local archaeological implications that are derived. Each of these topics has a specific section and they are developed according to the level of interest that each one has for this study.

The Pampa is a grassland located in southeastern South America on the Atlantic slope between 31° and 39° SL and 57° and 65° WL. The vegetation coverage is divided between C_3 and C_4 plants and is thus classified as mixed grassland (Cabido et al. 2008; Collatz, Berry, and Clark 1998; Powell and Still 2009; Still et al. 2003). The altitude of the study area is below 120 masl, so that the altitudinal variable is not significant for our analysis. Within this region, we analyze two sectors. The first corresponds to the northeastern area, known as Pampa Ondulada or Rolling Pampa,

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and the second is the lower Paraná wetland, adjacent to the first one (Figure 1). All the samples analyzed here were recovered from Pre-Columbian Late Holocene archaeological sites. Based on the isotopic values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{18}\text{O}$) obtained from properly identified bone remains, the diets and habitat use of these three ungulates were inferred, as well as the paleoenvironmental, ecological and archaeological implications. We also compare the results with previous analyses carried out on samples obtained from archaeological sites in the southern Pampa that were based on guanaco and pampas deer in order to extend the analysis and to get a regional overview.

The landscapes and isoscapes

The Pampa Ondulada is located in the north of the Argentine Pampean plains. Its undulating aspect is due to a slight elevation of the crystalline basement and the related development of low round-topped hills composed of loess and covered with organic topsoils. The climate is temperate, averaging 11 °C in

winter and 25.5 °C in summer, with an annual precipitation of 1147 mm, and maximum temperature and rainfall in the warm season (Sträßer 1999). The Pampa plain is classified as mixed grassland, as it reaches the proper values of atmospheric CO_2 pressure, temperature and rainfall for C_3 and C_4 alternatively, depending on the month and season of the year. Its vast extent allows a clinal variation from almost pure C_3 in the south to significant C_4 coverage in the north and west, where suitable conditions over several months make the latter dominant in the landscape (Cabido et al. 2008; Collatz, Berry, and Clark 1998; Powell and Still 2009; Powell, Yoo, and Still 2012; Still et al. 2003) (Figure 2). This clinal variability is based on concurrent and non-variable factors through the archaeological time, such as the latitude and distance to the sea, which are translated into distinct light regimes, net irradiancies, isohyets and isotherms (Figure 2). These parameters are directly connected to the temperature, light and the availability of water during the growing season, which are key factors for the balance of C_3 and C_4 grasses (Collatz, Berry, and

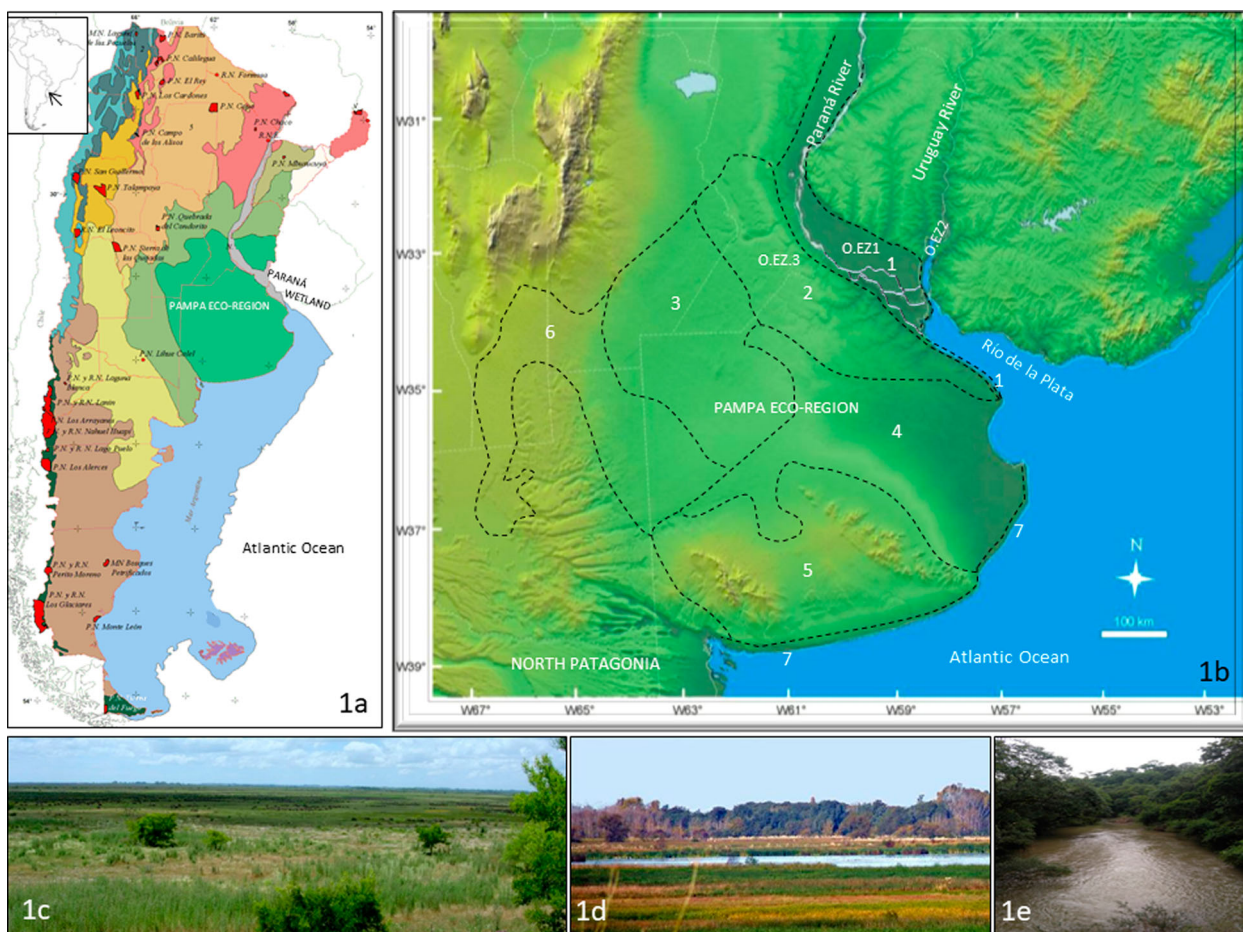


Figure 1. (a) Eco-regions in Argentina, with the Pampa Ondulada and wetland indicated (taken and modified from Burkart et al. 1999). (b) The regionalisation for this study is based on León (1991) 1: Wetland of the Lower Paraná River. 2: Rolling Pampa or Pampa Ondulada. 3: Inner Pampa (or Northwest Pampa). 4: Flooding Pampa. 5: Southern Pampa. 6: West Pampa. 7: Coastal sand dunes. O.EZ.1: Oxygen Ecozone 1. O.EZ.2: Oxygen Ecozone 2. O. EZ.3. Oxygen Ecozone 3. The original map was drawn by Damian Voglino. (c) Landscape at the Pampa Ondulada (image taken and modified from Administración Nacional de Parques Nacionales 2017). (d) Riverine prairies in the wetland with gallery forest on the horizon (image taken and modified from Administración Nacional de Parques Nacionales 2017). (e) Gallery forest in the wetland (image taken by authors).

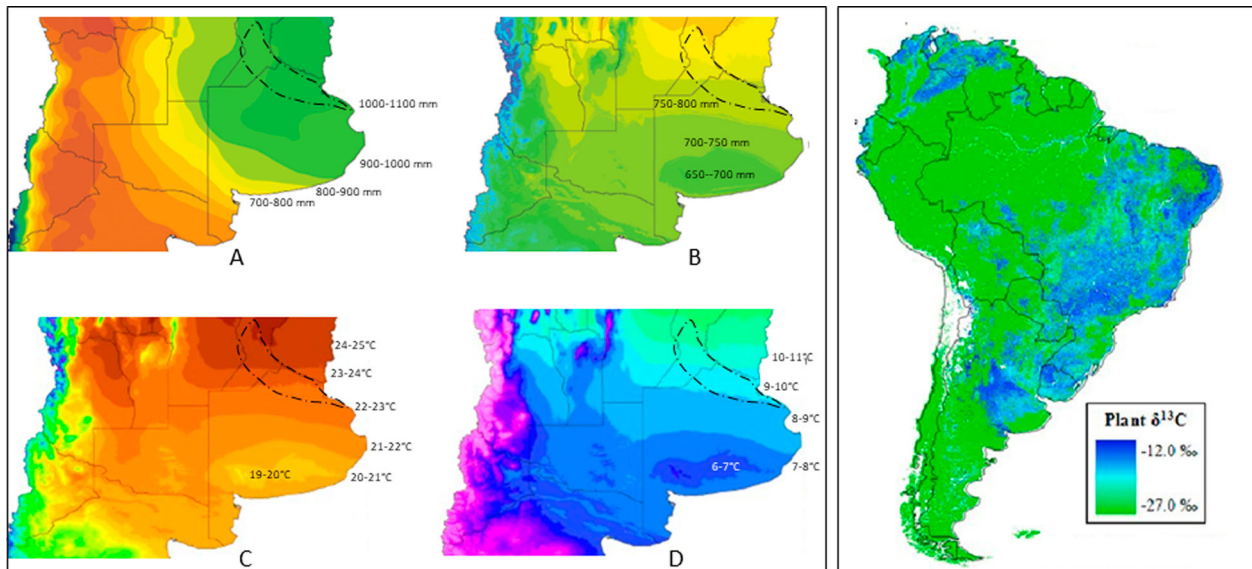


Figure 2. Left: Current climate parameters in the Pampa region. The Pampa Ondulada is indicated with a dotted line. A: Annual mean precipitation. B: Annual mean evaporation. C: Mean temperature in summer (January). C: Mean temperature in winter (July) (taken and modified from Bianchi and Cravero 2010). On the right-hand map is the current stable carbon isotopic distribution (vegetation cover) for the South American continent (taken and modified from Powell and Still 2009).

Clark 1998; Diefendorf et al. 2010; Ehleringer 1978; Ehleringer and Monson 1993; Ehleringer, Cerling, and Helliker 1997; Kohn 2010; Lattanzi 2010; Sage, Wedin, and Li 1999). Also, the higher proportion of C_4 grasses in the north compared to the south obeys the rule of increasing C_4 grasses as the latitude decreases (Powell and Still 2009; Sage, Wedin, and Li 1999). Although the *Piptochaetium* and *Stipa* Genera (both C_3) were abundant throughout the entire Pampa plain, in the north the C_4 *Aristida* (*i.e.* Genera *Aristida*), Chloridoideae and Panicodae subfamilies are well represented (Biganzoli and Zuloaga 2015; Cabido et al. 2008; Ghersa and León 2001; Soriano 1991; Tonello and Prieto 2009). Paleoenvironmental analysis supports this current distribution into the late Holocene. Indeed, some palynological studies, which are the best proxies available, carried out in the Pampas and the adjacent Campos in Uruguay indicate the existence of a climate similar to the current one during the Late Holocene since 3.0 ky or little later (Laprida et al. 2014; Mancini et al. 2005; Mourelle and Prieto 2016; Mourelle, Prieto, and García-Rodríguez 2017; Tonello and Prieto 2010). During this period, the environment could have varied from the current mesic prairie during wet years, to a dry-mesic during the driest ones (cf. Ghersa and León 2001; Tonello and Prieto 2009, 2010). In either of these two options, the coverage was composed predominantly of grasses, shrubs and no trees, as was the rest of the humid Pampa plain. We do not yet know for sure what the quantitative balance of the C_3 - C_4 vegetation coverage was during the entire Holocene, but a variation is expected throughout this period, mainly related to the Holocene Thermal Maximum, the

Medieval Climatic Anomaly and the Little Ice Age. On this plain, guanaco and pampas deer were regularly found until the biological invasion of cattle and horses from the XVI century. With the exception of the Flooding Pampa (Salado Depression) and the lower Paraná wetland, both of which were avoided by the guanaco troops (Loponte and Acosta 2008), the pampas deer and guanaco moved freely across this vast Pampa plain. The spatial continuity between the Pampa Ondulada and the rest of the humid Pampean region allowed the dispersal and gene flow of the flora and fauna, thus forming a wide and more or less continuous ecological landscape where the two main expected variability inputs for biocenosis distribution were related to clinal variation and climate change.

The other ecological unit we include in this paper is the lower Paraná wetland, located parallel to the Paraná River and adjacent to the Pampa Ondulada, which ends in the middle of the Río de la Plata estuary (Figures 1 and 3). A more or less continuous, narrow and xeric forest has developed between both environments. Although there are no differences in the annual rainfall or temperature in the Pampa Ondulada, the wetland has fewer frosts and more moderate extreme temperatures due to the microclimatic effect of the Paraná River (Daus 1973; Hoffman and García 1968; Saravia et al. 1987). This watercourse is 4000 km in length and a high-volume South American river, which originates from rainfall in the tropics (15° SL) and which extends the moisture and temperature along the Paraná Basin, thus allowing the development of the southernmost subtropical wetlands in the subcontinent and representing the end of the inland South American ecological conveyor belt. Here, along the large rivers

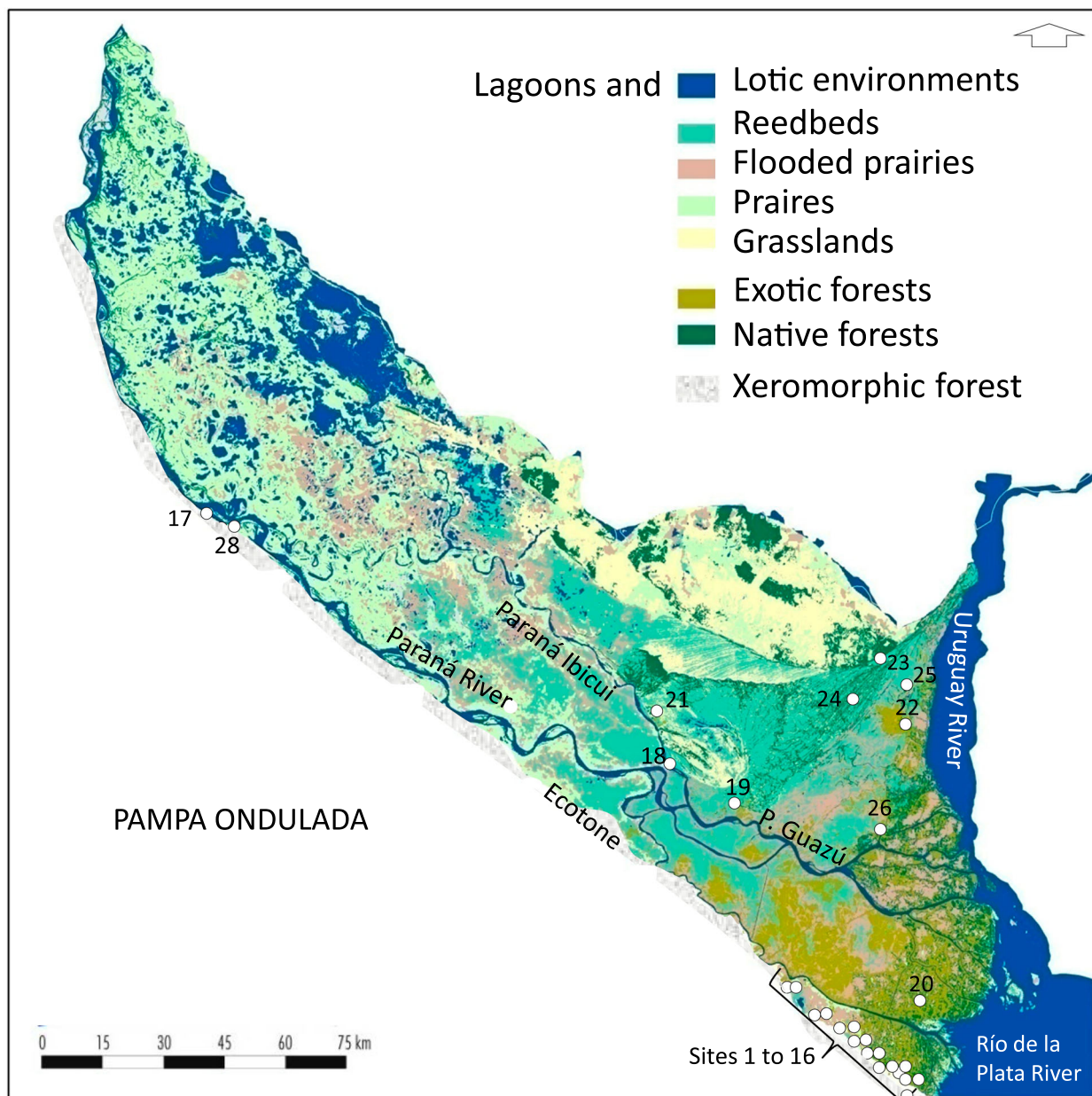


Figure 3. Wetland of the Lower Paraná River. We included the locations of sites 1–28 listed in Supplemental Data Table 1. Sites 1–17 and 28 are located on the edge of the wetland. The other sites are in the interior. The base-map was modified from an original drawing by P. Kandus.

and streams, a multilayered riparian forest has developed with a more or less continuous canopy 8–15 m in height along the main watercourses; the area is associated with small islands and riverine prairies that are fragmented by streams and shallow lakes (Cabrera 1976; Kalesnik et al. 2008; Roesler and Agostini 2012). This wetland has vast waterlogged prairies and islands, which are formed by the accretion of sediments on the Río de la Plata estuary, advancing on it and forming closed forests with low levels of light inside. Most of the vegetation and fluvial primary sources, which are the main isotopic input for the local biocenosis, have a C_3 pattern (Loponte et al. 2016a, 2016b; Madanes, Kalesnik, and Vargas 2013; Marchese et al. 2014; Powell and Still 2009). The current ecological conditions in this wetland were established by at least

2400 years BP, when the present-day biocenosis (see Haene and Pereira 2003) is still well represented in the archeological contexts (Loponte, Acosta, and Muciolio 2012) and where the marsh deer finds suitable ecological conditions to develop its lifecycle.

Water sources for local organisms

The Pampa Ondulada and wetland receive the same meteoric water mostly originated in the South Atlantic Ocean with an annual mean of $\delta^{18}O = -5.5$ ‰ (V-SMOW). To trace the isotopic water signal in the mammals we are studying, we have to perform a separate analysis. In the Pampa Ondulada the values of most of the superficial groundwater is around -5.7 | -5.0 ‰, demonstrating its direct meteoric origin (Dapeña et al.



Figure 4. Aeolian depressions filled with meteoric waters and groundwaters in the Pampa Ondulada with the quadrants in detail. In the first quadrant are the locations of the sites in the Pampa Ondulada included in this study (sites 32, 33 and 35), and the wetland sites in the southern extreme of this last environment (sites 29, 30 and 31). See Supplemental Data Table 1.

2001; Dapeña and Panarello 2004). The $\delta^{18}\text{O}$ that plants provide to the herbivores is approximately the same than meteoric waters. However, drinking water is a different matter. The availability of surface water in this sector is reduced to a few rivers separated by wide plains with vast numbers of small depressions and shallow lakes formed by aeolian erosion in-between, as well as small and intermittent streams (Figure 4). These natural reservoirs, also more or less permanent, are filled by meteoric and occasionally also by groundwater, as well as by the streams. Then, an evaporation process is triggered. The result is a well-stocked plain of water reservoirs with significant and variable $\delta^{18}\text{O}$ enrichment. Indeed, the surface water in the Pampa Ondulada and shallow lakes yield current values of $0.26 \pm 0.8 \text{ ‰}$ (based on Dapeña et al. 2001; Table 1). Frequent drinkers such as the guanaco and pampas deer (see Section 4) approach their isotopic signals to them. For an ecological application, we previously defined this area as the ecozone of the Pampa Ondulada, or Ecozone 3 (Buc and Loponte 2016). Since enrichment depends mainly on the frequency and amount of rainfall, air humidity and net irradiance (Dansgaard 1964), the isotopic values of oxygen can be used as proxy data for paleoclimate inference, using periodic drinkers such as the abovementioned two mammals as biosamplers.

In the wetland, the water available for mammals is quite different. The Paraná River is an allochthonous water course that fills the landscape with its water

and humidity along several major and minor branches, and extends its characteristics to water vapour. The contribution of the water from the rivers in the Pampa Ondulada is negligible. Indeed, during the frequent flooding the waters of the Paraná River flow upstream through the estuaries of the small rivers that descend from the Pampa plain.

This flux also floods the wetland prairies, transferring the isotopic signal from the Paraná water to most plants. It should be noted that the Paraná River has some biological and chemical heterogeneity in its different sections, which is typical of large rivers (Camponico, García, and Pasquini 2015). However, the Paraná wetland has developed in an area where the main geochemical contributions of the major tributaries of the Paraná River have already mixed hundreds of kilometres upstream, whereby the oxygen isotopic signal is homogeneous in its lower section. In fact, in the Paraná discharge area (Río de la Plata estuary), $\delta^{18}\text{O}$ has limited variability, with an average range of $-4.46 \pm 1.26 \text{ ‰}$ ($\pm 2\sigma$; range) (Loponte et al. 2016a; based on Panarello and Dapeña 2009). Thus, the expected values of the organisms that go through their lifecycles in the lower Paraná River valley have intervals of confidence (IC) between -5.72 ‰ | -3.20 ‰ . In fact, previous analyses of typical prey and local semi-sedentary humans here yielded magnitudes of $\delta^{18}\text{O}$ $-3.7 \pm 0.5 \text{ ‰}$ (IC = -3.83 ‰ | -3.16 ‰ V-PDB), and a recent analysis carried out on *Diplodon* sp.,

whose shell is in isotopic equilibrium with the Paraná's water, yielded values of $x_{36} = -4.0 \pm 0.15 \text{ ‰}$ ($CI = -4.29 \text{ ‰} \mid -3.68 \text{ ‰}$), thus defining this as an ecozone in the Paraná valley, or Ecozone 1 (Loponte et al. 2016a; Loponte and Corriale 2019; see section 5 for equivalences in the oxygen isotope values).

Isotopes and isotopic niche

There are many concepts of a niche, although all the contemporary definitions retain the idea of the niche as a multidimensional space with scenopoetic and bionomic axes (Hutchinson 1957, 1978). The bionomic axes define the resources that animals use, while the scenopoetic axes describe the bioclimatic scenario in which a species lives (Hutchinson 1978). Stable isotopes allow us to quantify these niches' dimensions in multivariate space (i.e. $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$) with coordinates that record bionomic and scenopoetic ecological information. This 'space' is comparable to n -dimensional space, which contains a so-called niche, because the chemical composition of an animal is directly influenced by what it consumes (bionomic) as well as by its habitat (scenopoetic) (Newsome et al. 2007). In this way, $\delta^{15}\text{N}$ is analogous to a bionomic axis; in turn, the axis of $\delta^{13}\text{C}$ is considered to be a bionomic and scenopoetic axis, and $\delta^{18}\text{O}$ is strictly a scenopoetic axis (Jackson et al. 2011). Therefore, the 'isotope niche' provides information on issues traditionally considered within the broad domain of the ecological niche, including the concepts of functional and bioclimatic niches, thus providing quantitative information on the use of resources (bionomic) and habitats (scenopoetic) to define ecological niche space. The isotopic niche is a broad concept useful for analyzing the lifestyle of each individual (Jackson et al. 2011; Martínez del Río et al. 2009; Newsome et al. 2007, 2009, 2012; Yeakel et al. 2016). In fact, it has been widely used to address the effective niches of organisms, their patterns of spatial distribution and for environmental reconstruction (Ayliffe and Chivas 1990; Bocherens and Drucker 2007; Bocherens et al. 1999, 2015; Drucker, Bocherens, and Billiou 2003, 2011a, 2011b; Feranec 2003; Fox-Dobbs, Leonard, and Koch 2008; Gil et al. 2016; Grocke, Bocherens, and Mariotti 1997; Heaton 1999; Koch, Diffenbaugh, and Hoppe 2004; Samec, Morales, and Yacobaccio 2014; Stevens, Lister, and Hedges 2006, among others). The isotopic values of ^{13}C was one of the most commonly used because the animals' tissues have a direct relationship with the isotopic signal of the food they ingested, and in this way with the ecology of the environment (Heaton 1999; Tieszen 1991;). These relations are mediated through a fractionation of approximately + 5 ‰ between the values of the plants and the carbon isotope values of the consumers. Thus, plant-based diets with C_3 photosynthetic patterns yield isotope values in bone collagen

of $\sim -21\text{‰}$, while in those with monoisotopic C_4 photosynthetic pathways they are $\sim -7 \text{‰}$ (DeNiro and Epstein 1978a, 1978b; Koch 2007; Krueger and Sullivan 1984; Lee-Thorp, Sealy, and van der Merwe 1989; Vogel 1978a, 1978b). In the inorganic fraction, this fractionation is around + 12 ‰, thus monoisotopic diets show magnitudes between $\sim -13.5 \text{‰}$ and $\sim -3 \text{‰}$, respectively (Ambrose and Norr 1993; Kellner and Schoeninger 2007; Lee-Thorp and van der Merwe 1987; Sullivan and Krueger 1981).

Collagen isotope values reflect dietary protein, while the inorganic fraction reflects the bulk diet (Ambrose and Norr 1993; Tieszen and Fagre 1993). The spacing between both sources in large herbivores is 7 ‰ or greater, which is due to the differential routing of macromolecules and differences in the digestive process related to the availability of proteins in their diets (Fogel and Tuross 2003; Hedges 2003). In warm and some temperate climates, browsers and mixed-feeding herbivores tend to exhibit depleted diets based on C_3 plants; on the contrary, grazers tend to eat C_4 grasses (DeNiro 1987; Gannes, Martínez del Río, and Koch 1998; van der Merwe 1982). Herbaceous and woody plants such as shrubs and herbs reflect a browsing component, and grass a grazing one. It is obvious that this global pattern must be analyzed within each ecological context. As we are going to compare the diets of two ruminants (*B. dichotomus* and *O. bezoarticus*) and one pseudoruminant (*L. guanicoe*), it should be noted that despite some differences, both digestive system have elevated spacing in their carbonate sources (Crowley et al. 2010).

Some aspects of these values that are important for this study should be treated with caution, such as the 'canopy effect' that occurs in closed environments (Farquhar, O'Leary, and Berry 1982; Vogel 1978b). The closed forest produces a negative bias related to the low recycling of CO_2 , the smaller amount of light and the greater availability of water (van der Merwe and Medina 1991; Broadmeadow et al. 1992).

Nitrogen has also been frequently used in the reconstruction organism's lifestyle and in paleoenvironmental analysis, as its values depend on diet and climate, the availability of environmental water, the water content of food and the frequency of drink intake (DeNiro and Epstein 1981; Drucker, Bocherens, and Billiou 2003; Murphy and Bowman 2006; Rabanus-Wallace et al. 2017; Stevens, Lister, and Hedges 2006). Animals obtain nitrogen from plants, reflecting their nitrogen isotopic signal. In turn, the plant's nitrogen content is related to the chemical composition of the soil, the rainfall average, the nitrogen composition of the atmosphere and microbiological processes (Hartman 2011; Rabanus-Wallace et al. 2017; Ugan and Coltrain 2011; Wrage, Kuchenmeister, and Isselstein 2011). Low $\delta^{15}\text{N}$ levels are more common in cold or wet ecosystems, and higher values are typical in arid or hot

environments (Austin and Vitousek 1998; Handley et al. 1999). This is related to a physiological response to heat, water stress and/or the amount of rainfall, as there is a well-established relationship between rainfall and the $\delta^{15}\text{N}$ content of plants on both regional and global scales (Austin and Vitousek 1998; Handley et al. 1999; Hartman 2011; Swap et al. 2004). As herbivores play the role of biosamplers with average nitrogen isotope values in their diets, the $\delta^{15}\text{N}$ in their tissues is frequently used in paleoenvironmental reconstructions (Hedges and Reynard 2007). Certain aspects of this methodology should also be treated with some caution; for example, the maturational status of the measured specimens, as young individuals have a significant influence on the 'carnivorous effect' related with breastfeeding, and in some females the values may also be influenced by the stress of pregnancy and breastfeeding (Barboza and Parker 2006; Dupras, Schwarcz, and Fairgrieve 2001; Jenkins et al. 2001; Richards, Mays, and Fuller 2002; conversely see Stevens, Lister, and Hedges 2006). In the isotopic studies of wildlife the gender and age of adult individuals are not usually taken into account as a source of variability, and in archaeology both gender and age certainly have different degrees of difficulty to be evaluated.

The $\delta^{18}\text{O}$ values of animal tissues are related to drinking water and the water content of food. These oxygen isotope values are incorporated without minor fractionation, retaining the value of the source, which is influenced by temperature, geomorphology, the annual amount of precipitation, the frequency of water intake, diet type and metabolism. Thus, they were used for environmental and mobility analysis, as well as for identifying the spatial locations where individuals went through their lifecycle (Balasse et al. 2002; Bocherens et al. 1996a, 1996b; Bryant et al. 1996; Dansgaard 1964; DeNiro and Epstein 1981; Eerkens et al. 2014; Grimes and Pellegrini 2013; Hobson 1999; Knudson and Price 2007; Kohn, Schoeninger, and Valley 1998; Longinelli 1984; Sponheimer and Lee-Thorp 1999). Herbivores that drink frequently incorporate their main oxygen isotopic signal from meteoric waters, mixed with their food's isotopic signal. In fact, plants incorporate meteoric water from the soil without fractionation (Wershaw et al. 1970), but an enrichment process is triggered in some parts of the plant. In the water in the roots, xylems and stems, there is no fractionation and the isotopic signal remains the same as in soil water or close, but in tissues that undergo a transpiration process such as leaves, there is an enrichment of the values which depends on the plant's physiology, the environmental humidity and the isotopic signal of the atmospheric water (Ometto et al. 2005). In turn, this enrichment has to be averaged with the non-enriched water in the plant and the direct water intake (Ehleringer and Dawson 1992; Flanagan et al. 1991). Another important issue

is herbivores that drink frequently from water sources such as isolated lakes, stagnant bodies of water or more or less intermittent streams with little water flow from their main collectors have more enriched isotopic signals than meteoric water (Sponheimer and Lee-Thorp 1999).

The ecology and behaviour of the guanaco, Pampas Deer and marsh deer

The guanaco is a large mammal weighing 80–110 kg, with a high adaptive capacity that allows it to range from northern Peru to southern South America, from 4500 masl to sea level, with temperatures ranging from 45 °C (Paraguayan Chaco) to several degrees below zero (Patagonia). Its historical distribution includes hardpan deserts, semideserts, shrublands, grasslands, savannas and scrublands on plains (Darwin 1839; Franklin 1982). The guanaco chooses from dry, xeric, mesic and open environments with except in Patagonian forests, the South American Arid Diagonal and on the wide Chaco savanna (Acebes 2010; Franklin 1982; González et al. 2006; Iranzo 2011; Montes, de Lamo, and Zavatti 2000; Puig and Videla 1995; Puig et al. 2008). Along with its ability to adapt to different landscapes, it is an opportunistic herbivore that changes its feeding behaviour from a dominant grazing strategy to another with a significant proportion of browsing, depending on the available options (Baldi et al. 2004; Franklin 1982; Hofmann 1989; Puig et al. 2001; Rivals, Rindel, and Belardi 2013). Different analyses suggest that where the available plants are as diverse as grasses, shrubs and trees, or where the competition with other herbivores is a key factor for survival (such as sheep), the guanaco has developed mixed strategies such as 'taking the opportunity', but where the possibilities for grazing are not limited, the guanaco will choose a grazing strategy (see discussions in Franklin 1982; Muñoz and Simonetti 2013; Ojasti 1997; Puig et al. 1996, 2001; Raedeke 1979, 1980). Its high level of adaptability in its feeding behaviour and physiology allows this species to develop isotopic diets ranging from a pure C_3 diet to others with significant proportions of C_4 plants, depending on the environment (see enriched and depleted isotope values in $\delta^{13}\text{C}_{\text{collagen}}$ in Barberena et al. 2009; Gil et al. 2016 and this study). In some populations behaviours have been observed that imply migrations, according to the time of year (Allen 1942; Bolgeri 2016; Franklin 1982; Ortega and Franklin 1995), which increases the expected variability in its diet. The guanaco is a frequent drinker when water is available (Franklin 1982). In the Pampa region, the guanaco has been found since the Pleistocene to Late Holocene (Darwin 1839; Loponte 1996–98, 2008; Menegaz 2001). In the Pampa Ondulada, the latest radiocarbon dates available today, obtained directly from guanaco bones, yield 540

± 40 , 560 ± 40 and 452 ± 24 ^{14}C years BP (Buc and Loponte 2016; Toledo 2010). This species has never inhabited wetlands, but local aboriginal populations used to hunt this camelid (and/or acquired it through trade) on the adjacent Pampa Ondulada from at least 2400 ^{14}C YBP, which is the oldest dated archaeological wetland site so far, until 400 ^{14}C YBP, when the Spanish arrived in the region (Buc and Loponte 2016). After that, the guanaco suffered a drastic decline on the Pampa due to the biological invasion of European herbivores (cattle and horses especially), predation by feral dogs and human manipulation of the environment, as Darwin's pioneering observations (1839) pointed out. Indeed, the Pampa Ondulada was the first area to be impacted by this ecological change in the Pampa region (Crivelli 1993–1994; Darwin 1839; Franklin 1982; Loponte 1996–98, 2008; Silveira 1997), followed by the rest of the Pampa plain and the Argentine Chaco, where the guanaco was seen until the XIX century (Loponte 1996–98; 2008). In the adjacent Paraguayan Chaco, there are still a few individuals (González et al. 2006). On the southern Pampa, the guanaco was continuously hunted from the end of the Pleistocene until at least 360 ± 40 ^{14}C years BP (Grill, March, and Rodríguez Loredo 2010), persisting until historical times outside the Pampas' livestock borders. Darwin (1839) caught a glimpse of one guanaco on the plain adjacent to the Tandil hills in the early 1800's, where this species had probably found one of its last refuges during the expansion of the large exotic herbivores over the Pampean plain toward the south and west.

The Pampas deer is a medium-sized mammal weighing 20–30 kg, widely distributed in South America, from central Brazil to northern Patagonia in Argentina, in tropical, subtropical, temperate and semidesert environments, where rainfall varies from 2000 to 250 mm/year, and temperatures range from 45°C (Brazil and Chaco) to several degrees below zero (northern Patagonia). This ungulate chooses in particular open environments and patchy landscapes (wooded/open) such as the tropical savannas in Brazil ('Cerrado'). It is classified as an opportunistic or intermediate feeder, depending on the seasonal variability and the environment. Its intestinal morphology is closer to browsers (see Cosse, González, and Gimenez-Dixon 2009; Weber and González 2003). This species comprises five subspecies. On the Pampa plain the form is *O. b. celer*; in the Chaco and probably throughout the Argentinian Mesopotamian, *O. b. leucogaster*; on the Uruguayan plain, *O. b. arerunguaensis* and *O. b. uruguayensis*; and in southern Brazil, *O. b. bezoarticus* (González 2004; González, Álvarez-Valin, and Maldonado 2002). Its diet includes, preferentially, grasses and tender stems, flowers and occasionally fruits and leaves from *Celtis tala*, the main species in the xeromorphic forest between the

Pampa Ondulada and the wetland. There are no references to migratory movements, but in Mato Grosso State (Brazil), they tend to increase their foraging range during the summer (Rodrigues and Monteiro-Filho 2000). It is a frequent drinker, or at least in semi-arid environments it usually uses artificial water reservoirs to drink from (Semeñuk and Merino 2014–2015). This mammal has suffered a 98% reduction compared to its historic distribution, which is related to human land use for cattle and agriculture (Weber and González 2003). On the northern Pampa, Darwin (1839) saw them in a river valley connected to a wetland, or in the wetland itself, adjacent to the Pampa Ondulada, but he highlighted this species' decline due to the environmental changes caused by the invasion of exotic herbivores and the human manipulation of the environment.

The marsh deer is the largest deer in South America. Adult males are two metres tall, while their body weight reaches 150 kg (Cabrera and Yepes 1940; Miranda et al. 2009; Weber and González 2003). It has a broad spatial distribution, from 10° SL on the right bank of the Amazon River to the Río de la Plata, including the central and southern sectors of Brazil, eastern Perú and Bolivia, central Paraguay, northeastern Argentina, and the fluvial and maritime coast of the Republic of Uruguay. Its habitat includes tropical and subtropical swamps, marshes and floodplains (Schaller and Vasconcelos 1978; Tomas and Salis 2000; Weber and González 2003). The marsh deer's diet consists mainly of grasses and aquatic macrophytes or other plants that can tolerate seasonal flooding (Tomas and Salis 2000; Tomas, Beccaceci, and Pinder 1997). The existence of multiple types of information has led to *B. dichotomus* being regarded as a deer with a mixed dietary strategy and some browsing tendencies (Coimbra Filho 1972; Hofmann, Ponce del Prado, and Otte 1976; Tomas and Salis 2000; Tomas, Beccaceci, and Pinder 1997; Weber and González 2003). Previous isotopic analysis has yielded a C_3 -based diet (Loponte and Corriale 2012). It is the only one of the three ungulates included in this paper whose archaeological record shows it being strictly limited to wetlands (Acosta, Loponte, and Mucciolo 2014; Loponte, Acosta, and Tchilinguirián 2010). In this sense, it is beyond doubt that it prefers waterlogged environments with subtropical characteristics, and for this reason, this species was spatially restricted, except perhaps during extensive flooding of the Paraná River complex, when this ungulate would have sought occasional refuge on the border of the Pampa Ondulada. Given that the lower Paraná River wetland was an area that was almost ignored during European colonisation, the deer survived with significant populations until the XIX century, and where there is today a small population (D'Alessio et al. 2006; Sastre 1858).

Samples, isotopes and statistical processing

In this paper, we include bone samples recovered from archaeological sites located in the northern Pampa region, which for the purposes of this paper includes the Pampa Ondulada and the lower Paraná wetland. In the latter area, there are two different locations for archaeological sites; those situated on the edge of the wetland, bordering the Pampa Ondulada, and those in the wetland interior, far away from this plain. The samples have direct radiocarbon dates or, failing that, they were recovered from specific archaeological layers that had been well dated. If there were several dates in the same layer within a tight chronological range (see Supplemental Data Table 1 and Figures 3 and 4 for chronology and location), the radiocarbon ages were averaged for the analysis of the temporal variability of the isotopic values. We have included some samples from the southern Pampa of guanaco and pampas deer in order to compare the north and south isotope values on this plain, and some minor comparisons with isotope values from the guanaco obtained in the Monte eco-region area of south Mendoza.

For this study, we gathered a certain amount of isotopic data and radiocarbon dates obtained over a number of years, which is why they come from different labs. Most of the isotopic analyses were performed at the Environmental Isotope Laboratory at the University of Arizona. We codified these results under the acronym 'EIL', as this lab does not have a code name. A few of the analyses were performed at the Institute of Geochronology Isotope in Buenos Aires (CONICET) (sample codes AIE). A few of the data were obtained from the Laboratory at the University of Utah, Center for Applied Isotope Studies at the University of Georgia (sample codes UGA). In order to expand the database, we also incorporated some $\delta^{13}\text{C}$ data obtained during the radiocarbon dating process at the NSF Arizona AMS Laboratory Department of Physics at the University of Arizona (sample codes AA). All the bone samples selected for this study were fragments of compact bone tissue with acceptable parameters of wt % C and wt % N (Ambrose 1990; Van Klinken 1999), and within a ratio C/N between DeNiro bounds of 2.9 and 3.6 (Ambrose 1990; DeNiro 1985). The protocol for extracting collagen follows Longin (1971) and Tykot (2004). We included in this study some isotope values obtained during the AMS dating process, which had no C/N ratio. Since the seminal work of DeNiro (1985) these values are not taken into account, but it must be recognised that the multiplicity of data with little dispersion should be considered as clues that serve to generate working hypotheses, which should be contrasted with information generated more adequately. The removal of diagenetic carbonates followed the protocol described in Koch, Tuross, and Fogel (1997); removing the

adsorbed carbonate, which is more soluble than the carbonate structural, and increasing the reliability of the readings for the paleodietary analysis (Ambrose and Krigbaum 2003; Garvie-Lok, Varney, and Katzenberg 2004; Grimes and Pellegrini 2013; Krueger 1991; Lee-Thorp and van der Merwe 1987, 1991; Tykot 2004). The values for the $\delta^{15}\text{N}$ and $\delta_{13}\text{C}$ collagen were measured on a continuous-flow gas-ratio mass spectrometer. The samples were burned using an elemental analyzer coupled to a mass spectrometer. The standardisation was based on acetanilide for elemental concentration, NBS - 22 and USGS - 24 for $\delta^{13}\text{C}$, and IAEA-N-1 and IAEA-N-2 for $\delta^{15}\text{N}$ (EIL). The precision was better than ± 0.08 ‰ for the $\delta^{13}\text{C}$ collagen (except in the INGEIS samples ± 0.2 ‰) and ± 0.2 ‰ for $\delta^{15}\text{N}$ ($\pm 1\sigma$), based on repeated internal standards. With the exception of the data related to oxygen, which is sensitive to pre-treatment methods, a recent study on the variability of results between different labs proved to be insignificant interpretatively, especially when the samples were well preserved (Pestle, Crowley, and Weirauch 2014). All the isotopic values in this paper are reported relative to the V-PDB, including $\delta^{18}\text{O}$. We compared the isotope values obtained from the carbonates with the V-SMOW values from the surface and groundwater without corrections, as the CO_2 was equilibrated with V-SMOW at 25°C and the CO_2 extracted with H_3PO_4 from VPDB at 25°C differed only by 0.22 - 0.27 ‰ (Coplen, Friedman, and O'neil 1984; Craig and Gordon 1965), allowing us to compare with virtually no corrections for the purposes of this study. The empirical results of this study support these equivalencies for our region.

General linear mixed models were used to analyze the differences between the isotopic values of the species in the distinct ecozones (Pampa Ondulada, wetland and southern Pampa). We considered the isotopic values to be dependent variables and each ecozone to be independent. The sites were included as a random factor. The relationships between the individuals' isotopic values over time were analyzed using general linear models. The differences between species were examined using t-tests, analysis of variance (ANOVA) and Tukey post-hoc tests with a significance level of 0.05. All the statistical analyses were performed using R 3.4.3 software. To calibrate the radiocarbon dates to Common Era years (CE), the Calib Rev 7.0.4 programme and SHCal - 13 curve (Hogg et al. 2013) were used.

Results and discussion

Guanaco

The bulk collagen isotope value for samples recovered from the northern Pampa (wetland + Pampa

Ondulada) shows a C₃ diet with a minor contribution of C₄ plants ($n = 22$; $\delta^{13}\text{C}_{\text{co}} -18.7 \pm 2.0 \text{ ‰}$) (Table 1). Two different tendencies can be observed here. Those recovered from wetland sites ($n = 18$) have a depleted average ($\delta^{13}\text{C}_{\text{co}} -19.0 \pm 2.1 \text{ ‰}$), close to a monoisotopic C₃ diet with a minor component of C₄ plants ($\sim \leq 5\%$), while the four samples recovered from the Pampa Ondulada (Cañada de Rocha site, late Holocene) and Laguna El Doce sites (middle Holocene), have a slightly enriched mean of $-17.3 \pm 0.3 \text{ ‰}$. This explains why the intervals of confidence for each area are not superimposed and the wetland values are depleted (IC wetland = $-20.1 \text{ ‰} \mid -18.0 \text{ ‰}$; Pampa Ondulada = $-17.8 \text{ ‰} \mid -16.7 \text{ ‰}$). However, the average gap between both sets of samples is small (1.7 ‰), which could easily be related to the small sample effect in the case of the latter, where only four values are available. In fact, in the wetland collection there are enriched and even more enriched values than the Pampa Ondulada ones. Thus, the difference between both sets of samples is not significant ($F = 2.61$; $p = 0.1216$). Moreover, the Pampa Ondulada collagen isotope values must be treated with caution, since they lack a measured C/N ratio, and this environment is proving to be quite detrimental to the proper conservation of collagen (Buc and Loponte 2016), so the values from the Pampa Ondulada should not be taken into account by now. Having said that and just only to consider, it should also be noted that most of the samples from the Pampa Ondulada were recovered from the Cañada de Rocha site, whose chronology matches one of the main events of the Little Ice Age (LIA), and the last ones from Laguna El Doce match the Holocene Thermal Maximum (HTM). Meanwhile, the wetland does not include samples from the HTM or the LIA; conversely, most fall within the Medieval Climatic Anomaly (MCA), and a few samples in the period immediately before that. We think that if the Pampa Ondulada samples were reliable, these mostly unmatched sets of samples from a chronological point of view could reflect distinct environmental conditions, which would explain differences (see section 7.5 for a discussion on the topic).

In the apatite, the bulk value (wetland + Pampa Ondulada) also shows a C₃ pattern with a minor contribution from C₄ plants ($n = 20$; $\delta^{13}\text{C}_{\text{ap}} -9.4 \pm 1.1 \text{ ‰}$, see Table 1). Here we have a better chronological distribution of the samples in order to make a suitable comparison between both areas (see Supplemental Data Table 1). The wetland ($n = 12$; $\delta^{13}\text{C}_{\text{ap}} -9.7 \pm 1.2 \text{ ‰}$) and Pampa Ondulada values ($n = 8$; $\delta^{13}\text{C}_{\text{ap}} -9.0 \pm 0.9 \text{ ‰}$) show no statistical differences ($F = 1.87$; $p = 0.18$). Indeed, the intervals of confidence (95%) are superimposed (wetland = $-10.5 \text{ ‰} \mid -8.8 \text{ ‰}$; Pampa Ondulada = $-9.8 \text{ ‰} \mid -8.3 \text{ ‰}$). This reflects exactly what is to be expected for a single population that lived during the same temporary block (end of the Late Holocene), as can equally be observed in the phalanx's morphometry

in both subsets of samples (see Buc and Loponte 2016) and oxygen magnitudes (see below).

Within the wetland samples, the spacing between both carbon sources is typical for large herbivores, $\Delta_{\text{co-ap}} = 9.7 \pm 2.1 \text{ ‰}$ (cf. Crowley et al. 2010; Lyut 2017). In turn, the nitrogen isotope magnitudes ($\delta^{15}\text{N} 6.4 \pm 1.8 \text{ ‰}$) are also usual for continental herbivores (Schoeninger and DeNiro 1984). One particular point which should be noted is the high nitrogen isotope level of the EIL 2031 outlier ($\delta^{15}\text{N} 10.4 \text{ ‰}$, see Table 1). This sample is an unfused metapodial which belongs to a juvenile individual below 18 – 36 months old (cf. Mengoni 2013). Therefore, its extreme value could be understood as being influenced by breastfeeding, physiological issues and/or nutritional stress. There are no other published values in the entire Pampa region to compare it with, but in Perú higher nitrogen isotope levels in juvenile camelids were also correlated with their dependency on their mother's milk (Szpak et al. 2014).

In the collection of wetland sites, the maximum intraspecific range in collagen isotope values (hereafter $\Delta^{13}\text{C}_{\text{co-co}}$) is 7.2 ‰ (samples AIE 20921 vs. EIL 2032/2, see Table 1). This variability is also present in the guanaco values post-2400 ¹⁴C YBP, recovered from the southern Pampa, where a difference of 7.1 ‰ was recorded (sample AA 95300 vs. AA 94557, see Table 2). The within-species range of values can be observed even in samples from a single wetland site, such as El Cazador site 3 ($\Delta^{13}\text{C}_{\text{co-co}} = 5.3 \text{ ‰}$, to compare samples EIL 2032/2 vs. EIL 1011, see Table 1). There is no equivalent collection from the southern Pampa with the same quantity of samples analyzed from one site and which also has such a small chronological range as El Cazador site 3. The only case which comes close is the Calera site, where six collagen isotope values yield $\Delta^{13}\text{C}_{\text{co-co}} = 4.1 \text{ ‰}$ (to compare samples AA 67732 vs. AA 71669, Table 2). This magnitude is similar to the one at El Cazador site 3, but within a somewhat more scattered timeline (and no informed C/N values, see below). In the apatite fraction, the intraspecific ranges in the northern Pampean samples also vary from the purest C₃ diet, as can be observed in the Garín sample (-13.1 ‰ , EIL 2033, recovered from the wetland), and the most enriched one in Hunter (-7.7 ‰ , EIL 2025 recovered from the Pampa Ondulada, see Table 1), giving a maximum of $\Delta^{13}\text{C}_{\text{ap-ap}} = 5.4 \text{ ‰}$.

The arithmetic mean of the oxygen isotope values of all the samples recovered from both areas (Pampa Ondulada + wetland; $n = 19$, including outlier EIL 2030) is $\delta^{18}\text{O} -0.3 \pm 1 \text{ ‰}$ (see Table 1). This magnitude is close to the average of the Pampa lakes and streams ($\delta^{18}\text{O} 0.26 \pm 0.8 \text{ ‰}$, calculated from Dapeña et al. 2001 Table 1). It does not matter if the guanacos were recovered from the Pampa Ondulada sites ($n = 7$; $\delta^{18}\text{O} 0.12 \pm 0.6 \text{ ‰}$ excluding outlier EIL 2030) or from the

Table 1. Isotopic values obtained from the guanaco samples on the northern Pampa (wetland + Pampa Ondulada). All the values are post-2400 ¹⁴C YBP except Laguna El Doce (AA89914). All the samples are in-between the DeNiro bounds (C/N 2.9 – 3.6), except those marked with * which lack C/N ratio.

Site	Location	Lab. Code	$\delta^{13}\text{C}_{\text{co}}$ ‰	$\delta^{13}\text{C}_{\text{ap}}$ ‰	Spacing	$\delta^{15}\text{N}$ ‰	$\delta^{18}\text{O}$ ‰
El Espinillo	Wetland	EIL 1001	-17.9	-8.3	9.6		-0.49
Garín	Wetland	EIL 2033	-22.4	-13.1	9.3	6.3	-1.36
Lechiguanas 1 (level IV)	Wetland	EIL 1009	-17.5	-9.2	8.3	5.5	0.09
Lechiguanas 1 (level IV)	Wetland	AA103660	-18.4*				
El Cazador sitio 3	Wetland	EIL 1010	-18.7	-8.8	9.9	5.5	-0.91
El Cazador sitio 3	Wetland	EIL 1011	-17.9	-9.1	8.8	5.1	-0.72
El Cazador sitio 3	Wetland	EIL 1012/1	-19.5	-9.4	10.1	4.9	-0.15
El Cazador sitio 3	Wetland	EIL 1013/1	-20.6	-10.9	9.7	7.1	
El Cazador sitio 3	Wetland	EIL 2032/2	-23.2	-9.0	14.2	8.4	-0.97
Túmulo de Campana 1	Wetland	AA 108370	-20.0*				
Túmulo de Campana 2	Wetland	EIL 2031	-22.4	-10.2	12.2	10.4	-1.78
Vizcach.	Wetland	AIE20921	-16.0	-9.5	6.5		-1.80
Rancho largo	Wetland	EIL 1007	-16.4	-9.7	6.7	4.8	-0.08
Punta Canal	Wetland	EIL 2030/1	-20.2	-9.5	10.7	6.3	-0.15
Playa Mansa	Wetland	UGAMS 3302	-18.6*				
San Clemente II	Wetland	AA 13822	-17.4*				
San Clemente IV	Wetland	AA 28412	-16.4*				
Las Marías	Wetland	NSRL 12252	-19.0*				
Meguay	Pampa Ondulada	AIE20923		-9.2			-0.90
Meguay	Pampa Ondulada	EIL 2030/2		-9.0			2.30
Meguay	Pampa Ondulada	EIL 2029		-10.3			0.66
Meguay	Pampa Ondulada	EIL 2028		-8.6			-0.01
Hunter	Pampa Ondulada	EIL 2027		-8.7			0.36
Hunter	Pampa Ondulada	EIL 2026		-8.5			-0.34
Hunter	Pampa Ondulada	EIL 2061		-10.2			0.77
Hunter	Pampa Ondulada	EIL 2025		-7.7			0.34
Cañada de Rocha	Pampa Ondulada	AA108389	-17.4*				
Cañada de Rocha	Pampa Ondulada	Beta 220693	-16.8*				
Cañada de Rocha	Pampa Ondulada	Beta 220695	-17.3*				
Laguna El Doce	Northwest Pampa	AA89914	-17.6*				
N			22	20	12	10	19
Mean			-18.7	-9.4	9.7	6.4	-0.3
SD			2.0	1.1	2.1	1.8	1.0
CV			10.9	12.1	22.0	27.8	291.5
25 prntil			-20.0	-10.0	8.3	5.0	-0.9
75 prntil			-17.4	-8.7	10.1	7.6	0.3

wetland sites ($n = 11$; $\delta^{18}\text{O} -0.76 \pm 0.7$ ‰, see Table 1). The values are all enriched. There is a slight depletion in the subset recovered from the wetland compared to the Pampa subset ($F = 9.727$; $p = 0.014$), but this is linked to three specific samples from the wetland; one of them has an enriched collagen isotope value (AIE 20921), but the other two exhibit more depleted ones in both carbon sources, indicating a pure C_3 diet or close to it (samples EIL 2031, 2033). This depletion in oxygen can be a random effect due to the small sample size. Indeed, some of the water in streams on the Pampa plain is depleted by as much as -1.8 ‰ (Dapeña et al. 2001). This could also be related to the more humid conditions, as they are during the warm and wetter MCA period, although other samples from the same time period are enriched, or rather they are less depleted (see section 7.5). These three depleted samples also would be slightly influenced by the wetland environment itself, which extends up to 7 – 10 km inside the eastern border of the Pampa Ondulada (Daus 1973; Hoffman and García 1968). It is expected that animals which went through their lifecycles in this area, or which frequented this border, reflect an isotopic niche affected by the Paraná valley environment; meanwhile, the other hunted guanacos, including most of the samples recovered from

wetland sites, show no influence by this environment at all. Thus, individuals who more frequently used the border area closest to the wetland would tend to have exhibited more depleted oxygen isotope values (and both carbon sources) values than those that occasionally or sporadically reached this ecotone or nearby. These movements towards the ecotone gave the guanacos the opportunity to feed on the western edge of the xeromorphic forest. We will see below the same trend towards depleted apatite and oxygen isotope values in pampas deer samples recovered from wetland sites, a trend that could be explained in the same way as the influence of the Paraná valley environment, and which reinforces this interpretation as one of the possible or concurrent explanations for these few samples of guanaco.

As all the guanaco oxygen isotope values are quite different from the regional meteoric waters ($\delta^{18}\text{O} - 5.5$ ‰) and the water in the Paraná valley (-4.5 ± 1.3 ‰), this species only used the Pampa plain as its habitat, avoiding the subtropical wetland and ingesting most of its body water from the enriched shallow lakes and streams of the Pampa Ondulada, behaving like a frequent drinker as described in areas with enough available surface water. The high coefficient of variation in the oxygen isotope values observed in

guanaco bones (291.5%), including extreme magnitudes like the outlier EIL 2030/2, is precisely what would be expected among frequent drinkers in the Pampa Ondulada, as the shallow lakes and streams there have an equally large coefficient of variation, rounded up to 318% (calculated from the values of the waters of the lakes and streams listed in Dapeña et al. 2001; Table 1). This large variation is related to water bodies with different volumes, distinct rates of evaporation and unequal proportional recharge rates from both the depleted phreatic and meteoric waters (cf. Levin et al. 2006). The evaporation processes in some of the plants' edible parts (mostly leaves) also enrich the oxygen isotope values with respect to the meteoric waters (Ayliffe and Chivas 1990; Kohn 1996; Levin et al. 2006), which could be another factor in this enrichment.

Within the available sample size (Pampa Ondulada + wetland), there is no significant regression between apatite and oxygen isotope values ($r_s = 0.26$, $p = 0.27$) or between collagen and oxygen isotope values ($r_s = 0.31$, $p = 0.34$), but it is positive and significant between oxygen isotope values and time ($R^2 = 0.04$; $F = 0.884$, $p = 0.36$) and between nitrogen isotope values and time ($R^2 = 0.080$ $F = 1.798$; $p = 0.194$). We discuss these trends in section 7.5.

A regional overview of the guanaco's isotopic values

In other areas of the Pampa region no apatite or nitrogen isotope values for the guanaco are available, except for a few samples (*i.e.* Barberena et al. 2009), and certainly no $\delta^{18}\text{O}$ analysis at all. But, there are numerous radiocarbon dates obtained in the Southern Pampa where $\delta^{13}\text{C}_{\text{collagen}}$ was obtained through the dating process (Barberena et al. 2009; Massigoge 2012; Messineo et al. 2013, 2014; Scabuzzo et al. 2016). Unfortunately, all these values lack a C/N ratio nor wt % C wt % N, or at least they are not informed. In this way, they have a potential bias and some isotopic studies discourage its use (DeNiro 1985; Szpak, Metcalf, and Macdonald 2017). Having said that, by now we have no option but to use them to compare the values from the south with those from the north, within the parameters of a hypothetical exercise. A previous analysis with 25 southern samples was performed by Barberena et al. (2009). In this paper, we included 42 values, all from the southern Pampa up to 39° SL, where this plain ends and the northern Patagonia environment begins, as well as one sample from the Inner Pampa (see Figure 1). This list is not exhaustive and some few values may have been left out (Table 2).

The average of all the samples listed in Table 2 is $\delta^{13}\text{C}_{\text{Cco}} -20.4 \pm 2.1$ ‰, IC = -21.06 ‰ | -19.74 ‰, including five outliers ≤ -23.9 ‰, four recovered from

a single site (Nutria Mansa), with extremely depleted values ($n = 4$, $\delta^{13}\text{C}_{\text{Cco}} = -24.9 \pm 0.3$ ‰). These 42 samples are distributed approximately through eight millennia, thus becoming a hypothetical average of the entire Holocene. To make an adequate comparison between north and south, we considered 17 samples post-2400 YBP from the last area (see Table 2), whose average is $\delta^{13}\text{C}_{\text{Cco}} -19.9 \pm 1.8$ ‰. These results show no statistical differences in collagen isotope values between northern samples (wetland + Pampa Ondulada) and the southern ones ($F = 3.747$; $p = 0.060$). If we compare the southern samples with the wetland ones only (which are more reliable as they have C/N ratios and match chronologically), the values are even closer ($F = 1.76$; $p = 0.19$). In fact, the intervals of confidence (95%) are almost perfectly superimposed between the wetland samples (-20.1 ‰ | -18.0 ‰) and the southern Pampa post-2400 ^{14}C YBP (-20.9 ‰ | 19.0 ‰, see Table 3 and Figure 5). Thus, we cannot statistically support a clinal variation in the guanaco's diet as we expected. However, the very mild enrichment of the wetland samples, which are ~ 0.9 ‰ enriched in the IC and $+1.4$ ‰ in the 75th percentile could be initial clues of this geographical variability (see Table 3).

Some other minor differences can be observed. In the south there is quite a tight conglomeration of values, except for the outliers (which influence the decreasing average value), along with a lower coefficient of variation, suggesting a less variable environment than the northern plain. This may be related to multiple factors, including greater regularity in some of the environmental parameters along with a maritime influence for a large sector in the south. However, some variability inputs for the isotopic diets must be expected in the southern Pampa, such as the influence of the narrow coastal environment along the southeastern border, as salinity can modify the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Stevens, Lister, and Hedges 2006), as well as movements of guanaco troops between the southern and the west Pampa and the north of the Patagonian steppe.

An extra-regional overview of the guanaco's isotopic values

The samples recovered from the Monte eco-region in south Mendoza, located around 700 km west of the Pampa Ondulada are quite interesting for two basic reasons. The first is that it helps us to understand the variability of the guanaco in its foraging behaviours, and second, these variations allow us to analyze the evolution of the Pampean climate, both objectives of this work. The climate in south Mendoza is also temperate, with an annual mean of 15.3°C , close to that of the Pampa Ondulada, but there is less rainfall, only ~ 340 mm per year (all the values

Table 2. $\delta^{13}\text{C}$ collagen isotope values from the southern Pampa. The sample codes beginning with a 'B' refer to the Beta Analytic Laboratory, 'AA' to the Arizona University Laboratory and 'CAMS' to the Center for Accelerator Mass Spectrometry. References: 1 = Barberena et al. (2009). 2 = Scabuzzo et al. (2016). 3 = Messineo et al. (2014). 4 = Messineo et al. (2013). 5 = This paper. 6 = Massigoe (2012). 7 = Politis et al. (2012).

	Code	Site	$\delta^{13}\text{C}_{\text{Cco}}$	^{14}C YBP	Ref.	Code	Site	$\delta^{13}\text{C}_{\text{Cco}}$	^{14}C YBP	Ref.
post – 2400 ^{14}C BP	B169820	Quequén Salado 1	-18.6	360 ± 40	1	AA67732	Calera	-18.5	3008 ± 46	1
	AA91414	Paso Vanoli	-19.5	714 ± 53	2	AA72844	Paso Otero 1	-19.0	3056 ± 42	1
	B157398	Quequén Salado 1	-19.0	790 ± 40	1	CAMS 4993	Zanjón Seco 2	-19.8	3070 ± 40	1
	B157397	Quequén Salado 1	-19.1	940 ± 40	1	CAMS 4994	Zanjón Seco 2	-19.5	3080 ± 40	1
	B169821	Quequén Salado 1	-18.9	960 ± 40	1	AA55115	Nutria Mansa 1	-25.0	3080 ± 110	1
	AA90374	El Puente	-22.4	1220 ± 340	3	AA94559	Empalme Querandíes 1	-18.6	3095 ± 50	4
	AA59507	La Barrancosa	-20.2	1676 ± 46	1	AA81453	Las Brusquillas 1	-19.0	3334 ± 43	6
	B169822	Quequén Salado 2	-19.3	1720 ± 40	1	AA71669	Calera	-22.6	3390 ± 170	1
	AA67735	Calera	-19.2	1748 ± 42	1	AA82709	Paso Mayor	-19.8	3820 ± 47	2
	AA7070	Tres Reyes 1	-20.4	1845 ± 50	1	AA81647	Fortín Necocha	-20.4	4024 ± 56	5
	AA95300	El Puente	-16.8	2069 ± 53	3	AA82709	Paso Mayor	-19.9	4046 ± 57	2
	AA94557	Empalme Querandíes 1	-23.9	2052 ± 62	4	AA90376	El Puente	-22.7	4500 ± 1400	3
	AA67773	Calera	-18.8	2075 ± 44	1	AA93220	Laguna de los Pampas	-18.1	5684 ± 61	7
	AA64617	Calera	-20.8	2232 ± 55	1	AA71656	Paso Mayor	-19.5	5877 ± 63	2
	AA7971	Tres Reyes 1	-19.9	2235 ± 50	1	AA80664	La Olla 4	-19.9	6960 ± 71	1
	AA67736	Cortaderas	-23.6	2270 ± 190	1	AA24052	Arroyo Seco 2	-19.8	7540 ± 80	1
	AA71655	García del Río	-18.6	2342 ± 47	2	AA52613	Arroyo Seco 2	-23.3	8390 ± 410	1
	AA55114	Nutria Mansa 1	-25.3	2705 ± 66	1	USF8751	Nutria Mansa 1	-25.0	n/d	1
	AA82714	Paso Mayor	-19.0	2774 ± 45	2	N		42		
	AA94558	Empalme Querandíes 1	-19.9	2816 ± 49	4	Mean		-20.4		
	AA90377	El Puente	-20.1	2900 ± 51	3	SD		2.1		
	AA55116	Nutria Mansa 1	-24.6	2920 ± 110	1	CV		10.3		
	AA81648	Escuela Agropecuaria	-19.3	2983 ± 51	5	25 prcnil		-20.8		
	AA71671	Calera	-19.1	3005 ± 66	1	75 prcnil		-19.0		

(*)This average includes five samples that lack C/N ratio (see Table 1). If we exclude them, the average is $\delta^{13}\text{C} -19.3 \text{‰}$ and CI $-20.7 \text{‰} | -17.9 \text{‰}$.

are for San Rafael city). Here there are increased heliophany and irradiance regimens due to the reduction in cloud cover (Grossi Gallegos and Righini 2007; Servicio Meteorológico Nacional 2017). All these environmental parameters give rise to a semi-arid environment suitable for C_4 grasses within the NAD-ME biochemical type and C_3 grasses, shrubs and trees endemic to or typical of the South American Arid Diagonal (Bruniard 1982). A significant quantity of the collagen isotope values of camelid bones were obtained in this eco-region, averaging $\delta^{13}\text{C}_{\text{Cco}} -16.3 \pm 2.3 \text{‰}$ (Gil et al. 2016; Table 2). The authors suggest an association between the enriched collagen isotope values and a significant proportion of natural C_4 plants. Within this collection are included four collagen isotope values from bones properly identified as guanaco (*Lama guanicoe*), recovered from the Aguas de los Caballos and Nacimiento de los Leones archaeological sites (Barberena et al. 2009; Gil et al. 2016). Both deposits are between 35° and 36° SL, almost the same latitude where the Pampa Ondulada ends (-35° L) albeit around 1000 masl. The mean of the collagen isotope values of these four samples yield $\delta^{13}\text{C}_{\text{Cco}} -17.1 \pm 1.6 \text{‰}$. In turn, the $\delta^{15}\text{N}$ average is $7.6 \pm 2.0 \text{‰}$ (based on Gil et al. 2016, samples MSRA-200, MSR-16; Barberena et al. 2009, samples USF 5906 and USF 8865 whom classified these last two samples as guanaco). Therefore, these values are slightly more enriched in collagen carbon and nitrogen isotope values than both the southern and northern Pampean samples, which is expected due to the greater aridity and net irradiancy. The availability of

nitrogen isotopes magnitudes allows us to plot them against the northern Pampean samples and to include the only two records of nitrogen obtained in the southern Pampa (Barberena et al. 2009). Although the latter two were obtained in bones dated 3070 ± 40 and 3080 ± 40 ^{14}C YBP, which is outside the temporal block we are analyzing here, the time difference is small and they are the only data available from this area. All these values are plotted in two different groups. The first corresponds to the Pampa region (north + south), and the second, enriched in collagen and nitrogen isotope values, to the Monte eco-region samples (see Figure 6).

Chronological trends in the guanaco isotopic values

With regard to all the Holocene values available for the guanaco in the northern and southern Pampa, and plotted with the chronology, there is an apparent positive enrichment with time. However, the association between the collagen isotope values and time fails to reach significant levels (adjusted R – squared: 0.11; $F = 0.199$, $p = 0.843$). In the same way, there is no significant relationship between the values, time and the area where the samples were recovered (wetland, Pampa Ondulada and southern Pampa) ($F = 0.074$, $p = 0.942$). In the inorganic fraction, based on the only values available (wetland) the apparent trend is inverse, as there is a declination toward depletion as the samples are modern. However, a significant regression could also not be found ($R^2 = 0.06$; $F =$

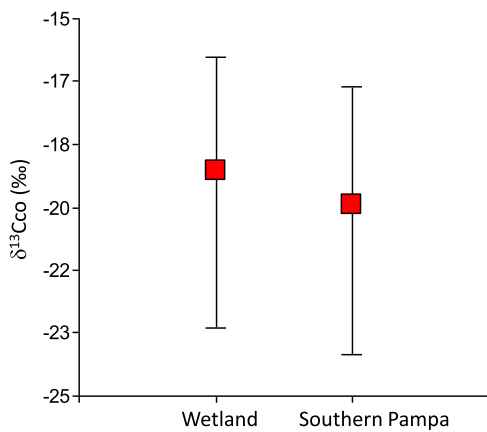


Figure 5. Average, maximum and minimum $\delta^{13}\text{C}$ collagen isotope values for the guanaco post-2400 YBP from the wetland ($n = 18$) and southern Pampa ($n = 17$).

1.14; $p = 0.299$). Thus, both observed trends show no temporal variation (Supplemental Data Figure 1).

Pampas deer

The collagen carbon isotope values of this species in the northern area are only based on three wetland samples, showing a C_3 monoisotopic diet ($\delta^{13}\text{C}_{\text{Cco}} -21.0 \pm 1.9$ ‰). There are no usable collagen data from the Pampa Ondulada. In the apatite, seven values are available (wetland + Pampa Ondulada), where a C_3 diet can also be observed ($\delta^{13}\text{C}_{\text{Cap}} -11.2 \pm 1.5$ ‰) (see Table 4). As in the guanaco's case, there are no significant differences in the average between the wetland subset ($n = 4$; $\delta^{13}\text{C}_{\text{Cap}} -11.6 \pm 1.9$ ‰) and the Pampa Ondulada ($n = 3$; $\delta^{13}\text{C}_{\text{Cap}} -10.6 \pm 0.7$ ‰), nor in the intervals of confidence (-14.75 ‰ | -8.60 ‰; -12.40 ‰ | -8.87 ‰, respectively). The more depleted mean and lower bound of the IC of the wetland values could be a random effect due to the sample size, or to the limited/partial use of this environment by this species. The $\Delta^{13}\text{C}_{\text{co-co}}$ is the smallest out of the species analyzed here (1.1‰). However, the sample size is too small to explore it. The spacing between both carbon sources ($\Delta^{13}\text{C}_{\text{co-ap}}$) is 10.1 ± 0.6 ‰ and $\delta^{15}\text{N}$ is 5.2 ± 0.5 ‰, both typical magnitudes for pure herbivores and continental diets (see Table 4).

The mean of $\delta^{18}\text{O}$ is -0.48 ± 0.9 ‰, close to the values of the Pampean lakes and streams, and far outside those of wetland organisms. This indicates the Pampa plain is the main habitat for this deer. It does not matter if the samples were collected in the wetland or the Pampa Ondulada, the values are enriched in $\delta^{18}\text{O}$. However, there are minor differences between the individuals recovered from the wetland sites ($n = 4$; $\delta^{18}\text{O} -1.15 \pm 0.3$ ‰; CI -1.70 ‰ | -0.6 ‰) compared with those obtained from the Pampa Ondulada sites ($n = 3$; $\delta^{18}\text{O} 0.43 \pm 0.4$ ‰; CI -0.5 ‰ | 1.35 ‰). These variations sustain the idea

that most pampas deer recovered from the wetland sites went through deer their biological cycles on the Pampa plain close to the wetland and in the narrow forest between both ecozones, and that they used the floodplains and drier prairies of the wetland itself, where they were probably hunted. Indeed, their archaeological representation shows that complete carcasses were transported to the wetland sites (Acosta 2005; Acosta and Mucciolo 2014; Acosta, Loponte, and Mucciolo 2014; Loponte 2008). The within-species variability in oxygen isotope values is close but slightly broader than those observed in the guanaco, which could be explained as a more adaptive behaviour which allowed the pampas deer to use the wetland environment on a more frequent basis.

A regional overview of the isotopic values of the pampas deer

The collagen isotope values included in this study (all post-2400 ^{14}C YBP) from the southern Pampa correspond to two samples from the El Picadero site (-21 ‰ and -21.4 ‰) (Colombo 2013), one from the Las Brusquitas site 2 (-25.2 ‰) (Massigoge 2011) and another from the Puente de Fierro site (-20.0 ‰) (Scabuzzo et al. 2016). This list is not exhaustive and a few values may have been left out. The average of these four samples is $\delta^{13}\text{C}_{\text{Cco}} -21.9 \pm 2.3$ ‰, which is a monoisotopic C_3 diet, similar to but slightly more depleted than the northern samples (-21.0 ± 1.9 ‰). The difference in the average is 0.9 ‰, which is the difference in the mean between the guanacos from the south and from the wetland (see Table 3). The maximum $\Delta^{13}\text{C}_{\text{co-co}}$ in collagen in all the samples from this deer (northern + southern Pampa) is 6.4 ‰ (samples Guazunambí UGA 9908 vs. Las Brusquitas site 2), close to the maximum recorded in the guanaco (7.2 ‰), even with such a small sample.

Chronological trends in the pampas deer isotopic values

There is a limit to the size of a sample when analyzing temporal trends. If we take into account the northern and southern Pampa regions, an enrichment of the isotopic values of the collagen can be observed, as the samples are more recent ($R^2: 0.542$, $F = 4.738$ $p: 0.095$). For the inorganic fraction we only have the northern samples, where, on the contrary, there is a tendency toward depletion, although not significant ($R^2: 0.129$, $F = 0.7414$ $p = 0.4286$) (Supplemental Data Figure 2).

Marsh deer

Both of this deer's carbon sources yield a C_3 monoisotopic diet ($\delta^{13}\text{C}_{\text{Cco}} -20.7 \pm 1.5$ ‰; $\delta^{13}\text{C}_{\text{Cap}} -12.2 \pm 1.9$ ‰). The $\Delta^{13}\text{C}_{\text{co-co}}$ is 7.1 ‰ (AA108383 vs.

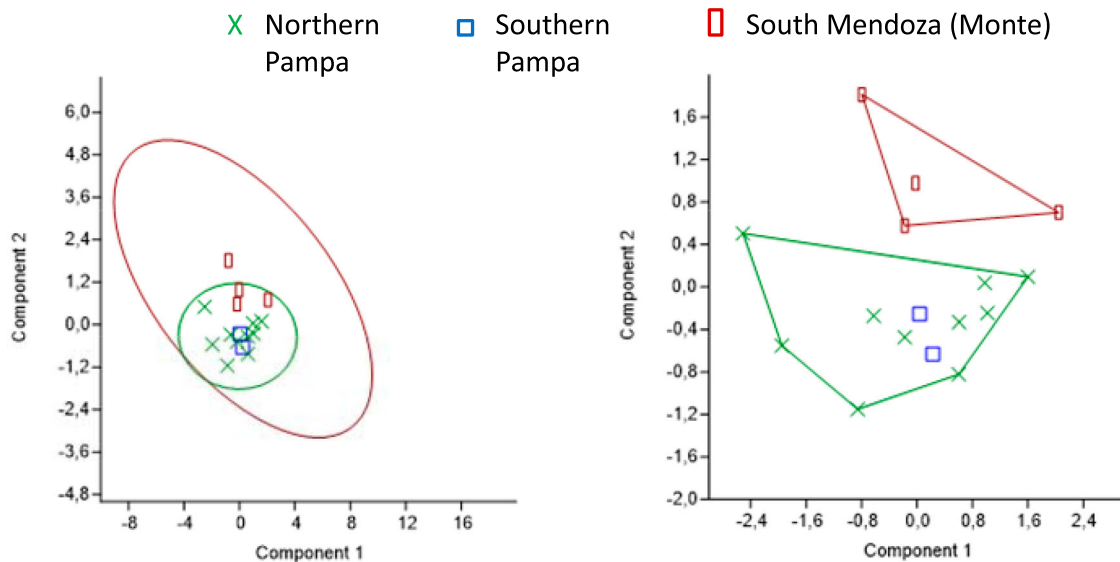


Figure 6. Overview of the guanaco's isotopic values. Principal component analysis ($\delta^{13}\text{C}$ collagen and $\delta^{15}\text{N}$) including the wetland, southern Pampa and south Mendoza samples. In the left-hand graph, the green line is the 95% ellipsis and the external one represents the tendency. In the right-hand graph, all the values are clustered in convex hull areas.

AA108385, see Table 5), while in the archaeologically synchronous samples (AA108387 and AA108383) it reaches 6.5 ‰. This within-species variability is more equal in the apatite than in the collagen ($\Delta^{13}\text{C}_{\text{ap-ap}}$ 7.2 ‰, comparing AIE 26923/4 vs. AIE 26931/2, see Table 5), both close to the guanaco. The spacing between carbon sources is to be expected for large herbivores ($\Delta^{13}\text{C}_{\text{co-ap}}$ 8.1 ± 1.2 ‰). The nitrogen isotope values (5.9 ± 1.3 ‰) are also typical for continental herbivores. The only $\delta^{18}\text{O}$ magnitude available today for this mammal is a typical value for the Paraná valley (-3.38 ‰, UGA 9907). Indeed, the archaeological record shows that this deer selected strictly wetland as its habitat (Acosta and Mucciolo 2013; Acosta, Loponte, and Mucciolo 2014), extending to the outer estuary of the Río de la Plata River in the south and including the mixohaline wetland of Samborombón Bay. This expansion to the south during the late Holocene was predicted some years ago (Loponte 2004) and archaeological studies have recently confirmed it (Acosta and Mucciolo 2014; Silveira et al. 2010). The hypothesis that this record is 'anomalous', as alleged by Politis et al. (2011), is based on a highly hypothetical model which is also contradictory and not supported by the archaeological record or the type of habitat selected by this mammal (see Acosta and Mucciolo 2014).

No isotopic data are available for the southern distribution of this deer (the middle estuary of the Río de la Plata River, the Salado Depression and Samborombón Bay). But, to the north in the Iberá wetland, the mean of the currently available values is $\delta^{13}\text{C}_{\text{co}} - 23.1$ ‰ (Loponte and Corriale 2012).

Chronological trends in the marsh deer's isotopic values

The collagen isotope values in this species tend to be enriched when the samples are more recent (R^2 : 0.20, F = 6.82, p = 0.015). The most enriched samples are chronologically arranged between ca. 700 – 1100 ^{14}C YBP (n = 13; $\delta^{13}\text{C}_{\text{co}}$ -19.8 ‰), while the depleted ones are clustered between ca. 1500–2300 ^{14}C YBP (n = 14; $\delta^{13}\text{C}_{\text{co}}$ -21.6 ‰). Conversely, and with smaller samples, the apatite carbon isotope values are more depleted in more recent samples, but not significant (R^2 : 0.103, F = 1.0322, p = 0.3362) (Supplemental Data Figure 3). We discuss these trends in section 7.5.

General trends

Habitat use

We have already seen that the oxygen isotope values support the guanaco and pampas deer having selected

Table 3. $\delta^{13}\text{C}$ collagen isotope values for guanacos from the northern, wetland and southern Pampa (post-2400 YBP). LB = lower bound of the 95% confidence interval. UB = upper bound of the 95% confidence interval. The $\Delta^{13}\text{C}_{\text{co-co}}$ value for the Pampa Ondulada was not calculated due to the small sample size. (*) This average includes five samples that lack C/N ratio (see Table 1). If we exclude them, the average is $\delta^{13}\text{C} -19.3$ ‰ and CI -20.7 ‰ | -17.9 ‰.

Area	<i>n</i>	Mean (‰)	SD (‰)	CV (%)	Min. (‰)	Max. (‰)	$\Delta^{13}\text{C}_{\text{co-co}}$	<i>P</i> .75 (‰)	LB (95%)	UB (95%)
Wetland alone	18	-19.0*	2.1	11.0	-23.2	-16.0	7.2	-17.5	-20.1	-18.0
Pampa Ondulada alone	3	-17.2	0.3	1.7	-17.4	-16.8	-	-16.8	-18.0	-16.4
Wetland + Pampa Ondulada	21	-18.8	2.1	11.1	-23.2	-16.0	7.2	-17.4	-19.7	-17.8
Southern Pampa	17	-19.9	1.8	9.0	-23.9	-16.8	7.1	-18.9	-20.9	-19.0

the Pampa Ondulada plain as their habitat. Given this spatial overlap throughout the entire Holocene, they probably both formed an interspecific guild with a low level of competition for food, where mutualistic relationships would not have been discarded (see examples for herbivores in Sinclair and Norton-Griffiths 1982). The slightly depleted values for some individuals of both species collected at wetland sites could be related to some environmental changes during the Holocene (see section 7.5) and/or are concurrently linked to eastern herds/troops that are subject to the wetland environment's influence and a less continental climate. Although there are no statistical differences in the oxygen isotope values between the pampas deer and the guanaco ($F = 0.415$ $p = 0.526$) and that their IC of $\delta^{18}\text{O}$ are superimposed throughout almost the entire range ($-1.31\text{‰} \mid 0.36\text{‰}$ vs. $-0.74\text{‰} \mid 0.20\text{‰}$ respectively), there are slight differences according to each species. With the exception of one pampas deer sample (UGA 9908, see Table 4), the values of this mammal recovered from wetland sites tend to be slightly more negative ($n = 4$, $\delta^{18}\text{O} -1.15 \pm 0.3\text{‰}$) than the guanaco recovered from the same area ($n = 11$, $\delta^{18}\text{O} -0.76 \pm 0.70\text{‰}$). We think this difference could be random or related to the pampas deer's direct use of the wetland prairies and the estuaries of the Pampa Ondulada's streams, which are connected to the wetland and are regular pathways for this deer's movement through both landscapes, where it had the opportunity to drink depleted waters and eat the plants under their influence, and where historical records also mention its presence (Darwin 1839). This ability to use different habitats shows a greater adaptability with respect to the guanaco. In fact, the archaeological record shows that pampas deer also inhabited the Salado Depression wetland with high humidity levels and frequently waterlogged prairies. Conversely, for the guanaco, the xeromorphic forest probably constituted the first barrier against its dispersion into the wetland, and the adjacent and subtropical flooded prairies were a definitive ecological barrier to the east. In the same way, the guanaco troops were absent from the Salado Depression (cf. Aldazabal and Eugenio 2008; Aldazabal, Silveira, and Eugenio 2007; González 2005;

Loponte 1996–98). The anatomical representation of both mammals at the archeological sites located in the wetland but adjacent to the Pampa Ondulada supports this distribution, as there are complete carcasses of pampas deer, while, on the contrary, guanacos tend to be represented by a specific anatomical selection (phalanxes and distal metapodials) which has been linked to fur-related activities (Loponte 1996–98; Buc and Loponte 2016). Indeed, when the archaeological sites are located in the wetland interior far from the ecotone with the Pampa Ondulada, both mammals are rarely found in or absent from archaeofaunal collections. This can also be observed throughout the entire archaeological record currently available for the wetland (2400–400 ^{14}C YBP) (Buc and Loponte 2016). Exactly the same happens with other prey typical of the Pampa Ondulada such as the ñandú (*Rhea americana*). It is common at wetland sites in the ecotone or adjacent to the Pampa plain, but absent or quite rare in the wetland interior. Its $\delta^{18}\text{O}$ values are more equally enriched than those of the guanaco or the pampas deer; and it follows the same general rule, which is a general trend toward slightly depleted values in individuals hunted near the ecotone (at the El Espinillo site it is $\delta^{18}\text{O} 1.4\text{‰}$) than those obtained in the inner Pampa Ondulada (at the Hunter site it is $\delta^{18}\text{O} 2.3\text{‰}$) (see Figure 7).

The ecological barrier of the Paraná River also meant a border for the pampas deer, encouraging the differential distribution of subspecies; in the humid Pampa the *O. b. celer* subspecies, on the Entre Ríos plain the *O. b. leucogaster* subspecies and on the Uruguay plain from the eastern bank of the Uruguay River the *O. bezoarticus arerunguaensis* and *O. bezoarticus uruguayensis* forms (González, Álvarez-Valin, and Maldonado 2002; Weber and González 2003) (see Figure 8).

The marsh deer was strictly limited to wetlands. Although we only have one oxygen isotope value, which coincides with this distribution, the archaeological record shows no evidence at all of its presence or transportation by humans to other environments other than wetlands. Thus, two very significant and partial overlaps can be observed between the guanaco

Table 4. Isotopic values of the pampas deer (*O. bezoarticus*) from the northern Pampa region.

Site	Location	Lab. Code	$\delta^{13}\text{Cco}\text{‰}$	$\delta^{13}\text{Cap}\text{‰}$	Spacing	$\delta^{15}\text{N}\text{‰}$	$\delta^{18}\text{O}\text{‰}$
Garín	Wetland	EIL 2023	-22.5	-12.3	10.2	5.7	-1.25
Garín	Wetland	EIL 2024	-21.8	-11.2	10.6	4.8	-1.17
Guazunam.	Wetland	UGA 9908	-18.8	-9.3	9.5	5.2	-0.68
Guazunam.	Wetland	AIE20924		-13.9			-1.5
Hunter	Pampa Plain	EIL 2022		-11.4			0.7
Hunter	Pampa Plain	EIL 2021		-10.0			0.0
Hunter	Pampa Plain	EIL 2020		-10.5			0.57
N			3	7	3	3	7
Mean			-21.0	-11.2	10.1	5.2	-0.48
SD			1.9	1.5	0.6	0.5	0.9
CV			9.3	13.6	5.5	8.6	189.5
25 prcnil			-22.5	-12.3	9.5	4.8	-1.25
75 prcnil			-18.8	-10.0	10.6	5.7	0.57

Table 5. Isotopic values of the marsh deer.

Site	Location	Lab. Code	$\delta^{13}\text{Cco} \text{‰}$	$\delta^{13}\text{Ccap} \text{‰}$	Spacing	$\delta^{15}\text{N} \text{‰}$
Arroyo Sarandí	wetland	AIE 26925/6	-20.9	-12.8	8.1	4.7
Bajada Guereño	wetland	AIE26944		-12.2		
Playa Mansa	wetland	AIE 26946		-9.8		
Punta Canal	wetland	AIE 26931/2	-17.7	-8.3	9.4	8.8
Cerro Lutz	wetland	AIE 26923/4	-21.6	-15.5	6.1	4.7
El Espinillo	wetland	AA103652	-21.4			
La Argentina	wetland	AA97463	-21.5			
Médanos Escobar	wetland	AA97465	-21.9			
Garín	wetland	AIE 26935/6	-20.7	-12.2	8.5	6.5
Anahí	wetland	UGA 9907	-20.3	-10.3	10.0	6.0
Anahí	wetland	AIE 26937/8	-20.1	-12.7	7.4	4.9
Arroyo Fredes	wetland	AIE 26927/8	-22.0	-14.9	7.1	4.5
Arroyo Guazunambí	wetland	Beta 147109	-19.0			
Arroyo Guazunambí	wetland	AIE 26929/30	-21.8	-12.9	8.9	
La Bellaca 2	wetland	AIE 26941/2	-17.1	-10.7	6.4	5.4
La Bellaca 3	wetland	AA108383	-16.0			
Túmulo Campana 2	wetland	Beta 172059	-21.1			
Túmulo Campana 2	wetland	AIE 26933/4	-21.5	-13.8	7.7	5.4
Túmulo Campana 1	wetland	AA108369	-22.4			
Cerro Mayor	wetland	AA97469	-21.7			
Cerro Mayor	wetland	AA97457	-21.2			
Islas Lechiguanas 1	wetland	AA97467	-21.4			
Islas Lechiguanas 1	wetland	AA97461	-21.2			
Río Luján site 2	wetland	AA97458	-21.3			
Escuela 31	wetland	AA103651	-20.6			
Escuela 31	wetland	AA103650	-21.7			
Escuela 31	wetland	AA103649	-21.8			
El Cazador site 3	wetland	AA97470	-16.8			
El Cazador site 3	wetland	AIE 26939	-22.0	-12.7	9.3	6.2
Cerro Bauer	wetland	AA108378	-19.8			
Cerro Lafría	wetland	AA108385	-23.1			
Campo Binaghi	Paraná valley	AIE 26947/8	-21.0	-12.3	8.7	7.6
Cerro Peter	wetland	AA108387	-22.5			
N			31	14	12	11
Mean			-20.7	-12.2	8.1	5.9
SD			1.7	1.9	1.2	1.3
CV			8.3	15.9	15.0	22.9
Perc. 25%			-21.8	-13.1	7.1	4.7
perc. 75%			-20.3	-10.6	9.2	6.5

and the pampas deer, which were sympatric species in North Pampa, while the marsh deer was distributed in a mostly parapatric form with respect to them (Figure 8).

Measures of central tendency in isotopic diets

An integrated view of the data obtained allows us to discuss the characteristics of the herbivorous guild in this region, and provide data for the understanding of the variability of the diet among large herbivores. The three mammals show a C_3 diet, but the guanaco's compared with the two deer is enriched by 2.0–2.3 ‰ in collagen and 1.8–2.8 ‰ in apatite (see Figure 9). This gap is statistically significant in the collagen isotope values between the guanaco and marsh deer ($T = -2.6$, $p = 0.011$; not enough samples to compare with the pampas deer). Likewise, the three mammals show significant differences in apatite between each other ($F = 14.33$; $p < 0.0001$). These variations reflect a more grazing strategy in the guanaco based on C_3 grasses with a subordinate and variable intake of C_4 grasses, and probably a minor consumption of leaves and stems from shrubs. On the other hand, mixed feeding behaviour was developed by both deer, based on C_3 grasses and shrubs (leaves, fruits and

tender stems), but in different environments for each of them. In the marsh deer a certain intake of C_4 can also be observed, probably related to C_4 aquatic macrophytes and grasses. The pampas deer's most negative values cannot be related to the canopy effect, nor indeed can the marsh deer's. However, the highly geomorphological dynamics of the wetlands and the patchy distribution of the forests and prairies in this environment make it tricky to determine what samples of marsh deer might have been subject to a certain canopy effect. Besides, there are no observations of the feeding behaviour of this mammal in this area, but in the Iberá wetland (500 km north) this ungulate prefers to eat on open prairies alongside lentic waters, while forest areas are used preferentially for shelter (D'Alessio et al. 2001; Pinder 1996; Piovezan et al. 2010). If we transfer these observations to the area under study, a low incidence of the canopy effect is expected, but it not cannot be ruled out, especially in samples recovered from sites whose main catchment area was undoubtedly within heavily forested areas with no prairies, such as the islands in the mouth of the Delta. To be precise, a marsh deer sample recovered from this area was the most depleted in both carbon sources (sample AIE 26927/8, see Table 5).

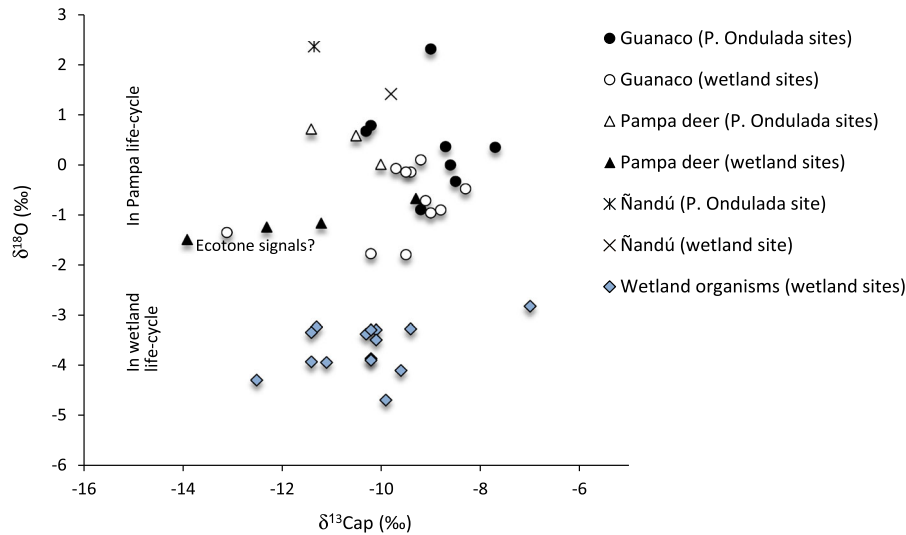


Figure 7. $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ apatite isotope values of the guanaco, pampas deer and ñandú. The values of wetland organisms (including a marsh deer sample) were taken from Buc and Loponte (2016), excluding human samples EIL-1003 and EIL-1004 (for a discussion, see Loponte et al. 2016a).

The $\Delta^{13}\text{C}$ values in the entire collection of these three mammals vary from 8.1 ± 1.2 ‰ to 10.1 ± 0.6 ‰, which is to be expected for pure herbivores (Ambrose and Krigbaum 2003; Ambrose and Norr 1993; Lee-Thorp, Sealy, and van der Merwe 1989). In the guanaco (pseudo-ruminant) the spacing is significantly greater than in the marsh deer (ruminant) ($T = 6.33$ $p = 0.020$). Larger spacing was predicted and observed in ruminants compared to non-ruminants (Hedges 2003; Kellner and Schoeninger 2007; Lyut 2017), which is not the case. Also, differences related to the sizes of the animals were predicted (Lyut 2017), which is not the case either. The differences in $\Delta^{13}\text{C}$ between both mammals (guanaco and marsh deer) might have been related to the distinct proportions of proteins, carbohydrates and fats in their diets, but also to the different humidity levels in their environments (Murphy, Bowman, and Gagan 2007a, 2007b; Lyut 2017). Although there are few samples of pampas deer, they support the latter idea (see Figure 9).

The nitrogen isotope levels are close between these three ungulates, ranging from 5.2 ± 0.5 ‰ to 6.4 ± 1.8 ‰, which also supports the nitrogen isotopes magnitudes for local large herbivores. Both deer have an IC of $\delta^{15}\text{N}$, almost exactly overlapping (marsh deer = 4.98 ‰ | 6.79 ‰; pampas deer = 4.11 ‰ | 6.35 ‰), while in the guanaco the bounds are slightly displaced (5.15 ‰ | 7.71 ‰). However, there are no statistical differences between the guanaco and marsh deer ($T = 0.41$ $p = 0.688$; not enough samples to compare with the pampas deer) (see Figure 9). This slight and not significant difference could also be an incipient trend related to the differences in the environmental humidity between the wetlands and the Pampa Ondulada, although more samples from these and other taxa are needed to explore this proposition (work in progress). Along with this idea, the nitrogen isotope values of the four guanaco samples recovered from the more arid Monte eco-region area (see section 6.3) are higher (average) than those from the humid Pampa. This geographical trend could reflect the ambient humidity

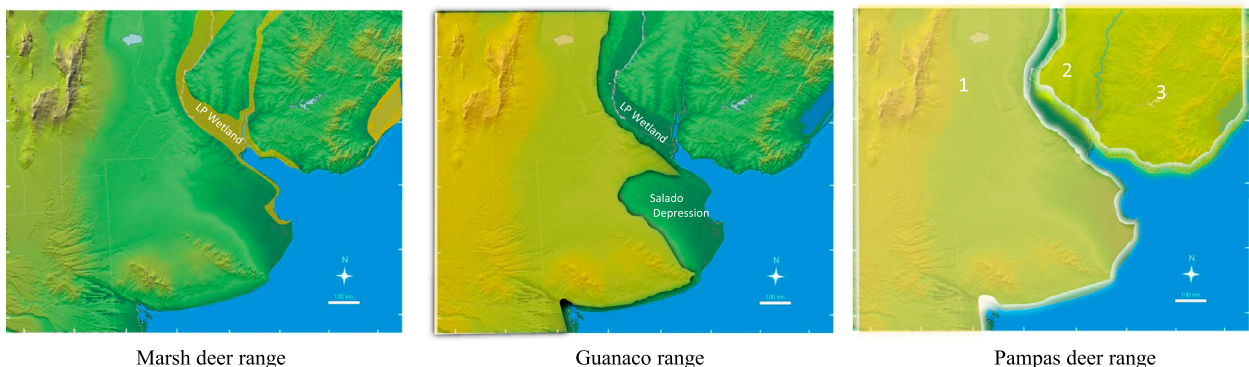


Figure 8. Distribution of the marsh deer, guanaco and pampas deer in the late Holocene up to historical times. In the pampas deer range, the number '1' reflects the western distribution of the *O. bezoarticus celer* subspecies; the number '2' the *O. b. leucogaster* subspecies (Entre Ríos province), and the number '3' the *O. b. arerunguensis* and *O. uruguayensis* forms.

gradient along with the isohyets distribution, not with the thresholds themselves which varied throughout the Holocene, but with their morphology. This overview is well supported in semi-desert samples recovered even from a lower latitude environment as in northeastern Patagonia, on the lower banks of the Colorado River, where two guanaco samples also yield high nitrogen isotope values (10.1 and 10.8 ‰; Flensburg, Martínez, and Tessone 2018) (see Figure 9). However, this general trend contradicts those obtained in the northwestern Patagonian desert, whose mean is 5.0 ± 0.7 ‰ (Gil et al. 2016, see Table 2). This range is even smaller than the marsh deer's values (5.9 ± 1.3 ‰). Moreover, the authors did not find a correlation between the nitrogen isotope values and rainfall in the deserts of central western Argentina. Thus, the guanaco could have been a species that was insensitive in this matter in some areas of its geographical range. However, other explanations for the northwestern Patagonia's values could be applied here, but they are beyond the scope of this paper.

Niche ecomorphology and resource partitioning

We saw above the segregated habitat use between the guanaco and the pampas deer on one side, and the marsh deer on the other. The latter mammal developed a narrow and selected isotopic niche in the wetland, where the correlation between the $\delta^{13}\text{C}_{\text{co}}$ and $\delta^{13}\text{C}_{\text{ap}}$ values is significant ($r_s = 0.75$, $p = 0.004$), quite different from the broader one in the guanaco, where no significant correlations between either carbon sources were found ($r_s = 0.13$, $p = 0.70$, excluding outlier EIL 2031). Two guanaco individuals differ substantively from the broader niche of this mammal. One of them corresponds to a juvenile EIL 2031 which we have already dealt with above. The other corresponds to the EIL 2032/2 specimen whose medium-high level of nitrogen and spacing could respond to a stochastic variability, a physiological particularity or it could correspond to an allochthonous specimen to the region, perhaps from the more arid environment that surrounds to the north the Pampa Ondulada. In the pampas deer, which shared its habitat with this camelid, the few

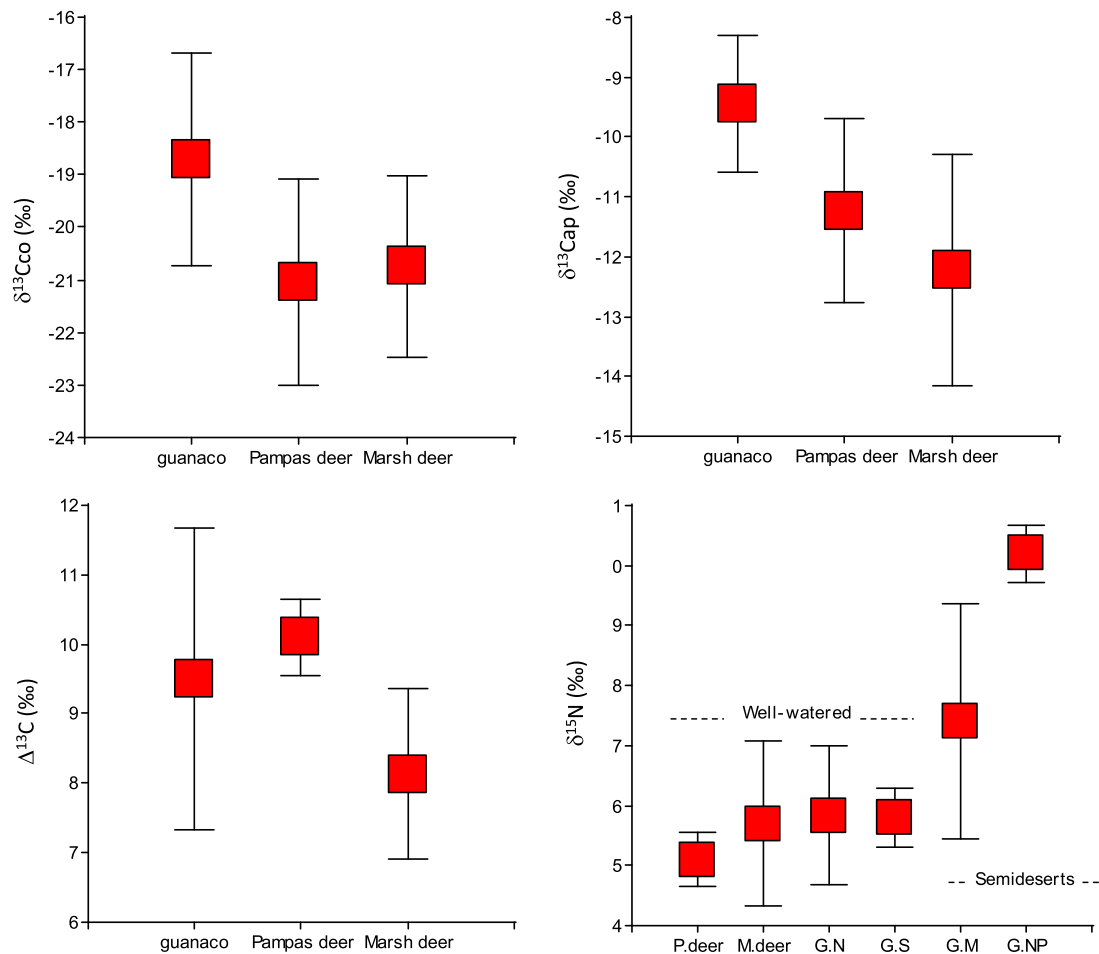


Figure 9. Mean values and standard deviation of $\delta^{13}\text{C}_{\text{collagen}}$, $\delta^{13}\text{C}_{\text{apatite}}$ and $\Delta^{13}\text{C}$ in guanaco from the northern Pampa (wetland + Pampa Ondulada), pampas deer (wetland + Pampa Ondulada) and marsh deer (wetlands). The $\delta^{15}\text{N}$ graph shows the values for the pampas deer (P. deer); marsh deer (M. deer); guanaco from the northern Pampa (G.N. – except juvenile outlier EIL 2031-); guanaco from the southern Pampa (G.S); guanaco from south Mendoza province (G.M) in the Monte eco-region; and guanaco from northeastern Patagonia (G. NP) (see also section 6.3).

available data show a closer but peripheral distribution to the guanaco's isotopic niche. More equal than the marsh deer, both carbon sources have a significant correlation ($r_s = 1$, $p = 0.33$), also showing a narrow isotopic niche (Figure 10). The differences in the correlations in the collagen and apatite isotope values between both deer on one side, and the guanaco on the other, suggest a different chemical composition of their food and/or different allocations of protein-derived carbon and whole diet-derived carbon related to their distinctive physiologies. In turn, the marsh deer and guanaco exhibit a positive and significant correlation between $\Delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($r_s = 0.74$, $p = 0.009$ and $r_s = 0.57$, $p = 0.11$ respectively).

Intraspecific variability

The intraspecific variation in feeding behaviour is a key factor in the adaptability of the species to their environments and for the population's stability in the landscape, thus constituting one of the main traits of evolution (Bolnick et al. 2003, 2011; Codron et al. 2012; Darwin 1859; Dobzhansky 1937; Gilbert and Brassil 2014). Multiple inputs have been pointed out as being responsible for this, such as the social organisation of each species, inter and intraspecific competition, age at the moment of death, sex, and/or distinct individual or social foraging behaviour, including significant mobility ranges which would also have been sensitive to clinal variations and the productive states of the environments (Lecomte et al. 2011; Lehmann 2015; Lyut 2017; Roth 2002; Stevens, Lister, and Hedges 2006). The intraspecific variability between herbivores is not a well-developed topic, as few studies have gathered enough information to discuss it, and certainly no previous discussions about the region under study are available.

In the northern Pampa samples, the intraspecific variability in collagen and apatite isotope values reaches 7.2 and 5.4 ‰ in the guanaco, and 7.1 and 7.2 ‰ in the marsh deer, respectively. In the southern Pampa, the guanaco's ranging in collagen (7.1 ‰) has equal variability to the northern samples (see Figure 11). A fraction of this variability could certainly be connected to the chronology (see below), but we also identified this within-species variability (around $\delta^{13}\text{C}_{\text{CO}}$ 5.3 ‰ – 4.1 ‰ in the guanaco and 6.5 ‰ in the marsh deer) as more or less synchronous in archaeological time. This archaeological time is, of course, scattered in terms of the synchronicity of the studies on living populations (see examples in Codron et al. 2016; Lehmann 2015; Lyut 2017). The intraspecific variability of both the guanaco and marsh deer is greater than that reported in modern populations of other herbivores such as *Cervus elaphus* (maximum 2.6‰, Stevens, Lister, and Hedges 2006; Table 2), which is predominantly a browser in a mostly C_3

monoisotopic environment. The same small intraspecific variability can be observed in archaeological samples of horses (grazers) in northern Europe. Here, in samples covering 38 and 13.5 ka YBP, the intraspecific range is only 2.6 ‰. Between 13.5 and 8 ka YBP it is 3.5 ‰, and from 8 ka to the present it is 1.8 ‰ (based on Stevens and Hedges 2004, 979). However, in mixed environments in South Africa, higher intraspecific ranges were recorded in bone tissue in modern populations. These values are equal to or even higher than those observed in the archaeological samples of guanaco and marsh deer. For instance, in grazers such as *Oryx gazelle* (in the Gemsbok biome) the intraspecific range for collagen isotope values is 9.7 ‰ (samples UCT 16.215 vs. UCT 16.220), in *Panacochoreus africanus* it is 8.9 ‰ (Albany Thicket biome, samples UCT 14.300 vs. UCT 14.296), in *Alcelaphus bucelaphus* it is 8.1 ‰ (Fynbos biome, samples UCT 16.370 vs. UCT 16.375), in *Syncerus caffer* it is 4 ‰ (Albany Thicket biome, samples UCT 2.645 vs. UCT 14.288), and in the mixed feeder *Antidorcas marsupialis* it is 4.3 ‰ (Nama Karoo biome, samples UCT 13.993 vs. UCT 13.979) (based on Lyut 2017; appendix 7). Another analysis in Namibia, but of a short timeline based on tail hair, shows the same wide intraspecific range in *O. gazelle* (5.9 ‰) and *A. marsupialis* (6.8 ‰) (Lehmann 2015, 64; there are also differences within individuals which are beyond the scope of this paper). On the other hand, in the same biomes from South Africa analyzed by Lyut, the browsers tended to show less variability (typical ranges varied from 3.2 ‰ – 2 ‰, based on Lyut 2017; appendix 7). Thus, the investigations into this topic suggest that it is reasonable to expect more interspecific variability in grazers at low and intermediate latitudes, where the C_3 and C_4 options are available in the coverage, and smaller ranges at high latitudes, where C_3 monoisotopic landscapes prevail. On the other hand, browsers tend to be more conservative, with less intraspecific variability at both low and high latitudes. In the case of the guanaco in the Pampa region, that is a grazer at middle latitudes with broad foraging behaviour, it fits this overview. Here, the annual or even seasonal variability in temperature, cloud cover and rainfall dynamically impacts the thresholds in the coverage balance between the different photosynthetic patterns, leading to a changing isotopic landscape and encouraging competition between the herbivores themselves, as well as between this guild and the plants. Colder years (dry or humid, but preferentially the latter, along with lower irradiance) favoured C_3 plants; hot and humid years were suitable for the NADP-ME biochemical type of C_4 plants, while hot, light and dry years favoured the NAD-ME biochemical type of C_4 plants (see section 7.5). Another certain source of variability is the migratory movements observed in this species, as there is a clinal variation in this grassland's

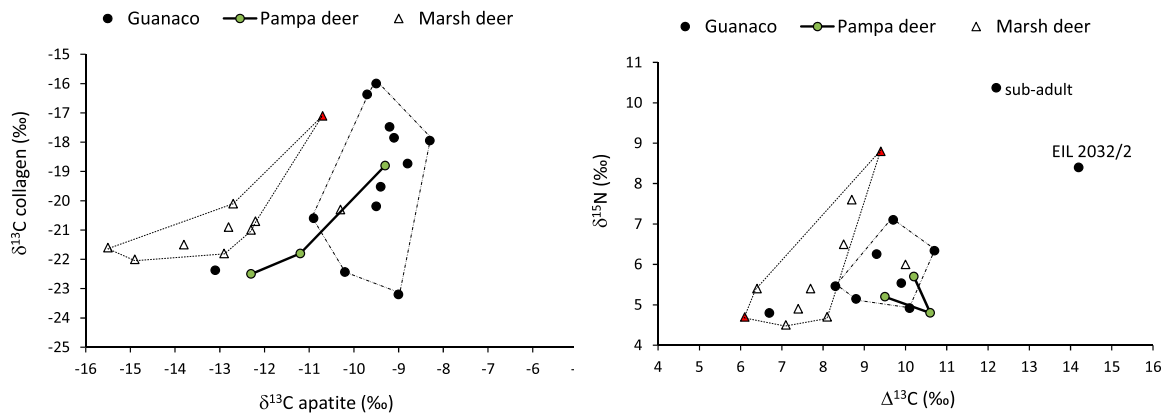


Figure 10. Some dimensions of the isotopic niche of the marsh deer, pampas deer and guanaco. In the left-hand graph, the polygon surrounds the $\delta^{13}\text{C}_{\text{co}}$ and $\delta^{13}\text{C}_{\text{ap}} \pm 2$ SD values. In the right-hand graph, the polygon surrounds the $\Delta^{13}\text{C}$ and $\delta^{15}\text{N} \pm 1$ SD values. The red filling indicates that one of the two plotted values is outside the range of the standard deviation considered in each graph.

vegetation coverage and its connection to the peripheral arid belt further inland (see Figure 1). All these factors lead to an isotopic variability, as expected in a grazer such as the guanaco. Indeed, the continental human diets heavily based on guanaco hunting, recovered from sites located in this arid belt or near it, show enriched values (Barrientos, Catella, and Oliva 2015).

In the case of the marsh deer, a browser with some mixed feeding behaviour distributed over a fluvial wetland, its intraspecific variability must be analyzed separately from the above general overview. Its range could be primarily related to the annual flooding, which is in fact highly irregular. This affects the distribution, type and quantity of vegetation coverage on a very narrow time base (Kandus 1997), where afterward individual behaviours overlap, thus adding more variation. In this sense, albeit the wetland and the Paraná River itself must be considered basically and predominantly a C_3 isoscape (Madanes, Kalesnik, and Vargas 2013; Marchese et al. 2014; Loponte, Acosta, and

Corriale 2016b), the increase in the frequency, intensity and extent of the flooding events has favoured some C_4 aquatic plants such as Genera *Echinochloa*, *Paspalum* and *Panicum*, allowing them to cover significant parts of the Paraná riverbanks and floodplain channels (Marchese et al. 2014). Moreover, some of this variability appears to be increased by temporal irregularities related to major climatic change (see section 7.5).

Temporal trends and paleoenvironmental inferences

The collagen isotope values of the three analyzed mammals show a slightly enriched trend for each species, as the samples are more recent (see sections 6.4, 6.7 and 6.9). In both deer we saw that these correlations are significant. Due to their chronological distribution, they have been narrowed down to a late Holocene tendency, showing an enriched peak around 1100–700 ^{14}C YBP (~900–1300 CE), overlapping with the Medieval Climatic Anomaly (MCA), which covered the time period between ca. 950–1250 CE (Mann et al. 2009). Leaving aside the small sample size of the pampas deer, the marsh deer shows an enrichment and increase in the range of its collagen isotope values during this period, which could have been related to the greater intensity and frequency of flooding and rainfall, reflecting a more unstable environment favouring oscillations between C_4 and C_3 plants (see section 7.4). The variable flooding must be mainly related to the El Niño–Southern Oscillation (ENSO), which impacts heavily the Paraná Basin with an interdecadal base, but it is highly variable, even influencing the magnitude of the annual flooding (Jaime and Menéndez 2003). Meanwhile, some authors have found no significant relationship between the MCA and LIA and the ENSO's frequency or intensity; others have noted important variations in its incidence in South America during the whole MCA period (Henke, Lambert, and

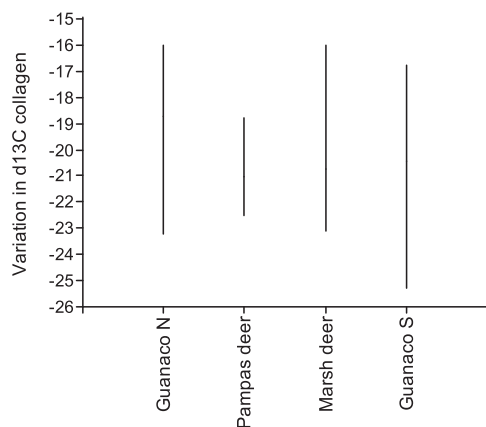


Figure 11. Range of $\delta^{13}\text{C}_{\text{co}}$ values of the ungulates analyzed in this study. References: Guanaco N = North Pampas guanaco samples (Pampa Ondulada + wetland). Guanaco S = South Pampas guanaco samples with a chronological range ~8.5–0.36 ka ^{14}C YBP, including depleted outliers (see section 6.2).

Charman 2017; Ledru et al. 2013; Mann et al. 2009). Beyond this discussion, which we will not go into here, what is significant for now is that there was an increase in the variability of the marsh deer's diet, as well as a trend toward the enrichment of collagen isotope values, which fell during the MCA, probably related to a wetter or/and a more variable environment.

With regard to the guanaco, although it has an irregular date base, we have a certain general overview of most of the Holocene. We think that the slight guanaco enrichment trend is not significant (see section 6.4) due to its polynomial distribution, which looks to have been synchronised with the major Holocene climatic variations. In fact, two enriched peaks can be observed (Figure 12). The first matches the Holocene Thermal Maximum (HTM) during the early – middle Holocene (post ~8.5 ka to 6 – 5 ka YBP, depending on the author). During this period, in the southern hemisphere the climatic belts migrated around 10° to the south, increasing the temperature and rainfall in the Pampa region, although some authors suggest an oscillating climate, with arid and wet periods, some of them with extreme peaks of precipitation. However, there are certainly no strong arguments against considering it a warmer period than the current one, with significant humid events. The second peak of the guanacós values overlaps with the MCA, which was a warmer and a mostly wetter phase than today, with a migration of tropical isotherms and isohyets toward the south, and where the guanaco is well represented throughout the entire archaeological record of the Pampa region. In the middle of the HTM and MCA, an intermediate period developed with a similar climate to the current one, as indicated by some authors, while others indicate the existence of periods of arid conditions, with a later shift to a more humid environment like the present one after 2.0 – 1.5 ka ¹⁴C YBP (see these climatic changes during the Holocene on a local and global scale, but with some internal differences, in Bartlein et al. 2011; Bjune et al. 2005; Bonadonna, Leone, and Zanchetta 1999; Cioccale 1999; Clapperton 1993; Guerra et al. 2015; Iriondo 1994, 1999; Iriondo and García 1993; Iriondo, Bunetto, and Kröhling 2009; Jansen et al. 2007, 2008; Laprida et al. 2014; Ledru 1993; Mancini et al. 2005; Panigatti 1981; Prieto et al. 2014; Teta et al. 2005; Tonello and Prieto 2010; Renssen et al. 2012; Soilbenzon, Medina, and Abba 2013; Stutz et al. 2012; Waldmann et al. 2010). During the warm and wet periods of the HTM and the MCA, C₄ species of the NADP–ME biochemical type, especially those in the Panicoideae and Aristidoideae subfamilies which are now broadly represented in the Pampa Ondulada, must also have been widely distributed in the coverage during both phases, as they found suitable parameters in wet and hot environments. In turn, if arid and warmer minor periods developed during the HTM, the development of C₄ plants of the NAD–ME biochemical

type, associated with high net irradiancy would have been encouraged. Conversely, C₃ species are not well adapted to or avoid warm, wet and high-irradiancy environments (cf. Cabido et al. 2008; Ehleringer and Monson 1993; Ghannoum, von Caemmerer, and Conroy 2002; Hattersley and Watson 1992; Rao and Dixon 2016). Thus, one probable explanation for these two slightly enriched peaks during the early/middle Holocene and late Holocene is an overlap with these warm and wet (or oscillating) periods, matching an expansion of the NADP – ME/NAD – ME C₄ grasses. Additional information supports this trend. A human sample recovered from the northwestern Pampa at the Laguna El Doce site and dating directly to the early Holocene (8274 ± 68 ¹⁴C YBP), thus matching the HTM, yielded a δ¹³C_{co} value of –15.1 ‰ (Avila and Ceruti 2013), which is substantially enriched and according to the local past subsistence based on guanaco hunting (Cornaglia 2013). A little further south, already in the sector indicated as Northwestern Pampa (see Figure 1), at the Laguna de Los Pampas sites two human samples, although with earlier dates of 8971 ± 77 and 8835 ± 83 ¹⁴C YBP, yielded a mean δ¹³C_{co} –15.6 ‰ (based on raw data published by Politis et al. 2012; Table 3). For all these values, it is reasonable to leave out any possibility of influence from marine foods, or at least a significant quantity of them (unlike with what happened with the human isotopic values from the southern Pampas region; *i.e.* Catella 2014; Scabuzzo et al. 2016). Unfortunately, all these samples lacked informed C/N ratios, but they allow us to support the working hypothesis of mixed isotopic diets on the northern Pampa plain during the HTM.

Both enriched peaks cannot mask the guanaco average's mainly C₃ pattern for the entire Holocene. On the Pampa plain, C₃ plants are quite rare or absent when the rainfall is lower than 600 mm/annual and the average temperature is >17°C / annual (Cabido et al. 2008). As there is no solid evidence of the Patagonian isotherms migrated to humid Pampa during the period ~8000 year BP – LIA, we have to conclude that C₃'s predominance on the Pampa plain is linked to these climatic parameters of temperature (~ 17°C / annual) and rainfall (minimum threshold 600 mm / annual), which would have been the most frequently established conditions in the humid Pampa region environment. Then, this plain would have shifted between a more recurrent mesic and temperate environment with minor phases of dry-mesic conditions as other proxy-data indicated, to humid and warm ones during the peaks of the HTM period and MCA phase. Concurrent information within this environmental framework can be observed in the low δ¹⁵N values of the guanacos and pampas deer from both the southern and northern Pampa, which are typical of well-watered environments and different

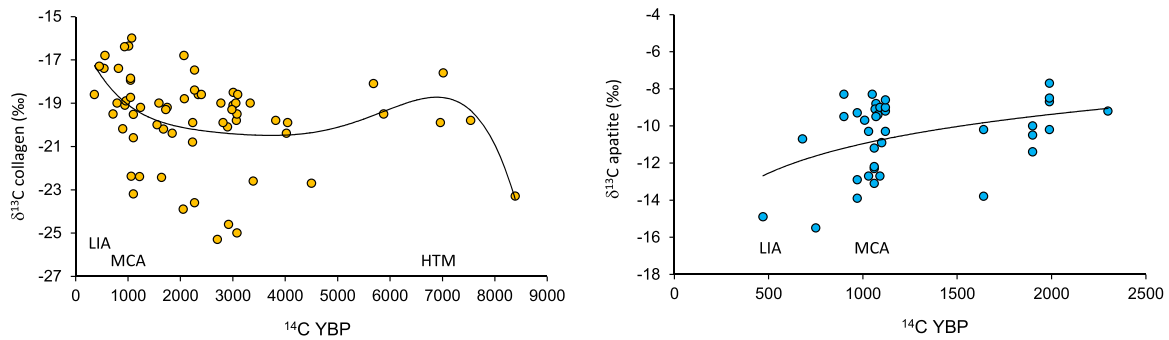


Figure 12. The left-hand graph includes all the available guanaco collagen isotope values in the Pampa Ondulada, wetland and southern Pampa. The right-hand graph shows the apatite isotope values of the three species under consideration, based on the Pampa Ondulada and wetland samples. References: LIA = Little Ice Age. MCA = Medieval Climatic Anomaly. HTM = Holocene Thermal Maximum.

from the higher levels of the semideserts of the Monte eco-region and northeastern Patagonia (see section 6.3 and 7.2).

After the MCA, at the end of the pre-Columbian sequence and at the beginning of the Spanish conquest, the Spörer Minimum period, which was the first and one of the main events of the Little Ice Age (LIA), was affecting the Earth. It developed within a well-calibrated time span, between ~1400 – 1600 CE (Eddy 1976; Masiokas et al. 2009; Miller et al. 2012; Ruiz, Masiokas, and Villalba 2012; Solomina et al. 2016; Villalba 1994). During this period, arid and cold conditions were established, sustained locally by different biotic and abiotic proxies. It was also well described in the first historical records of the XVI century (Cioccale 1999; Guerra et al. 2015; Laprida et al. 2014; Ledru et al. 2013; Mann et al. 2009; Prieto and Jorba 1990; Tonello and Prieto 2010). During this cold and arid period, the environment was also suitable for species such as the guanaco. It is expected that there should have been a replacement of the vegetation coverage, as indicated in adjacent regions (Bonnin et al. 1987). The NADP-ME biochemical type of the C_4 plant species may have decreased their presence, but this shift toward drought and higher net irradiance (due to a decrease in the average annual cloud cover) was an opportunity for an increase in C_4 grasses of the NAD-ME biochemical type, which prefers dry and high net irradiance environments, due to its more efficient water use. Included in this type, there are many other species of the Panicodae and especially Chloridoideae subfamilies (cf. Cabido et al. 2008; Ehleringer and Monson 1993; Ghannoum, von Caemmerer, and Conroy 2002; Hattersley and Watson 1992; Rao and Dixon 2016). In fact, 500 years BP there is a peak of representation of Chenopodiaceae Family in the polinic sequence of Empalme Querandies, 250 km southwards the Pampa Ondulada, which is a xerophytic taxa most composed by C_4 species (Tonello and Prieto 2010).

Therefore, during the LIA mixed grassland is also to be expected, with a significant proportion of C_4 grasses, and thus the enriched – mixed trend that prevailed during the MCA should have been sustained or could have increased until historical times. Unfortunately, the LIA period is not well represented in the sampling. There are the three guanaco values obtained at the Pampa Ondulada (Cañada de Rocha site, see Table 1) and only one published by an international research team from the southern Pampa (sample B169820, see Table 1). The average of these four samples is $\delta^{13}C_{Co} -17.5 \pm 0.8$ ‰, which is an enriched mean close to the Monte ecoregion's values (see section 6.3). Unfortunately, no $\delta^{18}O$ or $\delta^{15}N$ records are available yet. These samples cover the interval 1400 – 1600 CE (corrected with the SHCal 13 curve), falling entirely within the Spörer Minimum. Indeed, intensive droughts were recorded at the nearby Lake Melincué, starting in ~1492 CE and continuing until ~1880 CE (Guerra et al. 2015), which was the beginning of the Spörer Minimum and covering the more recent Maunder–Dalton Minimums, including the short and variable intermediate period at the beginning of the XVII century (Cioccale 1999). Moreover, at the beginning of the XVI century, during the first LIA pulse, the historical records describe a dry environment in the northern Pampean region (Loponte 1996–98). Although we do not know how reliable the collagen isotope values from the Cañada de Rocha and Laguna El Doce sites are, as no C/N ratios are available for the moment they allow us to support the hypothesis of significant C_4 plant coverage during the LIA in the Pampas grasslands, equal to or probably more than the previous MCA period, conforming to the typical Pampean landscape of the historical records during the European exploration and the later colonial periods.

On the contrary, the apatite isotope values show an inverse tendency in each species, and are restricted to the final phase of the late Holocene (see Figure 12). These trends toward depletion in more recent samples

are all within non-significant levels, although if the apatite isotope values of the three mammals are included as a single sample, the correlation becomes weak but significant ($R^2 = 0.12$; $F = 4.66$; $p = 0.038$). However, it is strongly based on the marsh deer's wetland values, and particularly in two samples recovered from the Arroyo Fredes and Cerro Lutz sites (AIE 26927/8 and AIE 26923/4, respectively, see Table 5). Both are the most depleted and a canopy effect should not be ruled out (see section 7.2). Therefore, we believe that this tendency reflects the particular influence of the wetland samples and the current sampling level, so it should not be confirmed as an opposite trend until the database can be improved and analyzed again.

The trend observed in the values of $\delta^{13}\text{C}$ cannot be contrasted in its entirety with the values of $\delta^{18}\text{O}$ because we have very little data here. By now, a decrease in oxygen isotope values has been observed through time ($r_s = 0.54$, $p = 0.004$), but the time span covered by this trend is reduced (ca. 2300 – 900 ^{14}C YBP). The depleted oxygen isotope values are clustered between ca. 1100 – 900 ^{14}C YBP, corresponding with the MCA (see Figure 16), which is expected during for a humid phase, related basically to the 'amount effect' and the increase of cloudiness (cf. Dansgaard 1964). A fraction of this trend is based on guanaco and pampas deer values, probably influenced by the isotopic oxygen-depleted waters in $\delta^{18}\text{O}$ of the wetland landscape. Indeed, two of the three most depleted guanaco samples show the purest C_3 diet, thus suggesting this influence (see section 6.1). However, this depletion in $\delta^{18}\text{O}$ toward the MCA is clear within the entire collection (see Figure 13).

The chronological distribution of nitrogen isotope values is also circumscribed, covering the period ca. 2300 – 470 ^{14}C YBP. During this time span, a weak and significant decrease in the nitrogen isotope values as the samples become more recent can be observed ($R^2 = 0.080$; $F = 1.798$; $p = 0.1943$) (see Figure 13) (we have excluded the outlier EIL 2031). The magnitudes show a lot of variability around 1.0 ka ^{14}C YBP, matching the MCA, and after that a depleted peak at the end of this phase. This depletion is also expected during this wet (or variable) phase. However, the samples are clustered around 1.0 ka YBP, which is not very useful for seeing temporal tendencies, and the post-1.0 ka YBP depletion is based on marsh deer bones (see Figure 13), recovered of course from wetland, where the availability of water depends essentially on the flooding that is related to extra-regional rainfall. As the current state of the sampling is quite fragmentary, the temporal variations in the oxygen and nitrogen isotope values are more of a work agenda than confirmed trends; however, for now we can preliminarily conclude that these values coincide with a humid phase around 1100 – 1000 ^{14}C YBP, thus matching the MCA.

Archaeological implications

The main conclusion for this section is the obvious variability in the isotopic signals transferred from prey to humans, especially to hunter-gatherers whose subsistence was based heavily on the guanaco in the Pampa Ondulada throughout the entire Holocene, although there is certainly more evidence for this subsistence pattern for the late Holocene between 2.0 – 0.45 ka ^{14}C YBP (Ameghino 1880 [1947]; Avila and Ceruti 2013; Buc and Loponte 2016; Cornaglia 2013; Loponte, Acosta, and Tchilinguirían 2010; Toledo 2010). Also quite important is the range recognised in the marsh deer, where some enriched values transferred to humans could be mistaken for maize intake, as in wetlands this crop could be cultivated on a small scale by complex hunter – gatherer groups, and significantly by the Amazonian horticulturalist populations historically known as the Guaraní (Loponte et al. 2016a, 2016b). Therefore, to confirm the impact of the isotopic range of any of the targeted animals, not only are several samples from each resource needed, as pointed out by other authors (Stevens, Lister, and Hedges 2006), they must also be within suitable temporal and spatial parameters where each specific isoniche can be analyzed.

Another quite obvious implication of this study is the adaptability of the guanaco to the climatic changes during the Holocene, including warm and humid (or variable) peaks such as the HTM and the MCA. The guanaco was the main taxon hunted at the Laguna El Doce site during the HTM, as well as at the Hunter site during the pre – MCA period, the Meguay site during the MCA and the Cañada de Rocha site during the LIA. Today this mammal have no adaptation problems to the current climate of the Pampa Ondulada (Loponte 1996–98). This adaptability is also clear in the continuous record of this mammal at archaeological sites located on the edges of wetlands throughout the known archaeological sequence between 2400 and 500 ^{14}C YBP, including several assemblages dating from the pre-MCA, the MCA and the LIA periods (see Table 1 and Figure 14; see also Buc and Loponte 2016 and historical sources in Loponte 2008). In the southern Pampa, is the main hunted taxon along the entire Holocene, including La Toma site, in the archaeological layer dating just inside the MCA (cf. Rabassa et al. 1989; Salemme 1987), and it is the most abundant species in the latest aboriginal occupation in that area (Quequén Salado site 1; Grill, March, and Rodríguez Loredó 2010) with direct radiocarbon dates for guanaco bones (360 ± 40 ^{14}C YBP) matching the LIA. At other sites in the southern pampa, guanaco bones are also found in the archaeological layers formed during the LIA (Ceresole and Slavsky 1985; Colombo 2013; Mazzanti and Quintana 2001). Conversely, in the

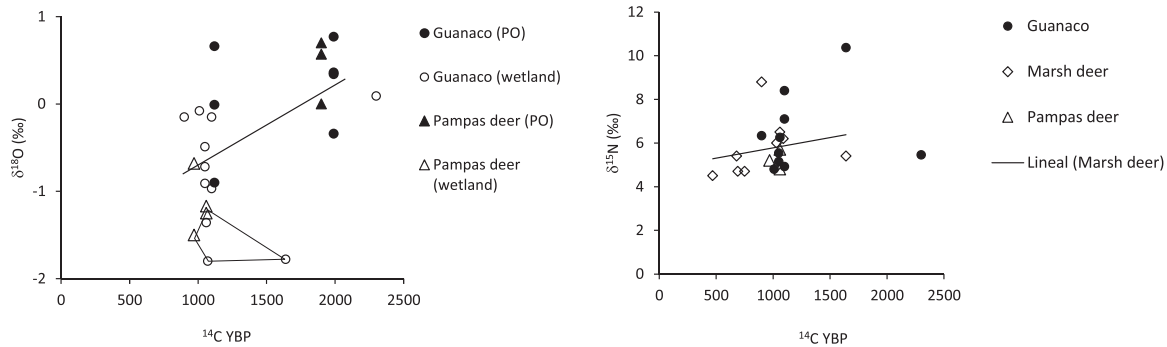


Figure 13. The left-hand graph shows the $\delta^{18}\text{O}$ dispersion values against chronology. The trend is for all of the samples including those depleted within the polygon. The right-hand graph shows the $\delta^{15}\text{N}$ values plotted with the time line.

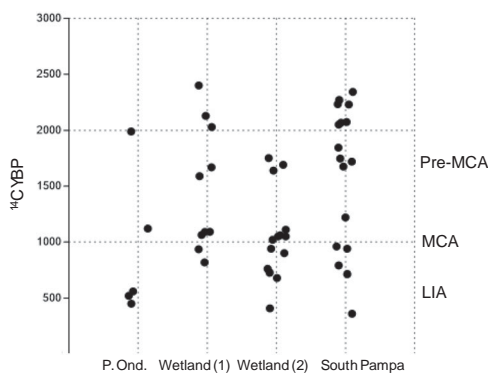


Figure 14. Direct radiocarbon dates on guanaco bones from the humid Pampa post-2400 ^{14}C YBP (taken from Tables 1 and 3), except 'wetland (2)', which are based on well-dated archaeological layers within a small time span (see Supplemental Data Table 1). References of climatic periods: LIA: Little Ice Age; MCA: Medieval Climatic Anomaly; Pre-MCA: pre-Medieval Climatic Anomaly period.

entire humid Pampa there are no archaeological base-camp sites from the pre-Columbian MCA or LIA periods without guanaco bones. Moreover, the LIA environment would typically be associated today with an appropriate habitat for this mammal. In this way, it is evident that the guanaco adapted to this plain, which varied from mesic to semi-mesic conditions, with peaks of humidity and temperature, as well as drier and colder conditions like those established during the LIA, when the Europeans arrived in this region. For all these reasons, the hypothesis that this camelid retracted due to climatic causes (Politis and Pedrotta 2006; Tonni and Politis 1980) during the MCA, or for the entire LIA, has no ecological, environmental, archaeological or historical support. The sudden introduction during the first LIA period (cool and dry in the first half of the XVI century) of cattle and horses, both larger grazers which competed for food, pushed the guanaco outside this suitable environment for European herbivores. After that, the historical distribution shows fragmentary populations, usually sighted as isolated individuals within the grassland biome and particularly on the borders of the expansion of the large exotic European herbivores, that is, nearby

or in the Pampean hills or in the arid ecotone between the humid and arid Pampa.

Final remarks

The marsh deer, pampas deer and guanaco were the major herbivores in the Pampa region in pre-Columbian Holocene times, but also in other areas of South America. Therefore, to study them is of great interest with regard to archeological, ecological and paleoenvironmental issues on this subcontinent, as well as to the ecology of large and endangered mammals. In the Pampa region, most of the topics analyzed in this work were almost totally undeveloped previously, and thus the available data are few and the ideas are many. Despite these limitations, we were able to analyze some aspects of the isotopic niche of these three herbivores, their habitat selection and significant relationships between the isotopic values, species, landscapes, environments and climatic changes. The picture presented here is a starting point, which intentionally seeks to stimulate discussion and contribute to a better understanding of the isotopic ecology of these large herbivores. This paper also serves as a starting point for filling in the gaps in the current information and for thinking in new ways about the ideas and hypothesis expressed here.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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