



# Variation in camelid $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in relation to geography and climate: Holocene patterns and archaeological implications in central western Argentina



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## ABSTRACT

Camelids are among the largest wild and domestic faunas in South America and represent one of the most important taxa to pre-hispanic South America human populations. Stable isotope data from these animals play an important role in improving our understanding of human paleodiet, past human-animal interactions, Holocene environmental change, and modern camelid management. This paper presents  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values taken from 91 camelid specimens distributed across western Argentina between 30° and 37° S. These samples come from three desert environments (Andean, Patagonia, and Monte) and include both modern and prehistoric samples. Camelid  $\delta^{13}\text{C}$  values range between  $-20.3\text{‰}$  and  $-10.7\text{‰}$ , while  $\delta^{15}\text{N}$  values vary between 2‰ and 10.2‰. Mean isotope values differ by environmental context, with significant difference in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  between Patagonian and Monte or Andean deserts. Camelid isotope values also vary with latitude, altitude and longitude, though differences in  $\delta^{15}\text{N}$  are weak, and these geographic differences are tied to climatic variables such as annual mean temperature, annual precipitation, and season of precipitation. When comparing camelid  $\delta^{13}\text{C}$  values from Central-western Argentina with those from Northwest Argentina and Patagonia, we see a latitudinal trend of decreasing  $\delta^{13}\text{C}$  values, with the most negative values occurring in southern Patagonia and the most positive values in Northwest Argentina. Variation in camelid stable isotope values and their association with particular environmental contexts shows their value as a geographic marker and possibly as a paleoecological proxy. These results highlight the need to consider the geographic origin of camelid isotope values when using them to reconstruct human diet.

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## 1. Introduction

Human isotope ecology is not only an innovative way to explore human diet but also a method to help understand other aspects of ecosystem structure such as biogeographical range, human mobility, animal husbandry, and climatic change (Bocherens et al., 2015; Fry, 2006; Koch, 1998; Martínez del Río et al., 2009; Newton,

2010; Rubenstein and Hobson, 2004; Samec et al., 2014; Szpak et al., 2014; Ugan and Coltrain, 2012). Our ability to apply stable isotope methods to these problems depends on our understanding of isotopic fractionation, which often depends not only on the species involved, but also on particular features of the local environment. For most wild animals, such natural, intraspecific variability in their stable isotope composition is neither well documented nor well understood (Stevens et al., 2006). There are insufficient data on relevant, free-living animals from similar environments to provide a clear indication of how much variability may be expected, and therefore what would constitute an adequate

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sample size to define the isotopic composition of a given species in a particular habitat. Most human palaeodietary reconstructions have been made on the basis of a sample size that is arguably insufficient to provide the statistical power needed to validate their conclusions, although the nature of palaeodeposits may give little choice in terms of the faunal assemblage used, the number of samples available, their contemporaneity, or the homogeneity of their original habitat. Without such a definition of the relevant baseline, palaeodietary reconstructions are hard to justify and may lead to circular arguments (Stevens et al., 2006).

In southern South America, the camelids are among the most significant resources in pre-hispanic diets (Politis et al., 2011; Otaola et al., 2012; Borrero, 1990; Miotti and Salemme, 1999; Mengoni Goñalons, 2009, 2010). They are also ubiquitous in the South America zooarchaeological record, and are some of the most important animals to explore in terms of their stable isotope signals. Not surprisingly, there has been an increasing use of stable isotopes from these animals in order to define their contribution to human diets. Researchers have also shown the potential of faunal isotopes to help define the geographic range of human exploitation, as well as their possible role of camelid isotopes as paleoenvironmental proxies (Thorton et al., 2011; Yacobaccio et al., 2009; Samec et al., 2014; Brookman and Ambrose, 2013). Given this, it is necessary to improve this line of research and the development of a relevant isotopic ecology (Barberena et al., 2009; Falabella et al., 2007; Giardina et al., 2014; Martínez et al., 2009; Laguens et al., 2009; Thornton et al., 2011; Zangrando et al., 2004; Izeta et al., 2009; Mengoni Goñalons, 2007; Szpak et al., 2014).

Research along these lines has taken place in three primary areas. In the Pampas and Patagonian regions of southern Argentina, recent stable isotope studies have focused largely on guanaco (*Lama guanicoe*; Barberena et al., 2009). This research was based on  $\delta^{13}\text{C}$  data from bone collagen, mostly generated as a byproduct of radiocarbon dating of samples found between 34° and 54° SL (Barberena et al., 2009; Fig. 1). Barberena et al. (2009) found no temporal trends in stable carbon values, nor did they identify correlations between latitude and  $\delta^{13}\text{C}$ . Although there is a gradual tendency towards enriched average values at lower latitudes, this tendency is neither strong nor linear. At this smaller scale it is not possible to isolate the role of latitude, as a direct conditioning of global climate, on guanaco isotopic values. The study found no significant correlation with altitude but did find higher  $\delta^{13}\text{C}$  values in the area of southern Mendoza (the southern part of Central-western Argentina), which was considered an outlier.

Additional research on camelid isotope signatures has taken place in the Central Andes and Northwestern Argentina, between 10° and 28° SL (Fernández et al., 1991; Fernández and Panarello, 1999–2001; Finucane et al., 2006; Mengoni Goñalons, 2007, 2009; Samec, 2012; Samec et al., 2014; Thornton et al., 2011; Yacobaccio et al., 1997). These researchers have explored stable isotope trends not only among guanacos, but also wild vicuñas and domesticated llamas and alpacas. These papers have focused on isotopic  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  variation among camelid species and its relationship with altitude, and on using stable isotope values to differentiate domestic and wild camelids. Fernández et al. (1991), for example, demonstrate that the stable carbon ratios of camelid tissues decline with altitude and suggest that these changes reflect concomitant declines in the availability of  $\text{C}_4$  plants. Other researchers have noted similar trends in carbon values (Fernández and Panarello, 1999–2001; Samec, 2012; Yacobaccio et al., 2009, 2010). Working in the Puna region, Samec (2012) notes that the  $\delta^{15}\text{N}$  signatures of vicuñas and llamas also covary with altitude. The pattern shows a negative correlation between altitude and camelid tissue  $\delta^{15}\text{N}$  values, which is thought to reflect greater water availability at higher altitudes (Samec et al., 2014). Looking at

interspecific variation among wild camelids, Samec et al. (2014) found no significant difference in  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  between wild guanacos and vicuñas. Finally, more recent research on taxonomic variation in camelid diet and stable isotope values in the region has proposed that higher  $\delta^{13}\text{C}$  values in domestic llamas may result from maize consumption (Dantas et al., 2014; Izeta et al., 2009).

This paper focuses on camelid isotope variability in Central-western Argentina, the third area in which work has been done. Central-western Argentina (Fig. 1) is an area of environmental, ecological and geographic transition between the two previously mentioned study cases (Northwest Argentina and Patagonia). Previous research in this area has focused on taxonomic differences in stable carbon isotope values and using those values to differentiate wild and domestic species. These early efforts were based on a small sample of camelid bones ( $n = 12$ ) and focused on stable carbon isotope data almost exclusively (Barberena et al., 2009; Gil et al., 2006). More recent research in this area has highlighted the difficulties encountered when trying to explain variation in camelid  $\delta^{13}\text{C}$  values in this manner (Falabella et al., 2007; Gil et al., 2010; Tykot et al., 2009).

This paper presents the results of a broader study of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values from camelid bone collagen distributed throughout Central-western Argentina between 30° and 37° S (Fig. 1). The analysis involves samples from three ecological contexts, the Andean, Patagonia, and Monte deserts (Cabrera, 1976), and includes modern and prehistoric samples. The study aims to improve our understanding of camelid dietary variation and discusses the mechanisms that might explain it. Key goals are to evaluate the degree to which climate and geography explain patterns in camelid stable isotope values and to assess how variation in those values is best considered in order to improve paleoecological and archaeological research.

## 2. Camelids in central-western Argentina: ecological, archaeological and isotopic framework

### 2.1. Project area and environment

Central-western Argentina is an appropriate location to explore the ecology of prehistoric camelid habitats analysis due to altitudinal variation in climate, hydrology, and vegetation. The study area (Fig. 1) is located between ca. 30° and 37° S latitude, and includes a combination of mountains in the west, plains to the east, and a volcanic area in the southeast. It is a temperate, continental region with an arid to semiarid climate. Three ecological units are defined within it: the Andea, Patagonia, and Monte deserts (Roig, 1972).

These ecological units are situated within the South American Arid Diagonal, where precipitation alternates seasonally between the Atlantic and Pacific anticyclone (Bruniard, 1982). From a climate perspective, these regions are highly contrasting due to their relief, dominant masses of maritime air and the season in which precipitation takes place. During the summer, the Atlantic anticyclone brings moisture from the Atlantic to the lowland Monte desert, in the eastern part of the region. During the winter, moisture is derived from the Pacific and precipitation primarily falls in the Andean and Patagonia deserts of the western mountains and fringing piedmont. Because of the great distance traveled, the humid winds of the Atlantic provide little precipitation, while the strong rain-shadow cast by the Andes results in most of the Pacific moisture falling in the mountains as snow, arriving further east as warm, dry winds (Abraham and Rodríguez, 2000).

The Andean desert includes the Altoandina and Puna phytogeography which comprises the Andean cordillera above 2500–3000 m asl, is characterized by cold, windy climatic conditions and winter dominant precipitation of 300–800 mm per year.

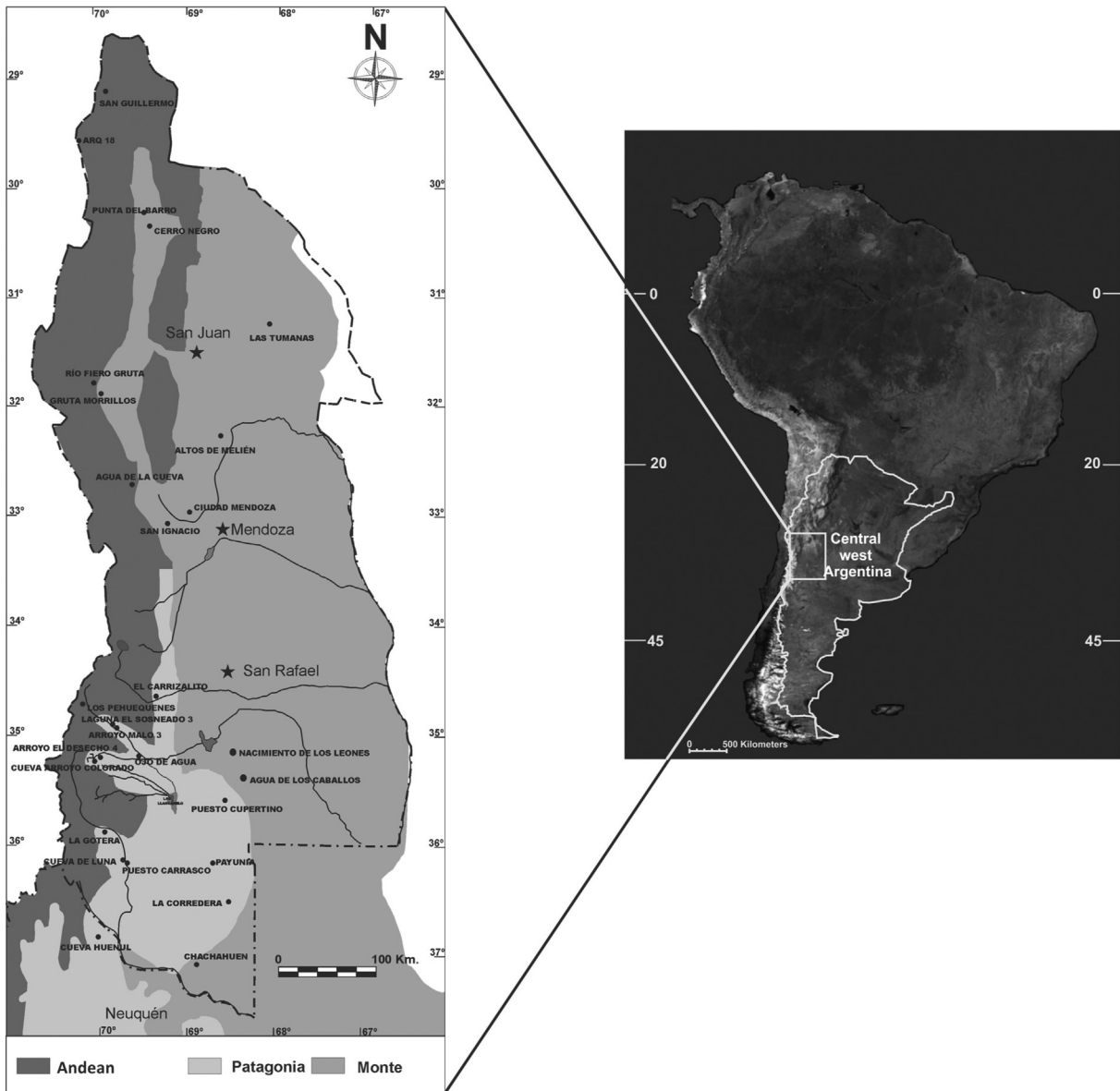


Fig. 1. Central Western Argentina with its major environmental zones and the location of camelid samples presented in the paper.

The northern samples include both Puna and Altoandino environments but the southern samples include only Altoandino samples. The shrubby and herbaceous steppes of this unit are composed mostly of  $C_3$  photosynthetic bunch grasses and shrubs such as *Adesmia* spp., *Oxalis muscoides* and *Mulinum spinosum* (Cabrera, 1976; Cavagnaro, 1988). We emphasize the similarities of Altoandino and Puna with similar expectations regarding  $^{13}C$  and  $^{15}N$  (see below). There are no significant differences in either  $^{13}C$  or  $^{15}N$  between camelids samples from the two environments, and for that reason we group them together here under “Andean” desert.

The Patagonian desert, extending south from ca.  $35^\circ$  S latitude, is located between 2200 and 1500 m asl. The Patagonian semi-deserts and steppe average 200 mm in annual precipitation, with a ranging of 120–600 mm (Pruel et al., 1998). Most rainfall also occurs during the winter. This desert is characterized by a xeric bushy steppe of *Mulinum* spp., *Chuquiraga* spp., and *Festuca* spp., among others (Cabrera, 1971; Roig et al., 2000), and the dominant vegetation is also characterized by  $C_3$  photosynthesis.

Finally there is the Monte desert, which covers the majority of

the study area. The Monte forms a wide fringe containing the eastern plains and eastern part of the La Payunia badlands. It is characterized by an arid climate with summer dominant precipitation of 150–350 mm per year. Here the shrubby and herbaceous steppes include numerous  $C_4$  plants such as *Atriplex lampa*, *Aristida subulata*, *Bouteloua curtipendula*, *Distichlis scoparia*, *Sporobolus rigens*, *Panicum urvilleanum*, *Trichloris crinita* and *Setaria leucopila*; various cacti with CAM metabolism (*Opuntia sulphurea* and *Trichocereus candicans*), and  $C_3$  plants such as *Larrea* spp., *Prosopis* spp., *Cercidium praecox*, *Chuquiraga erinacea*, *Lycium chilense*, and *Geophroea decorticans* (Abraham et al., 2009; Cabrera, 1976; Cavagnaro, 1988; Llano and Ugan, 2014).

## 2.2. Camelid taxonomy, biology, and distribution

Camelids are long known for being a species well-adapted to living in arid environments. They are the most successful ungulates to inhabit the Andean prairies and semiarid slopes, as well as the steppes and plains of Patagonia (Franklin, 1982). South America

camelids include two wild species, guanaco (*Lama guanicoe*) and vicuña (*Vicugna vicugna*), and two domestic species, llama (*Lama glama*) and alpaca (*Vicugna pacos*). The adaptive plasticity that camelids possess owes to their long evolution in arid climates and has made them very efficient in the use of vegetation present in marginal habitats (Bas and Bonacic, 2003). Their unique digestive physiology increases their ability to digest low-quality forage by prolonging the particle retention time in the pseudo-rumen. This promotes high water use efficiency, especially when there is low food intake (González et al., 2006). Foraging behavior and digestive adaptations to harsh environments have allowed the guanaco to become the dominant large herbivore of the scrubland and steppes of South America.

There are certain differences in South American camelids in terms of feeding behavior. The guanaco and llama are considered to be grazers and browsers, while the vicuña and alpaca are grazers only (Franklin, 1982). Camelid diet varies throughout the year depending upon forage availability and quality. Domesticated llamas and alpacas in the Puna alter their diet during the dry and rainy seasons (winter and summer respectively) (Castellaro et al., 1996). Borgnia et al. (2010) show that wild vicuñas show less seasonal variation in diet, but clear dietary differences depending on their geographic location. Vicuña diets include vegetation from all habitats, all vegetation strata, and all functional groups of plants, suggesting that vicuñas can use a large range of the plant species distributed across their range and that they behave as a generalist ungulate (Borgnia et al., 2010).

Guanaco may also be classified as a generalist or opportunistic (mixed) feeder (González et al., 2006), as they, too, forage on a highly diverse range of food sources (Puig et al., 1996, 1997; Puig and Videla, 2000). They forage mainly on the herbaceous vegetation stratum during the year, with preferences displayed for some plant species (Puig et al., 1997; Puig and Videla, 2000). Nevertheless, when the availability of herbaceous strata decreases during winter, guanacos will also feed on shrub or tree strata (González et al., 2006; Puig et al., 1996, 1997). This dietary flexibility extends to the consumption of lichens and succulent plants (González et al., 2006) and to the tree leaves of the deciduous Magellanic forest (González et al., 2006).

Today, the camelids that inhabit Central-western Argentina are wild species (*Lama guanicoe* and *Vicugna vicugna*), with vicuña restricted to the Andean desert of the extreme northwest (30° S) part of the region (Gil et al., 2011; González et al., 2006; Lichtenstein et al., 2008; Marín et al., 2007). The zooarchaeological record shows that during the Holocene, vicuña could have had a slightly more southern distribution of up to 32° S (Gil et al., 2011). Archaeological research posits the use of domestic camelids (probably *Lama glama*) as far south as 30–32° S latitude, but not further (Aguilar, 2009; Aguilar and Iniesta, 2007; Bárcena, 2001; Gambier, 2000; Gasco et al., 2011; Lagiglia, 2001; Otaola et al., 2012).

### 3. Camelid isotopic ecology, camelid diet, deserts, and expectations

Paleoecological and paleodietary reconstruction and sourcing of archaeological animal remains is possible because the isotopic ratios of consumer tissues vary predictably with the ratios of the foods consumed (Ben-David and Flaherty, 2012; Fry, 2006; Koch et al., 2009; Luz et al., 1984; Szpak et al., 2013). Herbivores consume plants and it is the isotopic composition of those plants which is incorporated into their biological tissues (in our case bone). In this study, variation in carbon ( $^{13}\text{C}/^{12}\text{C}$ ), and nitrogen ( $^{15}\text{N}/^{14}\text{N}$ ) stable isotopes of camelid bone are explored with respect to isotopic variation of plants growing under different

environmental contexts throughout Central-western Argentina. Natural variation in isotopic signatures across these ecological zones allows the reconstruction of ancient camelid diet and the exploration of their potential geographic range, with implications for understanding their distribution and migration, as well as human mobility and subsistence organization. The stable isotope ratios of carbon and nitrogen are expressed as ratios relative to a standard in parts per mil (‰) using  $\delta$  notation, where

$$\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1] * 1000$$

Here  $R = ^{13}\text{C}/^{12}\text{C}$  for the measurement of carbon and  $^{15}\text{N}/^{14}\text{N}$  for the measurement of nitrogen. The standards to which samples are compared are the Vienna-PDB (V-PDB) and atmospheric nitrogen (AIR) for carbon and nitrogen, respectively. As most materials have less  $\delta^{13}\text{C}$  than V-PDB,  $\delta^{13}\text{C}$  values are typically negative. The majority of plants photosynthesize using the Calvin Cycle or  $\text{C}_3$  pathway and have an average  $\delta^{13}\text{C}$  value of  $-26.5\text{‰}$ . The  $\delta^{13}\text{C}$  values of plants using the Hatch-Slack photosynthetic pathway ( $\text{C}_4$ ), mainly tropical grasses, millet, and sugarcane, are much higher, averaging  $-12.5\text{‰}$ . Finally, a smaller group of plants including species of bromeliads, cacti, and other succulents utilize a third pathway, Crassulacean Acid Metabolism (CAM), and have  $\delta^{13}\text{C}$  values ranging from  $-27$  to  $-12\text{‰}$ . The  $\delta^{13}\text{C}$  values of the collagen of large herbivores eating these plants are typically enriched by about  $5\text{‰}$  relative to their dietary average (Hedges et al., 2005).

Controlled feeding studies of laboratory animals reveal that the carbon isotope signature of animal proteins, such as collagen in bone, predominantly reflects the protein component of diet, as essential amino acids are preferentially routed from diet to be incorporated into body tissue (Ambrose and Norr, 1993; Tieszen and Fagre, 1993). For pure  $\text{C}_3$  feeders the expected collagen  $\delta^{13}\text{C}$  value is around  $-21.5\text{‰}$ , and for pure  $\text{C}_4$  feeders the expected collagen value is around  $-7.5\text{‰}$ . Intermediate values are expected for mixed diets (Cerling and Harris, 1999).

In the case of nitrogen, consumer  $\delta^{15}\text{N}$  values reflect average diet plus an offset caused by trophic level effects. This offset is generally held to be a  $3\text{‰}$  increase in  $\delta^{15}\text{N}$  among trophic levels (Pate, 1997; but see Szpak, 2014). Recent studies have shown the effects of climate and environment on both plant and animal  $\delta^{15}\text{N}$  values (Ambrose, 2000; Ambrose and DeNiro, 1986; Amundson et al., 2003; Hedges and Reynard, 2006; Samec et al., 2014; Szpak, 2014). Herbivore bone collagen nitrogen enters into the animal as plant protein, which can be traced to both mineralized and organic nitrogen sources in the soil (Richards and Hedges, 2003). Large effects attributable to environmental influences have been recognized in some situations, for example, aridity and water stress in fauna (Heaton et al., 1986), and of temperature and precipitation on vegetation and nitrogen cycling (Amundson et al., 2003; Handley et al., 1999; Hartman, 2011).

Since bone remodels slowly, the isotopic signature recorded in bone reflects long-term, average diet (Ambrose, 1991). Wild and domesticated camelids live on average 10–12 and 15–20 years, respectively (Bonavia, 2008). While individuals may have moved between habitat zones, those feeding for extended periods of time in Altoandean and Patagonian deserts should yield more negative  $\delta^{13}\text{C}$  values than those feeding in the Monte due to the increased availability of  $\text{C}_4$  plants below 1500 m asl (Fig. 2; Cavagnaro, 1988; Gardina et al., 2014). Camelids feeding on maize, a  $\text{C}_4$  plant, should also exhibit more enriched  $^{13}\text{C}$  values. Camelids primarily residing in the Monte Desert would also be expected to have higher  $\delta^{15}\text{N}$  values due to increased aridity and salinity, reduced vegetative cover, and a presumably more open nitrogen cycle (Ambrose and DeNiro, 1986; Ambrose, 1991; Amundson et al., 2003; Heaton et al., 1986; Szpak, 2014). Finally, the extensive use of compost,

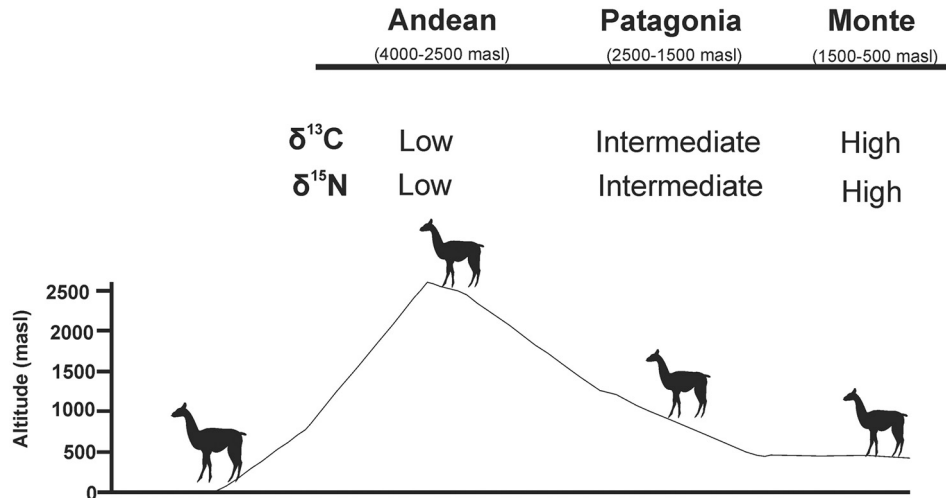


Fig. 2. Expected relationship between camelids stable isotopes values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) and environmental zone in Central-western Argentina.

manure or guano as crop fertilizer could also raise the  $\delta^{15}\text{N}$  values in camelids feeding primarily on human cultigens, or on weeds growing in fallow fields (Szpak, 2014).

#### 4. Materials and methods

Extraction of bone collagen and apatite was performed in the Museo de Historia Natural de San Rafael (samples code MSR) and the Laboratory for Archaeological Science at the University of South Florida (code USF; Gil et al., 2010; Tykot, 2004). The samples processed in MSR followed the procedures reported in Coltrain and Stafford (1999) and were measured at the University of Wyoming Stable Isotope Facility and the Stable Isotope Ratio Facility for Environmental Research (SIRFER) at the University of Utah. The samples processed at USF followed the procedures reported in Tykot (2004). Table 1 details the stable isotope information for 83 archaeological and eight modern camelid samples identified as *Lama* sp. (n = 43), *Lama guanicoe* (n = 42), and *Vicugna vicugna* (n = 6). Taxonomic identification of archaeological camelids is limited by the difficulty of distinguishing between wild and domesticated species based on post-cranial osteological evidence alone (e.g., *L. guanicoe* vs. *L. glama* or *V. vicugna* vs. *V. pacos*; Wheeler et al., 1995; Wheeler, 2012; Yacobaccio, 2010). However, of the 43 specimens identified as *Lama* sp., only 17 are young enough (<3000 cal BP) and located far enough north (above 32° south latitude) to potentially be domesticated *Lama glama*. The rest are almost assuredly guanaco, but we remain conservative in our taxonomic assignment.

Table 1 also details the anatomical part of bone, estimated chronology, and environmental context of the samples. Most age determinations were obtained via radiocarbon dating of associated material rather than directly dating the faunas themselves. In terms of the environmental context, the present study includes 28 Andean, 35 Patagonian, and 28 Monte samples from a range of different latitudes and altitudes (Table 1; Fig. 1).

We note that bone turnover rates vary according to the type of bone tissue, skeletal element, and health of the individual (Lamb et al., 2014; Sealy et al., 1995). In humans, dense, cortical bone such as the femur has a relatively slow turnover rate of 2.5%/year and isotope values for collagen from the femur are thought to represent an average of at least 10 years prior to death in adults (Cox and Sealy, 1997; Hedges et al., 2007). In contrast, cancellous bone is more active and will turn over at a faster rate (Hill and Orth,

1998), estimated to be as much as 10%/year (Cox and Sealy, 1997). Values for juveniles are substantially higher yet owing to their rapid growth and somatic development. While specific data for animals such as camelids are lacking, similar effect can be expected insofar as both are mammalian vertebrates. Incorporating higher turnover skeletal elements or those from juveniles decreases the temporal window over which diet is sampled and increases the variation in observed isotope values, making it more difficult to tease apart differences in sample means. However, only eleven samples come from elements with substantial amounts of cancellous or trabecular bone, and just eight from clearly juvenile animals.

Statistical analyses were performed using PAST Software, statistical computing package R (R Development Core Team, 2007) and specific geospatial analysis with Spatial Analysis in Macroecology (SAM; Rangel et al., 2010). Isotopic differences among regions and environmental zones were evaluated using ANOVA and boxplots that describe differences in sample ranges. Specific pairwise comparisons were made using Tukeys Honest Significant Difference (HSD) test. Temporal trends were assessed using a simple linear regression of sample isotope value against age.

Spatial statistical analyses were performed in order to describe the spatial structure of isotopic and climatic variables, and to evaluate the association between them (Diniz-Filho et al., 2007). The spatial analysis include Moran's I correlograms for exploring the existence of a geographical pattern for each variable, as well as spatial regression analysis and multi-inference models for studying the association among isotopic and climatic variables in order to evaluate if variation in the latter explains variation in the former.

First, Moran's I correlograms were calculated for isotopic variables ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) and climatic data. The relevant climate data were obtained from a group of ten variables available in the WorldClim database. WorldClim is a set of global climate layers (climate grids) with a spatial resolution of about 1 square kilometer. The data can be used for mapping and spatial modeling in a GIS or with other computer programs. Detailed information about the methods used to generate the climate layers, and the units and formats of the data can be found in Hijmans et al. (2005).

The correlogram is a graph of Moran's I autocorrelation values calculated at different distance classes. The autocorrelation values are plotted on the ordinate and distance classes among sampling localities on the abscissa (Legendre and Fortin, 1989 Sokal and Oden, 1978). Moran's I values near 1 or -1 indicate geographic clustering of data while a value near 0 indicates geographic

**Table 1**  
Raw information of modern and/or archaeological camelid bone collagen isotopic analysis.

ID	Status	Provenience	msnm	Lat	Long	Desert	$\delta^{13}\text{C}$	Crr $\delta^{13}\text{C}^*$	$\delta^{15}\text{N}$	Atomic C:N	Taxa	Bone element	Fused	Years BP**
MSR-A300	Modern	San Guillermo	3000	-29.16	-69.33	Andean	-18.54	-16.54	5.41	3.2	<i>Vicugna vicugna</i>	Metapodial	Yes	20
MSR-A298	Modern	San Guillermo	3000	-29.16	-69.33	Andean	-18.03	-16.03	5.76	3.4	<i>Vicugna vicugna</i>	Carpal	Yes	20
MSR-A299	Modern	San Guillermo	3000	-29.16	-69.33	Andean	-17.85	-15.85	6.9	3.2	<i>Vicugna vicugna</i>	First Phalange	Yes	20
MSR-A301	Modern	San Guillermo	3000	-29.16	-69.33	Andean	-18.68	-16.68	5.74	3.2	<i>Vicugna vicugna</i>	Metapodial	Yes	20
MSR-236	Archaeological	ARQ 18	3.761	-29.33	-70	Andean	-17.55	-17.55	4.59	3.2	<i>Lama sp.</i>	Phalange	Yes	1900
MSR-238	Archaeological	ARQ 18	3.761	-29.33	-70	Andean	-17.32	-17.32	5.55	3.2	<i>Vicugna vicugna</i>	Mandibule	Yes	1900
MSR-239	Archaeological	ARQ 18	3.761	-29.33	-70	Andean	-17.71	-17.71	6.79	3.2	<i>Lama sp.</i>	First Phalange	Yes	2300
MSR-240	Archaeological	ARQ 18	3.761	-29.33	-70	Andean	-18.48	-18.48	8.37	3.2	<i>Lama sp.</i>	Humerus	Yes	4900
MSR-241	Archaeological	ARQ 18	3.761	-29.33	-70	Andean	-17.14	-17.14	6.03	3.2	<i>Vicugna vicugna</i>	Scapule	Yes	3700
MSR-237	Archaeological	ARQ 18	3.761	-29.33	-70	Andean	-17.55	-17.55	7.21	3.2	<i>Lama sp.</i>	Astragalus	Yes	4500
MSR-200	Archaeological	Punta del Barro	1.700	-30.03	-69.17	Monte	-17.39	-17.39	7.13	3.1	<i>Lama sp.</i>	Metapodial	Yes	1700
MSR-203	Archaeological	Punta del Barro	1.700	-30.03	-69.17	Monte	-16.26	-16.26	8.13	3.1	<i>Lama sp.</i>	First Phalange	Yes	1700
MSR-204	Archaeological	Punta del Barro	1.700	-30.03	-69.17	Monte	-15.31	-15.31	7.13	3.1	<i>Lama sp.</i>	First Phalange	Yes	1700
MSR-205	Archaeological	Punta del Barro	1.700	-30.03	-69.17	Monte	-16.27	-16.27	6.78	3.1	<i>Lama sp.</i>	First Phalange	Yes	1700
MSR-262	Archaeological	Punta del Barro	1.700	-30.03	-69.17	Monte	-15.53	-15.53	8.5	3.1	<i>Lama sp.</i>	First Phalange	Yes	1700
MSR-263	Archaeological	Punta del Barro	1.700	-30.03	-69.17	Monte	-13.13	-13.13	7.69	3.2	<i>Lama sp.</i>	Astragalus	Yes	1700
MSR-264	Archaeological	Punta del Barro	1.700	-30.03	-69.17	Monte	-14.98	-14.98	9.14	3.2	<i>Lama sp.</i>	Second Phalange	No	1700
MSR-265	Archaeological	Punta del Barro	1.700	-30.03	-69.17	Monte	-17.99	-17.99	6.27	3.2	<i>Lama sp.</i>	First Phalange	Yes	1700
MSR-97	Archaeological	Punta del Barro	1.700	-30.03	-69.17	Monte	-17.43	-17.43	7.1	3.1	<i>Lama sp.</i>	First Phalange	Yes	1700
MSR-98	Archaeological	Punta del Barro	1.700	-30.03	-69.17	Monte	-14.56	-14.56	3.72	3.1	<i>Lama sp.</i>	Humerus	Yes	1700
MSR-201	Archaeological	Cerro Negro	1.638	-30.29	-69.26	Monte	-14.07	-14.07	5.42	3.2	<i>Lama sp.</i>	n/d	-	1050
MSR-99	Archaeological	Cerro Negro	1.638	-30.29	-69.26	Monte	-13.21	-13.21	8.91	3.1	<i>Lama sp.</i>	n/d	-	1050
MSR-190	Archaeological	Alero Las Tumanas	460	-30.86	-67.33	Monte	-12.06	-12.06	10.16	3.2	<i>Lama sp.</i>	n/d	-	1000
MSR-202	Archaeological	Río Fiero Gruta 2	3.012	-31.68	-69.72	Andean	-19.36	-19.36	8.62	3.2	<i>Lama sp.</i>	n/d	-	2250
MSR-206	Archaeological	Los Morrillos Gruta 1	3.012	-31.72	-69.12	Monte	-17.89	-17.89	6.3	3.1	<i>Lama sp.</i>	First Phalange	Yes	2250
MSR-A192	Archaeological	Altos de Melián	540	-32.2	-68.15	Monte	-10.66	-10.66	9.27	3.2	<i>Lama sp.</i>	Astragalus	Yes	200
MSR-242	Archaeological	Agua de la Cueva	2.900	-32.62	-69.15	Andean	-18.91	-18.91	5.18	3.2	<i>Lama sp.</i>	Femur	No	400
MSR-243	Archaeological	Agua de la Cueva	2.900	-32.62	-69.15	Andean	-19.25	-19.25	3.86	3.2	<i>Lama sp.</i>	Astragalus	Yes	1400
MSR-244	Archaeological	Agua de la Cueva	2.900	-32.62	-69.15	Andean	-17.7	-17.7	5.38	3.2	<i>Lama sp.</i>	Metacarpal	Yes	1350
MSR-245	Archaeological	Agua de la Cueva	2.900	-32.62	-69.15	Andean	-18.73	-18.73	5.29	3.1	<i>Lama sp.</i>	Astragalus	Yes	1300
MSR-246	Archaeological	Agua de la Cueva	2.900	-32.62	-69.15	Andean	-14.04	-14.04	9.58	3.2	<i>Lama sp.</i>	Femur	Yes	1400
MSR-247	Archaeological	Agua de la Cueva	2.900	-32.62	-69.15	Andean	-17.48	-17.48	4.35	3.1	<i>Lama sp.</i>	Radius	No	9500
MSR-248	Archaeological	Agua de la Cueva	2.900	-32.62	-69.15	Andean	-18.9	-18.9	4.97	3.1	<i>Lama guanicoe</i>	First Phalange	Yes	1300
MSR-249	Archaeological	Agua de la Cueva	2.900	-32.62	-69.15	Andean	-18.31	-18.31	4.52	3.2	<i>Lama sp.</i>	Maxilar	Yes	1300
MSR-250	Archaeological	Agua de la Cueva	2.900	-32.62	-69.15	Andean	-17	-17.00	6.77	3.2	<i>Lama sp.</i>	Third Phalange	No	9500
MSR-251	Archaeological	Agua de la Cueva	2.900	-32.62	-69.15	Andean	-19.15	-19.15	4.31	3.2	<i>Lama sp.</i>	Second Phalange	Yes	1300
MSR-252	Archaeological	Agua de la Cueva	2.900	-32.62	-69.15	Andean	-18.3	-18.3	4.94	3.2	<i>Lama guanicoe</i>	First Phalange	Yes	400
MSR-253	Archaeological	Agua de la Cueva	2.900	-32.62	-69.15	Andean	-18.87	-18.87	3.21	3.2	<i>Lama sp.</i>	Pelvis	No	400
MSR-254	Archaeological	Agua de la Cueva	2.900	-32.62	-69.15	Andean	-16.61	-16.61	6.73	3.1	<i>Lama sp.</i>	Carpal	Yes	9500
MSR-255	Archaeological	Agua de la Cueva	2.900	-32.62	-69.15	Andean	-18.19	-18.19	6.43	3.1	<i>Lama sp.</i>	Maxilar	Yes	1200
USF-8863	Archaeological	Agua de la Cueva	2.900	-32.62	-69.15	Andean	-17.5	-17.5	6.5	-	<i>Lama sp.</i>	Second Phalange	Yes	-
MSR-A302	Archaeological	Ciudad de Mendoza	500	-32.88	-68.88	Monte	-18.63	-18.63	3.97	3.2	<i>Lama sp.</i>	Tibiae	Yes	200
MSR-A303	Archaeological	Ciudad de Mendoza	500	-32.88	-68.88	Monte	-18.44	-18.44	9.39	3.2	<i>Lama sp.</i>	Second Phalange	Yes	200
MSR-256	Archaeological	San Ignacio	1.400	-32.97	-69.17	Monte	-17.47	-17.47	4.24	3.1	<i>Lama sp.</i>	Tibiae	No	1500
MSR-257	Archaeological	San Ignacio	1.400	-32.97	-69.17	Monte	-17.96	-17.96	2.06	3.0	<i>Lama sp.</i>	Astragalus	Yes	1500
MSR-258	Archaeological	San Ignacio	1.400	-32.97	-69.17	Monte	-18.35	-18.35	1.95	3.2	<i>Lama sp.</i>	Femur	No	1500
MSR-266	Archaeological	San Ignacio	1.400	-32.97	-69.17	Monte	-18.48	-18.48	4.61	3.1	<i>Lama sp.</i>	Second Phalange	No	1500
MSR-267	Archaeological	San Ignacio	1.400	-32.97	-69.17	Monte	-18.85	-18.85	4.58	3.1	<i>Lama sp.</i>	Astragalus	Yes	1500
MSR-268	Archaeological	San Ignacio	1.400	-32.97	-69.17	Monte	-14.48	-14.48	3.51	3.2	<i>Lama sp.</i>	Humerus	Yes	1500
MSR-A6	Archaeological	El Carrizalito	2.311	-34.53	-69.45	Patagonia	-19.01	-19.01	4.72	3.1	<i>Lama guanicoe</i>	Metapodial	Yes	n/d
MSR-A14	Archaeological	Los Peuquenes	3.089	-34.6	-70.09	Andean	-19.17	-19.17	3.09	3.3	<i>Lama guanicoe</i>	Metapodial	Yes	200
MSR-A15	Archaeological	Los Peuquenes	3.089	-34.6	-70.09	Andean	-19.28	-19.28	5.42	3.2	<i>Lama guanicoe</i>	Cuboid	Yes	200
MSR-A11	Archaeological	Laguna Sosneado 3 LS3	2.000	-34.83	-69.9	Patagonia	-19.09	-19.09	5.27	3.2	<i>Lama guanicoe</i>	Isquium	Yes	2000
USF-8357	Archaeological	Laguna Sosneado 3 LS3	2.000	-34.83	-69.9	Patagonia	-18.9	-18.9	6.1	-	<i>Lama guanicoe</i>	n/d	-	2000
USF-8355	Archaeological	Arroyo Malo 3	2.000	-34.87	-69.9	Patagonia	-18.8	-18.8	4.8	-	<i>Lama guanicoe</i>	n/d	-	n/d

Table 1 (continued)

ID	Status	Provenience	msnm	Lat	Long	Desert	$\delta^{13}\text{C}$	Crr $\delta^{13}\text{C}^*$	$\delta^{15}\text{N}$	Atomic C:N	Taxa	Bone element	Fused	Years BP**
MSR-A8	Archaeological	Ojo de Agua	1.576	-35.15	-69.64	Patagonia	-19.45	-19.45	5.92	3.2	<i>Lama guanicoe</i>	Humerus	Yes	500
USF-8356	Archaeological	Ojo de Agua	1.600	-35.15	-69.64	Patagonia	-18.7	-18.7	6.6	-	<i>Lama guanicoe</i>	n/d	-	500
MSR-A10	Archaeological	Cueva Arroyo Colorado	2.000	-35.18	-70.05	Patagonia	-19.18	-19.18	4.72	3.2	<i>Lama guanicoe</i>	Vertebrae	Yes	1300
MSR-A7	Archaeological	Arroyo El Desecho-4	2.000	-35.18	-70.05	Patagonia	-19.45	-19.45	4	3.1	<i>Lama guanicoe</i>	Radius	Yes	5000
MSR-A9	Archaeological	Cueva Arroyo Colorado	2.000	-35.18	-70.05	Patagonia	-20.14	-20.14	5.03	3.1	<i>Lama guanicoe</i>	Metapodial	Yes	700
USF-5905	Archaeological	Cueva Arroyo Colorado	2.000	-35.18	-70.05	Patagonia	-19.1	-19.1	4.3	-	<i>Lama guanicoe</i>	n/d	-	-
USF-5913	Archaeological	Cueva Arroyo Colorado	2.000	-35.18	-70.05	Patagonia	-18.8	-18.8	4.3	-	<i>Lama guanicoe</i>	n/d	-	-
MSR-A200	Archaeological	Nacimiento de Los Leones	1.100	-35.2	-68.4	Monte	-17.6	-17.6	7.94	3.2	<i>Lama guanicoe</i>	Metapodial	Yes	-
MSR-A16	Archaeological	Agua de los Caballos	1.025	-35.37	-68.3	Monte	-17.47	-17.47	9.91	3.13	<i>Lama guanicoe</i>	Metapodial	Yes	300
USF-6171	Archaeological	Agua de los Caballos	1.025	-35.37	-68.3	Monte	-14.7	-14.7	5	-	<i>Lama sp.</i>	First Phalange	Yes	300
USF-8865	Archaeological	Agua de los Caballos	1.025	-35.37	-68.3	Monte	-18.5	-18.5	7.6	-	<i>Lama sp.</i>	Second Phalange	Yes	300
MSR-A110	Modern	Puesto Cupertino	2.300	-35.52	-68.55	Patagonia	-22.11	-20.11	4.14	3.16	<i>Lama guanicoe</i>	First phalange	Yes	20
MSR-A350	Modern	Puesto Cupertino	2.280	-35.52	-68.55	Patagonia	-22.24	-20.24	3.33	3.19	<i>Lama guanicoe</i>	First Phalange	Yes	20
USF-8354	Archaeological	La Gotera	1.800	-35.87	-69.95	Patagonia	-18.7	-18.7	6.2	-	<i>Lama guanicoe</i>	n/d	-	1000
MSR-A1	Archaeological	Cueva de la Luna A	1.300	-36.08	-69.72	Patagonia	-19.69	-19.69	4.18	3.1	<i>Lama guanicoe</i>	Metatarsal	Yes	200
MSR-A2	Archaeological	Cueva de la Luna A	1.300	-36.08	-69.72	Patagonia	-19.15	-19.15	5.01	3.11	<i>Lama guanicoe</i>	Metatarsal	Yes	200
MSR-A3	Archaeological	Cueva de La Luna B	1.300	-36.08	-69.72	Patagonia	-19.89	-19.89	4.42	3.1	<i>Lama guanicoe</i>	Phalange	Yes	1000
MSR-A4	Archaeological	Cueva de La Luna C	1.300	-36.08	-69.72	Patagonia	-19.75	-19.75	4.97	3.14	<i>Lama guanicoe</i>	Phalange	Yes	1500
MSR-A5	Archaeological	Cueva de La Luna B	1.300	-36.08	-69.72	Patagonia	-19.75	-19.75	4.94	3.28	<i>Lama guanicoe</i>	Cervical Vertebrae	Yes	1500
USF-5907	Archaeological	Cueva de Luna	1.300	-36.08	-69.72	Patagonia	-19.4	-19.4	4.6	-	<i>Lama guanicoe</i>	Metapodial	Yes	-
MSR-A12	Archaeological	Alero Puesto Carrasco	1.300	-36.1	-69.69	Patagonia	-18.62	-18.62	5.35	3.12	<i>Lama guanicoe</i>	Phalange	Yes	1400
MSR-A13	Archaeological	Alero Puesto Carrasco	1.300	-36.1	-69.69	Patagonia	-19.85	-19.85	4.61	3.15	<i>Lama guanicoe</i>	Metapodial	Yes	700
MSR-A46	Modern	Payunia	1.500	-36.15	-68.69	Patagonia	-16.93	-14.93	4.78	3.14	<i>Lama guanicoe</i>	Patella	Yes	20
USF-8864	Archaeological	La Corredera	1.300	-36.52	-68.53	Patagonia	-19.3	-19.3	6.3	-	<i>Lama guanicoe</i>	Patella	Yes	1000
MSR-A233	Archaeological	Cueva Huenuil	1.000	-36.93	-69.82	Patagonia	-17.98	-17.98	6.52	3.21	<i>Lama guanicoe</i>	Radius Ulnae	Yes	1500
MSR-A236	Archaeological	Cueva Huenuil	1.000	-36.93	-69.82	Patagonia	-19.94	-19.94	5.35	3.33	<i>Lama guanicoe</i>	Lumbar Vertebrae	Yes	1500
MSR-A237	Archaeological	Cueva Huenuil	1.000	-36.93	-69.82	Patagonia	-19.94	-19.94	4.17	3.29	<i>Lama guanicoe</i>	First Phalange	Yes	1600
MSR-A239	Archaeological	Cueva Huenuil	1.000	-36.93	-69.82	Patagonia	-19.49	-19.49	4.51	3.23	<i>Lama guanicoe</i>	Tibiae	Yes	9300
MSR-A241	Archaeological	Cueva Huenuil	1.000	-36.93	-69.82	Patagonia	-18.17	-18.17	4.92	3.24	<i>Lama guanicoe</i>	Radius Ulnae	Yes	9300
MSR-A244	Archaeological	Cueva Huenuil	1.000	-36.93	-69.82	Patagonia	-19.8	-19.8	5.11	3.22	<i>Lama guanicoe</i>	First phalange	Yes	1500
MSR-A50	Archaeological	Cueva Huenuil	1.000	-36.93	-69.82	Patagonia	-19.67	-19.67	5.37	3.2	<i>Lama guanicoe</i>	First phalange	Yes	-
MSR-A51	Archaeological	Cueva Huenuil	1.000	-36.93	-69.82	Patagonia	-20.33	-20.33	5.78	3.11	<i>Lama guanicoe</i>	Tibiae	Yes	-
MSR-A52	Archaeological	Cueva Huenuil	1.000	-36.93	-69.82	Patagonia	-19.58	-19.58	4.69	3.19	<i>Lama guanicoe</i>	Metapodial	Yes	-
MSR-A53	Archaeological	Cueva Huenuil	1.000	-36.93	-69.82	Patagonia	-19.54	-19.54	5.31	3.13	<i>Lama guanicoe</i>	Metacarpal	Yes	-
MSR-A54	Archaeological	Cueva Huenuil	1.000	-36.93	-69.82	Patagonia	-19.37	-19.37	5.87	3.16	<i>Lama guanicoe</i>	Cervical Vertebrae	Yes	-
MSR-A120	Modern	Sierra de Chachauen	1.200	-37.08	-68.92	Monte	-21.62	-19.62	3.94	3.16	<i>Lama guanicoe</i>	Caudal vertebrae	Yes	20

Note: Lat/Long is in decimal degrees,  $\delta^{13}\text{C}$  (‰ VPDB) and  $\delta^{15}\text{N}$  (‰ AIR) values of bone collagen. \* (modern +2‰); \*\* chronology estimated by associated with radiocarbon or contextual association.

dispersion. The shape of the correlogram may also reflect the type of spatial structure underlying the studied variables (Sokal, 1979). Correlograms display a characteristic asymptotically decreasing shape when the pattern of variation has a strong geographical signal (Barbujani, 2000), while when correlograms show a random pattern, a cline, or a depression, other factors are involved.

In order to evaluate the association between isotopic and climatic variables we performed regression analyses, using climatic data as independent variables and isotopic data as dependent variables. This model can be described as  $y = Xb + \varepsilon$ , where  $y$  is the vector that describes isotopic variation,  $X$  is the matrix of independent climatic variables,  $b$  is the vector of regression coefficients,  $\varepsilon$  is the error term with a covariance matrix  $C$  among residuals  $C = \sigma^2 I$ , where  $\sigma^2$  is the variance of the residuals, and  $I$  is an identity matrix (Perez et al., 2010).

Given that most of our data are spatially autocorrelated—that is, observations that are closer to each other in space have more similar values—we used autoregressive models instead of ordinary regression (Legendre and Legendre, 2003). These methods model spatial effects within the error term, which is predefined from a neighborhood matrix, and then parameters are estimated using a generalized least squares framework (Dormann et al., 2007; Perez et al., 2010). Here, we used the conditional autoregressive model (CAR; Dormann et al., 2007; Perez et al., 2010), an error model with all first order neighbors and equal weighting of all neighbors. Finally a multi-model inference was done to evaluate the combination of climatic variables that best explain isotopic variation. This analysis is based on the Akaike Information Criterion (AIC), which is a measure of the relative quality of a statistical model for a given data set, providing a means for the selection of models. It is based on the entropy of information and thus offers a relative estimate of the information that is lost when a particular model is used to represent the process that generates the data. Given a set of possible models to explain the data, the preferred model is the one that has the minimum AIC value.

## 5. Results and discussion

Table 1 shows camelid  $\delta^{13}\text{C}$  values for the three desert environments of Central-western Argentina. These range from  $-20.3\text{‰}$  to  $-10.7\text{‰}$ , with a mean of  $-17.9\text{‰}$ , suggesting that camelid diets are highly variable and include both  $\text{C}_3$  and  $\text{C}_4$  plants. Camelid  $\delta^{15}\text{N}$  values vary between  $2\text{‰}$  and  $10.2\text{‰}$ , with a mean value of  $5.7\text{‰}$ . A simple regression of carbon and nitrogen values against sample age reveals no temporal differences in either  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  ( $\delta^{13}\text{C} f = .015$ ,  $p = .903$ ;  $\delta^{15}\text{N} f = .036$ ,  $p = .851$ ). The mean contribution of  $\text{C}_3$  plants to the diet is on the order of 60–70%, while individual contributions vary between 100% and 20%  $\text{C}_3$ . These estimates assume an herbivore diet composed of  $\text{C}_3$  and  $\text{C}_4$  plants, where a 100%  $\text{C}_3$  diet produces a bone collagen  $\delta^{13}\text{C}$  value of  $-21.5\text{‰}$  and a 100%  $\text{C}_4$  generates a  $\delta^{13}\text{C}$  of  $-7.5\text{‰}$ . Taken as a whole, the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values considered here fit expectations for a mixed feeder herbivore species inhabiting an arid setting (Hartman, 2011; Pate and Anson, 2008).

### 5.1. Camelids taxonomy, deserts and variability of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

Mean carbon and nitrogen isotope values of the camelid samples differ across geographic regions (Table 2;  $F_{13\text{C}} = 27.13$ ,  $p < .001$ ;  $F_{15\text{N}} = 5.73$ ,  $p = .005$ ). All pairwise comparisons of carbon  $^{13}\text{C}$  values are significant (Tukey's HSD,  $p < .003$ ), and values from Patagonian deserts are more negative than those from either Monte or Andean environments (Fig. 3). Nitrogen  $^{15}\text{N}$  values from Patagonian camelids are also generally lower (Fig. 3), though the only significant difference is between Patagonia and Monte samples

(Tukey's HSD,  $p = .003$ ); Monte and Andean samples are broadly similar.

These results refute the expectation presented in Fig. 2. Our original hypothesis, based on the ecology and spatial distribution of  $\text{C}_3$  and  $\text{C}_4$  photosynthesizing plants, predicted differences among all of the desert environments, with  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  declining with elevation. Monte and Patagonia camelids differ in the manner expected, with Monte samples having more positive average values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . The Andean samples, on the other hand, are higher than expected and surprisingly similar to those recovered from the lower, Monte desert environment rather than the intervening Patagonia fringe.

The high Andes have few if any  $\text{C}_4$  plants, so it is difficult to explain the observed values as a consequence of local camelid diet. We suspect this unexpected departure reflects, at least in part, a combination of geography and extreme seasonality in the camelids use of this desert. The Andean region is largely uninhabitable during winter months due to extremely low temperatures and heavy snowpack, being accessible only between October and late March/April. Some part of this desert also has permanent snow. Furthermore, most of the Andean bone samples (26 of 28) come from the region north of  $30^\circ$  S latitude, where the Monte environment abuts almost directly against the high Andes rather than a fringing piedmont of Patagonian vegetation (Fig. 1). As Martinez Carretero et al. (2013) note, a strong bioclimatic change occurs between 1900 and 2200 m asl in this area. Within the space of 40 km, the environment changes from Monte desert, with annual average temperature  $11.4^\circ\text{C}$  and annual precipitation of 28 mm (mostly in summer), to an Andean environment with an annual average temperature of  $7.5^\circ\text{C}$  and precipitation of 102 mm (mostly in winter).

Given this geography, one possibility is that the unexpectedly positive  $\delta^{13}\text{C}$  signal among the Andean samples reflects seasonal movements between Andean and Monte deserts in the northern region (Fig. 1). If so, the diet of Andean camelids, which occupy Monte habitats seasonally, should still include a higher proportion of  $\text{C}_3$  plants than those using Monte habitats exclusively. Consistent with this observation, northern Andean samples have mean  $\delta^{13}\text{C}$  values  $2.5\text{‰}$  more negative than northern Monte samples ( $-17.6\text{‰}$  vs  $-15.1\text{‰}$ ;  $t = 4.12$ ,  $p < .001$ ; Fig. 4). A similar pattern can be seen among the southern camelids (Fig. 5). Although there are only two individuals from Andean contexts, their  $\delta^{13}\text{C}$  values are slightly more negative than those of animals found further north ( $\delta^{13}\text{C}_S = -19.2\text{‰}$ ,  $\delta^{13}\text{C}_N = -18.0\text{‰}$ ) and mirror the adjacent Patagonian sample ( $\delta^{13}\text{C} = -19.2\text{‰}$ ) rather than being more positive. The same issue may apply to animals migrating to or from the Pacific face of the Andes, though there are currently no isotopic studies available to explore this in detail.

The northern, Andean samples also include all six of the vicuñas present in our data. These vicuñas possess distinctly higher mean carbon values than sympatric *Lama* sp. ( $-16.6$  vs.  $-18.0\text{‰}$ ; Fig. 4). They are also more restricted in their distribution and generally limited to habitats above 3000 m, making it less likely that their patterns are solely the result of seasonal shifts in habitat use. The exact reason for the differences in carbon isotopes values is

**Table 2**

Variation in camelids  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  between ecological areas in Central-western Argentina.

	Andean			Patagonia			Monte		
	n	Mean	SD	n	Mean	SD	N	Mean	SD
$\delta^{13}\text{C}_{\text{col}}$	28	-17.7	1.2	35	-19.2	0.9	28	-16.3	2.3
$\delta^{15}\text{N}$	28	5.75	1.5	35	5.0	0.7	28	6.4	2.3



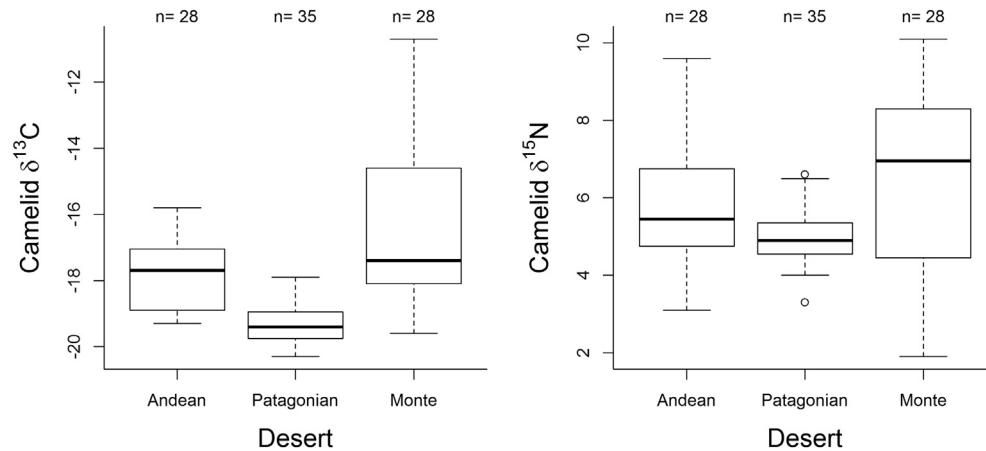


Fig. 3. Boxplot of camelid  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values by environmental zone.

unknown, but the contrast between *Lama* sp. and vicuñas in northern Central-west Argentina suggests a degree of dietary separation, perhaps related to differences in feeding niche and reduced competition for forage.

#### 5.2. Camelids, geography, climate and variability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

In order to explore the spatial, geographical and ecological patterning in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in more detail, these values are studied along with geographic and climatic variables through spatial analysis (Rangel et al., 2010). The Moran's I correlograms (Fig. 6) confirm the strong spatial variation of  $\delta^{13}\text{C}$  values but weak spatial pattern of  $\delta^{15}\text{N}$  values.

When considering only the geographic variables, the results indicate that the best models are those where isotopic variation is explained by three variables: latitude, longitude and altitude. Fifty-six percent of the spatial variation in  $\delta^{13}\text{C}$  values is explained by a combination of geographical location and altitude ( $r^2 = 0.565$  and  $\text{AIC} = 315$ ). This value is lower for  $\delta^{15}\text{N}$ , where only 21% of its variation is explained using these variables ( $r^2 = 0.216$  and  $\text{AIC} = 344$ ). In relation to climatic variables,  $\delta^{13}\text{C}$  models have more explanatory power, with higher  $r^2$  values than  $\delta^{15}\text{N}$  models. The model that best explains the variation of  $\delta^{13}\text{C}$  includes mean annual temperature, annual precipitation, and precipitation during the warmest and coldest quarters of the year. The combination of these variables explain nearly 64% of the isotopic variation ( $r^2 = 0.639$

and  $\text{AIC} = 300.999$ ). The model that best explains the distribution of  $\delta^{15}\text{N}$  values includes annual mean temperature, temperature annual range, annual precipitation, and precipitation of the warmest and coldest quarters, which together explains 35% of the  $\delta^{15}\text{N}$  isotope values variation ( $r^2 = 0.355$  and  $\text{AIC} = 331.597$ ). Notably, the same variables help to explain the distribution of both isotopes values; only temperature annual range is added for the  $\delta^{15}\text{N}$  model. Clearly, both isotopes can be explained by geography, and more strongly, by climatic variables. In both cases, the combination of geography and climate account for a larger part of the variation in  $\delta^{13}\text{C}$  than  $\delta^{15}\text{N}$ .

Camelid  $\delta^{13}\text{C}$  shows a positive correlation with summer precipitation and mean annual temperature and a negative one with winter precipitation and mean annual precipitation. These results echo previous research on the relationship between climate and variation in plant photosynthetic pathway in central Argentina (Cabido et al., 2008), which find  $\text{C}_4$  photosynthesizing plants occurring more frequently in areas with summer dominant rainfall and high average temperatures. These are precisely the conditions which characterize the Monte Desert, and not surprisingly, these results mirror and confirm the geographic comparisons made earlier. Together they suggest the more positive camelid samples are reflecting the higher natural abundance of  $\text{C}_4$  vegetation, not necessarily a camelid diet based on maize. This highlights the need to control for natural contributions to  $^{13}\text{C}$  enrichment before evaluating the use of maize in the camelid diet (Dantas, 2012; Dantas

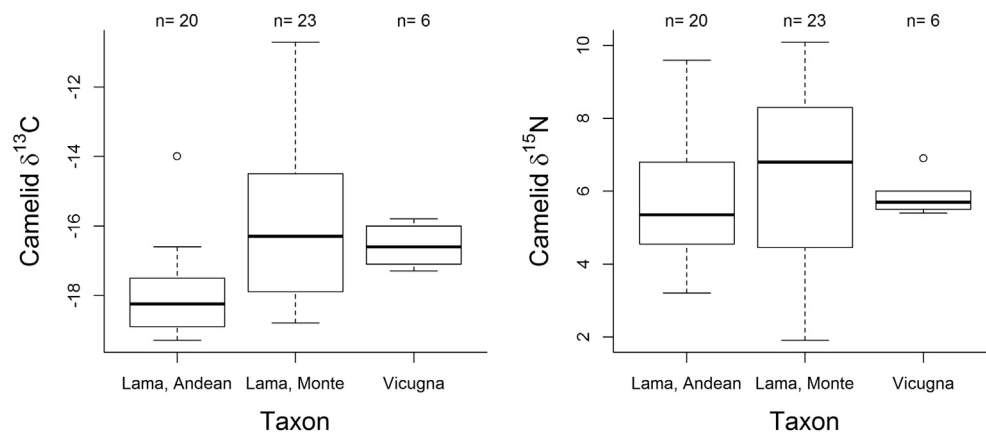


Fig. 4. Boxplot of camelid  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values by environmental zone, northern Central-western Argentina (30–33° SL).

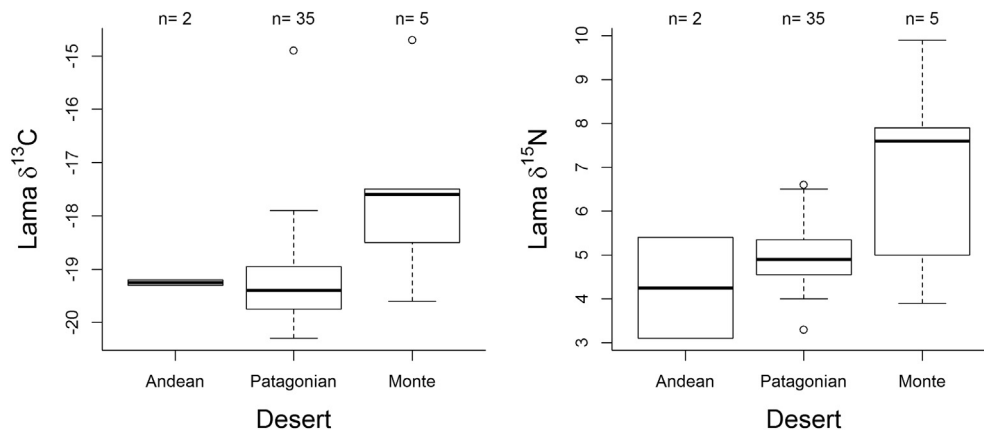


Fig. 5. Boxplot of camelid  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values by environmental zone, southern Central-western Argentina (below  $33^\circ\text{S}$ ).

et al., 2014).

In terms of  $\delta^{15}\text{N}$ , the results indicate that climatic variables serve as weak predictors of nitrogen variation, with a positive relationship between nitrogen values and mean annual temperature and summer (warmest quarter) precipitation and a negative one between nitrogen values and winter precipitation and annual temperature range. Various studies have recognized the influence of rainfall and other environmental factors on the  $\delta^{15}\text{N}$  values of animal tissues (e.g., Ambrose, 1991; Ambrose and DeNiro, 1986; Heaton et al., 1986; Sealy et al., 1987). The central west camelids did not show a strong correlation with precipitation, and climatic variables as a group can only explain 35% of the observed variation in nitrogen values. In this regard, the climatic models echo the analysis by biogeographic area, with substantial variability and no clear differences between deserts. Future studies need to explore other ecological and climate factors to improve our understanding of  $\delta^{15}\text{N}$  variability in mammalian diet and physiology (Amundson et al., 2003; Ugan and Coltrain, 2011).

5.3. Central-western, northwest and Pampa-Patagonia camelids: comparative in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$

The camelid data from central-western Argentina presented here greatly increase the amount of information available on isotopic variation among Andean camelids. The comparison of the

central-western camelid bone isotope data with that from other regions allows us to consider broader spatial patterns that are not visible locally. To do this, we compare our data with published reports throughout the Andes (Fernández et al., 1991; Yacobaccio et al., 2009, 2010; Samec et al., 2014; Mondini et al., 2010; Mengoni Goñalons, 2009; Laguens et al., 2009; Izeta et al., 2009; Tessone and Belardi, 2010; Barbererna et al., 2009; Tessone, 2010; Tessone et al., 2014). These include samples from both Patagonia and northwestern Argentina (NOA). These regions also contain various biogeographic subdivisions, but because not all studies provide detailed environmental information for individual samples, we limit ourselves to interregional comparisons (Patagonia, Central-western Argentina, and the NOA). We also limit ourselves to studies of lama and guanaco (*Lama* spp.) and exclude the vicuñas, which are restricted to the NOA and the northern part of Central-western Argentina.

An analysis of variance indicates clear differences among mean carbon and nitrogen values for the three regions ( $F_{\text{carb}} = 63.6$ ,  $F_{\text{nitro}} = 20.19$ ;  $p < .001$ ). A further comparison of differences by region indicate significant differences in all pairwise samples of carbon and nitrogen isotope values (Tukey's HSD,  $p < .001$  for all comparisons except Central-western and Patagonian nitrogen values;  $p_{\text{cw-p}} = .05$ ). Mean carbon values differ by more than one per mil ( $\delta^{13}\text{C}_{\text{pat}} = -18.9$ ,  $\delta^{13}\text{C}_{\text{c-w}} = -17.9$ ,  $\delta^{13}\text{C}_{\text{noa}} = -16.3$ ), and nitrogen values by half a mil or more ( $\delta^{15}\text{N}_{\text{pat}} = 6.2$ ,  $\delta^{15}\text{N}_{\text{c-w}} = 5.7$ ,

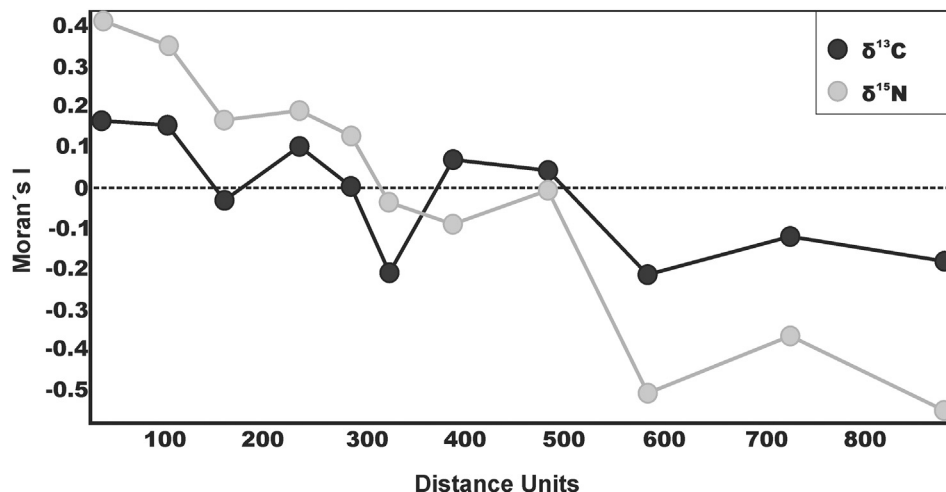


Fig. 6. The Moran's I correlograms showing the degree of spatial structure in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .

$\delta^{15}\text{N}_{\text{noa}} = 7.4$ ). Fig. 7 shows the distribution of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for the camelids from each region. As can be seen in the figure, the median  $\delta^{13}\text{C}$  values for samples from Patagonia and Central-western Argentina are actually very similar ( $-18.6$  and  $-18.5\text{‰}$ , respectively), though significantly different (Wilcoxon test  $W = 6505$ ,  $p = .007$ ). However the Patagonian samples are skewed more negatively and the Central-western samples more positively.

It is this difference which is pulling the means apart, and it reflects geographic patterning in the distribution of both  $\text{C}_4$  plants and the camelid samples. Latitudinal variation in precipitation and temperature (Bremond et al., 2012; Ehleringer et al., 1997; Domingo et al., 2012), are associated with a change in the frequency of  $\text{C}_3$  and  $\text{C}_4$  plant taxa (Cabido et al., 1997), with the latter increasing in frequency the farther north one goes. It is the increasing fraction of  $\text{C}_4$  plants at more northern latitudes that likely accounts for the higher average  $\delta^{13}\text{C}$  values of camelids (in this case *Lama* sp.) from those areas. Here the NOA clearly stands out. The bulk of the camelid samples from both Central-western Argentina and Patagonia come from the middle latitudes, with substantial overlap in  $\delta^{13}\text{C}$  values from camelids in those areas. At the same time, the majority of the very positive and negative values from those two areas (the tails in Fig. 7) come from the northern and southernmost samples.

Stable nitrogen values were analyzed in the same way as carbon, but while mean values differ by region, there is no latitudinal trend. Samples from the NOA are the most positive. The warm, arid northern Andes are where one would arguably expect to see more positive values owing to higher frequencies of saline areas, lower vegetation densities, and more open soil systems, all of which contribute to enriched  $\delta^{15}\text{N}$  values in soils, plants, and the herbivores. However these characteristics are not unique to the NOA, and it is not surprising that very positive nitrogen values are often found in other regions, including the much cooler areas of Patagonia. This is a case in which more detailed biogeographic information for each sample is needed, and represents an obvious direction for future research.

## 6. Final remarks

The paper shows how ecological, geographic and climatic variables can explain variation in camelid bone stable isotopes values, particularly spatial patterning in  $\delta^{13}\text{C}$ . Camelid carbon values exhibit a strong spatial pattern that reflects ecological differences between deserts that are themselves a reflection of geographic differences in temperature, precipitation, seasonality, and other climatic variables. The work here represents a first attempt to

describe isotope spatial patterns in Argentina and explore how climatic variables can influence in them. As the results show, there are strong trends in  $\delta^{13}\text{C}$  but much weaker or non-existent ones for  $\delta^{15}\text{N}$  in Central-western Argentina. Significantly, the research shows that similar trends in isotope variation hold over a broader spatial scale when northwestern Argentina and Patagonia are included in the analysis.

The study confirms the high variability underlying camelid bone isotope ratios and, as consequence, in its diet. As was previously proposed by Puig et al. (2014), the dietary generalism of camelids (mostly guanacos) appears as an adaptive mixture of diverse foraging strategies which confer an important survival advantage in the diverse, arid habitats that characterize their extensive range. In Central-western Argentina camelid  $\delta^{13}\text{C}$  ranges between  $-20.3\text{‰}$  and  $-10.7\text{‰}$ , with an average of  $-17.9\text{‰}$ . These values indicate a diet mostly based on  $\text{C}_3$  plants but with the presence of individuals for whom  $\text{C}_4$  plants were the dominant resource. These differences are associated with changes in plant distributions across the analyzed areas. Within Central-western Argentina, the camelids from Patagonian desert environments have isotope values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) that differ significantly from those guanacos inhabiting Monte and Andean deserts. Patagonian  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values tend to be lower, as was predicted. The very positive carbon values for the Andean samples comes as a surprise and cannot be explained in terms of local plants composition since the Andean community is almost entirely composed of  $\text{C}_3$  plants. We propose that this trend is driven in large part by the fact that almost the entire Andean sample, including the small set of vicuñas, comes from the northernmost part of the region, where Monte and Andean deserts directly abut. Elevated camelid  $\delta^{13}\text{C}$  values reflect seasonal movement between these two environments, at least on the part of the lamas (*Lama* sp. and *L. guanicoe*).

A significant amount of research in the archaeology of Central-western Argentina has been devoted to understanding farming and the significance of maize in the human diet (Gil et al., 2015). In this framework a number of studies have used stable isotopes to assess the significance of maize in human diets and have accepted a depleted value of  $-19\text{‰}$  to be characteristic of camelids when doing dietary reconstructions (Chiavazza et al., 2015; Gil et al., 2006, 2014). In these previous studies, the few enriched camelids bone samples were considered outliers and were not seriously included in the discussion. Here we see positive  $\delta^{13}\text{C}$  values can characterize camelids occur in all of the environments common to Central-western Argentina, and that in the Monte Desert mean values average almost  $3\text{‰}$  greater than previously assumed.

At the same time, these researches noted that human

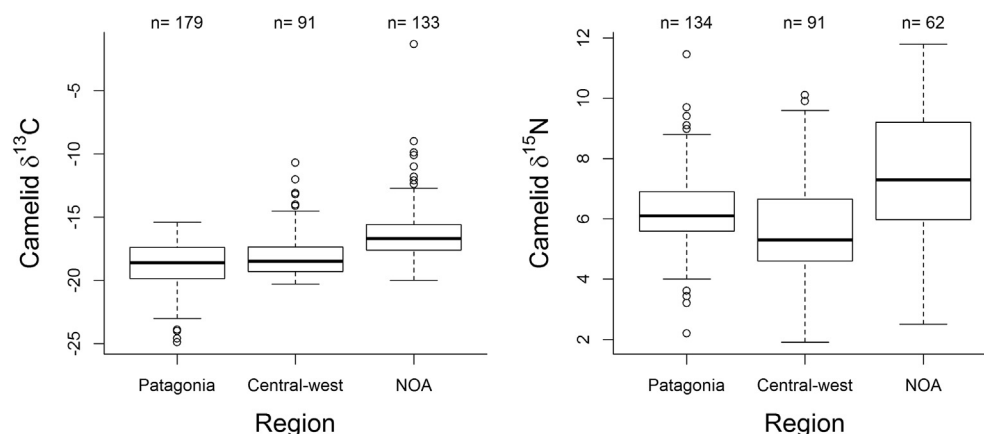


Fig. 7. Variation in camelid  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values comparing Patagonia, Central-western Argentina, and Northwest Argentina (NOA).

archaeological bone exhibited greater enrichment of collagen  $\delta^{13}\text{C}$  relative to apatite, contrary to what might be expected if maize (plant) consumption was driving the process. Such a collagen-apatite offset indicates that a protein was influencing the human dietary signal, resulting in a more positive total diet than the expected (Ambrose and Norr, 1993). These results indicate a need to consider the possible contribution of animals rather than plants to elevated human collagen  $\delta^{13}\text{C}$  values. Camelids are clearly one, though not the only, such potential animal, and a resource that needs to be understood in terms of its intra- and interregional isotopic variation in order to improve our understanding of past human diets.

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