



Stable isotope compositions of South American camelids in the Dry Puna of Argentina: A frame of reference for the study of prehistoric herding and hunting strategies

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ABSTRACT

The prehistoric pastoralist groups that inhabited the Dry Puna of Argentina employed a combination of subsistence strategies that included the herding of domestic South American camelids and the hunting of wild ones since ca. 3500 years BP. The relative importance of both subsistence strategies to the prehistoric economy of these groups can be established through traditional zooarchaeological techniques, although how exactly herding and hunting practices developed and interacted both in space and time remains unknown. The general purpose of this work is to provide a tool to explore these questions through stable isotope analyses of animal tissues.

We measured bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of modern *llamas* and *vicuñas*, with the aim to account for the variation in the isotopic compositions of domesticated and wild South American camelids from the Dry Puna of Argentina in order to develop an appropriate frame of reference to address archaeofaunal and paleodietary data. Both $\delta^{13}\text{C}$ ($n = 140$, mean = -18.4‰) and $\delta^{15}\text{N}$ ($n = 109$, mean = $+6.3\text{‰}$) values showed a negative and significant correlation with altitude for *llamas* and *vicuñas*, which can be explained by the variation identified in plant $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and their correlation with altitude, as discussed in previous investigations. Based on these results we elaborated linear regressions models for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of both species, which will allow us to predict expected $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for archaeofaunal materials recovered at archaeological sites using altitude as the explanatory variable.

1. Introduction

One of the main characteristics of highland pastoralism is that it makes use of resources that are heterogeneous in space and time (Genin, 1995). In this sense, most of the contemporary pastoralist groups that inhabit the Andean highlands employ traditional herding strategies that often involve the use of different pastures located in different altitudinal ranges at different moments of the annual cycle. Particularly in the Dry Puna of Argentina, contemporary pastoralist groups maintain various herds and combine the exploitation of several animal species, such as domestic South American camelids (SAC) (*llamas*) and caprines (sheep and goats) (Yacobaccio, 2007). In contrast, the prehistoric pastoralist groups of the same area employed a combination of subsistence strategies that included not only the maintenance and culling of domestic SAC, but also the hunting of wild ones (*vicuñas* and *guanacos*), since ca. 3500 years BP (Mengoni Goñalons and Yacobaccio, 2006). The relative importance of both subsistence strategies to the prehistoric economy of Dry Puna pastoralist groups can be established through traditional zooarchaeological

techniques (Cartajena et al., 2007; Olivera and Grant, 2009), although how exactly herding and hunting practices developed and interacted both in space and time remains unknown. The general aim of this work is to provide a new tool to explore these questions through stable isotope analyses of animal tissues.

Recently, several studies have explored the potential of stable isotope analyses to investigate prehistoric herding strategies in various parts of the globe (Balasse et al., 2002; Britton et al., 2008; Towers et al., 2011; among many others). In this sense, stable isotope analyses of animal tissues represent a new approach to investigate how human groups exploited and managed animals in the past, allowing us to address issues such as mobility and foddering, which usually escape the scope of traditional zooarchaeological techniques applied to the study of archaeofaunal remains (Balasse et al., 2002; Finucane et al., 2006; Makarewicz and Tuross, 2006; Stevens et al., 2013). Many of these studies employ modern isotopic data as a comparison material to explore variation in archaeofaunal isotopic data (Thornton et al., 2011) and to posit models to test archaeological hypotheses (Balasse and

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Ambrose, 2005). So far, these methods have been applied mostly to the study of domesticated species, but are also useful to study seasonal habitat use, dietary habits, movements and physiology of wild animals also exploited by human groups (Drucker et al., 2012). These are key aspects to deal with palaeoclimatic, palaeoenvironmental and palaeobiological questions but also provide the means to study the hunting strategies employed by human populations in the past (Hartman et al., 2015; Hoppe, 2004).

The main purpose of our work is to account for the variation in the isotopic composition of modern domesticated and wild SAC from the Dry Puna of Argentina and to develop an appropriate frame of reference to address archaeofaunal and paleodietary data. We measured carbon and nitrogen stable isotope compositions on bone material of domestic SAC managed by pastoralists employing traditional herding strategies and wild SAC from previously studied populations, following the lead of previous research performed in the area (Fernández et al., 1991; Fernández and Panarello, 1999-2001a, 1999-2001b; Samec, 2012, 2014; Yacobaccio et al., 2009, 2010). It is important to mention that the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values presented here were measured on bone collagen, a protein potentially resistant to diagenetic alteration, with the future perspective of using these results in order to interpret isotopic compositions measured on archaeological bones (Bocherens et al., 1996).

As a first step towards the development of an isotopic ecology for the Dry Puna of Argentina, the results discussed here have enormous implications in the investigation of prehistoric herding and hunting strategies, human dietary reconstructions and palaeoenvironmental reconstructions through stable isotope analyses. In this sense, the development of studies that address the variation in the isotopic compositions of plants and animals is one of the main concerns among most users of stable isotope analyses in disciplines like archaeology and paleoecology.

2. The study area: the Dry Puna of Argentina

The Puna of Argentina is located between 22° and 25° S and between 3000 and 5000 masl. This region is a highland desert that contains several NE-SW oriented mountain ranges. It is characterized by wide temperature variation between day and night, high solar radiation and low atmospheric pressure due to altitude. Primary productivity is concentrated on stable hydrological systems such as primary basins, high ravines and wetlands. The only sources of freshwater are a few rivers and several springs scattered throughout the landscape. Precipitation occurs during summertime, governed by the South American monsoon system (Zhou and Lau, 1998). This system produces about 80% of the annual rainfalls between December and February (Vuille and Keimig, 2004). At the same time, precipitation exhibits a NE-SW gradient that delimits two sub-regions within the Dry Puna of Argentina: the north eastern sector with a mean annual precipitation of 300 mm/year; and the south western sector with a mean annual precipitation that barely reach 100 mm/year (Bianchi et al., 2005; Baldassini et al., 2012).

Four main vegetational communities have been identified in the Dry Puna (Cabrera, 1976; Ruthsatz and Movia, 1975; Samec et al., 2017):

1. Shrub steppe (*tolar*) is located between 3500 and 3900 masl. It is dominated by species like *Parastrephia lepidophylla* and *Fabiana densa*, and exhibits a low proportion of herbs (5%). It includes mainly C_3 (shrubs and grasses) and some C_4 (mostly grasses) plant species.
2. Grass steppe (*pajonal*) is located between 4100 and 4700 masl. It is dominated by *Festuca* spp. and other grasses, like *Poa* spp. and *Stipa* spp. It includes predominantly C_3 plant species.
3. Wetlands (*vegas*) are scattered along the landscape between 3500 and 4700 masl. These are restricted patches with high plant cover all year round, mainly composed of hygrophilous grasses such as *Deyeuxia* spp. and *Muhlenbergia* spp. These plant communities

include mainly C_3 plant species.

4. Mixed steppes are located between 3900 and 4100 masl. These ecotonal landscapes are composed of grasses and shrubs in which mainly C_3 plant species are represented.

3. South American camelids

South American camelids (SAC) are classified into two genera (*Vicugna* and *Lama*) based on their physical appearance and mtDNA sequence data (Wheeler, 1995). Four species are recognized: two wild, the *vicuña* (*V. vicugna*) and the *guanaco* (*L. guanicoe*), and two domesticated, the *llama* (*L. glama*) and the *alpaca* (*L. pacos* or *V. pacos*) (Wheeler, 1995). The origins of SAC domestication and the development of indigenous herding practices are restricted to the Andes, particularly the Central and South-Central portion, since ca. 5000 years BP (Yacobaccio and Vilá, 2016). During prehistoric times, domesticated SAC were herded to obtain both primary and secondary products such as meat, hide, fiber and dung, and in the case of the *llama* they were also used as beasts of burden (Mengoni Goñalons and Yacobaccio, 2006). On the other hand, wild SAC were hunted by pastoralist groups to obtain meat supplies, acting as a buffer in periods of shortage, and to use their fiber and hide to make clothes (Yacobaccio, 2009).

The *llama* is the only domesticated SAC that is currently herded in the Dry Puna of Argentina, whereas the *alpaca* is practically absent in the area today as it was in the past given its almost complete absence in the archaeological record of the area (Mengoni Goñalons and Yacobaccio, 2006). At the same time, the *vicuña* and the *guanaco* are the two species of wild SAC that currently inhabit within the Dry Puna of Argentina. The *vicuña* is well distributed within the area, whereas the *guanaco* is present only in small patches along the landscape, an aspect that makes extremely difficult to obtain modern tissue samples. For these reasons, we will focus on *llamas* and *vicuñas*, the most important SAC species in the area both in the present and the past (Fig. 1).

3.1. Traditional herding strategies employed by llama herders

The human groups that currently inhabit the Dry Puna of Argentina base their subsistence on the herding of domestic animals. In this area, livestock is mainly composed of *llamas*, sheep and goats, being these last ones introduced since the Spanish conquest in the XVIth Century (Yacobaccio et al., 1998). *Llama* breeding is mostly oriented towards the production of fiber and meat, whereas sheep are used to obtain wool and meat, and goats are used to obtain meat and milk in good years (Yacobaccio, 2007). Herds feed on natural pastures, only



Fig. 1. A *vicuña* and two *llamas* feeding together in a wetland near the town of Santa Catalina (Jujuy Province, Argentina, 3770 masl) (Photo: Yanina Arzamendia).

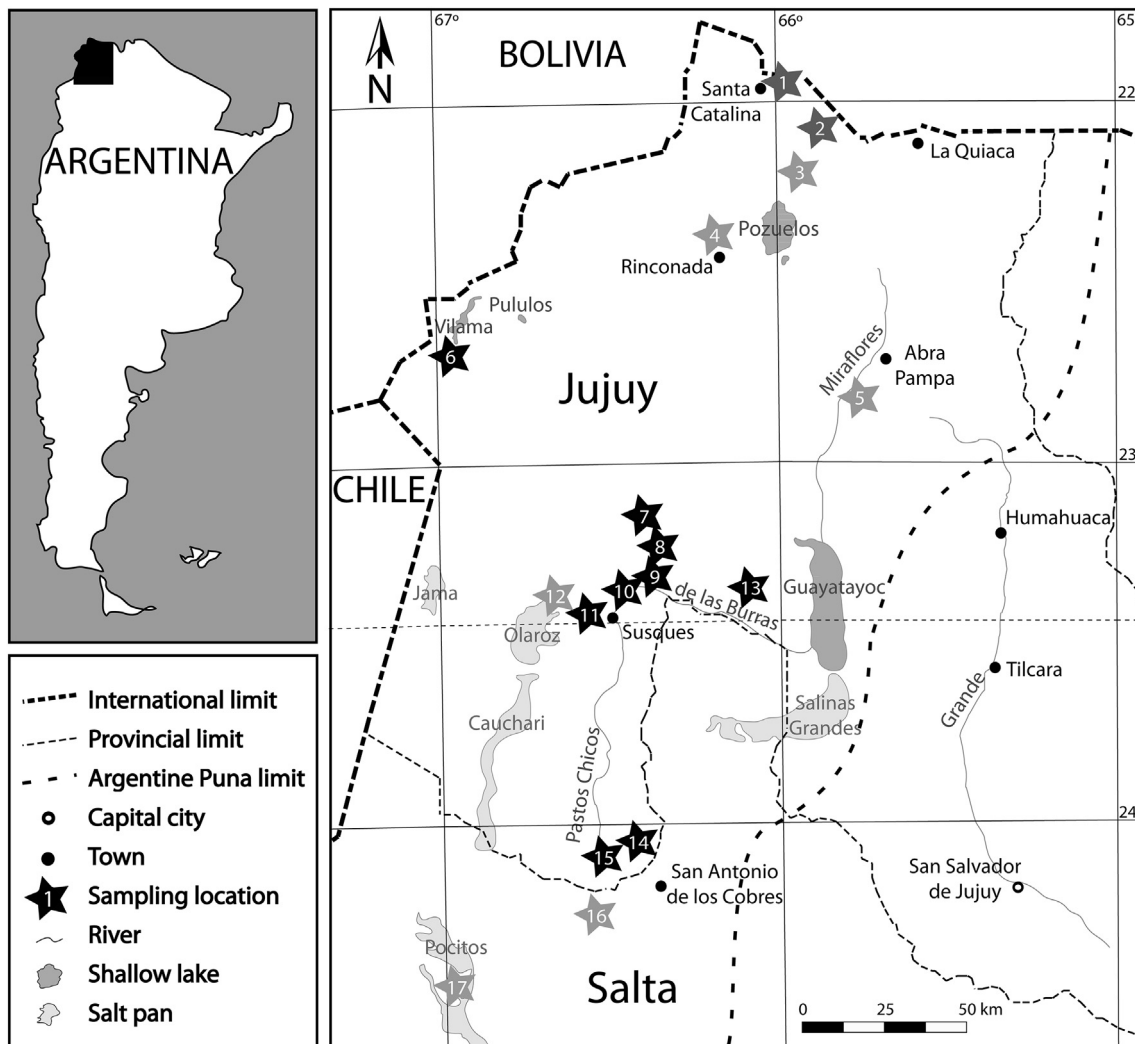


Fig. 2. Map showing the location of the sampling sites comprised within this study, where *llama* (black stars), *vicuña* (light grey stars) or both species (dark grey stars) bones were collected. Sampling locations: 1. Santa Catalina, 2. Cieneguillas, 3. Pasajes, 4. San José, 5. Abra Pampa, 6. Vilama, 7. Agua Chica, 8. Punta de la Pista, 9. Estancia, 10. Lapao, 11. Taire, 12. Olaroz, 13. Barrancas, 14. Tres Pozos, 15. Tuzgle, 16. Tocomar, 17. Pocitos.

occasionally caprines are foddered, whereas *llamas* are not, because South American camelids are more adapted to pasture shortage (Göbel, 2001).

The temporal availability and spatial separation of pasture lands is managed by mobilizing herds and people (Yacobaccio, 2007). As a consequence of this mobility strategy the settlement pattern is disperse over the landscape, comprising sites that are not homogeneously employed during the annual cycle (Yacobaccio et al., 1998). Two types of settlements can be distinguished: residential bases (*casas*) and temporary sites (*estancias*) (Yacobaccio, 2007). Particularly in the Susques area, herders and their animals stay at the residential base for more than eight months a year, making use of the pastures that grow in the vicinity of the settlement (Yacobaccio et al., 1998). In contrast, a part of the family group and their animals occupy temporary sites for two to three months during the winter, herding their llamas at the different plant communities located near these sites (Caracotche, 2001). In this sense, the use of these different settlements follows a seasonal pattern and determines the access to different kinds of vegetation to be included in the diet of the herds (Yacobaccio and Madero, 2001).

It is important to mention that this transhumant land use system involving different pasture lands has prevailed for thousands of years in the Dry Puna, as shown by the distribution of archaeological sites and the characteristics of the archaeological record of the area (Yacobaccio et al., 1998). Nowadays herding is the main economic activity since

agriculture is almost nonexistent or only practiced at a very small scale due to unsuitable climatic conditions and high environmental unpredictability (Yacobaccio, 2007).

3.2. Foraging and territorial behavior of *vicuñas*

Vicuñas are wild SAC adapted to live in desert and semi-desert environments (Franklin, 1982; Koford, 1957). Water location operates as a limiting factor for the distribution of the species since *vicuñas* are obligate drinkers (i.e. they must drink water every day) (Franklin, 1982; Vilá, 2000). Studies performed at several areas of the Andes have shown that *vicuñas* spend more time in habitats associated to permanent water sources with high overall plant cover dominated by grasses (*pajonales* and *vegas*) than in habitats with low cover dominated by shrubs (*tolares*) (Arzamendia et al., 2006; Franklin, 1982). Initially, the species had been classified as a strict grazer, as it feeds preferably on grasses (Franklin, 1982; Koford, 1957), exhibiting great efficiency for processing C₄ plants (Borgnia et al., 2010). Nevertheless, some authors have found that it also feeds on variable proportions of shrubs in steppe habitats, thus considering the species as a generalist herbivore with a strong selectivity towards grasses (Benítez et al., 2006; Borgnia et al., 2010). In this sense, Benítez and coauthors (2006) have found that *vicuñas* can eat shrub vegetation at the end of the rainy season in order to obtain specific proteins when these plant communities offer better

Table 1
SAC bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values statistics according to species and altitude.

Species	Altitude masl	Number of specimens sampled ^a	Mean $\delta^{13}\text{C}$ (‰)	Median $\delta^{13}\text{C}$ (‰)	Range $\delta^{13}\text{C}$ (‰)	SD $\delta^{13}\text{C}$ (‰)	Variance $\delta^{13}\text{C}$ (‰)	Mean $\delta^{15}\text{N}$ (‰)	Median $\delta^{15}\text{N}$ (‰)	Range $\delta^{15}\text{N}$ (‰)	SD $\delta^{15}\text{N}$ (‰)	Variance $\delta^{15}\text{N}$ (‰)
<i>Llamas</i>	(3550–4700)	72 (54)	−18.5	−18.4	−23.5 to −13.8	1.62	2.63	+6.8	+7.2	+2.1 to +9.7	1.60	2.56
<i>Vicuñas</i>	(3480–4500)	68 (55)	−18.4	−18.7	−20.6 to −14.6	1.46	2.13	+5.8	+5.7	+2.2 to +11.3	2.01	4.01
Total both species	(3480–4700)	140 (109)	−18.4	−18.5	−23.5 to −13.8	1.54	2.37	+6.3	+6.5	+2.1 to +11.3	1.89	3.57

^a Number of SAC specimens measured for $\delta^{13}\text{C}$ (including the ones published by Fernández et al., 1991; Fernández and Panarello, 1999–2001a; Samec, 2012, 2014; Yacobaccio et al., 2009, 2010) and number of SAC specimens measured for $\delta^{15}\text{N}$ between parentheses.

quality forage than the *vegas*. In this sense and despite its dependence on water resources and territorial behavior, *vicuñas* can feed on different plant communities on a seasonal basis employing specific habitats such as shrublands at specific moments of the year (Benítez et al., 2006).

The *vicuña* presents a stable social structure with territorial and non-territorial animals. Family groups are composed of one male, three or four females and two offspring and remain territorial throughout the year (Vilá, 2000). On the other hand, non-territorial animals are represented by bachelor groups, composed of calves that are expelled of the family group during the new birth season, and males without an established territory (Franklin, 1982; Koford, 1957).

4. Materials and methods

4.1. Skeletal samples

The SAC remains analyzed in this study were collected in the Dry Puna of Argentina between the years 1989–1995 and 2006–2013. In the case of *llamas*, the bones were recovered from the discard areas of eleven pastoral settlements located at different altitudes between 3600 and 4700 masl (Fig. 2). It is important to mention these pastoral settlements were mainly residential bases, where most of the culling activities take place and where the herds feed most of the year (Yacobaccio et al., 1998). In the case of *vicuñas*, the bones were recovered along the field at eight different sampling sites located between 3480 and 4400 masl (Fig. 2). In this case it is important to mention that these sampling sites were located within the territories of previously studied populations of *vicuñas* in most of the cases (Arzamendia and Vilá, 2006; Arzamendia et al., 2006). When it was possible only adult skeletal remains were selected (age-at-death was determined by dental eruption and wear in the case of skulls and by fusion in the case of long bones) in order to avoid $\delta^{13}\text{C}$ and mostly $\delta^{15}\text{N}$ values affected by a residual “suckling effect” (Balasse et al., 2002; Britton et al., 2008).

4.2. Bone collagen extraction

All bone samples were prepared following the collagen extraction method developed by Tykot (2004). A 1g chunk of compact tissue preferentially from midshaft sections of skeletal elements was removed for each sample. These bone samples were physically cleaned with a Dremel® tool and sonicated in deionized water to remove visible dirt and debris and then air dried. The next step involved the elimination of humic acids with sodium hydroxide at 0.1 M dilution for 24 h before and after the demineralization. For the collagen extraction itself, the bone was demineralized in 2% hydrochloric acid for 72 h.

4.3. Mass spectrometry

Measurements of each sample $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were made on a CarloErba Elemental Analyzer (CHONS) coupled to a Finnigan MAT

Delta V continuous-flow isotope ratio mass spectrometer (CF-IRMS) through a Thermo ConFlo IV interface using internal standards calibrated against VPDB and AIR reference standards for carbon and nitrogen (Coplen et al., 1992; Craig, 1957). Replicates of internal standards showed analytical errors (SD) to be on the order of ± 0.2 ‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

5. Results

We present 66 new $\delta^{13}\text{C}$ values measured on bone collagen of *llamas* ($n = 28$) and *vicuñas* ($n = 38$) from the Dry Puna of Argentina, which add to the 74 values already published for the two species (see Fernández et al., 1991; Fernández and Panarello, 1999–2001a; Samec, 2012, 2014; Yacobaccio et al., 2009, 2010). Thus, the isotopic values considered here make for a total of 140 $\delta^{13}\text{C}$ values of *llamas* ($n = 72$) and *vicuñas* ($n = 68$) for the area. At the same time, our study presents 83 new $\delta^{15}\text{N}$ values measured on modern *llamas* ($n = 28$) and *vicuñas* ($n = 55$), which add to the 26 values already published for the first species within the study area (see Samec, 2014). All reported samples fell within the acceptable range of atomic C:N values (2.9–3.6) and ranges for ‰C (22.6–47) and ‰N (8–17.3) as expected for well-preserved and uncontaminated modern bone collagen (Ambrose, 1990; DeNiro, 1985) (Supplementary Table 1).

The $\delta^{13}\text{C}$ values for the two species ($n = 140$) range from -23.5 ‰ to -13.8 ‰ with a mean value of -18.4 ‰ and a normal distribution (Shapiro-Wilk Test $W = 0.98$; $p = 0.14$). The $\delta^{15}\text{N}$ values ($n = 109$) range from $+2.1$ ‰ to $+11.3$ ‰ with a mean value of $+6.3$ ‰ and a normal distribution (Shapiro-Wilk Test $W = 0.99$; $p = 0.48$) (Table 1, Fig. 3).

Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the two species present a negative correlation with altitude ($r = -0.69$ $p = 8.17E^{-21}$ for $\delta^{13}\text{C}$ values and $r = -0.69$ $p = 1.62E^{-16}$ for $\delta^{15}\text{N}$ values). This correlation between altitude and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values is also strong when considering both

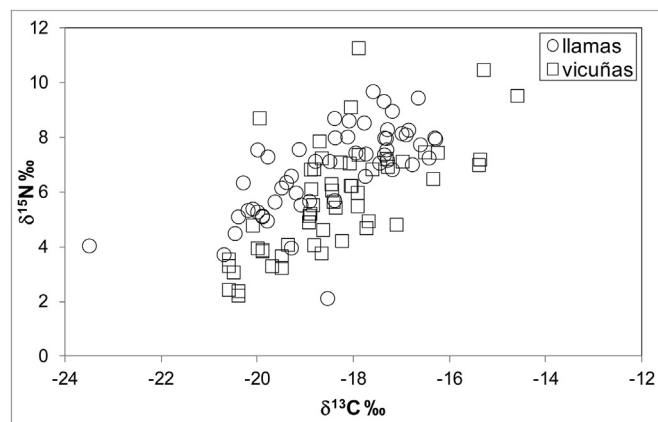


Fig. 3. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *llamas* ($n = 54$) and *vicuñas* ($n = 55$).

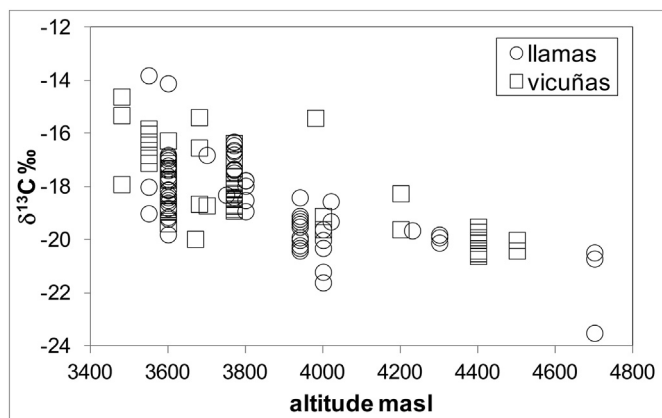


Fig. 4. $\delta^{13}\text{C}$ values of llamas ($n = 72$) and vicuñas ($n = 68$) according to altitude (masl).

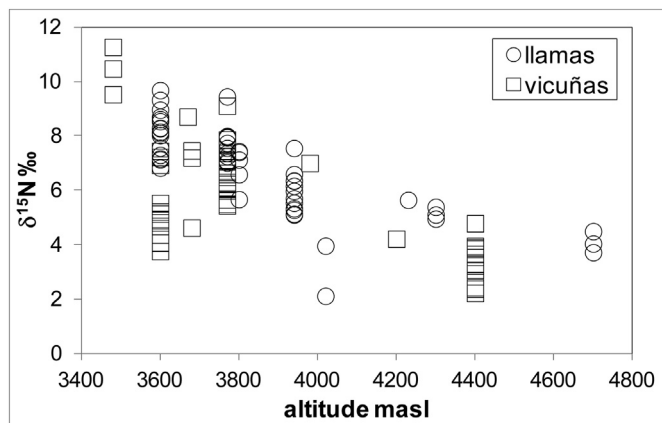


Fig. 5. $\delta^{15}\text{N}$ values of llamas ($n = 54$) and vicuñas ($n = 55$) according to altitude (masl).

species separately ($r = -0.68$ $p = 5.15\text{E}^{-11}$ for llamas $\delta^{13}\text{C}$ values and $r = -0.79$ $p = 1.15\text{E}^{-11}$ for llamas $\delta^{15}\text{N}$ values; $r = -0.72$ $p = 6.81\text{E}^{-12}$ for vicuñas $\delta^{13}\text{C}$ values and $r = -0.68$ $p = 1.48\text{E}^{-08}$ for vicuñas $\delta^{15}\text{N}$ values) as can be seen in Figs. 4 and 5.

Llamas $\delta^{13}\text{C}$ values range between -23.5 ‰ and -13.8 ‰ with a mean of -18.5 ‰ and a SD of 1.62 ‰, exhibiting a normal distribution (Shapiro-Wilk Test $W = 0.97$ $p = 0.14$). Vicuñas $\delta^{13}\text{C}$ values range between -20.6 ‰ and -14.6 ‰ with a mean of -18.4 ‰ and a SD of 1.58 ‰, but do not exhibit a normal distribution (Shapiro-Wilk Test $W = 0.96$ $p = 0.03$) (Table 1). Llamas $\delta^{15}\text{N}$ values range between $+2.1$ ‰ and $+9.7$ ‰ with a mean of $+6.8$ ‰ and a SD of 1.60 ‰, exhibiting a normal distribution (Shapiro-Wilk Test $W = 0.97$ $p = 0.13$). Vicuñas $\delta^{15}\text{N}$ values range between $+2.2$ ‰ and $+11.3$ ‰ with a mean of

$+5.8$ ‰ and a SD of 2.01 ‰, exhibiting a normal distribution (Shapiro-Wilk Test $W = 0.97$ $p = 0.23$) (Table 1).

Both species present similar $\delta^{13}\text{C}$ values exhibiting no statistically significant differences (Mann-Whitney Test $U = 2441.5$, $z = -0.03$, $p = 0.98$) although llamas present greater variation. In opposition, both species present different $\delta^{15}\text{N}$ values exhibiting significant differences (Mann-Whitney Test $U = 922$, $z = -3.41$, $p = 0.001$) given that llamas present higher values, although in this case vicuñas present greater variation (see Fig. 6 and Supplementary Table 1).

To evaluate the influence of both altitude and taxonomy in the patterning of our results we divided the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of both species into two groups: below and above 3900 masl. The 3900 masl threshold was selected according to the characteristics of the vegetational communities and their differences in the relative abundances of C_3 and C_4 plant species (Samec et al., 2017). The $\delta^{13}\text{C}$ values present differences according to altitude regardless of taxonomy (Kruskal Wallis Test $H = 78.14$ $p = 7.63\text{E}^{-17}$) given that llamas and vicuñas from the same altitudinal range present similar values in spite of the presence of some outliers. No statistically significant differences are found between llamas and vicuñas from the same altitudinal range (Mann Whitney Test: llamas and vicuñas < 3900 $U = 881$ $p = 0.22$, llamas and vicuñas > 3900 $U = 283.5$ $p = 0.79$) although significant differences are found when comparing llamas and vicuñas from different altitudinal ranges (Mann Whitney Test: llamas < 3900 and > 3900 $U = 27$ $p = 1.51\text{E}^{-11}$, vicuñas < 3900 and > 3900 $U = 75$ $p = 1.66\text{E}^{-08}$). On the other hand, the $\delta^{15}\text{N}$ values present differences related to both altitude and taxonomy (Kruskal Wallis Test $H = 61.71$ $p = 2.54\text{E}^{-13}$) given that llamas $\delta^{15}\text{N}$ values are higher than those of vicuñas inhabiting the same altitudinal range. Statistically significant differences are present between llamas and vicuñas from the same altitudinal range (Mann Whitney Test: llamas and vicuñas < 3900 $U = 267$ $p = 1.36\text{E}^{-05}$, llamas and vicuñas > 3900 $U = 44$ $p = 0.0003$). These same differences are present when a comparison between the same species at different altitudinal range is performed (Mann Whitney Test: llamas < 3900 and > 3900 $U = 20$ $p = 7.28\text{E}^{-09}$; vicuñas < 3900 and > 3900 $U = 36$ $p = 6.37\text{E}^{-07}$).

6. Discussion

Our results show that bone collagen $\delta^{13}\text{C}$ values measured on llamas and vicuñas from the Dry Puna of Argentina exhibit a significant correlation with altitude, as expected from previous results carried out within the study area (Fernández et al., 1991; Fernández and Panarello, 1999-2001a; Samec, 2012, 2014; Yacobaccio et al., 2009, 2010). At the same time, our results show that bone collagen $\delta^{15}\text{N}$ values of these two SAC species also present a significant correlation with altitude, as expected from previous results carried out within the study area and other regions of the Andes (Thornton et al., 2011; Dufour et al., 2014; Szpak

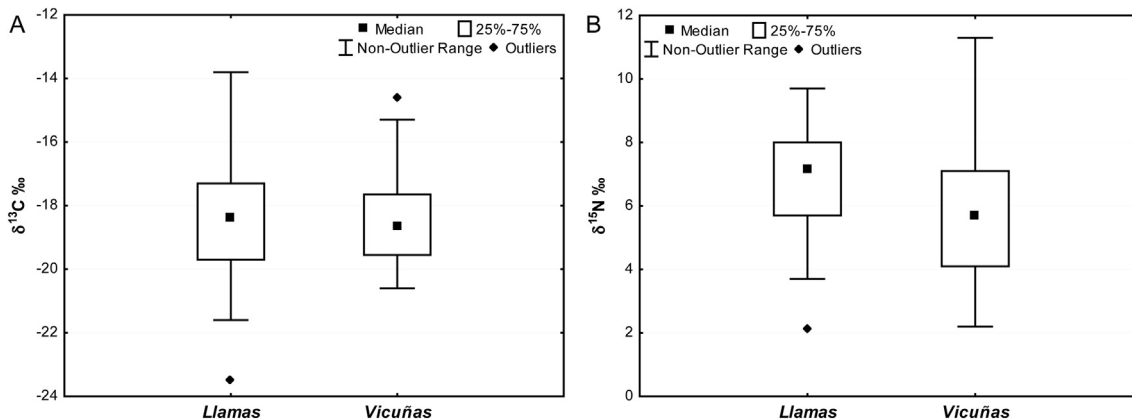


Fig. 6. A) $\delta^{13}\text{C}$ values of llamas ($n = 72$) and vicuñas ($n = 68$) and B) $\delta^{15}\text{N}$ values of llamas ($n = 54$) and vicuñas ($n = 55$).

et al., 2014; Samec, 2014).

Previous studies have established that carbon isotope composition of bone collagen in herbivorous ungulates is controlled by two main factors: the distribution of C₃ and C₄ plants and their relative abundances according to environmental factors such as temperature and precipitation, and the selective feeding habits particular to the species considered (Koch et al., 1994; Stevens et al., 2006; Cerling et al., 2003; among others). These two main aspects affect C₃ and C₄ plants proportions included in herbivorous diets, which are reflected in the $\delta^{13}\text{C}$ values measured on these animals bone collagen (Bocherens et al., 1996; Bocherens, 2000).

Considering the first aspect, several studies have found that the distribution of C₃ and C₄ plants is affected by altitudinal variation, according to its effects on temperature, water availability and irradiance (Cavagnaro, 1988; Llano, 2009; Tieszen et al., 1979; Tieszen and Chapman, 1992). These studies demonstrate that C₄ plants are mostly present at lower elevations due to increased temperature and water stress, and practically disappear above a certain threshold (between 3000 and 4000 masl depending on the specific area considered) where these conditions are no longer found (Tieszen et al., 1979). In this sense, the llamas and vicuñas bone collagen $\delta^{13}\text{C}$ values presented here indirectly reflect the manifestation of a differential distribution of C₃ and C₄ plants according to variation in temperature and water stress. The higher $\delta^{13}\text{C}$ values of the SAC sampled at lower altitudes indicate the intake of a mixed diet composed of C₃ and C₄ plants in variable proportions, since both photosynthetic pathways are present below 3900 masl. In contrast, the lower $\delta^{13}\text{C}$ values of the SAC sampled at higher altitudes indicate the intake of a diet with a higher proportion of C₃ plants, since C₄ plants presence notably diminishes above the 3900 masl threshold (Samec, 2014; Samec et al., 2017). These results are in line with previous studies that presented a strong negative correlation between altitude and bone collagen $\delta^{13}\text{C}$ values of both wild and domesticated SAC in relation to variations in C₃ and C₄ plants distribution at the Dry Puna of Argentina (Fernández and Panarello, 1999-2001a; Samec, 2012, 2014; Yacobaccio et al., 2009, 2010). It is important to mention that even though some $\delta^{13}\text{C}$ values measured in llama bone collagen are relatively high (as -13.8‰ and -14.1‰) and point to a diet that included a considerable amount of C₄ plants (near 50%), we can easily discard maize foddering for these herds, being no record of these practices within the area nowadays. In fact, these results can be easily explained by the herding of these llamas within certain areas where C₄ plants are dominant, such as isolated grasslands covered by *Muhlenbergia fastigiata* and *Bouteloua simplex* located in the NE corner of the study area, as explained by Fernández and Panarello (1999-2001a).

Considering the second aspect mentioned above, no significant differences were found between the $\delta^{13}\text{C}$ values of both llamas and vicuñas. The distribution of both species $\delta^{13}\text{C}$ values overlap, even considering that llamas show a higher variation and comprise the most negative values. The absence of such a difference is again evident when we compare both species at the different altitudinal ranges considered (below and above 3900 masl). Based in our previous work we expected to find a significant difference between llamas and vicuñas feeding below 3900 masl (Samec, 2012), however our new results obscured such a difference showing that both species can consume equally and non-preferentially C₃ and C₄ plants, according to its relative abundances at the area where they fed. The absence of a significant difference between llamas and vicuñas is related to the fact that they can share the habitats sampled without developing any forcible displacements or agonistic interactions (Arzamendia and Vilá, 2015).

On the other hand, several authors have established that variations in the $\delta^{15}\text{N}$ values measured on bone collagen extracted from herbivorous animals can be related to spatial differences in local environments and particularly to the influence of variables like temperature and water availability on soil and plants $\delta^{15}\text{N}$ values (Ambrose, 1991; Hartman, 2011; Towers et al., 2011). These aspects will affect the

nitrogen stable isotope composition of the diet, which is reflected in the enriched $\delta^{15}\text{N}$ values measured on bone collagen as a consequence of the fractionation produced from plant to consumer tissues during incorporation (Schoeninger and DeNiro, 1984; Bocherens, 2000).

Previous reports have established that $\delta^{15}\text{N}$ values of plants can be influenced by environmental and physiological factors including climate, soil type, water and nitrogen availability, salinity, root depth and age, among others (Amundson et al., 2003; Austin and Vitousek, 1998; Virginia and Delwiche, 1982; among many others). Overall, the $\delta^{15}\text{N}$ values of terrestrial plants exhibit a range from -5 to $+20\text{‰}$, in which the highest values are found in arid and saline environments, whereas the lowest ones are found in wetter environments with increased rainfall and elevation (Ambrose, 1991; Virginia and Delwiche, 1982). Several studies have found a strong negative correlation between rainfall and $\delta^{15}\text{N}$ values measured on soils (Amundson et al., 2003; Austin and Vitousek, 1998) and plants (Heaton, 1987; Swap et al., 2004; among others). Moreover, a negative correlation has also been found between rainfall and herbivore bone collagen $\delta^{15}\text{N}$ values (Murphy and Bowman, 2006; Sealy et al., 1987; among many others). Initially some authors have proposed that physiological mechanisms to cope with water stress could explain the high $\delta^{15}\text{N}$ values measured on animal tissues in arid environments (see Ambrose, 1991 for details on the models suggested by: Schoeninger and DeNiro, 1984; Sealy et al., 1987). Nevertheless, the results of both experimental and field research provide support to reject physiological explanations in favor of those that emphasize diet as the main cause of variation in nitrogen isotope composition, explaining the higher $\delta^{15}\text{N}$ values in animal tissues as a result of higher $\delta^{15}\text{N}$ values in soils and plants (Ambrose, 2000; Hartman, 2011; Murphy and Bowman, 2006). In this sense, variation in the $\delta^{15}\text{N}$ values within a food web and its correlation with water availability can be related to the different nitrogenous compounds available in the soil and the relative openness of the nitrogen cycle (open systems with preferential loss of ^{14}N versus closed systems with very limited loss of ^{14}N) (see Amundson et al., 2003; Austin and Vitousek, 1998 for details). These correlations are relevant in highland ecosystems since humidity rises along the altitudinal gradient making expectable to find lower $\delta^{15}\text{N}$ values measured on plants and herbivores from high altitude locations, as shown by our results (Samec et al., 2017). Thus, the correlation between altitude and SAC $\delta^{15}\text{N}$ values exhibited by our results can be explained considering the influence of variables such as humidity and temperature, which vary with altitude, in the mean $\delta^{15}\text{N}$ values of the plants consumed.

On the other hand, llama $\delta^{15}\text{N}$ values are higher compared to vicuña ones in both altitudinal ranges considered here (below and above 3900 masl). These differences respond to altitude, given that vicuñas below and above 3900 masl and also llamas below and above 3900 masl present significant differences, but also to taxonomy, given that significant differences are also present when species inhabiting at the same altitudinal range are compared. We believe that this pattern has several potential explanations that no necessarily are mutually-exclusive. In the first place, the difference identified in the $\delta^{15}\text{N}$ values of llamas and vicuñas can be related to an uneven distribution of sampling locations of both species since vicuña specimens were predominantly sampled in the NE corner of our study area where mean annual precipitation reaches 200 mm whereas llama specimens were mainly sampled on the SW corner of this area where mean annual precipitation is around 100 mm (based on World Clim data) (see Fig. 2). Another possible explanation is that even in those cases were llamas and vicuñas are feeding on the same vegetational patches, both species are consuming different plant forms and species with different mean $\delta^{15}\text{N}$ values (Arzamendia and Vilá, 2015). In any case further research is needed in order to establish a more thoroughly understanding of this variation.

Finally, taking into consideration the results exposed in the previous section and in order to develop a tool that could become useful for the interpretation of carbon and nitrogen stable isotopes measured in archaeofaunal materials, we decided to elaborate four lineal regression

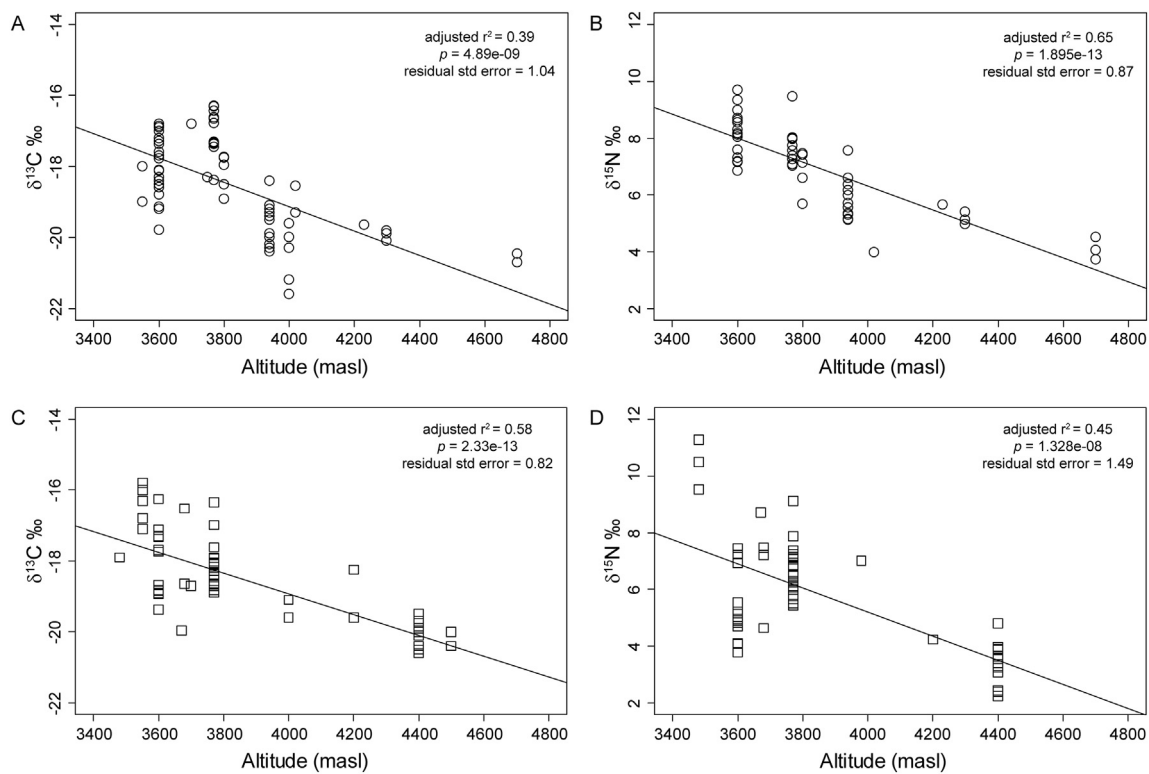


Fig. 7. Linear regression models for $\delta^{13}\text{C}$ values of llamas (A) and vicuñas (C) and for $\delta^{15}\text{N}$ values of llamas (B) and vicuñas (D).

models to explain the variation exhibited by the SAC $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in relation to altitude. Species-specific linear regression equations were proposed for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, taking each species values separately and eliminating the outliers and extreme values for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and thus ascribing to accepted normality and variance homogeneity assumptions. The results of the linear models created for both llamas and vicuñas $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are exposed in Fig. 7. We expect that these calculations will help us to evaluate and discuss prehistoric herding and hunting strategies through the analysis of archaeofaunal remains recovered at archaeological sites from the same area in future research outcomes.

7. Conclusions

The results presented here show that herbivore carbon and nitrogen stable isotope compositions can vary significantly between different areas within the same climatic and geographic region. In this sense, we believe that the patterns exhibited by our results reflect the influence of variables such as temperature and water availability, which in turn depend on altitude, in the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the diet consumed by wild and domesticated SAC (Ambrose, 1991; Britton et al., 2008; Fernández and Panarello, 1999–2001a). Moreover, the patterns exhibited by the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values measured on bone collagen from llamas and vicuñas and their correlation with altitude can be used as a frame of reference to evaluate the variation exhibited by the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of SAC bone remains from archaeological contexts, in order to address questions concerned with prehistoric animal herding and hunting strategies (Yacobaccio et al., 2010). Particularly in the case of llamas, the manifestation of herd management strategies in the bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values can help us to evaluate the mobility exercised by the pastoralist groups that occupied the Dry Puna of Argentina in the past. The results of the linear regression models presented here will allow us to propose expected $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the different altitudinal ranges considered, calculating mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and prediction intervals for pastoralist archaeological sites

according to their location and altitude. In general terms, this method will be useful to test archaeological hypothesis about the altitudinal range employed by the pastoralist groups that occupied the Dry Puna in the past. Thus, if the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values measured on archaeological bones present similarities when compared to the modern $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and no significant differences are found between domesticated and wild SAC recovered at archaeological sites, we can propose the existence of a mobility system that combined herding and hunting activities in the same locations, in which llamas and vicuñas would share the same feeding areas, making it easily for pastoralist groups to access wild resources as well as domesticated ones. This hypothesis could challenge the idea that high altitude sites were preferentially involved in hunting activities, as was proposed to explain the settlement pattern of herders in the southern portion of the Puna of Argentina for the same time-period (Olivera and Grant, 2009). At the same time, the patterns exhibited by both domesticated and wild SAC bone collagen isotopic compositions can be used to develop human paleodietary and palaeoenvironmental studies, establishing baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to perform dietary and environmental reconstructions (Killian Galván et al., 2012, 2016; Samec et al., 2014).

This study represents a new and comprehensive approximation to the isotopic variability among domesticated and wild SAC in the highlands of the South-Central Andes. In the future, we hope to be able to apply the patterns discussed here to the study of the isotopic variability in archaeofaunal remains and thus gain a new perspective in the investigation of herding and hunting strategies employed by the pastoralist groups that occupied this area ca. 3500 years BP.

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