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Carbon and nitrogen isotopic ecology of Holocene camelids in the Southern Puna (Antofagasta de la Sierra, Catamarca, Argentina): Archaeological and environmental implications

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ABSTRACT

This article focuses on camelid isotope ecology from archaeological sites dating to the Holocene (c. 9800–420 BP) located in the Southern Argentine Puna. We present 92 carbon and nitrogen stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) extracted from wild (*Vicugna vicugna* and *Lama guanicoe*) and domesticated (*L. glama*) camelid bone collagen. The samples come from the following archaeological sites: Quebrada Seca 3, Cueva Salamanca 1, Peñas de la Cruz 1.1, Casa Chávez Montículos 1 and 4, Bajo del Coypar II, Cueva Cacao 1A, Real Grande 1, and Real Grande 6, all of them located over 3300 masl in Antofagasta de la Sierra, Catamarca, Argentina. Mean carbon isotopic relationship ($\delta^{13}\text{C}$) was -17.2‰ , ranging from -20.1‰ to -11.6‰ , and mean nitrogen isotopic relationship ($\delta^{15}\text{N}$) was 6.8‰ , ranging from 3.4‰ to 10.8‰ . We interpret these isotope values against the background of environmental and cultural changes that occurred throughout this period. Variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were generally not structured per the availability of different pasture areas across varying altitude. Instead, there was an appreciable increase of some $\delta^{13}\text{C}$ values in domesticated camelids, suggesting the use of complementary forage in their diet. That aside, the isotope values do not differ significantly among the different camelid taxa. More generally, a noticeable increase in $\delta^{15}\text{N}$ values, and to a lesser extent in $\delta^{13}\text{C}$ values, was noted at around 8000 BP, coinciding with a palaeoclimatic phase of extreme regional aridity. Yet, no significant increase of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values was recorded during a later arid phase (1500 BP), and no significant variations were observed in isotope values during the arid and wet fluctuations (sub-phases) within each of the principal Holocene palaeoenvironmental phases recorded for the region. These results highlight the varying magnitude of past climatic changes and their differential impact, and emphasise the need to investigate further into the environmental aspects that produce variation in isotope data.

1. Introduction

The archaeofaunal record from North-Western Argentina, and generally from the South-Central Andes, shows that for thousands of years South American camelids were a key resource for the human populations of the region (Mengoni Goñalons, 2008; Mondini et al., 2013; Mondini and Elkin, 2014; Olivera and Grant, 2008; Yacobaccio, 2001). From the earliest human occupation (c. 10,000 BP) of the Antofagasta de la Sierra basin, in the Southern Argentine Puna, animal resources were obtained through hunting. In this scenario, wild camelids—vicuña (*Vicugna vicugna*) and guanaco (*Lama guanicoe*)—represented key species for the hunter-gatherers of the area (Mondini et al., 2013; Mondini

and Elkin, 2014). Later, different populations across the Andean area experienced a series of processes that led human groups to undergo profound social and economic changes. In Antofagasta de la Sierra, these changes, possibly involving the local domestication of the llama (*Lama glama*) (Aschero et al., 2012; Elkin, 1996; Grant, 2014; Olivera and Elkin, 1994), date to the late Middle Holocene and the early Late Holocene (c. 4500–3000 BP), and culminated in the adoption of an agro-pastoralist way of life. From this moment onwards, hunting, herding and agriculture have played varied social and economic roles, with each enjoying greater or lesser importance through time (Olivera and Grant, 2008).

In this article, we present the results of carbon and nitrogen stable

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isotope analyses on camelid bone collagen from different archaeological sites in the Antofagasta de la Sierra region, with the aim of investigating the diet of these animals and, ultimately, the strategies employed in their exploitation by the prehispanic populations of the area. The archaeological occupations considered here date to the length of the Holocene (c. 9800–420 BP), although some periods, notably that from c. 6100–2100 BP, are not represented. Anyway, this broad temporal framework provides the necessary depth to consider not only the cultural changes occurring in the area, but also the environmental fluctuations that impacted on the Southern Puna after the Pleistocene. These fluctuations would have affected camelid ecology and, concomitantly, human decisions regarding their exploitation. Furthermore, the sites considered are located throughout the basin, ranging across all areas from the basin bottom (c. 3300 masl) to the high ravines (at over 4000 masl). This in turn allows us to assess variability in vegetation cover at different altitudes.

The faunal samples analysed here belong to wild camelids from hunter-gatherer contexts from the following archaeological sites: Quebrada Seca 3 (QS3), Cueva Salamanca 1 (CS1) and Peñas de la Cruz 1.1 (PCz1.1); while wild and domesticated camelid samples were obtained from agro-pastoralist levels at the following sites: Casa Chávez Montículos 1 and 4 (CChM1, CChM4), Bajo del Coypar II Sector 3 (BCII), Cueva Cacao 1A (CC1A), Real Grande 1 (RG1) and Real Grande 6 (RG6) (Fig. 1, Table 1) (Pintar, 2014; Olivera and Grant, 2008; including bibliography therein). We present and discuss a total of 92 carbon and nitrogen stable isotopes extracted from camelid bone collagen. These isotope values were collected from a series of studies and research projects, the results of which—including some of the first samples from the high Andes in general to be reported for the chronological period considered—have only been partially presented in conferences and articles (Grant, 2017; Grant and Olivera, 2016; Mondini et al., 2010; Mondini and Panarello, 2014; Motta, 2013). Therefore, this is the first time that these values have been compared and interpreted altogether.

Based on these analyses, we explore here the diet and pasturage areas utilised by the different camelid species through space and time as suggested by these isotopes, and evaluate the importance of vegetation variability according to altitude, as well as environmental change throughout the Holocene. Given the results of previous studies in the Andean region (Fernández and Panarello, 1999–2001; López et al., 2013; Mengoni Goñalons, 2007; Yacobaccio et al., 2010; Samec et al., 2014; Szpak et al., 2014; among others), we proposed the hypothesis that isotope values varied according to the altitudinal location of

feeding areas, as well as due to palaeoenvironmental change throughout the Holocene. This would result in less negative carbon values at lower altitudes and more positive nitrogen values for the drier palaeoenvironmental phases. Our data implies that the case is not as clear-cut. Indeed, many of our results, both on carbon and nitrogen values, did not develop as expected.

1.1. Environmental and palaeoenvironmental setting

Antofagasta de la Sierra is located between 25°50' and 26°10'S and between 67°30' and 67°10'W, at over 3000 masl. It is part of the Southern Argentine Puna, and environmentally belongs to the Salt Puna (Fig. 1). It is characterised by extreme aridity (arid Andean *puna* climate), with annual summer rainfalls ≤ 150 mm, including virtually no rain some years. Mean annual temperature is 9.5 °C, with substantial daily and seasonal amplitude, and low atmospheric pressure. The hydrological network is endorheic, fed by meagre precipitations, ice-melt (November to March), and subterranean aquifers (García Salemi, 1986; Olivera, 1992).

Phytogeographically, the lower part of this region belongs to the Puna Province of the Andean Domain, where the dominant vegetation is steppe shrub, with herbaceous, halophilic and samophilic steppe also present (Cabrera, 1976). Plants with a C₃ photosynthetic cycle are predominant, although C₄ and CAM plants are also found. In the High Andean Province, whose lower boundary varies between 3000 and 4000 masl across the region, C₄ plants are not commonly found (Fernández and Panarello, 1999–2001; Grant, 2016; Panarello and Mondini, 2015). Nevertheless, a recent study in Jujuy has found plants with this photosynthetic signature within this altitudinal range, and even at above 4000 masl (Samec et al., 2015).

In the Antofagasta de la Sierra basin, the lower and intermediate areas are dominated by *tolar* formations, composed principally of shrubs and with a low proportion of herbs. The *tolar* includes mainly C₃ (shrubs and grasses) and C₄ (mostly grasses) plant species. At a higher altitude—presently above c. 3900 masl—, the *pajonal* predominates, composed of pastures and a variety of herbaceous species which are all non-C₄ plants (Cabrera, 1976; Cabrera and Willink, 1980; Fernández and Panarello, 1999–2001; Haber, 1991; Olivera, 2006; among others). Both ecozones—*tolar* and *pajonal*—also include moor-like *vegas* associated to water streams. The archaeobotanical samples recovered from Holocene levels in Antofagasta de la Sierra sites are also mainly C₃, excepting a single CAM Cactaceae (*Trichocereus pasacana*, which grows in the Prepuna but may also grow in the Puna) dated after c. 7600 BP,

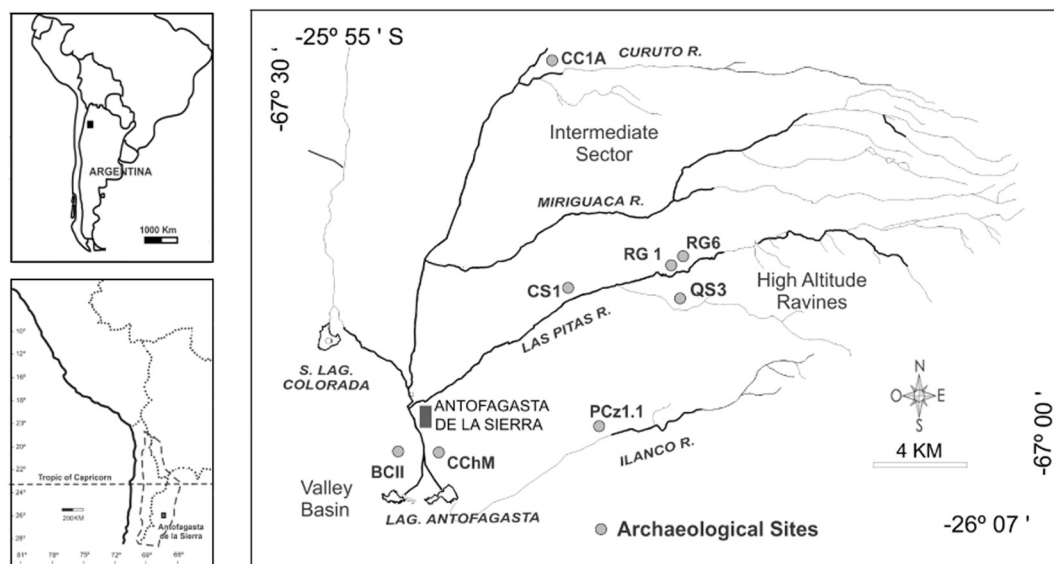


Fig. 1. Antofagasta de la Sierra and the archaeological sites considered in this study.

Table 1
Archaeological occupations considered in this study.

Archaeological site		Altitude (masl)	Age (^{14}C) of sampled levels	Societal-economic organization	References
Full name	Short name				
Quebrada Seca 3	QS3	4050	c. 9790–6080 BP	Hunter-gatherers	Pintar (2014a) and bibliography cited there
Cueva Salamanca 1	CS1	3665	c. 8100–6250 BP		
Peñas de la Cruz 1.1	PCz1.1	3665	c. 7910–7270 BP	Agro-pastoralists	Olivera and Grant (2008); Olivera and Vigliani (2000/2002); and bibliography cited there
Casa Chávez Montículos 1 and 4	CChM1, CChM4	3360	c. 2120–1440 BP		
Bajo del Coypar II Sector 3	BCII	3349	c. 780–670 BP		
Cueva Cacao 1A	CC1A	3700	c. 990		
Real Grande 1	RG1	4050	c. 680		
Real Grande 6	RG6	4050	c. 1170–420 BP		

and some C_4 plants (*Munroa andina* from the *tolar* formation, and introduced *Zea mays*) after c. 3500 BP (Rodríguez, 2014).

Camelids have been the dominant ungulates both in the past and present. In the past, these included the ubiquitous vicuñas; the guanacos, a larger wild species that is no longer present in the region, and later, the domesticated llamas (Grant, 2010; Mondini and Elkin, 2014; Olivera and Elkin, 1994). The other domesticated camelid species, the alpaca (*Vicugna pacos*), is virtually inexistent in the Argentine Puna, given that the area is too dry for the environmental requirements of this animal (Vilá, 2000).

The *puna* environment is characterised by a high degree of heterogeneity. Therefore, significant variability can be observed within a few kilometres. This variability is based fundamentally on topography and altitude. In the Antofagasta de la Sierra basin, three micro-environmental sectors have been identified, containing concentrated patches of resource-rich areas: Basin Bottom (3400–3550 masl), Intermediate Sectors (3550–3800 masl), and High Altitude Ravines (3800–4600 masl) (Olivera, 2006).

Data obtained from a variety of palaeoenvironmental records—sedimentary facies, palaeo-soils, diatoms, ostracods and geomorphology—suggest that the study area has undergone a number of sharp environmental changes throughout the Holocene (Grana et al., 2016; Olivera, 2006; Tchilinguirian, 2009; Tchilinguirian and Olivera, 2012, 2014). Tchilinguirian (2009) has proposed a palaeoenvironmental model for Antofagasta de la Sierra that establishes 6 distinct phases over the last 15,000 years, including environmental fluctuations (sub-phases) within each of them.

Based on this model, the onset of the Holocene would have been characterised by a wetter and more resource-rich landscape than at present. Later on, between c. 7900–4500 BP, a predominantly arid and unstable phase followed. Within this arid phase, Tchilinguirian (2009) has identified a wetter sub-phase occurring between c. 6300–5800 BP. Subsequently, between c. 4500–1500 BP, the area experienced a very wet and water-rich period that included drier and intermediate conditions during a sub-phase between c. 3900–3400 BP. It is only towards c. 3400 BP that the environment becomes more stable and water availability increases including a higher river water-flow, in respect to the earlier Middle Holocene. This stability increased the abundance and geographic extension of the hydric, animal and plant resources available to human groups in the area (Grana et al., 2016; Tchilinguirian, 2009).

Finally, during the last 1500 years, arid conditions again predominated. From this time onwards, lakes retreated and some of the moor-like *vegas* degraded or only survived in the highest sectors of the valleys and ravines. Consequently, there was a decline in the availability of hydric and biotic resources (Tchilinguirian, 2009). Nevertheless, a salient fact concerning the dynamic environmental history of Antofagasta de la Sierra is that, even in moments of extreme aridity, there have always been active, permanent water sources and associated

flora and fauna available in the basin (Grana et al., 2016; Tchilinguirian and Olivera, 2012). What has varied most throughout the Holocene is thus the relative abundance and distribution of water and associated biotic resources.

1.2. Archaeological sequence of Antofagasta de la Sierra

The available archaeological evidence for Antofagasta de la Sierra reveals the presence of hunter-gatherers from the onset of the Holocene (since at least c. 10,190 BP), focused on the hunting of wild camelids—vicuña and guanaco—(Mondini et al., 2013; Mondini and Elkin, 2014; Martínez, 2014; Reigadas, 2014). These populations developed distinct landscape management strategies for the different ecozones, concomitant with a high degree of residential movement and logistics (Aschero and Martínez, 2001; Pintar, 2014b). Across millennia, these groups underwent numerous changes, which would have included the selective management of certain camelid populations from an early period (c. 4000–5000 BP), and the subsequent transition to camelid herding (Aschero et al., 2012; Olivera and Elkin, 1994; Reigadas, 2014; Yacobaccio, 2001).

From approximately 3000 BP, there is a consolidation of more sedentary groups vis-à-vis the earlier hunter-gatherers. During this period, llama herding became the principal economic strategy of the area, with agriculture occupying a secondary role (Olivera, 2006). Nevertheless, vicuña hunting continued playing a significant role within the economic strategies of these societies (Escola, 2002; Grant, 2010). Towards 1800 BP, the human population increased, and there was an intensification in agricultural production (Olivera and Vigliani, 2000/2002). During this period, wild camelid hunting seems to have diminished (Olivera and Grant, 2008).

Finally, c. 1000 BP, there is a further population increase, and semi-urban settlements appear, associated to increased social complexity. There is a marked growth in agricultural production and there is evidence for a more complex management of domesticated camelids, seen in the development of morphologically specialised breeds selected for fibre production and transport (Olivera, 1997; Reigadas, 2014). During this late period, hunting increased again, underlining its importance within the regional economy (Grant, 2010; Ortiz and Urquiza, 2012).

2. Materials and methods

2.1. Archaeological sites and analysed faunal assemblages

The analysed camelid faunal remains were obtained from different stratigraphic levels from eight archaeological sites located at varying altitudes throughout the Antofagasta de la Sierra region (Fig. 1, Table 1). They date between 9790 ± 50 and 420 ± 70 BP. In all cases, the date assigned to each sample is expressed in non-calibrated radiocarbon years before present, and is calculated from the dating (or

mean of dates) of the stratigraphic level from which the samples came. In the case of samples from undated levels, we took the average of existing dates from the levels immediately above and below, or just the date of the lower level in the case of late sites. This allowed us to organise our samples chronologically.

The samples from hunter-gatherer occupations were obtained from selected levels at the following sites: QS3, CS1 and PCz1.1, at intermediate and high altitudes (Table 1). In all cases, these were rather short and redundant multiple activity occupations in rock-shelters. While QS3, one of the highest sites in the area, was occupied throughout the Holocene, CS1 and PCz1.1, located at an intermediate altitude, were occupied mainly during the Early and Middle Holocene (see Pintar, 2014a, and bibliography cited there).

For the agro-pastoralist period set after 3000 BP, we analysed camelid samples from site CChM 1 and 4, a multi-activity residential base located on the basin bottom (Table 1). Also at this location, we sampled the domestic and storage residential site BCII sector 3. For intermediate sectors, we sampled the upper stratigraphic levels of CC1A, used as a residential base with recurrent seasonal occupations. Finally, faunal remains were analysed from the upper levels of sites RG1 and RG6, interpreted as high altitude camps dedicated to hunting and herding (Olivera and Grant, 2008; Olivera and Vigliani, 2000/2002; and bibliography cited there).

The analysed bone assemblages from these archaeological sites are, in general, very well preserved (Grant, 2014; Mondini and Elkin, 2014). Osteometrics were used to determine the different camelid species represented in each of the studied assemblages. To this end, the measurements of modern camelids from the region were used as the osteometric standards (Elkin, 1996; Grant, 2010, 2014; Mondini and Muñoz, 2017). Nevertheless, given the high degree of bone fragmentation present in many of the archaeological occupations—especially those of hunter-gatherers—, it was not possible to apply osteometric methods to all the samples. In these other cases, we used qualitative criteria to assign the camelid samples to large or small body sizes, as long as the difference in size was appreciable and a strong correlation with the reference collection was noted. When this was not possible, determination was only done to the family level, leaving these samples as indeterminate camelids. In this manner, the camelid samples were assigned to three main groups: small sized camelids, comprising vicuñas (*Vicugna vicugna*); large sized camelids, comprising guanacos (*Lama guanicoe*) and llamas (*L. glama*), and indeterminate camelids. The large camelid group was further sub-divided into two, wild and domestic: the former included those samples identified as guanacos from all periods, plus those of large-sized individuals pre-dating camelid domestication in the study area, and the latter including those samples from later periods that were consistent with modern llamas.

2.2. Methods

A total sample of 92 camelid bone specimens were analysed from the above mentioned archaeological sites. These bones were identified at least to the family level, and if possible to the genus and species level. We also took note of the stratigraphic location of each sample. Only one individual was sampled from each stratigraphical level, taking into consideration issues of anatomic determination, age and laterality. On this basis, we collated a sample made up from 38 small camelids (cf. *Vicugna vicugna*), 30 large camelids (cf. *Lama* sp.), and 24 indeterminate camelids. Following the osteometrical and the chronological criteria previously stated, the large camelid group in turn comprises 16 guanacos and guanaco-sized individuals (cf. *L. guanicoe*), and 14 llamas (*L. glama*). All selected samples were in a good state of preservation, with minimal or no weathering, and no thermal alteration. The dense tissue of these samples was extracted, and bone collagen from it was then used to measure the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes.

Sample preparation and analysis were conducted at the Instituto de Geocronología y Geología Isotópica (INGEIS, CONICET-UBA), Argentina.

Sample preparation for isotope analysis followed the standard procedures set by Tykot (2004), with some modifications. After abrasive cleaning and an ultrasonic wash with bi-distilled water, approximately 1 g from each bone element (one per individual) was selected; humic acids were then eliminated using 0.1 M sodium hydroxide for 24 h. To obtain collagen, the bone was demineralised in 2% hydrochloric acid solution for 72 h; the solution was changed every 24 h. Finally, each sample was soaked in sodium hydroxide for another 24 h. The final material was rinsed and dried at $<60^\circ\text{C}$ (Tykot, 2004; Yacobaccio et al., 2010).

The bone collagen was weighed on an analytic balance, and placed within a silver capsule. These capsules were then positioned, using an automatic sampler, into a CARLO ERBA EA1108 elemental analyser, that was linked to a (IRMS) Thermo Delta V Advantage isotope mass spectrometer, using a CONFLO IV™ interface. The results were expressed as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic deviations in respect to the international standard references VPDB and AIR respectively:

$$\delta = 1000 \frac{R_S - R_R}{R_R}$$

where $\delta = \delta^{13}\text{C}$ or $\delta^{15}\text{N}$, R = isotope ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, respectively. S denotes sample and R, reference standard (Coplen et al., 1992; Craig, 1957). The standard error (1σ) margin was $\pm 0.2\text{‰}$ for both isotopes.

In order to explore the variation in carbon and nitrogen values and test our hypothesis, we then grouped the results according to different criteria—taxon, altitude, chronology—and compared the medians using box-plots. We also calculated the coefficient of determination (R^2) to assess the proportion of the variance in the isotope values—the dependent variable—that is predictable from the independent variable (e.g., environmental phase), and applied some variance analyses using the null hypothesis that there was no difference between the means (Student test, one-way ANOVA in the case of more than two groups).

3. Results: isotope values

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the 92 archaeological camelid samples are presented in Table 2 and shown in Fig. 2. Table 2 also details the C/N relationship, showing that the selected samples were within the accepted range for collagen (2.9–3.6; De Niro, 1985), with a minimum value of 2.9 and a maximum of 3.6 (median = 3.3). These values are consistent with the good state of preservation observed macroscopically.

Aside from these values, a sample from CS1 produced an outlier with $\delta^{13}\text{C} = -9.9$ and $\delta^{15}\text{N} = 10.9$ (C/N = 3.3) (Mondini et al., 2010). We did not consider this sample any further within this study as it could have belonged to an immature individual, and therefore the isotope values could have been affected by this condition, unlike the rest of the samples.

The mean isotopic relationship for carbon ($\delta^{13}\text{C}$) in the studied camelid samples was -17.2‰ , ranging from -20.1‰ to -11.6‰ . The nitrogen relationship varied between 3.4‰ and 10.8‰ , with a mean of 6.8‰ . In Fig. 2, the relationship between carbon and nitrogen isotope values in the analysed samples is displayed, and a moderate correlation ($R^2 = 0.3707$) is inferred between them.

3.1. Taxonomic variability

On segregating the camelid samples by species or body size groups, a significant overlap is observed (Fig. 3). The correlation between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values was $R^2 = 0.5066$ for vicuñas/small camelids ($n = 38$); $R^2 = 0.4625$ for guanacos/large wild camelids ($n = 15$), based on the assumption that pre-6000 BP samples will be wild, and $R^2 = 0.125$ for llamas ($n = 15$). Thus the llama group displays the lowest relationship between nitrogen and carbon isotope values. This is so because in some llama cases, the $\delta^{13}\text{C}$ values were significantly less negative in relation to the $\delta^{15}\text{N}$ values. A Student test between wild camelids—vicuñas and

Table 2
Stable isotope ratios of archaeological camelid samples from the Antofagasta de la Sierra Basin, Argentina.

Archaeological site	Sample	Stratigraphic level	Level date (^{14}C)	Altitude (masl)	Species/size group	Anatomical element	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C/N
RG 6	RG 6241	II	420 ± 70	4050	<i>Vicugna vicugna</i>	Metapodial	-17.9	6.5	3.2
RG 6	RG 6259	III	670 ± 100	4050	<i>Vicugna vicugna</i>	Metapodial	-18.5	4.9	3.3
RG 6	RG 6213	III	670 ± 100	4050	<i>Vicugna vicugna</i>	1st Phalanx	-19.0	5.4	3.2
RG 6	RG 6219	III	670 ± 100	4050	<i>Vicugna vicugna</i>	Metapodial	-18.3	5.4	2.9
RG 6	RG 6217	III	670 ± 100	4050	<i>Vicugna vicugna</i>	1st Phalanx	-18.0	5.4	3.0
RG 6	RG 6256	III	670 ± 100	4050	<i>Vicugna vicugna</i>	Metapodial	-18.1	6.1	2.9
RG 1	RG 1 64	I	680 ± 70	4050	<i>Vicugna vicugna</i>	Metapodial	-18.5	5.4	3.1
RG 1	RG 1 62	I	680 ± 70	4050	<i>Vicugna vicugna</i>	Metapodial	-19.0	5.7	3.3
RG 1	RG 1183	II	680 ± 70–770 ± 60	4050	<i>Vicugna vicugna</i>	Metapodial	-18.6	7.0	3.0
RG 1	RG 1177	II	680 ± 70–770 ± 60	4050	<i>Vicugna vicugna</i>	Metapodial	-18.7	5.7	3.1
RG 1	RG 1 72	II	680 ± 70–770 ± 60	4050	<i>Vicugna vicugna</i>	Humerus	-18.2	5.1	2.9
RG 1	RG 1 3	II	680 ± 70–770 ± 60	4050	<i>Vicugna vicugna</i>	1st Phalanx	-19.7	4.7	3.2
BCII s3	BCII 265	I	670 ± 60	3349	<i>Vicugna vicugna</i>	1st Phalanx	-17.5	6.9	3.2
BCII s3	BCII 264	III	690 ± 50	3349	<i>Lama glama</i>	2nd Phalanx	-13.7	5.4	3.0
BCII s3	BCII 210	III	690 ± 50	3349	<i>Vicugna vicugna</i>	Metapodial	-17.8	4.5	3.4
BCII s3	BCII 211	Vib	780 ± 60	3349	<i>Vicugna vicugna</i>	1st Phalanx	-17.9	3.4	3.1
CCIA	CC 1268	I	990 ± 60	3700	<i>Vicugna vicugna</i>	Metapodial	-18.1	7.4	3.4
CCIA	CC1 270	I	990 ± 60	3700	<i>Vicugna vicugna</i>	2nd Phalanx	-18.1	6.7	3.2
CCIA	CCIA-N1	I	990 ± 60	3700	<i>Vicugna vicugna</i>	2nd Phalanx	-17.7	8.5	3.1
RG 6	RG 6230	IV	1170 ± 110	4050	<i>Vicugna vicugna</i>	1st Phalanx	-18.3	4.6	3.0
CChM 1	16.1102	IX?	1440 ± 70	3360	<i>Lama glama</i>	Metapodial	-17.3	7.6	2.9
CChM 1	16.1100	IX	1440 ± 70	3360	<i>Vicugna vicugna</i>	1st Phalanx	-18.2	5.1	2.9
CChM 1	16.1 99	IX	1440 ± 70	3360	<i>Vicugna vicugna</i>	Metapodial	-18.2	5.4	3.1
CChM 1	16.1120	II	1530 ± 70	3360	<i>Lama glama</i>	1st Phalanx	-18.0	5.1	3.0
CChM 1	16.1141	Va	1530 ± 70	3360	<i>Lama glama</i>	2nd Phalanx	-16.3	6.2	3.0
CChM 1	16.1140	IV	1660 ± 60	3360	<i>Lama glama</i>	Scapula	-16.2	7.7	3.0
CChM 1	16.1138	IV	1660 ± 60	3360	<i>Vicugna vicugna</i>	2nd Phalanx	-18.4	4.3	3.2
CChM 1	16.1121	III	1670 ± 60	3360	<i>Lama glama</i>	1st Phalanx	-17.9	4.9	3.0
CChM 1	16.1 58	III	1670 ± 60	3360	<i>Vicugna vicugna</i>	Scapula	-16.8	5.5	3.3
CChM 1	16.1 82	VI	1740 ± 60	3360	<i>Lama glama</i>	Metapodial	-17.0	6.4	3.3
CChM 4	16.4205	V	1740 ± 100	3360	<i>Lama glama</i>	1st Phalanx	-18.5	4.9	3.5
CChM 4	16.4 3	III	1740 ± 100–1530 ± 70	3360	<i>Lama glama</i>	Radioulna	-17.2	6.1	3.3
CChM 4	16.4 6	IV	1740 ± 100–1530 ± 70	3360	<i>Lama glama</i>	Scapula	-17.3	6.5	3.3
CChM 4	16.4 80	IVa	1740 ± 100–1530 ± 70	3360	<i>Lama glama</i>	2nd Phalanx	-13.1	7.6	3.0
CChM 4	16.4184	IVa	1740 ± 100–1530 ± 70	3360	<i>Lama glama</i>	1st Phalanx	-11.6	7.1	3.0
CChM 4	16.1 59	III	1740 ± 100–1530 ± 70	3360	<i>Lama guanicoe</i>	Scapula	-19.1	4.4	3.0
CChM 4	16.4186	IV	1740 ± 100–1530 ± 70	3360	<i>Vicugna vicugna</i>	1st Phalanx	-16.1	7.0	3.3
CChM 1	16.1156	VI	1740 ± 60	3360	<i>Vicugna vicugna</i>	1st Phalanx	-16.6	6.2	2.9
CChM 1	16.1 26	VII	1930 ± 70	3360	<i>Lama glama</i>	Metapodial	-19.3	7.3	3.3
CChM 1	16.1155	VII	1930 ± 70	3360	<i>Vicugna vicugna</i>	1st Phalanx	-18.0	4.5	3.0
CChM 1	16.1129	VII	1930 ± 70	3360	<i>Vicugna vicugna</i>	2nd Phalanx	-17.5	5.6	3.2
CChM 1	16.1 57	VII	1930 ± 70	3360	<i>Vicugna vicugna</i>	Metapodial	-17.3	6.0	3.0
CChM 1	16.1335	VIII	2120 ± 60	3360	<i>Lama glama</i>	Humerus	-17.1	7.9	3.2
CChM 1	16.1 10	VIII	2120 ± 60	3360	<i>Lama glama</i>	1st Phalanx	-19.0	4.1	3.2
CChM 1	16.1 74	VIII	2120 ± 60	3360	<i>Vicugna vicugna</i>	1st Phalanx	-18.6	6.1	2.9
QS3	564/4	2b(10)	6080 ± 70	4050	Small Camelid	Metapodial	-18.32	6.3	3.5
QS3	243/1	2b(9)	6160 ± 100–6080 ± 70	4050	Small Camelid	Metapodial	-18.28	6.3	3.4
QS3	119/5	2b(8)	6160 ± 100	4050	Camelid (indet.)	1st Phalanx	-16.25	8.1	3.3
CS1	286/1	2(2)	6250 ± 60	3665	<i>Lama guanicoe</i>	Metacarpal	-16.73	8.4	3.3
CS1	285/1	2(2)	6250 ± 60	3665	Large Camelid	Tarsal	-18.6	7.1	3.6
CS1	199/1	2(2)	6250 ± 60	3665	Camelid (indet.)	2nd Phalanx	-14.18	9.7	3.5
CS1	194i/1	2(2)	6250 ± 60	3665	Camelid (indet.)	Mandible	-14.3	9.4	3.3
QS3	228/1	2b(11)	6490 ± 100–7130 ± 110	4050	Camelid (indet.)	Metatarsal	-18.26	5.0	3.3
QS3	232/1	2b(12)	6490 ± 100–7760 ± 80	4050	Large Camelid	Vertebra	-17.09	7.4	3.3
PCz1.1	32/1	2(3a)	7270 ± 40	3665	<i>Vicugna vicugna</i>	Metapodial	-16.66	8.9	3.3
PCz1.1	23anexo/1	2(2a)	7270 ± 40	3665	Camelid (indet.)	Metapodial	-18.44	8.4	3.5
PCz1.1	30-Jan	2(3a)	7270 ± 40	3665	<i>Vicugna vicugna</i>	Metapodial	-16.78	8.6	3.4
PCz1.1	23anexo/2	2(2a)	7270 ± 40	3665	Camelid (indet.)	2nd Phalanx	-15.69	7.4	3.4
PCz1.1	11-Jan	2(1a)	7270 ± 40	3665	<i>Lama guanicoe</i>	Metacarpal	-18.35	6.9	3.5
PCz1.1	39/1	2(5a)	7270 ± 40	3665	Camelid (indet.)	Metapodial	-14.87	7.9	3.4
QS3	255/9	2b14	7350 ± 80	4050	Small Camelid	1st Phalanx	-16.33	8.3	3.3
CS1	99/1	2(4)	7500 ± 60	3665	Camelid (indet.)	Femur	-16.3	7.9	3.3
CS1	75/1	2(3)	7410 ± 100–7630 ± 40	3665	Camelid (indet.)	Humerus	-16.4	8.7	3.4
CS1	244/1	2(6)	7540 ± 50	3665	<i>Lama guanicoe</i>	Radioulna	-18.8	7.8	3.4
CS1	239/1	2(6)	7540 ± 50	3665	<i>Lama guanicoe</i>	Metatarsal	-15.3	8.9	3.3
CS1	129/1	2(5)	7550 ± 60	3665	Camelid (indet.)	Tibia	-16.4	9.4	3.4
CS1	464/1	2(7)	7620 ± 60	3665	Camelid (indet.)	Rib	-14.79	9.5	3.5
CS1	436/1	2(7)	7620 ± 60	3665	<i>Vicugna vicugna</i>	Humerus	-14.18	7.7	3.3
CS1	427/1	2(7)	7620 ± 60	3665	<i>Vicugna vicugna</i>	Astragalus	-14	10.4	3.4
CS1	285i/1	2(7)	7620 ± 60	3665	Camelid (indet.)	Skull	-17.6	9.7	3.3
QS3	245/7	2b(13)	7760 ± 80	4050	Camelid (indet.)	1st Phalanx	-17.74	4.9	3.3
QS3	265/7	2b(15)	7350 ± 80–8330 ± 110	4050	Camelid (indet.)	Metapodial	-18.87	5.6	3.5
PCz1.1	45/2	3(2a)	7910 ± 100	3665	Camelid (indet.)	Humerus	-15.93	8.3	3.3
PCz1.1	45/1	3(2a)	7910 ± 100	3665	Large Camelid	Rib	-18.6	7.8	3.6

(continued on next page)

Table 2 (continued)

Archaeological site	Sample	Stratigraphic level	Level date (^{14}C)	Altitude (masl)	Species/size group	Anatomical element	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C/N
PCz1.1	43anexo/1	3(1a)	7910 \pm 100	3665	Camelid (indet.)	Innominate	-17.36	8.5	3.5
PCz1.1	41/1	3(1a)	7910 \pm 100	3665	Camelid (indet.)	1st Phalanx	-15.58	9.7	3.4
CS1	510/1	2(10)	8100 \pm 50	3665	<i>Lama guanicoe</i>	1st Phalanx	-17.5	7.6	3.3
CS1	508/1	2(10)	8100 \pm 50	3665	Camelid (indet.)	Carpal	-15.04	9.2	3.3
CS1	505/1	2(10)	8100 \pm 50	3665	Camelid (indet.)	Tibia	-15.12	8.8	3.3
CS1	181/1	2(10)	8100 \pm 50	3665	Camelid (indet.)	Femur	-15.4	9.5	3.3
CS1	507/1	2(10)	8100 \pm 50	3665	Camelid (indet.)	Rib	-15.3	9.2	3.5
QS3	1603/4	2b(16)	8330 \pm 110	4050	Large Camelid	Tibia	-16.5	6.3	3.3
QS3	1672/2	2b(18)	8640 \pm 80	4050	Large Camelid	Tibia	-18.15	6.0	3.3
QS3	1457/1	2b(18)	8640 \pm 80	4050	Large Camelid	Metapodial	-18.32	5.9	3.2
QS3	1391/4	2b(17)	8660 \pm 80	4050	Small Camelid	1st Phalanx	-18.59	4.6	3.4
QS3	1517/2	2b(22)	9050 \pm 90	4050	Camelid (indet.)	Tibia	-17.53	8.4	3.4
QS3	1740/z2	2b(23)	9050 \pm 90–9410 \pm 120	4050	Camelid (indet.)	Sacrum	-19.41	5.9	3.4
QS3	1753/1	2b(24)	9050 \pm 90–9410 \pm 120	4050	Small Camelid	Radioulna	-15	10.8	3.6
QS3	1767/1	2b(25)	9250 \pm 100–9410 \pm 120	4050	Camelid (indet.)	Tibia	-18.5	5.3	3.3
QS3	1506/2	2b(20)	9790 \pm 50–9050 \pm 90	4050	Large Camelid	Vertebra	-20.09	4.9	3.6
QS3	1484/2	2b(19)	9790 \pm 50	4050	Large Camelid	Innominate	-18.9	6.0	3.4
QS3	1680/1	2b(19)	9790 \pm 50	4050	Camelid (indet.)	Tibia	-17.86	7.1	3.3

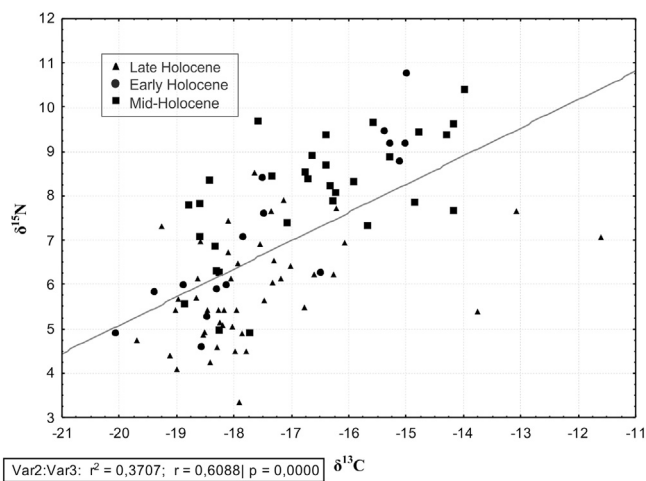


Fig. 2. Camelid bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic ratios from archaeological sites in Antofagasta de la Sierra, Argentina.

guanacos/early large camelid group altogether—and domestic camelids elucidates this variation in carbon values ($t = -2.62$, $p = 0.011$), while the variation in nitrogen values is not significant ($t = 0.12$, $p = 0.904$). Such difference between wild and domestic camelids is also observed in variance analysis (one-way ANOVA): $F = 3.78$, $p = 0.02792 > 0.01$ for carbon isotopes and $F = 0.62$, $p = 0.54369 > 0.01$ for nitrogen isotopes.

3.2. Chronological variability

Isotope relationships were also analysed from a chronological perspective, taking into consideration the different Holocene stages: Early (c. 10,000–8000 BP), Middle (c. 8000–4000 BP) and Late (c. 4000 to present). This allowed us to infer variations throughout the Holocene, especially during the Late Holocene for carbon values, and during the whole sequence for nitrogen values (Fig. 4).

While according to one-way ANOVA tests no statistically significant differences were noted between the $\delta^{13}\text{C}$ values of the Early and Middle Holocene ($F = 1.76$, $p = 0.19 > 0.01$), or between the Early and Late Holocene ($F = 0.36$, $p = 0.54 > 0.01$), there were differences between the Middle and Late Holocene values ($F = 6.65$, $p = 0.0019 < 0.01$). In the case of the $\delta^{15}\text{N}$ values, we likewise did not observe a statistically significant difference between the Early and Middle Holocene ($F = 2.83$, $p = 0.0992 > 0.01$), although we did between the Middle and Late Holocene ($F = 54.66$, $p = 0.000018 < 0.01$), as well as between the

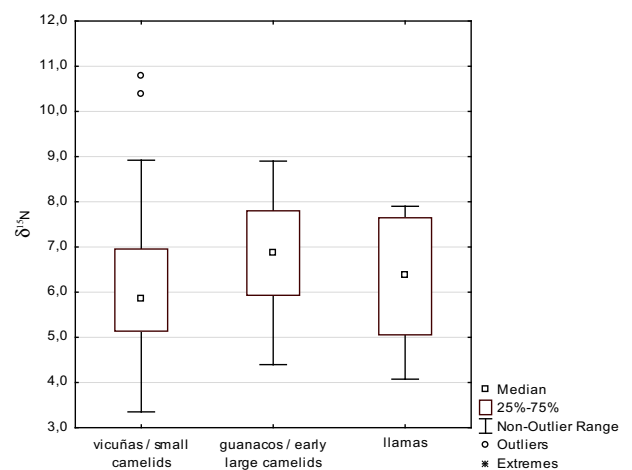
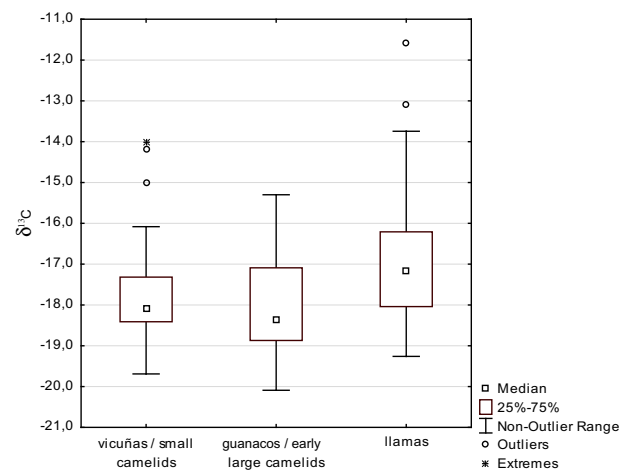


Fig. 3. Archaeological camelid bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope variation according to taxon and body size criteria, as expressed in box-plots.

Early and Late Holocene, albeit less pronounced ($F = 11.29$, $p = 0.00136 < 0.01$). While some of this variation might relate to the taxonomy of camelids as shown above, and the eventual consolidation of herding in Antofagasta de la Sierra, it might also relate to environmental changes, as considered next.

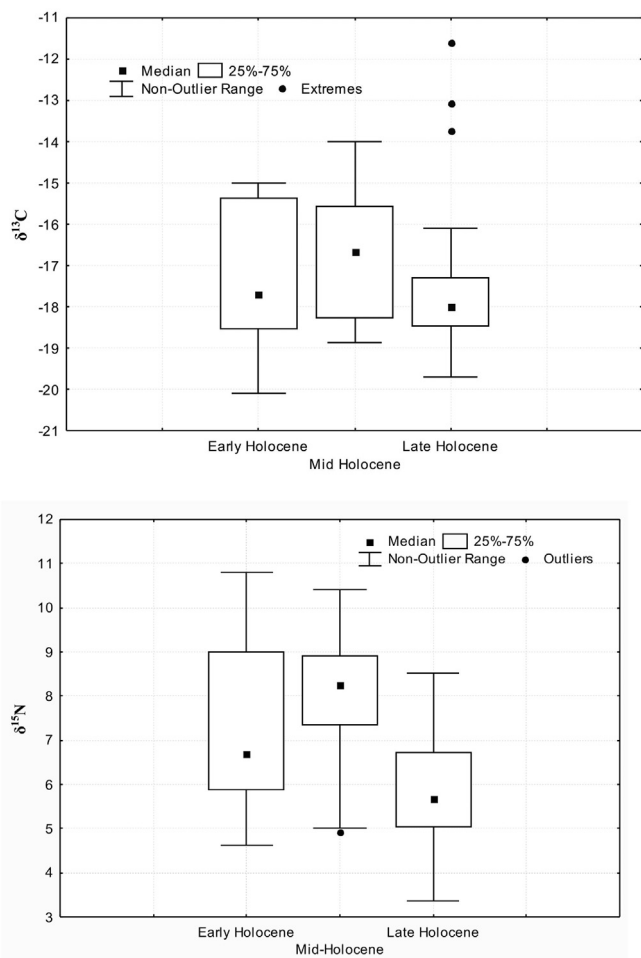


Fig. 4. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values according to chronological criteria.

3.3. Palaeoenvironmental variability

In evaluating possible environmentally related variability, we organised the data according to the palaeoenvironmental phases suggested for the region by Tchilinguirian (2009) and Tchilinguirian and Olivera (2014) (see Section 1.1). If we compare the data in accordance to the wet (shown in Fig. 5 under ‘W’) and dry (shown as ‘D’) phases and sub-phases, a concordant variation in isotope values is observed across some of the Holocene phases, although it is not as pronounced in the wet sub-phase that occurs in the Middle Holocene. A Student test renders no statistically significant differences when the isotope values were grouped around the three wet (sub-) phases on the one hand and the two arid ones on the other: $t = 0.641$, $p = 0.523$ for carbon and $t = 0.64$, $p = 0.523$ for nitrogen. It is important to note, that we could not include in this study samples from the 5800–4500 BP arid sub-phase, given that the archaeological signal during this harshest period of aridity was weak (Martínez et al., 2010, among others).

3.4. Altitudinal variability

Another factor we evaluated was altitude as a proxy of environmental factors that could affect isotope values. In this case, we did not observe a correlation of altitude with carbon values ($R^2 = 0.0831$), or with nitrogen values ($R^2 = 0.0001$) (see Fig. 6).

Taking into account that the plant communities that predominate in each altitudinal range are basically *pajonal* above 3900 masl and *tolar* below such altitude, we decided to group the samples to above and below 3900 masl. In this manner, we aimed at exploring variations in isotope values in relation to these plant communities (Fig. 7). While the

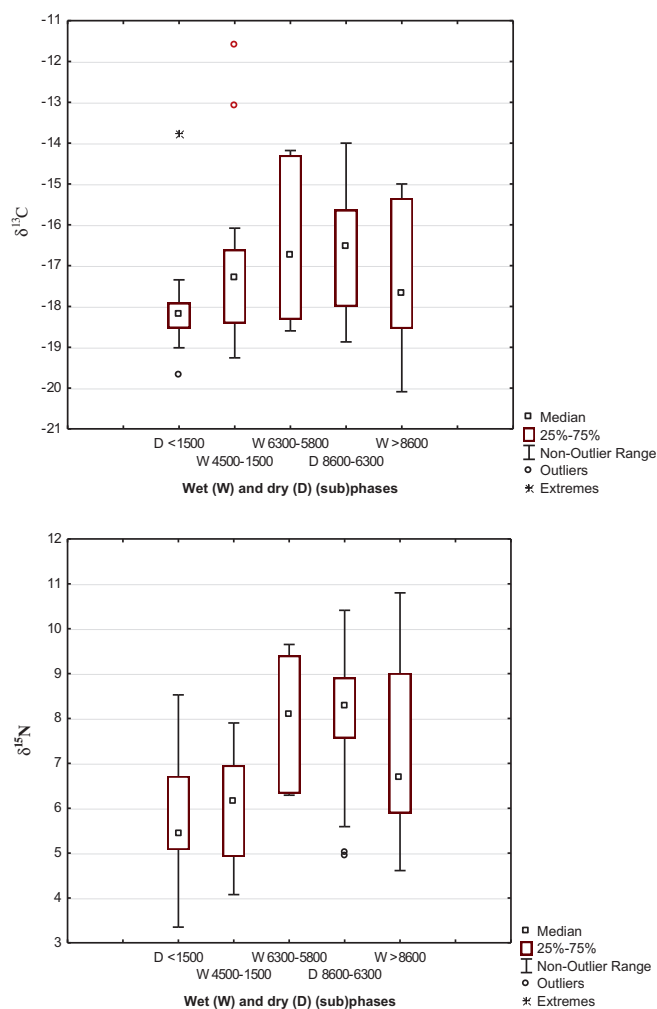


Fig. 5. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values according to palaeoenvironmental criteria.

results displayed some variation according to these categories, they did not reveal significant structured differences as there was a great deal of overlap ($t = 4.30$, $p = 0.000$ for carbon, and $t = 3.24$, $p = 0.002$ for nitrogen).

Given that the variability observed in the samples below 3900 masl was substantial, we segregated the values from the intermediate zone and the basin bottom, where C_4 and CAM plants concentrate—although the latter only included late samples of domesticated camelids (one-way ANOVA: $F = 11.71$, $p = 0.00003 > 0,01$ for carbon, and $F = 47.14$, $p = 0.00000 > 0,01$ for nitrogen). The main difference, especially in respect to nitrogen, was between the intermediate sectors and the others, and not so much between the *pajonal* and the basin bottom (Fig. 8).

4. Discussion

Our analyses suggest that the consumption of C_3 plants by camelids has been dominant, as expected for *puna* environments such as this where natural C_3 pastures predominate, even though C_4 did contribute to varying degrees—sometimes significantly—to their diet. This is consistent with what is known from other Andean areas (Fernández and Panarello, 1999–2001; López et al., 2013; Mengoni Goñalons, 2007; Samec et al., 2014; Szpak et al., 2014; Yacobaccio et al., 2010; among others).

When the first isotope results from hunter-gatherer contexts in Antofagasta de la Sierra (c. 8100–3500 BP) were obtained, one of the hypotheses proposed was that guanacos were feeding on different

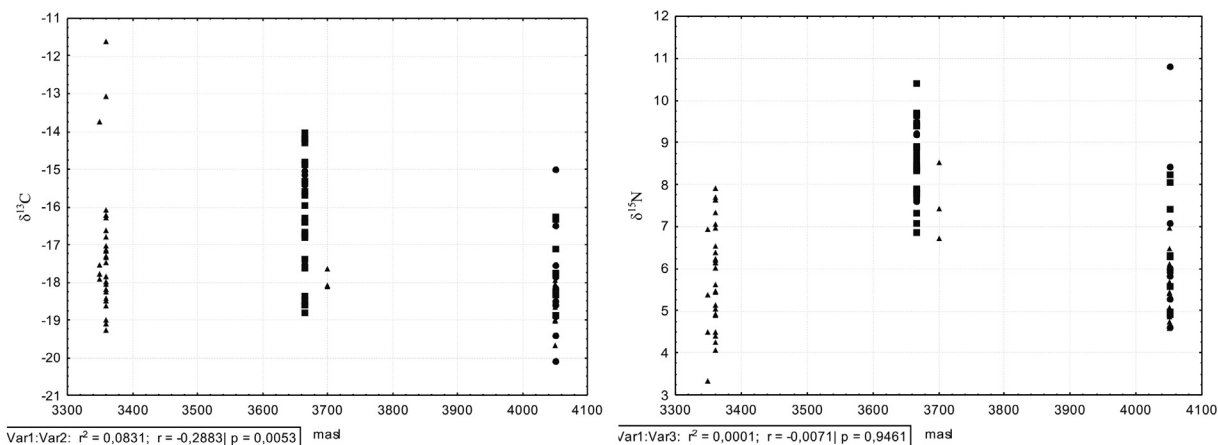


Fig. 6. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values according to altitude (masl).

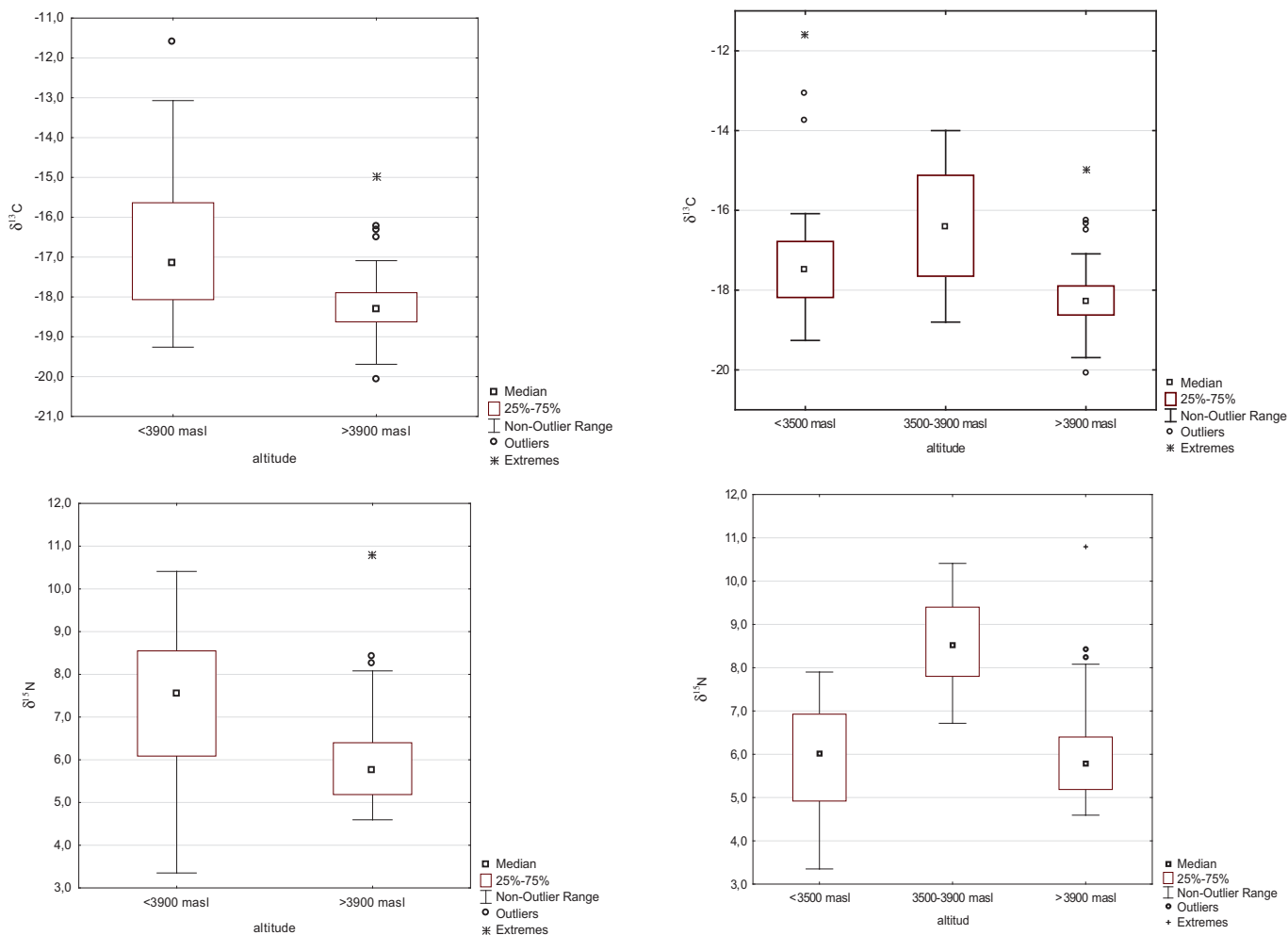


Fig. 7. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic variation as expressed in boxplots at altitudinal levels above and below 3900 masl.

Fig. 8. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic variation as expressed in boxplots at three altitudinal levels.

pastures from vicuñas, thereby implying divergent isotopic signatures (Mondini et al., 2010). Yet, having analysed this larger database, we realise that the variation between large and small wild camelids is not as structured as to suggest any consistent, significant difference in pasturage ($t = 1.02$, $p = 0.311$ for carbon, and $t = -1.06$, $p = 0.296$ for nitrogen; see also Samec et al., 2014).

Nevertheless, there is an appreciable difference in the case of certain camelid samples obtained from agro-pastoralist contexts—dating to after 3000 BP—and assigned, on osteometry grounds, to domesticated

camelids (*Lama glama*) (Grant, 2010, 2014). In this case, even at similar nitrogen isotopic levels, several $\delta^{13}\text{C}$ values were significantly less negative. The Student test between wild and domesticated camelids revealed a variation in carbon ($t = -2.62$, $p = 0.011$), while the nitrogen values did not exhibit a significant difference ($t = 0.12$, $p = 0.904$).

In earlier articles (Grant, 2017; Grant and Olivera, 2016), the hypothesis was proposed that these less negative carbon values were due

to a change in the management strategies of domesticated camelids in the study area beginning at c. 1800 BP, when Prehispanic pastoralists started complementing the llamas diet with C_4 plants, specifically maize and its bi-products (stem, husk and leaves). Nevertheless, it was difficult to test this hypothesis given that there was no direct correlation between high $\delta^{13}C$ values—disassociated from high $\delta^{15}N$ —and a diet complemented with maize, especially in ecological environments where wild C_4 plants also grow (Thornton et al., 2011).

In this sense, a more complete isotope database such as the one presented here, coupled with a greater temporal depth, provided further support to the concept of a managed control of llamas using maize agricultural residues. This is so, given that such carbon stable isotope less negative values are recorded before the return to more unstable and arid conditions in the area at c. 1500 BP, and furthermore these higher values were not detected during previous arid phases.

Likewise, even though we did not find significant statistical correlation between the different camelid isotope values and chronology, we did observe certain differences in the samples from the Middle Holocene, during which most of the carbon and nitrogen isotope values show a marked increment (see also Samec et al., 2014). The fact that no archaeological samples from one of the driest Mid-Holocene periods could be analysed (5800–4500 BP) should be recalled. For the Late Holocene, both isotopes had more impoverished values.

Several $\delta^{15}N$ values in fact came close to the higher end of the known range for these herbivores, and were high when compared to those of other camelid samples (Barberena et al., 2009; Mengoni Goñalons, 2007; Samec et al., 2014; among others). In this respect, then, we need further studies, especially concerning the possible effects of hydric stress due to arid conditions (see for example, Ambrose, 1991; Pate, 1994; Sillen et al., 1989).

On the other hand, as explained previously, the values obtained only correlate partially to the different palaeoclimatic phases and sub-phases registered for the area (Grana et al., 2016; Tchilinguirian and Olivera, 2014). During the most arid phase in the Middle Holocene, more positive nitrogen values were observed, while the drier phase of the Late Holocene registered no such difference, and the differences in nitrogen isotope values for the arid and wet palaeoclimatic (sub-) phases—when grouped—are not statistically significant. Therefore, the hypothesis that the isotopic values have varied according to past palaeoenvironmental parameters, with more positive nitrogen values expected for drier phases, has only received partial support (also see Samec et al., 2014). In any case, and even though we could not analyse samples from the harsh arid phase between 5800 and 4500 BP, some variation in nitrogen seems to relate to palaeoenvironmental conditions when aridity is intense.

As regards altitude-mediated factors, a negative correlation between altitude and $\delta^{13}C$ values of modern camelids has been suggested for the Northern and Southern Puna in Argentina (Fernández and Panarello, 1999–2001; Grant, 2016; Yacobaccio et al., 2009). Yet, the camelids in our samples did not display a direct, significant relationship with altitude; rather, they evidenced a high degree of overlap above and below 3900 masl. If we further subdivide the values between those in the intermediate and basin bottom sectors, we notice that the former are the most divergent, while the *pajonal* and basin bottom ones share broader similarities. Thus, the hypothesis that the isotopic values have varied in accordance to the altitudinal location of feeding areas, with higher carbon values at lower altitudes, has not received significant support out of the analysed samples, which reveal a more complex pattern.

In any case, the fact should be considered that in this analysis we have averaged different camelid species, subjected to varying degrees of control by humans, across a wide temporal range, ensconced in changing economic and environmental conditions, and that the samples present various biases that could impact on the results. For instance, the basin bottom samples are only represented by Late Holocene

domesticated camelids, which may have been pastured at varying altitudinal ranges and could have had their diet complemented by forage. A future increase in the number of available samples will allow researchers to elucidate between the different possible scenarios presented above and the relative influence of different factors in the isotopic ecology of these camelids.

5. Conclusions

The Holocene camelid isotope data from the Southern Puna presented here show a variable range of isotope values and a complex relationship with the factors that could affect them. We analysed the $\delta^{13}C$ and $\delta^{15}N$ isotope relationships in 92 bone collagen samples of wild and domestic camelids from archaeological sites at different altitudes in Antofagasta de la Sierra, dating to the whole Holocene. The average carbon ($\delta^{13}C$) isotope relationship was of -17.2‰ , with a range between -20.1‰ and -11.6‰ , and the average nitrogen ($\delta^{15}N$) isotope relationship was of 6.8‰ , with a range between 3.4‰ and 10.8‰ .

To understand the factors affecting this isotopic variability, we looked at several possible ones as suggested in the literature. We considered camelid taxonomy, of two wild species (*Vicugna vicugna* and *Lama guanicoe*), and a domesticated one (*L. glama*). The principal difference observed was that some of the llama $\delta^{13}C$ values were considerably less negative in relation to $\delta^{15}N$ values, suggesting that complementary forage was being employed as part of an agro-pastoralist strategy.

Chronologically, the main observed variation was carbon less negative and nitrogen more positive values in the Middle Holocene. We thus evaluated whether palaeoclimatic changes in the area throughout the Holocene might have impacted on the carbon and nitrogen isotope values of the camelid populations. While no statistically significant differences were observed between the isotope values during the wet and dry (sub-)phases as a whole, we did observe less negative carbon values, and especially more positive nitrogen values, during the regional extremely arid phase that occurred during the Middle Holocene.

Finally, we considered altitude as a proxy for plant community variability that might have impacted on isotope values. Nevertheless, we did not find statistically significant variation in this regard, even if the intermediate sectors did show less negative carbon and more positive nitrogen isotope values.

The data presented here bears some consistency with those from other archaeological studies in the Andean region (López et al., 2013; Mengoni Goñalons, 2007; Szpak et al., 2014; Yacobaccio et al., 2010; among others), although in our case-study variability is not as clearly structured in relation to the environmental variables considered. This could be partly explained by the broader chronological scale of our study, and its location in the Southern Andes, within a drier area of the Puna. The temporal reach of this study is wider than in most other studies. Thus, a more complex array of factors might impinge upon isotopic relationships. In any case, what this study does underline is that the apparently lineal relationship between isotopes and environmental factors often elicited is not as clear-cut when the parameters are expanded or under varying conditions. Furthermore, the Puna is not a homogeneous entity, and cross-comparisons between the Dry and the considerably more arid Salty Puna could well be one of the factors behind the differences revealed here.

In conclusion, the present study should caution us against the use of some models displaying a direct relationship between carbon or nitrogen isotopes and some environmental factors in contexts where such relationship might not be working. It suggests that we do not yet fully understand all of the complex factors that may impact on isotope variability, or the interactions among them. Therefore, we believe that only by expanding our database and refining our questions can we better understand the past ecology of this key resource—the camelids—for human populations in the Andean region and the proximate

and ultimate factors that moulded the variability in their isotopic signatures.

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