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Towards an Isotopic Ecology of Herbivory in the Puna Ecosystem: New Results and Patterns on *Lama glama*

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ABSTRACT We present stable isotopic data obtained in order to elucidate the diet of current domestic camelids and their feeding areas, as a necessary step for the interpretation of archaelogical assemblages, and to answer questions regarding past diet, herd structure, foraging zones and interaction with human populations. Seventeen new $\delta^{13}C$ collagen isotope values from *Lama glama* bones were measured in order to start a systematic study of the isotopic ecology of herbivory in the Puna ecosystem of Jujuy province, Argentina. These values were compared with those previously available, and a reliable correlation between altitude and variation in isotopic values was found: of the order of −2‰ depletion for each 500 m increase in altitude. These results were interpreted as related to variation in vegetal assemblage due to altitude. We consider that the outcomes of this research exceed the scope of our study area, being important to the Argentine Puna as a whole, and will also contribute to the development of current animal population ecological models applied to the interpretation of archaeological remains. Copyright © 2009 John Wiley & Sons, Ltd.

Key words: $\delta^{13}C$ isotopes; collagen; *Lama glama*; archaeology; Puna

Introduction

Stable isotope analysis provides an important tool for answering archaeological questions surrounding human diet, mobility and herd management in the past, among many others (Schoeninger, 1995). In our research area, the Puna of Jujuy, isotopic studies are poorly developed and mainly oriented towards the analysis of human remains (Yacobaccio *et al.*, 1997; Olivera & Yacobaccio, 1999). The generation of new data is of central importance in building an isotopic ecology including several trophic levels of the Puna ecosystem. Isotopic data from plants and faunal resources exploited by human groups will be useful to engender a more accurate interpretation of the information obtained from palaeodietary studies of human remains. The results presented in this paper reveal new patterns in collagen isotopic values of the domestic camelids, one of the most important resources for humans in the area for the past 3000 years (Yacobaccio, 2001).

In the last 20 years stable isotope analysis of carbon and nitrogen has become a major tool for animal ecologists, answering questions regarding the foraging role of particular consumers in food webs or the importance of certain resources in the diet (Ambrose, 1993; Pate, 1994). One of the main uses of this technique has been the description of animal diet and the determination of migration routes in wild ungulate populations (Hobson, 1999;

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McKechnie, 2004). Within domesticated animals, isotopic analysis has been used for studying human strategies of sheep feeding at Neolithic sites in Orkney, Scotland (Balasse *et al*., 2006); for characterising patterns of seasonal mobility among prehistoric herders in South Africa (Balasse *et al*., 2002); and for distinguishing between sheep and goats in C_4 grass environments in East Africa (Balasse & Ambrose, 2005). Copley *et al*. (2004) also examined the potential of bio-molecular components (including $\delta^{13}C$ values) of bones from domesticated animals, like sheep, goats and cows, for reconstructing diet, foddering, foraging behaviours, and management strategies.

The Puna ecosystem

The Puna region comprises the arid highland of Argentina between 22° and 27°S and between 3000 and 4700 m.a.s.l. (Figure 1). This area is defined as a highland desert plateau crossed by several NE–SW oriented mountain ranges. This wide altitudinal range produces variations in plant assemblages from *'tolar'* (shrub steppe) to *'pajonal'* communities (herbaceous grasslands), with patched *'vegas'* (wetlands) placed in both of these main vegetal communities (see Figures 2,3 and 4, respectively).

The Puna is characterised by high solar radiation due to altitude, wide daily thermal variation, marked seasonality in rainfall, and low atmospheric pressure. Primary productivity is mainly concentrated on stable hydrological systems like primary basins, high valleys and wetlands (Dollfus, 1991). Few permanent freshwater basins, salt lakes, pans and playas constitute the general hydrological net. A few rivers and several springs, irregularly distributed over the landscape, are the only sources of fresh water, which is a critical resource for past and present human populations. The summertime precipitations are largely governed by the so-called South American Monsoon-like System (Zhou &

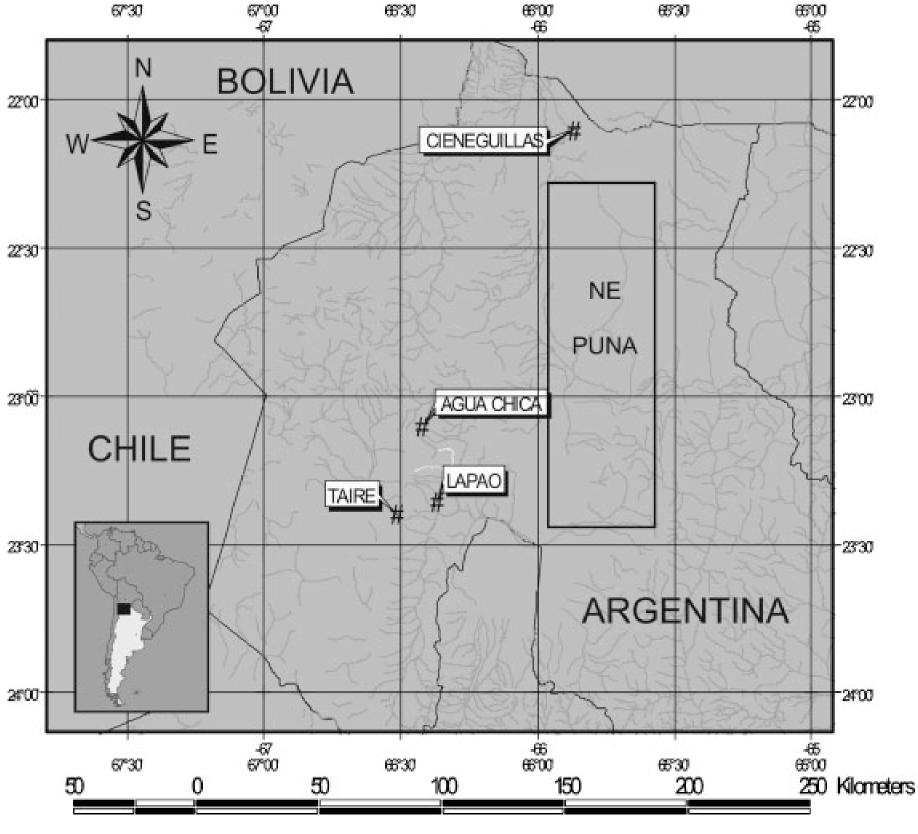

Figure 1. Locations of the study areas.

Figure 2. View of typical shrub steppe (*tolar*) vegetation zone.

Figure 3. View of typical herbaceous steppe (*pajonal*) vegetation zone.

Figure 4. View of typical wetlands (*vegas*) vegetation zone.

Lau, 1998). This system produces about 80% of annual precipitation occurring in the Andean highlands between December and February (Vuille & Keiming, 2004). In the Puna of Argentina the precipitation ranges from 340 mm/year in the northwest corner of the region to less than 100 mm/year in the southwest. Two sectors can be distinguished: the Dry Puna and the Salt Puna; they have similar vegetational compositions, but in the latter salt-lakes and saline soils are dominant features of the landscape. These conditions set a patchy distribution of vegetal and animal resources; however, three main plant communities can be identified (Cabrera, 1976; Arzamendía *et al.*, 2006; Borgnia *et al.*, 2006):

1. Shrub steppe (*tolar*) dominated by *Parastrephia lepidophylla* and *Fabiana densa* with a low proportion of herbs (5%) is the most extensive pasture area of the zone and is located between 3500 and 3900 m.a.s.l. (Figure 2).
2. Herbaceous steppe (*pajonal*) dominated by *Festuca* spp. and other grasses, like *Poa* spp. and *Stipa* spp., can be found between 4100 and 4700 m.a.s.l. (Figure 3). Above 4300 m.a.s.l., shrub presence diminishes almost completely.
3. Wetlands (*vegas*) are composed of short grasses and restricted swamp areas, with dense grassland of *Deyeuxia* spp. and *Mulembergia* spp. (Figure 4).

In ecotone areas (i.e. between 3900/4100 m.a.s.l.) mixed steppes of shrubs (only eight *genera* are present) and *Gramineae* can be found. In sum, two main altitudinal ranges with different plant assemblages are present in the Dry Puna: the *pajonal* and the *tolar*. The first is largely composed of *Poaceae* and *Gramineae*, while the second includes a lesser amount of herbs and grasses plus a wide variety of *Compositae* and *Cactaceae*. The *vegas*, considered as the main source of C_4 grasses, are present in both altitudinal settings (Ruthsatz & Movia, 1975). Consequently, the compositional differences in plant communities between both altitudinal ranges might be the main factor affecting mean isotopic values in herbivores, instead of the total abundance of C_4 plants. Notwithstanding, it must be kept in mind that intra-specific differences in vegetal isotopic values within both ranges could be registered and must be controlled in future research.

The quality of forage in these vegetal communities deserves further consideration. The foraging potential varies between different plant communities and, furthermore, the *vegas* have distinct properties at diverse altitudes. Recently, Benítez (2005) studied the pasture quality in the southern sector of the Salt Puna, analysing the nutritional chemical components' proportion of plants eaten by wild and domesticated camelids. This study included the percentage of proteins, neutral and acid fibre, and lignin. Her results showed that the majority of the shrubs have high yields of proteins, greater than 5%, but only three grasses reach this value (*Deyeuxia brevifolia*, *Stipa frigida*, and *Distichlis spicola*) (Table 1). It is worth noting that the percentage of proteins is greater in the shrub steppe than in the wetlands. On the other hand, grasses have higher values of fibres, also important in diet because they improve digestibility. Consequently, as proteins and fibres are a key factor, it can be asserted that a diet of better quality is available in the shrub steppe. Moreover, camelids have a great efficiency for processing C_4 plants which have high content of cellular walls and low nitrogen concentration (Sponheimer *et al.*, 2003). However, the relationship between the nutritional chemical components of plant communities and their isotopic signal remains to be studied.

Herding practice in the Puna

Traditionally, pastoralism has been the main economic activity of Puna inhabitants, complemented by some agriculture of quinoa, Andean tubers, and maize in the northwestern area of the region, which has most precipitation. Currently, livestock is mainly composed of camelids (llamas) and caprines (sheep: *Ovis aries*; and goats: *Capra hircus*), although cows (*Bos taurus*) are also present in some places. Llamas and alpacas (*Lama pacos*) were the only ungulates domesticated by pre-Hispanic people in the Americas. Prehistoric Andean societies relied on llamas for obtaining food, raw materials for textiles, ropes, and other artefacts, and also used them as pack-animals. The importance of the llama can be observed in the rock-art and other depictions, such as ceramic modelled vessels, mythology and ceremonial activities. Nowadays, camelid breeding is oriented towards the production of fibre and meat, whereas sheep are maintained to obtain wool and meat, and finally goat breeding is oriented to meat and milk production in good years. Each family or domestic unit of herders is composed of three generations: grandparents, parents and their children. Women and children usually work in daily herding, whereas men are recruited when physical demanding labours like shearing, castration, building of corrals or Pachamama ceremonies are carried out.

The spatial separation and temporal availability of pasturelands is managed by mobilising herds and people. As a consequence of this mobility, the settlement pattern is dispersed over the landscape. Two types of settlements can be identified: (1) residential bases (*casas*); and (2) temporary sites (*estancias*). The residential bases are located near water sources or *vegas* and constitute complex structures with many rooms as kitchens and bedrooms. They are usually occupied for 7–8 months per year, mainly in the wet season; however, one or several members of the family group not directly engaged in the care of the herds reside there permanently. Temporary sites are smaller, usually composed of one room and a corral, and are mainly occupied for two or three months during the winter (Yacobaccio *et al.*, 1998).

Table 1. Chemical composition of main plant species of the Puna

Plant group	*n*	% protein	% neutral fibre	% acid fibre	Lignin
Dicotyledonae*	11	7.45 ± 2.47	41.2 ± 10.96	32.71 ± 12.18	14.71 ± 4.47
Monocotydelonae**	13	4.70 ± 2.85	70.1 ± 10.93	42.67 ± 6.79	12.66 ± 5.27

Source: Benítez (2005: Table 4).

*Shrubs and herbs (Acantholippia salsoloides; Adesmia horrida; Atriplex argentinensis; Ephedra breana; Fabiana densa; Gochnatia glutinosa; Juniella serphioides; Parastrepia sp.; Senecio filagenoides; Baccharis acaulis; Arenaria catamarcensis).

**Grasses (Aristida cfr.subulata; Cortaderia rudiuscula; Deyeuxia brevifolia; Distichlis humilis; Distichlis spicata; Festuca argentinensis; Panicum chloroleucum; Sporobolus rigens; Stipa frigida; Stipa vaginata; Eleocharis albibracteata; Juncus sp.; Amphiscirpus nevadensis).

Methods and techniques in carbon isotope analysis

Methodology

The general framework of this paper assumes that isotopic composition in any trophic level depends on the original values of primary productivity in the area (Schoeninger, 1995; Tykot, 2004). In settings like the Argentine Puna, where vegetal cover depends on the altitudinal range (i.e. an altitudinal zonation of vegetal cover), it is expected that isotopic mean values in a herbivore's diet will correspond to this variation (Tieszen *et al.*, 1979). In order to test this suggestion, we sampled 17 individuals from four different llama herds feeding in two different altitudinal ranges in the Jujuy Province. The samples collected in the Lapao and Cieneguillas locations (Figure 1) correspond to 13 llamas that have fed in the highland shrublands at less than 4000 m.a.s.l. On the other hand, the samples from Taire and Agua Chica (Figure 1) correspond to four llamas that have fed in the highland grasslands at 4000 m.a.s.l. or more. Camelids used in this research fed on natural pastures and were not being foddered.

The resulting values are further compared with 12 previously published values (Fernández & Panarello, 1999–2001) obtained from llamas at both ranges of the Puna of Jujuy (Table 2). The general results from both studies are plotted separately and together in box-plots, and multivariate tests were performed to analyse the statistical significance of the results.

Techniques

The collagen samples were obtained from bones with dense tissues; usually shaft sections of different long bones were preferred. The preservation of the bones was good and they did not show any significant weathering. The bones were

Table 2. Isotopic results and setting of the samples

Code	Locality	Alt. (masl)	$\Delta^{13}C_{COL}$	Bone	Reference
Sample 1	NE Puna	3550	−13.8	Skull	Fernández & Panarello (1999)
Sample 2	NE Puna	3550	−18	Skull	Fernández & Panarello (1999)
Sample 3	NE Puna	3550	−19	Skull	Fernández & Panarello (1999)
Sample 4	NE Puna	3600	−16.8	Mandible	Fernández & Panarello (1999)
Sample 5	NE Puna	3600	−17.7	Mandible	Fernández & Panarello (1999)
Sample 6	NE Puna	3750	−18.3	Skull	Fernández & Panarello (1999)
Sample 7	NE Puna	4000	−19.6	Mandible	Fernández & Panarello (1999)
Sample 8	NE Puna	4000	−20	Skull	Fernández & Panarello (1999)
Sample 9	NE Puna	4000	−20	Skull	Fernández & Panarello (1999)
Sample 10	NE Puna	4000	−20.3	Skull	Fernández & Panarello (1999)
Sample 11	NE Puna	4000	−21.2	Mandible	Fernández & Panarello (1999)
Sample 12	NE Puna	4000	−21.6	Skull	Fernández & Panarello (1999)
UGA 7192	Cieneguillas	3600	−19.2	Phalanx	This work
UGA 7193	Cieneguillas	3600	−18.6	Phalanx	This work
UGA 7194	Cieneguillas	3600	−18.3	Phalanx	This work
UGA 7196	Lapao	3600	−18.5	Phalanx	This work
AIE-19140	Lapao	3653	−17.0	Humerus	This work
AIE-19149	Lapao	3653	−17.2	Femur	This work
AIE-19142	Lapao	3653	−17.2	Metatarsal	This work
AIE-19147	Lapao	3653	−17.2	Radius	This work
AIE-19139	Lapao	3653	−17.3	Humerus	This work
AIE-19148	Lapao	3653	−17.6	Metacarpal	This work
AIE-19145	Lapao	3653	−18.1	Humerus	This work
AIE-19150	Lapao	3653	−18.4	Femur	This work
AIE-19146	Lapao	3653	−18.8	Femur	This work
AIE-19143	Agua chica	3940	−19.4	Mandible	This work
AIE-19141	Agua chica	3940	−19.5	Metatarsal	This work
AIE-19138	Agua chica	3940	−19.9	Radius	This work
AIE-19144	Taire	4021	−19.3	Vertebrae	This work

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recovered from discard areas in or near the settlements, except for the Cieneguillas samples which were obtained from llamas sacrificed for making an economic anatomy study.

The sample preparation for isotopic $\delta^{13}C_{COL}$ measurements followed the procedures described by Tykot (2004). In the first place, physical cleaning was performed followed by an ultrasonic wash. The next step involved the elimination of humic acids with sodium hydroxide at 0.1 M dilution for 24 hours before and after the demineralisation. For the collagen extraction, the bone was demineralised in 2% hydrochloric acid for 72 hours. The isotopic ratio ($\delta^{13}C/\delta^{12}C$) measurement was performed at the INGEIS facilities using a Finnigan MAT mass spectrometer with a triple collector.

New $\delta^{13}C_{COL}$ isotope data: trends and patterns in Lama glama

Published and new isotopic values obtained are shown in Table 2. Figure 5 shows the altitudinal distribution of isotopic values. Three box-plots summarise the isotopic values obtained for samples from both altitudinal ranges (Figures 6, 7, 8). Figure 6 displays the 17 new measurements, while Figure 7 shows the 12 previously available (Fernández & Panarello, 1999–2001), and Figure 8 joins both data-sets ($n = 29$).

No substantial latitudinal variation in isotopic values was recorded from Lapao and Cieneguillas samples (both from less than 3700 m.a.s.l.). On the other hand, a strong variation in the values can be observed between samples obtained in llamas from Taire and Agua Chica (>3900 m.a.s.l.) and those from Lapao and Cieneguillas (<3900 m.a.s.l.), showing a relevant pattern in the values obtained at different altitudes. There were significant non-overlapped distributions, with mean values separated by −1.6‰ ($\mathrm{Mean}_{>3900masl} = -19.5$‰; $\mathrm{Mean}_{<3900masl} = -17.9$‰). The published information shows the same pattern (Figure 7) ($\mathrm{Mean}_{>3900masl} = -20.4$‰; $\mathrm{Mean}_{<3900masl} = -17.3$‰), although the dispersion of this data-set is noticeably greater when comparing their standard deviations ($SD_{>3900masl} = 0.779$; $SD_{<3900masl} = 1.845$; $n = 12$) with those obtained by us ($SD_{>3900masl} = 0.262$; $SD_{<3900masl} = 0.735$; $n = 17$) (Figure 6).

Pooling our data with the previous sample (Figure 8), the variation in isotopic values shows more than −2‰ of difference for each 500 m increase in altitude ($\mathrm{Mean}_{>3900masl} = -20.1$‰; $\mathrm{Mean}_{<3900masl} = -17.7$‰), with those samples of higher altitude more depleted. The statistical significance was tested by one-way ANOVA ($F = 7.94$, $P = <0.001$), supporting a significant mean difference in the distributions of isotopic values between both altitudinal ranges.

If we consider the altitude as a continuum, an inverse correlation between altitude and isotopic

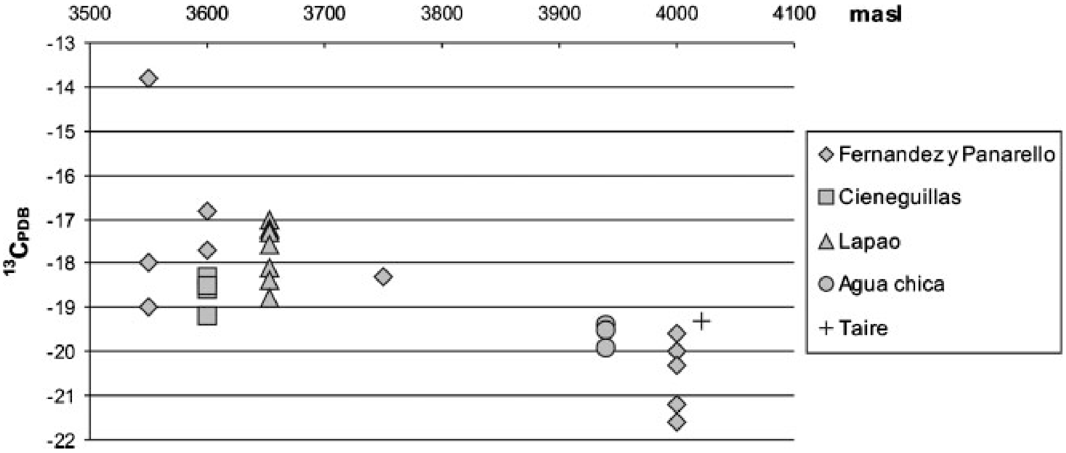

Figure 5. Altitudinal distribution of $\delta^{13}C_{PDB}$ values for the samples in this study.

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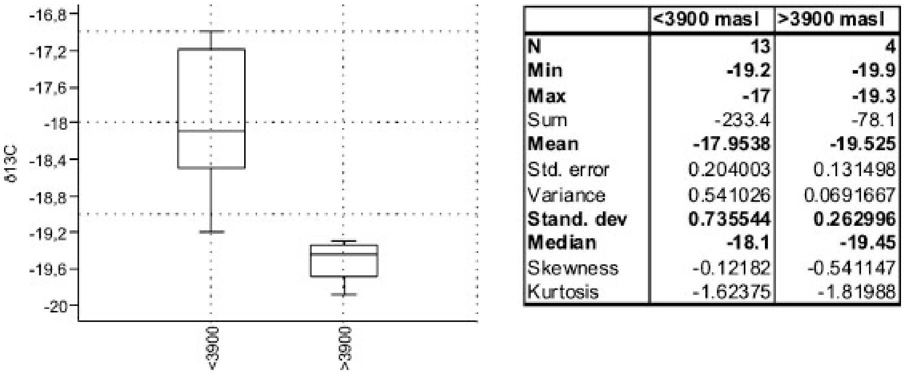
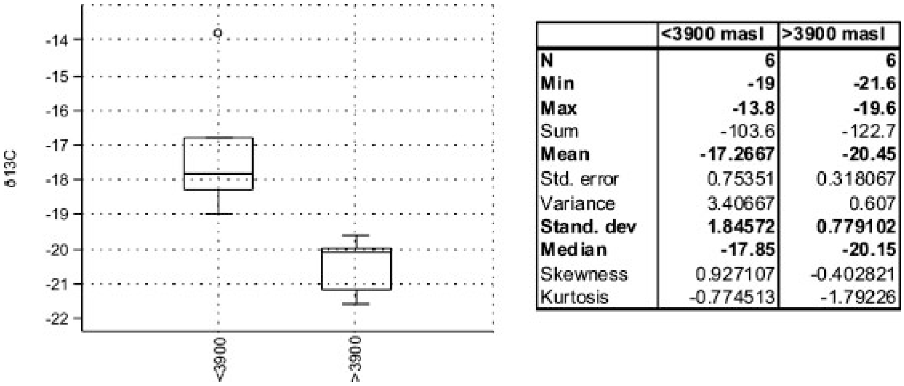


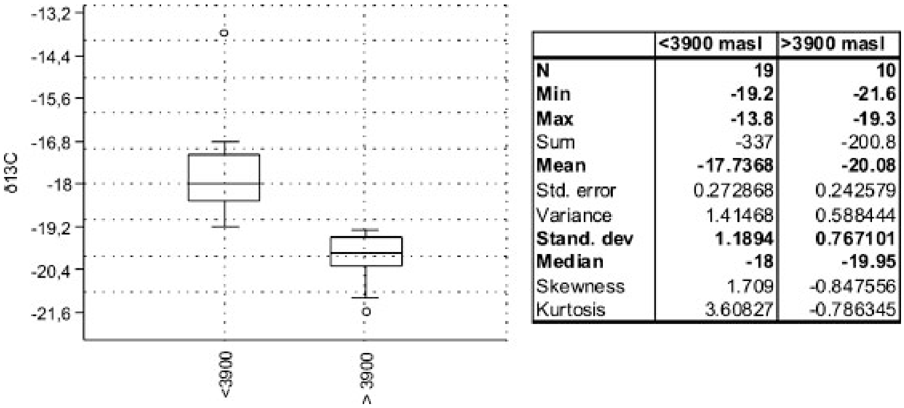
	<3900 masl	>3900 masl
N	**13**	**4**
Min	**-19.2**	**-19.9**
Max	**-17**	**-19.3**
Sum	-233.4	-78.1
Mean	**-17.9538**	**-19.525**
Std. error	0.204003	0.131498
Variance	0.541026	0.0691667
Stand. dev	**0.735544**	**0.262996**
Median	**-18.1**	**-19.45**
Skewness	-0.12182	-0.541147
Kurtosis	-1.62375	-1.81988

Figure 6. Box-plot of the distribution of δ^{13}C values for the samples in this study.



	<3900 masl	>3900 masl
N	**6**	**6**
Min	**-19**	**-21.6**
Max	**-13.8**	**-19.6**
Sum	-103.6	-122.7
Mean	**-17.2667**	**-20.45**
Std. error	0.75351	0.318067
Variance	3.40667	0.607
Stand. dev	**1.84572**	**0.779102**
Median	**-17.85**	**-20.15**
Skewness	0.927107	-0.402821
Kurtosis	-0.774513	-1.79226

Figure 7. Box-plot of the distribution of δ^{13}C values from the previous study by Fernandez & Panarello (1999–2001).



	<3900 masl	>3900 masl
N	**19**	**10**
Min	**-19.2**	**-21.6**
Max	**-13.8**	**-19.3**
Sum	-337	-200.8
Mean	**-17.7368**	**-20.08**
Std. error	0.272868	0.242579
Variance	1.41468	0.588444
Stand. dev	**1.1894**	**0.767101**
Median	**-18**	**-19.95**
Skewness	1.709	-0.847556
Kurtosis	3.60827	-0.786345

Figure 8. Box-plot of the δ^{13}C values from the previous study combined with this study ($n=29$).

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values is also supported by a Pearson correlation coefficient ($r = 0.7424$, $P < 0.001$), suggesting a possible linear trend between them. Another interesting pattern emerges when we compare the variance of the samples at both latitudes in the new and published data. The variance values in new data ($\mathrm{Var}_{<3900\mathrm{masl}} = 0.54$ and $\mathrm{Var}_{>3900\mathrm{masl}} = 0.069$) show more clustered values than the more sparse ones from Fernández & Panarello (1999–2001) ($\mathrm{Var}_{<3900\ \mathrm{masl}} = 3.4$ and $\mathrm{Var}_{>3900\mathrm{masl}} = 0.6$). This probably reflects the absence of dietary complements in the foddering of the individuals from the herds analysed by us, or greater mosaic diversity in vegetal communities in the northeast Puna area (Fernández & Panarello, 1999–2001). Nevertheless, in both cases and consequently in the pooled data ($\mathrm{Var}_{<3900\mathrm{masl}} = 1.414$ and $\mathrm{Var}_{>3900\mathrm{masl}} = 0.599$), the values above 3900 m.a.s.l. show reduced variance values compared with those located below this altitude, reflecting the differential distributions in plant communities which have a higher presence of Compositae (a greater abundance of shrub genera) and Cactaceae below 4000 m.a.s.l.

Discussion

The detectable difference in the isotopic values between the two altitudinal ranges considered sets some methodological questions to be answered, but also, and more importantly, has a variety of interesting implications for archaeological problems. We recorded a differential pattern in $\delta^{13}C_{COL}$ isotopic values from domestic camelids related to the altitude where they had been feeding. Is the difference in vegetal composition the exclusive cause of the isotopic variation between both altitudinal ranges? Probably not, since the differences in environmental variables (i.e. precipitation, temperatures and insolation) at both ranges could be affecting the intra-specific values of plants in a moderate way (Cavagnaro, 1988; Bocherens *et al*., 1995). At first sight, a difference of −2‰ in the llama values from these areas supports the incidence of these environmental variables.

An interesting point addressed in this research is how biased would these data be in relation to human intervention in pastures, for example, by the inclusion of foreign grasses in camelid diet. The compact clusters found in our data at both altitudinal ranges and the narrow variability between different localities of the same altitude seems to rule out this problem. An outlier value of −13.8‰ obtained by Fernández & Panarello (1999–2001) may show human intervention in the feeding, and was probably obtained from an animal that was being foddered with C_4 plants, perhaps maize.

Considering the archaeological implications of this study, we can point out several aspects regarding the isotopic study of past human diets. Of course, human diet was not only composed of camelids, but they have proven to be the most important source of animal proteins in the Andes, at least in the past 8000 years (Yacobaccio, 2004). Consequently, and taking into account that several other important elements in the diet must be considered, such as maize (Tykot *et al*., 2006), we think that the identified pattern will help us to understand isotopic signatures, while improving the interpretation of those values obtained from human tissues (Olivera & Yacobaccio, 1999).

Furthermore, these results allow us to address more particular archaeological topics. Altitudinal variations in isotopic values of llamas could help us to establish past herds' foraging radius and pasture management, implying a deeper knowledge of mobility patterns and risk management strategies by pastoralist societies in the past. Regarding this and several other archaeological problems, multi-scale palaeoenvironmental studies have been carried out by us in the Dry Puna (Morales, 2004; Yacobaccio & Morales, 2005). These studies might help us to isolate human intervention in pasture management from the isotopic changes climatically modelled. We consider that only intense and, more importantly, sustained environmental changes are the main reason for substantial modifications in vegetal arrangements, such as altitude adjustments in ecotonal ranges (Morales, 2004; Yacobaccio & Morales, 2005). Taking this into account, we consider that isotopic values in zooarchaeological llama remains can also be used as a proxy data for identifying environmental modifications. More depleted or enriched values than those expected in the same altitudinal range could reflect a displacement of vegetal zone boundaries and, consequently, environmental modifications and changes in the composition of the available pastures. We consider the future possibility of measuring values of $\delta^{15}N$ on bone collagen from archaeological specimens because, as has been recorded in other regions of the world, enriched $\delta^{15}N$ values may show more arid conditions (Sillen *et al*., 1989). These data will help us to deal with the influence of long-term and directional environmental modifications affecting the spatial distribution of plant communities on a regional scale, and consequently to tell apart the role of human intervention in camelid diet in the past.

Conclusions

The data presented in this paper allow us to detect a negative correlation between altitude and $\delta^{13}C_{COL}$ values of *Lama glama*. This correlation might be explained by the varying isotopic signal of plant communities at different elevations (Tieszen *et al*., 1979). Protein content of plants is a key factor to measure the quality of forage, although fibre is also important, because llamas select plants with high fibre content to improve their digestibility (Benítez, 2005; Benítez *et al*., 2006). Therefore, llamas' plant selectivity includes a wide range of species, which are representative of the plant community at certain altitudinal ranges and, consequently, the isotopic values of bone collagen are independent of their feeding selectivity. Nevertheless, these values are indicative of the diet along the time-span comprised in the turnover of bone collagen. On the other hand, we know that seasonal variation in llama foraging settings could also have an effect on the isotopic signal. Although this issue cannot be evaluated with the data currently available, we hope tackle it in the future by analysing fatty acids ($C_{16:0}$, $C_{18:0}$) of lipids, which are short-term indicators of the actual diet (Copley *et al*., 2004). These patterns could be used as frames of reference for the study of prehistoric herding practices, in which the range of mobility between different altitudes is still unknown.

In order to pursue this line of analysis, the generation of isotopic values from archaeological bone specimens is the next step for studying the development of early camelid herding and the diversification of management strategies, as have been recently demonstrated for caprines in Southwest Asia (Pearson *et al*., 2007). Also, the isotopic values from archaeological bones will improve their interpretative potential if they rest over a robust corpus of current isotopic herbivory study.

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