



Environmental diversity and stable isotope variation in faunas: Implications for human diet reconstruction in Argentine mid-latitude deserts



Clara Otaola^{a,*}, Andrew Ugan^b, Adolfo F. Gil^a

^a CONICET-IANIGLA Grupo Vinculado San Rafael/Museo de Historia Natural de San Rafael, UTN Facultad Regional San Rafael, Centro Tecnológico de Desarrollo Regional Los Reyunos, Parque Mariano Moreno, San Rafael, Mendoza, Argentina

^b Far Western Anthropological Research Group, Museo de Historia Natural de San Rafael, San Rafael, Mendoza, Argentina

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ABSTRACT

This paper presents the results of an isotopic study of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for bone collagen from 209 modern faunas from central-western Argentina. The samples come from two ecologically distinct areas: the Monte and Patagonian Deserts. The results confirm high intra- and inter-taxonomic variation in both isotopes. Previous studies of camelids, rodents and ostrich eggshells in this region showed a clear relation between animal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, altitude, and the percentage of C_3 and C_4 plants. This pattern was not fully met among the species considered in this paper. No statistical differences were seen between $\delta^{13}\text{C}$ values from Monte and Patagonian Deserts, although differences in $\delta^{15}\text{N}$ were found. When samples from saltmarsh contexts were considered separately, differences among $\delta^{15}\text{N}$ isotopic values become more pronounced, pointing to a relation between $\delta^{15}\text{N}$ isotopic signatures and soil salinity. Archaeological human diet reconstruction based on isotopic data needs to pay attention to this significant variation in resources isotopic patterns in order to be used as a reliable dietary indicator.

1. Introduction

The stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of plants and animals available for human consumption in a given environment provide a basis for inferring human diets, resource exploitation, and mobility (Ambrose and DeNiro, 1986; Weber et al., 2011; Sandias and Müldner, 2015; Salazar-García et al., 2014). These data must be obtained locally and with reference to the archaeological problem at hand, since vegetal and animal isotopic values vary depending on climate, nutrient availability, type of soils, the existence of marine or terrestrial isotopic reservoirs, and physiological adaptations (Bocherens et al., 2015a, 2015b; Casey and Post, 2011; Koch, 1998, 2007; Martínez del Río et al., 2009; Newton, 2010; Rubenstein and Hobson, 2004; Samec et al., 2014; Szpak et al., 2014; Ugan and Coltrain, 2011). In order to make accurate inferences concerning human diet using isotopic information, one needs to know something about variation in resource stable isotope values in the area where samples come from.

Isotopic evidence used to discuss past human behavior in Central-western Argentina has mainly focused on the introduction of maize agriculture and interactions between foragers and farmers (Gil et al., 2010; Gil et al., 2011; Gil et al., 2014). Other issues such as human mobility (Giardina et al., 2014a; Neme et al., 2015; Ugan et al., 2012),

climate changes, and geographic variability in resource isotope values (Fernández et al., 2016; Gil et al., 2016) have been incorporated recently, and more refined models of human diet using mixing models have been used (Giardina et al., 2014b; Bernal et al., 2016). All of these analyses have been based on relatively few floral or faunal resources, often averaging values across ecosystems and over time. More extensive datasets have been limited to various cactaceae, rodents, and camelids (Gil et al., 2016; Fernández et al., 2016; Llano and Ugan, 2014). This weak isotopic baseline is problematic (Post, 2002; Casey and Post, 2011; Phillips et al., 2014) and more clearly risky in areas of high environmental diversity such as Central-western Argentina. This region exhibits altitudinal variation in climate, hydrology, and vegetation, all of which may influence the isotopic signatures of floral and faunal communities. These differences are seen in the two contiguous phyto-geographic areas present in this region: the Monte and Patagonian Deserts. In order to accurately characterize the isotopic ecology of Central-western Argentina as a whole, it is important to consider variation in the stable isotope signatures of resources within these two deserts (Fig. 1). The objective of this paper is to analyze $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from the bone collagen of additional animal species not considered before and to explore variation in their isotopic values in relation to environmental differences associated with the two deserts.

* Corresponding author.

E-mail addresses: claraotaola@conicet.gov.ar (C. Otaola), agil@mendoza-conicet.gov.ar (A.F. Gil).

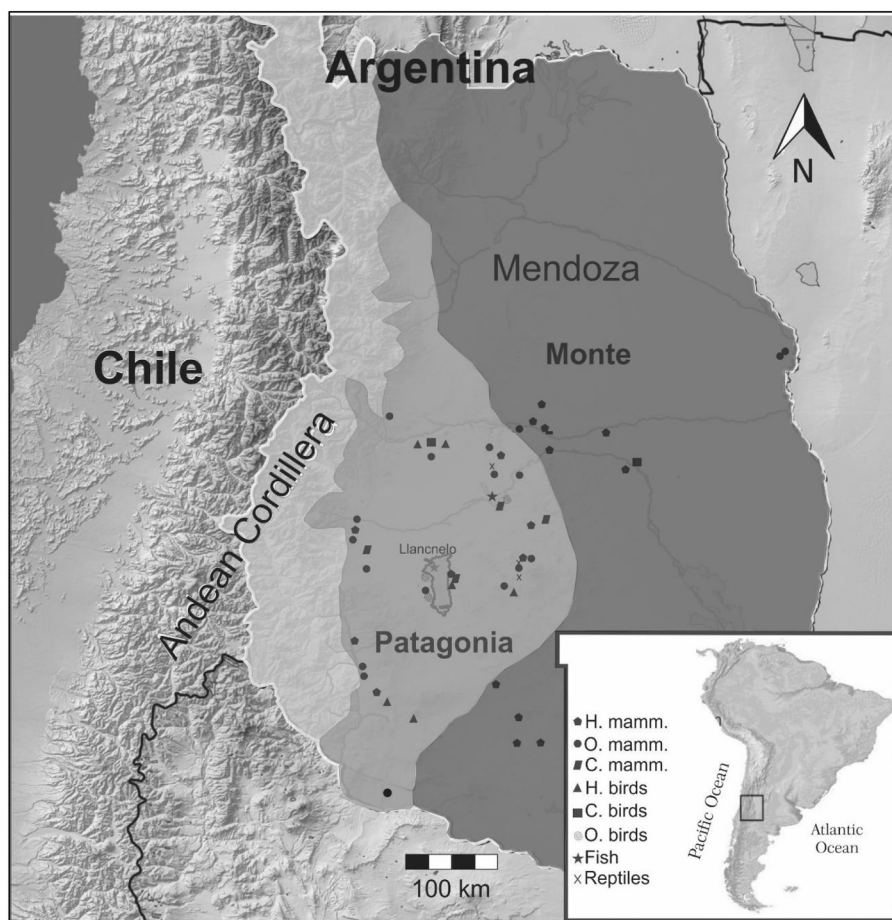


Fig. 1. Provenience of the faunal samples and the Monte and Patagonian Deserts. “H” herbivorous, “O” omnivorous, “C” carnivorous, and “Mamm” mammal.

2. The study area

Our area of focus is southern Mendoza (34° – 37° SL), in Central-western Argentina (Fig. 1). The climate in this region is continental, with warm temperatures in lowland areas, cold temperatures at higher elevations, and marked seasonal changes. Annual precipitation ranges from 200 mm in the lowlands to over 1000 mm in the upper cordillera (Norte, 2000). Differences in precipitation reflect differences in relief, the dominant masses of maritime air, and the season in which precipitation takes place (Abraham and Rodríguez, 2000; Norte, 2000). In the eastern lowlands (Monte Desert) most precipitation falls in the summer, while in the piedmont and Andean cordillera area (Patagonian Desert) precipitation occurs mostly in winter (Norte, 2000). Vegetation differences and phytogeographic provinces generally correspond to the topographic regions that characterize the area. From west to east and high to low these include the Andean, Patagonia and Monte Deserts (Fig. 1) (Abraham et al., 2009; Cabrera, 1976; Roig et al., 2009). Because the Andes rise abruptly, sharp changes in plant and animal communities can occur over short distances. Samples treated in this paper come from the Patagonia and Monte Deserts. Differences in the vegetation, rainfall pattern and temperature of these two desert regions are summarized in Table 1.

The Monte Desert extends across Argentina from the foothills of the Andes in Salta ($24^{\circ}30'$ S) to the Atlantic coast in Chubut ($44^{\circ}20'$ S). The portion of Monte Desert treated in this paper occurs along a lowland plain between 1000 and 325 m a.s.l., extending from the base of the piedmont to the margin of the Río Desaguadero on the eastern edge of the province of Mendoza. The Monte Desert is a temperate region with a rainfall regime produced by a combination of westerlies from the Pacific Ocean, the rain shadow effect of the Andes, and the winds from

Table 1

Principal ecological characteristics of Monte and Patagonian Deserts.

	Patagonia	Monte
Altitude (m a.s.l.)	1000 to 2000	325 to 1000
Mean annual temperature ($^{\circ}$ C) ^a	12.8	15
Mean annual maximum ($^{\circ}$ C) ^a	20.5	26
Mean annual minimum ($^{\circ}$ C) ^a	4.4	7.5
Range of annual precipitations (mm) ^b	120–600	150–300
Precipitation regime ^{ca}	Winter	Summer
Main photosynthetic pathways of grasses ^c	C ₃ (59%)	C ₄ (95%)

^a Gonzalez Loyarte et al. (2009) and historical weather information (1976–2015) published from weather stations from Malargüe and San Rafael airports.

^b Abraham et al. (2009), Paruelo et al. (1998),^{ca}Capitanelli (1972), Norte (2000), and Roig et al. (2000).

^c Cavagnaro (1988) (Area I in his paper for Monte and Area V for Patagonian Desert).

the Atlantic anticyclone, which provide limited humidity due to the great distance to the Atlantic Ocean (Abraham et al., 2009; Labraga and Villalba, 2009). The climate is semiarid to arid, with high evaporation enhanced by windy conditions. Precipitation occurs mainly in summer. Annual rainfall varies between 100 and 350 mm.

The complexity of the biota of the Monte Desert results from the extensive area of contact between the two principal biotas of South America: Brazilian biota (or tropical biota) and Patagonian biota (Roig et al., 2009). The vegetation of this biome is rather uniform in terms of its floristic composition. Creosote shrub steppes dominated by *Larrea* spp. are the typical landscapes (Abraham et al., 2009; Roig et al., 2009).

These are usually interspersed with a range of other xeric taxa including CAMS (Crassulacean Acid Metabolism) photosynthesizing columnar cacti (locally termed *cardones*), opuntia, and various bunch grasses. Most grasses found in this region are C₄ photosynthesizers, as is at least one species of widely distributed chenopod, the South American salt-bush (*Atriplex lampa*). The other characteristic plant community of the Monte is the algarrobal, a mesquite woodland of *Prosopis flexuosa* or *P. chilensis* (Roig, 1972) which occurs in open areas where ground water is accessible (Cabrera, 1976). These leguminous shrubs or trees can reach 8 to 10 m in height (Roig et al., 2000) and are C₃ photosynthesizers.

The fauna found in the Monte are typically what are considered plains fauna (*fauna de las llanuras*; Roig, 1972), which includes mammals such as wild cats (*Oncifelis geofroyi*), armadillos (Dasipodidae), puma (*Felis concolor*), guanacos (*Lama guanicoe*), and rodents of different sizes such as Patagonian mara (*Dolichotis patagonum*), mountain viscacha (*Lagidium viscacia*), plains viscacha (*Lagostomus maximus*), southern cavy (*Microcavia australis*), yellow-tooth cavy (*Galea luoblephara*), Andean akodon (*Akodon andinus*), and gray leaf-eared mouse (*Graomys griseiflavus*), among others. Other common taxa include birds such as the greater rhea (*Rhea americana*), elegant tinamou (*Eudromia elegans*), and various falconiforms, columbiforms, and passeriforms. A number of reptiles, particularly liolaemid lizards and the Chaco tortoise (*Liolaemus* sp., *Chelonoidis chilensis*), are also found in this area.

The transition to Patagonian Desert reflects changes in the influence of Pacific air masses (Paruelo et al., 1998) and a gradual shift from summer dominant to winter dominant rainfall (Prohaska, 1976). The Patagonian Desert extends from the Andean precordillera of Mendoza to northern Tierra del Fuego (35° S to 54° S) (Cabrera, 1971; Morrone et al., 2002). Within the study area it occurs in a transitional piedmont fringe of late Cenozoic alluvial fans that border the Andes between 2000 and 1000 m.a.s.l. These produce a series of gently sloping surfaces where the present fluvial system is degraded and represent a transitional unit between the mountains and the plains. Vegetation of this piedmont fringe is generally considered part of the Patagonian phytogeographic province. It borders the Andean vegetation province on its western margin and forms an ecotone with the Monte Desert in the east (Fig. 1). The vegetation of the Patagonian Desert is characterized by shrub steppe, psammophilous xeric grasses (*coirones*) in sandy areas and dunes, and relict gallery forests of molle (*Schinus* spp., Cabrera, 1971; Roig et al., 2000). Most vegetation is characterized by C₃ photosynthesis. Zoogeographically this region includes montane fauna and fauna of the Patagonian steppe (*Fauna de Montaña* and *Fauna de la Estepa Patagónica*). These faunas consist of large mammals like the puma and guanaco, medium size mammals like plains viscacha, mountain viscacha, red fox (*Lycalopex culpaeus*), and Patagonian mara (*Dolichotis patagonum*). It also includes flightless birds like the Lesser Rhea (*Rhea pennata*), migratory birds that live in small lagoons and creeks (e.g., *Anas* sp. and *Chloephaga picta*), and scavenger birds such as *Vultur gryphus*.

3. Carbon and nitrogen isotopes as dietary indicators

In terrestrial foodwebs, variation in carbon isotope ratios begins with plants. When CO₂ is taken up by plants during photosynthesis, metabolic processes alter the ratio of ¹³C/¹²C, depleting plant tissues in ¹³C relative to the atmosphere. Carbon isotope fractionation depends primarily on which of three photosynthetic pathways (C₃, C₄, CAM) a plant uses to metabolize carbon dioxide. Most plants use C₃ photosynthesis (the Calvin Cycle). The process discriminates most strongly against heavy carbon isotopes and plants using the Calvin Cycle have tissues with an average $\delta^{13}\text{C}$ value of $-26.7 \pm 2.7\text{‰}$. A small set of forbs, bushes, and tropical grasses including maize, various millets, and sugarcane use C₄ (Hatch-Slack) photosynthesis. This path discriminates less against heavy carbon isotopes and produces average $\delta^{13}\text{C}$ values of $-12.5 \pm 1.1\text{‰}$. Another small number of species exhibit a third photosynthetic pathway, Crassulacean acid metabolism (CAM; Lambers

et al., 2008:75–81). Cacti and some members of the Agavaceae (yucca and agaves) use the CAM pathway, which can shift between C₃ and C₄ photosynthesis and produce varying isotope signatures ($\delta^{13}\text{C}$ -27‰ to -12‰).

While photosynthetic pathway is the major determinant of $\delta^{13}\text{C}$ values in terrestrial plants, their values also vary depending on soil salinity, temperature and water availability as they affect evapotranspiration and water-use efficiency (Ben-David and Flaherty, 2012). The process observed in salinity stressed plants is that salt stress causes partial closing of stomata, resulting in lower partial ¹²C pressure, leading the plant to assimilate more ¹³CO₂ and making $\delta^{13}\text{C}$ signatures of the newly formed plant tissue less negative (van Groenigen and van Kessel, 2002). Aridity has a similar influence on isotope values. It has been shown that there exists a negative correlation between mean annual precipitation and plant $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Weiguo et al., 2005; Hartman and Danin, 2010). Plant stomatal conductance is reduced with aridity, and this produces the concentration of $\delta^{13}\text{C}$ (Farquhar et al., 1989).

Regarding nitrogen cycles in terrestrial environments, this element enters the trophic chain from the absorption of soil NH₄⁺ and NO₃⁻, or through fixation of atmospheric N₂ via symbiosis with nitrogen-fixing bacteria in plants or living in the soil (Ambrose, 1991; Virginia and Delwiche, 1982). Among the different factors that can influence variation in nitrogen isotope values, research points to aridity, mean annual temperatures, and soil salinity (Pate, 1994; van Groenigen and van Kessel, 2002). There is a general pattern across the globe of ¹⁵N enrichment in soils and plants with increasing aridity (Aranibar et al., 2004; Austin et al., 1999; Díaz et al., 2016; Handley et al., 1999; Heaton, 1987; Schulze et al., 1998). The pattern of ¹⁵N enrichment of soils and plants observed with increasing aridity is thought to reflect the degree of “openness” in the nitrogen cycle (N losses relative to internal N cycling; Handley et al., 1999; Amundson et al., 2003). In arid environments, the input of atmospheric N₂ to the soil is low and $\delta^{15}\text{N}$ values of soils is high (Ambrose, 1991). In dry soils and soils with high pH and high temperatures, soil $\delta^{15}\text{N}$ increases because of the preferential volatilization of ¹⁴NH₃ (Ambrose, 1991). Other research shows a positive correlation between plant $\delta^{15}\text{N}$ values and mean annual temperatures (Amundson et al., 2003) and saline soils. With regard to the relation between soil salinity and $\delta^{15}\text{N}$ values, van Groenigen and van Kessel (2002) hypothesize that the enrichment observed in plants living in salty soils might be because of higher NH₃ volatilization caused by high pH combined with a relative increase of NH₄⁺ uptake by the plant under saline conditions.

4. Expectations for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in Monte and Patagonian faunas

As outlined in the previous section, isotopic signals in terrestrial faunas depend mainly on the isotopic composition of the plants that form the base of the food chain. All sources of isotope variation in plants are passed up the food chain (Cormie and Schwarcz, 1996; Hartman, 2011; Pate and Anson, 2008; Stevens et al., 2006 among others), leading to $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ enrichment (DeNiro and Epstein, 1981; Ambrose and Norr, 1993). The isotopic values of herbivore tissues correlate positively with the values of the plants they eat (Ambrose, 1991), carnivore tissues reflects the isotopic values of the protein derived from the herbivorous animals consumed and omnivores reflect the isotopic values of both plants and animals of their diet (Ambrose, 1991). The offset associated with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ enrichment is called tissue-diet discrimination factor (TDF).

There is variation in the literature concerning the TDF in $\delta^{13}\text{C}$ for various taxa and diets. Different researchers have found a range from +1‰ to +5‰ $\delta^{13}\text{C}$ enrichment for different types of food resources, though more substantial differences have been measured where the protein and carbohydrate components of the diet differ substantially (Bocherens and Drucker, 2003; Tykot et al., 2009; Frohele et al., 2010;

Hare et al., 1991). For $\delta^{15}\text{N}$, it is known that differences between consumers and their diets range from 3 to 5‰. Most animals, including humans, exhibit an approximately +3‰ shift in $\delta^{15}\text{N}$ values relative to their diet (Ambrose, 2000; Frohele et al., 2010; Hedges and Reynard, 2007; Pate, 1994; Schoeninger and DeNiro, 1984; but see O'Connell et al., 2012, Szpak, 2014).

Given the close relationship between consumers and their diet, the key factor that determines $\delta^{13}\text{C}$ values in animals is the distribution of C_3 and C_4 plants (Van der Merwe and Vogel, 1978; De Niro and Epstein, 1978). Ecological research in Mendoza shows an inverse relationship between altitude and C_4 grass frequency (Cavagnaro, 1988; Llano, 2009). There is a dominance of C_3 plants over C_4 plants between 2200 and 1500 m a.s.l. (58.9% C_3 vs. 41.1% C_4), the same altitude associated with the Patagonian Desert, and an increased availability of C_4 plants below 600 m a.s.l. (in Monte Desert) (95.5% C_4 ; 4.5% C_3) (Cavagnaro, 1988). There is also a correlation between the seasonal distribution of precipitation and C_3 and C_4 plants (Cabido et al., 2008), with C_4 plants most common in areas with summer-dominant rainfall like the Monte Desert (53 to 80% of the total annual rainfall; Cabido et al., 2008), and C_3 plants most common in areas with winter-dominant rainfall, such as the Patagonian Desert.

Considering the differences in altitude, and the mentioned studies about the ecology and spatial distribution of photosynthetic patterns in our area of study (Cavagnaro, 1988; Cabido et al., 1997; Cabido et al., 2008), animals feeding in the Monte Desert (less altitude, less water availability, greater availability of C_4 plants) should have more positive $\delta^{13}\text{C}$ values than those feeding in the Patagonian Desert. These expectations are at least partially supported by previous studies in the area. In Central-western Argentina, camelids primarily residing in the Monte Desert have, were found to have higher $\delta^{13}\text{C}$ values than those from Patagonian or Andean contexts (Gil et al., 2016), and a similar trend has been observed in studies of rodents and ostrich eggshells (Fernández et al., 2016; Giardina et al., 2014a). Camelids in the dry Puna of Argentina and in Central-western Argentina also show a negative correlation between altitude and carbon values (Samec, 2014; Samec et al., 2017; Yacobaccio et al., 2009, Gil et al., 2016). The higher $\delta^{13}\text{C}$ values have also been attributed to differing abundance of C_3 and C_4 plants, being the latter less abundant in the higher elevation areas (Samec et al., 2017; Cavagnaro, 1988).

Though less well studied, a similar pattern is expected for differences in $\delta^{15}\text{N}$ values. Lowland vegetation should have higher $\delta^{15}\text{N}$ values due to increased aridity and a more open nitrogen system (Samec et al., 2017; Gil et al., 2016), while animal values should be more positive as a consequence. This same trend has been noted in the $\delta^{15}\text{N}$ values of camelids in the dry Puna of northwestern Argentina (Samec, 2014; Samec et al., 2017; Yacobaccio et al., 2009).

5. Isotope samples and sample pretreatment

This stable isotope data ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) presented here come from 209 samples of modern animal bone. They include 26 different taxa (mammals, birds, fish and reptiles) distributed across both Monte ($n = 67$) and Patagonia ($n = 142$) deserts (Fig. 1). The samples come from various contexts, including animals provided by local herders (*puesteros*), rural police or park rangers, and others collected by ourselves during archaeological field work. All of them represent surface finds and most of them were skeletonized by the time we collected them. Extraction of bone collagen and apatite was mostly performed in the Museo de Historia Natural de San Rafael (sample code MSR, Supplementary material) and the Laboratory for Archaeological Science at the University of South Florida (code USF; Gil et al., 2010; Tykot, 2004, Table 1, Supplementary material). They were measured at the University of Wyoming Stable Isotope Facility and the Stable Isotope Ratio Facility for Environmental Research (SIRFER) at the University of Utah.

For each sample we cleaned approximately 1 g of cortical bone. The bone was then demineralized whole in 0.6 N HCl at 4 °C, changing the

acid daily until the supernatant became clear and homogeneous. After demineralization the collagen pseudomorph was rinsed to neutrality and treated with 5% KOH to remove organic contaminants and residual lipids, again changing the supernatant daily. The cleaned collagen pseudomorph was then rinsed to neutrality, lyophilized, and weighed to obtain an initial collagen yield. Approximately 100 mg of lyophilized collagen was retained for analysis and the rest was archived. The 100 mg sample was gelatinized in 5 ml of acidified water (pH 3) for 24 h at 120 °C. Water soluble and water insoluble phases were separated by filtration through a 0.45 mm poly vinylidene fluoride (PVDF) filter, the water soluble phase lyophilized, and a final collagen yield calculated. Additional details on methods can be found in Coltrain (1993) and Coltrain et al. (2006).

Collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were determined by flash combustion to produce CO_2 and N_2 . The resulting gases were analyzed using a Finnigan Delta Plus isotope ratio mass spectrometer (Finnigan, Bremen, Germany) coupled with a Carlo Erba Model 1110 elemental analyzer (Carlo Erba, Milan, Italy) through a CONFLO III open split interface (Finnigan, Bremen, Germany). Measurements were taken at the Stable Isotope Ratio Facility for Environmental Research (SIRFER). Stable carbon and nitrogen isotopic compositions were calibrated relative to VPDB and AIR scales using USGS40 and USGS41. Both stable isotope measurements and sample weight percent carbon and nitrogen were obtained from a single sample combustion. Analytic precision is 0.1‰ for carbon isotope ratios (VPDB) and 0.2‰ for nitrogen (AIR). C:N ratios for most specimens were in the range of 3.1 to 3.6, indicating generally excellent preservation (Ambrose, 1991).

All specimens presented in this paper are modern samples (after year 2000) and we make comparisons among samples which might have no more than ten years old. Modern $\delta^{13}\text{C}$ values are $\approx 2\%$ more negative than archaeological organisms which grown before fossil fuel depletion of atmospheric CO_2 (Bada et al., 1990; Long et al., 2005). If they are used to compare with isotopic data of fossil samples it is necessary to correct the $\delta^{13}\text{C}$ values for the so-called 'Industrial' or 'Suess' effect (Friedli et al., 1986) which has altered global isotopic ratios by introducing carbon derived from fossil fuels, depleted in ^{13}C , to the atmosphere (Sealy and van der Merwe, 1992). When modern samples are considered and we want to compare them with archaeological samples, it is recommended to adjust the $\delta^{13}\text{C}$ isotopic values following a formula which takes into account the year of death of the animal (Feng, 1998; Bocherens et al., 2015a, 2015b). In the present paper, most of the samples had been collected in the field skeletonized. So, in most of the cases we do not have the information of the year of death of each sample. For that reason, we just compare modern values without the correction but in Table 1 of Supplementary material we add a column with the Suess effect adjusted but estimated like +2‰.

Isotopic differences among regions and environmental zones were evaluated using non-parametric tests due to the lack of normality in the sample distributions (Shapiro-Wilk test for normal distribution was performed). Statistical analyses (Kolmogorov-Smirnov, Kruskal-Wallis and Mann-Whitney pairwise comparisons) used in the present paper were performed using PAST3.18 Software (Hammer et al., 2001).

6. Results

Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and standard deviations for each species are presented in Table 2, while summary descriptions for each species are provided in the Supplementary information section at the end of this paper. Isotopic values are presented by species, grouped by class and feeding behavior (carnivorous birds, omnivorous birds, herbivorous birds, carnivorous mammals, omnivorous mammals, herbivorous mammals, fish, and reptiles). We then present a comparison among mammalian samples from Monte and Patagonian Deserts, aggregating those samples by feeding behavior. This is the only taxonomic class with a sufficiently large and comparable number of samples from each desert.

Table 2
Descriptive statistics for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values by taxonomic group and feeding behavior.

Class	Feeding behavior	Taxon	Total				Patagonian Desert				Monte Desert							
			n	$\delta^{13}\text{C}_{\text{col}}$ (VPDB)		$\delta^{15}\text{N}_{\text{col}}$ (AIR)		n	$\delta^{13}\text{C}_{\text{col}}$ (VPDB)		$\delta^{15}\text{N}_{\text{col}}$ (AIR)		n	$\delta^{13}\text{C}_{\text{col}}$ (VPDB)		$\delta^{15}\text{N}_{\text{col}}$ (AIR)		
				Mean (‰)	Sd	Mean (‰)	Sd		Mean (‰)	Sd	Mean (‰)	Sd		Mean (‰)	Sd	Mean (‰)	Sd	
Mammals	Carnivore	Canidae	1	-17.3	–	5.5	–	1	-17.3	–	5.5	–	0	–	–	–	–	
		<i>Felis concolor</i>	6	-17.4	1.2	8.2	1.3	3	-17.3	1.8	7.0	0.2	3	-17.4	0.4	9.4	0.1	
		<i>Lycalopex culpaeus</i>	3	-20.2	0.6	6.9	0.9	3	-20.2	0.6	6.9	0.9	0	–	–	–	–	
		<i>Lycalopex griseus</i>	8	-18.4	1.4	7.5	1.3	4	-18.9	1.5	7.3	1.1	4	-17.9	1.4	7.7	1.5	
		<i>Oncifelis geofroyi</i>	5	-18.1	0.3	7.6	0.5	1	-17.8	–	6.7	–	4	-18.2	0.2	7.8	0.2	
		<i>Conepatus chingue</i>	3	-17.4	1.2	8.5	0.3	0	–	–	–	–	3	-17.4	1.2	8.5	0.3	
	Carnivore Mam. subtotals			26	-18.2	1.3	7.6	1.1	12	-18.6	1.6	6.9	0.8	14	-17.8	0.9	8.1	1.1
	Omnivore	Dasipodidae	1	-16.1	–	10.8	–	1	-16.1	–	10.8	–	0	–	–	–	–	
		<i>Chaetophractus villosus</i>	6	-18.6	1.4	8.5	1.6	0	–	–	–	–	6	-18.6	1.4	8.5	1.6	
		<i>Zaedyus pichiy</i>	30	-18.8	1.4	6.1	1.5	19	-18.6	1.4	5.7	1.3	11	-19.2	1.4	6.6	1.7	
	Omnivore Mam. subtotals			37	-18.7	1.4	6.6	1.9	20	-18.5	1.4	5.9	1.7	17	-19.0	1.4	7.2	1.9
	Herbivore	<i>Lama guanicoe</i>	4	-20.7	2.5	4.0	0.6	3	-20.4	3	4	0.7	1	-21.6	–	3.9	–	
		Chinchillidae	2	-20.3	0.9	6.2	5.8	2	-20.3	0.9	6.2	5.8	0	–	–	–	–	
		<i>Dolichotis patagonum</i>	5	-20.9	1.8	3.6	1	2	-19.1	0.5	3.7	0.7	3	-22.2	0.9	3.5	1.3	
		<i>Lagidium viscacia</i>	6	-21.1	1.3	3.5	1.5	5	-20.8	1.2	3.5	1.5	1	-22.8	–	4.1	–	
		<i>Lagostomus maximus</i>	24	-18.1	2.5	4.6	2.4	18	-18.5	2.1	4.1	2.4	6	-16.8	3.4	5.9	1.1	
		Cavidae	1	-17.6	–	6.3	–	1	-17.6	–	6.3	–	0	–	–	–	–	
		<i>Microcavia australis</i>	2	-22.4	0.4	3.5	0.2	1	-22.7	–	3.7	–	1	-22.1	–	3.4	–	
		<i>Ctenomys</i> sp.	13	-19.3	3.5	3.8	0.2	10	-21.9	0.5	3.5	0.7	3	-13.1	0.4	4.7	1.2	
<i>Galea leucoblephara</i>		9	-21.7	1.7	4.5	1.9	2	-19.1	1.8	1.6	0.4	7	-22.4	0.6	5.4	1.1		
<i>Myocastor coypus</i>		2	-23.4	0.35	4.6	0.2	2	-23.4	0.3	4.6	0.2	0	–	–	–	–		
Herbivore Mam. subtotals			68	-19.8	2.8	4.3	2	46	-19.9	2.1	3.9	2.1	22	-19.5	3.8	4.9	1.3	
Fish		Omnivore	<i>Percichthys trucha</i>	12	-12.6	1.02	9.1	2	12	-12.6	1.0	9.1	2	0	–	–	–	–
	<i>Odontesthes hatcheri</i>		6	-13.5	1.7	6.1	1.5	6	-13.5	1.7	6.1	1.5	0	–	–	–	–	
	Fish subtotals			18	-12.9	1.3	8.1	2.3	18	-12.1	1.7	8.1	2.3	0	–	–	–	–
Birds	Carnivore	Charadriidae	1	-12.4	–	8.6	–	1	-12.4	–	8.6	–	0	–	–	–	–	
		<i>Cathartes aura</i>	3	-17.7	1.5	11.1	0.4	2	-18.1	1.5	11.3	0.4	1	-16.8	–	10.4	–	
		<i>Milvago chimango</i>	1	-22.0	–	8.6	–	0	–	–	–	–	1	-22	–	8.6	–	
		<i>Phalacrocorax olivaceus</i>	1	-11.3	–	16.9	–	1	-11.3	–	16.9	–	0	–	–	–	–	
	Carnivore birds subtotals			6	-16.4	4.0	11.2	3	4	-15.0	3.8	12.0	3.4	2	-19.4	3.6	9.6	–
	Omnivore	Anatidae	1	-17.3	–	8.1	–	1	-17.3	–	8.1	–	0	–	–	–	–	
		<i>Coscoroba coscoroba</i>	21	-14.8	3.5	9.5	2.8	21	-14.8	3.5	9.5	2.8	0	–	–	–	–	
		<i>Phoenicopterus chilensis</i>	6	-13.0	0.9	11.1	1.6	6	-13.0	0.9	11.1	1.6	0	–	–	–	–	
		<i>Eudromia elegans</i>	4	-19.6	0.5	7.5	1.6	4	-19.6	0.5	7.5	1.6	0	–	–	–	–	
	Omnivore birds subtotals			32	-15.1	3.4	9.4	2.6	32	-15.0	3.4	9.4	2.6	0	–	–	–	–
	Herbivore	Rheidae	3	-22.0	1.1	5.0	1.2	2	-22.1	1.5	5.4	1.4	1	-22	–	4.2	–	
		<i>Rhea americana</i>	5	-21.5	0.8	5.7	1.2	4	-21.8	0.5	5.3	1.1	1	-20.4	–	7.1	–	
		<i>Rhea pennata</i>	8	-22.4	0.9	5.0	1.3	7	-21.2	1	5.7	0.9	1	-22.7	–	7.5	–	
<i>Zenaida auriculata</i>		1	-15.0	–	7.6	–	0	–	–	–	–	1	-15	–	7.6	–		
Herbivore birds subtotals			17	-21.6	1.9	5.3	1.3	13	-22.1	0.9	4.9	1	4	-20	3.4	6.6	1.6	
Reptiles	Herbivore	<i>Chelonoidis chilensis</i>	5	-16.1	4.9	5.4	3.1	0	–	–	–	–	5	-16.1	4.9	5.4	3.1	

6.1. Mammals

6.1.1. Carnivore mammals

There are twenty-six carnivorous mammals included in the sample. The species involved are pumas (*Felis concolor*, n = 6), red and grey foxes (*Lycalopex culpaeus*, n = 3 and *Lycalopex griseus*, n = 8), wild cats (*Oncifelis geofroyi*, n = 5) skunks (*Conepatus chingue*, n = 3), and one canid which could not be classified to species or genus (Fig. 2).

Considering $\delta^{15}\text{N}$ values, Monte samples are more enriched than those from Patagonia, as expected. Monte samples average 8.1‰ and

Patagonia samples 7.0‰. When comparing $\delta^{13}\text{C}$ values from Monte and Patagonia, however, the results are not as expected, and not so clearly differentiated. While overall averages are slightly more positive in Monte settings (–17.7 vs. –18.5‰), the differences are not significant and, at a species level, sometimes reversed. For example, mountain lions from either desert have similar carbon values, while wildcats from the Patagonian Desert are more positive than those from the Monte.

6.1.2. Omnivorous mammals

Samples of this taxonomic group comprise specimens from the

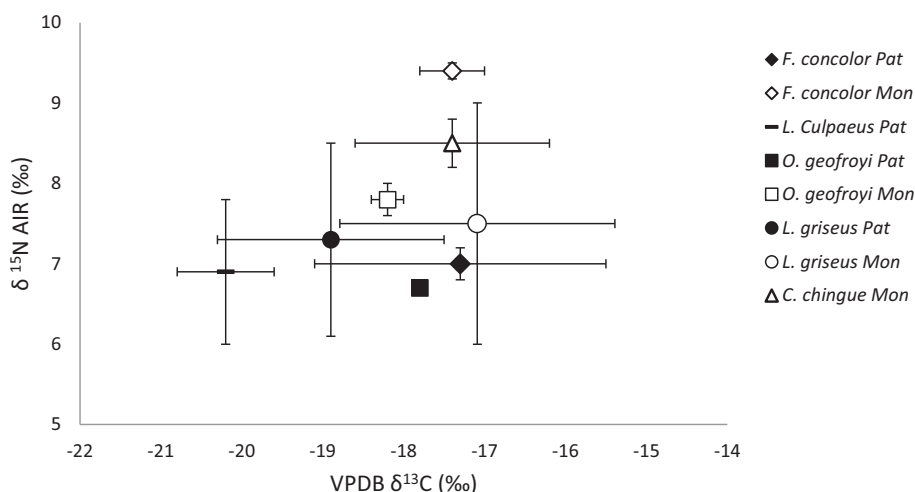


Fig. 2. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and one standard deviation error bars of carnivorous mammal species from Patagonian and Monte Deserts.

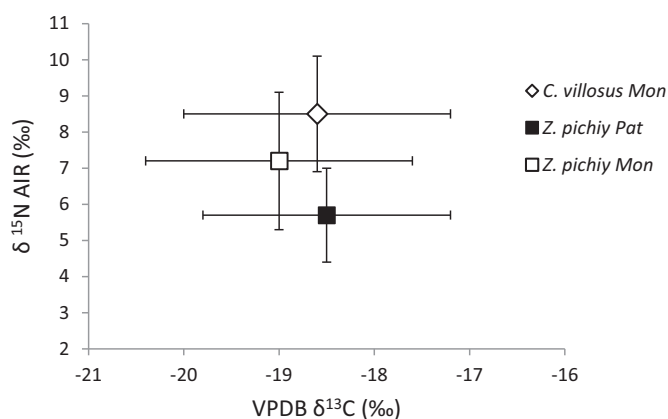


Fig. 3. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and one standard deviation error bars of omnivorous mammal species from Patagonian and Monte Deserts.

Dasipodidae family and include pichy (*Zaedyx pichiy*, $n = 30$) and big hairy armadillos (*Chaetophractus villosus*, $n = 6$). Armadillo $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values vary widely, from -21 to -15.4‰ , and from 4 to 10.8‰ respectively (Fig. 3), perhaps due to the broad geographical distribution of the samples and the fact that they have relatively small home ranges. Trends in armadillos are similar to those observed in carnivorous mammals. Mean $\delta^{13}\text{C}$ values are more negative in Monte rather than Patagonian samples, contrary to what was proposed. Mean $\delta^{15}\text{N}$ values for Monte specimens are more positive, as expected.

6.1.3. Herbivorous mammals

Herbivorous mammals are the best represented sample in this paper ($n = 68$). Included in this group are the most common ungulate in the archaeological record, the guanaco (*Lama guanicoe*, $n = 4$), as well as various rodents from the Chinchillidae, Cavidae and Ctenomidae families. Among the largest rodents are the plains viscacha (*Lagostomus maximus*, $n = 24$), southern viscacha (*Lagidium viscacia*, $n = 6$) and Patagonian mara (*Dolichotis patagonum*, $n = 5$). The smaller rodents include common yellow-toothed cavy (*Galea leucoblephara*, $n = 9$) and southern mountain cavy (*Microcavia australis*, $n = 2$). Some specimens could not be attributed to any Ctenomidae species in particular and have been classified as *Ctenomys* sp. ($n = 13$).

Fig. 4 shows that most of the samples of herbivorous mammals have $\delta^{13}\text{C}$ values between -18 and -22‰ and $\delta^{15}\text{N}$ values between 3.4 and 4.1‰ . Only Monte samples of *Ctenomys* sp. and plains viscacia exhibit more positive $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, as originally predicted. Monte sample of southern cavy, in contrast, have more positive $\delta^{13}\text{C}$ values,

but not $\delta^{15}\text{N}$, while mountain viscacia and yellow-tooth cavy from the Monte have more positive $\delta^{15}\text{N}$ values, but not $\delta^{13}\text{C}$. Finally, Patagonian guanacos and mara have values of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ that are more positive than conspecifics from the Monte Desert, contrary to what was expected for both.

6.2. Fish

The fish samples come from two species of fish, Patagonian silversides (*Odontesthes hatcheri*, $n = 6$) and Creole perch (*Percichthys trucha*, $n = 12$), and from two localities, Laguna Llanquanelo and the Embalse Nihuil. Both localities fall within the Patagonian Desert. Laguna Llanquanelo is a shallow, natural lake or lagoon fed by the Malargüe River, other smaller streams draining from the Andes, and several freshwater springs that upwell within the lake basin (Fig. 1). Since the basin in which the lake occurs lacks external drainage, its waters are warm and semi-saline to saline, with point sources of fresher water around the springs and where the Malargüe River and other streams enter the lagoon. Overall salinity changes with the depth of the lake, which has varied over time with changes in precipitation and evaporation (Bianchi et al., 2016). Due to the low depth of this lake, its surface area is extremely variable, fluctuating with drought or rainy periods from as low as 80 km^2 in dry seasons to four times this size in rainy years (Isla et al., 2005). The conditions producing the modern lake appear to have been in place for the last 2000 years (Giardina et al., 2014a), though diversion of the Malargüe River for irrigation has likely reduced levels somewhat below this average in the last 50 years. The depth of the lake seldom exceeds 3 m (Bianchi et al., 2016), favoring extensive wetland habitats throughout the area.

Unlike Llanquanelo, Nihuil is an artificial reservoir formed by the construction of the Nihuil Dam and does not support an area of extensive wetlands. This reservoir is fed by the Río Atuel which, along with the Río Diamante, is one of the two largest rivers draining the Andes in this region. The waters upstream of the dam are both deeper and colder than those of Llanquanelo, and also colder than those of the river where it flows naturally.

There are six silverside samples. Five come from el Nihuil reservoir, while the other is from Laguna Llanquanelo. The specimen from Llanquanelo exhibits a markedly more negative $\delta^{13}\text{C}$ value than the Nihuil samples (-16.7‰) and a more positive $\delta^{15}\text{N}$ (9.1‰) (Fig. 5). From the twelve samples of perch, eight are from Laguna Llanquanelo and four from the Nihuil reservoir. Unlike *Odontesthes*, *Percichthys* samples from Llanquanelo are more enriched in $\delta^{13}\text{C}$ than those from Nihuil, although the difference is small. $\delta^{15}\text{N}$ values, on the other hand, exhibit the same tendency as *Odontesthes*: Llanquanelo samples are notably more

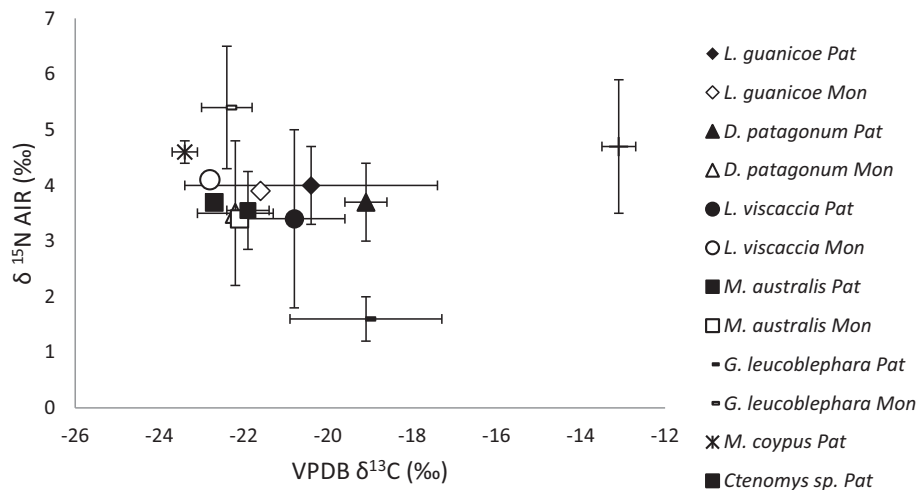


Fig. 4. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and one standard deviation error bars of herbivorous mammal species samples from Patagonian and Monte Deserts.

positive than those from Nihuil (Fig. 5).

6.3. Birds

6.3.1. Carnivorous birds

A small number of carnivorous bird samples were collected, including specimens of turkey vulture (*Cathartes aura* $n = 2$), chimango cara cara (*Milvago chimango* ($n = 1$)), olive cormorant (*Phalacrocorax olivaceus* $n = 1$), and two unidentified lapwings (Family: Charadriidae). Except for one cara-cara specimen, all samples are from the Patagonian Desert. The single Monte cara-cara sample exhibits the most negative values for both isotopes. In contrast, *Phalacrocorax olivaceus*, a frequent resident of Laguna Llanquanelo, has the most positive carbon and nitrogen isotope values, consistent with the values of the fish from Laguna Llanquanelo. Regardless of origin, carnivorous birds all exhibit very positive $\delta^{15}\text{N}$ values of 8‰ or more (Fig. 6).

6.3.2. Omnivorous birds

The largest sample of omnivorous birds comes from areas around Laguna Llanquanelo. The most well represented taxon by far is the Coscoroba swan (*Coscoroba coscoroba*, $n = 22$), all from this area, as are the Chilean flamingo specimens (*Phoenicopterus chilensis*, $n = 6$). In addition to the waterfowl, there is also a smaller sample of upland birds, all elegant tinamous (*Eudromia elegans*, $n = 4$). Although all of the bird samples come from the Patagonian Desert, we see a clear difference between the waterfowl and upland birds. The swans and flamingos from Laguna Llanquanelo have much higher $\delta^{13}\text{C}$ values, and

higher $\delta^{15}\text{N}$ values as well. Both are concordant with the higher isotopic values of carnivorous birds and fish from this lake (Fig. 7).

6.3.3. Herbivorous birds

Herbivorous birds include the lesser rhea and greater rheas (*Rhea pennata*, $n = 8$; *Rhea americana*, $n = 5$), large, flightless birds indigenous to Argentina. It also includes a small sample of specimens which could not be identified to species and which were classified at the family level instead (Rheidae, $n = 3$). In addition to these samples there was one dove (*Zenaida auriculata*, $n = 1$).

Mean *Rhea americana* $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are in agreement with our expectations, with more positive carbon and nitrogen values in the specimens from the Monte Desert (Table 2, Fig. 8). The opposite trend was observed in *Rhea pennata*, however, where the Patagonian samples were more positive. Finally, the single *Zenaida auriculata* specimen had the most enriched $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values.

6.4. Reptiles

The reptile sample consists of five Chaco tortoises (*Chelonoidis chilensis*), all from the Monte Desert. Four come from the area around Cerro Nevado and the other from southernmost Mendoza, 40 km north of the Rio Colorado. With the exception of one of the Cerro Nevado specimens, all were recovered from middens associated with herder (*puestero*) camps. Although the sample size is small, carbon values appear highly bimodal, with three more positive samples (-12.3 , -12.4 , and -12.9) and two much more negative ones (-21.2 and -21.8).

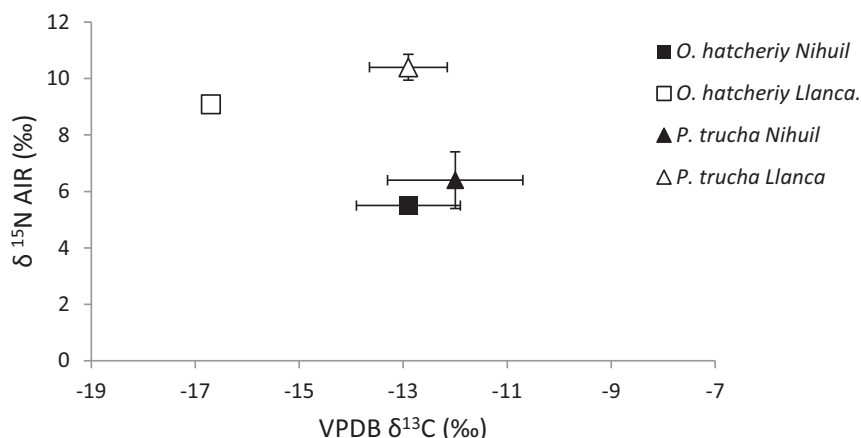


Fig. 5. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and one standard deviation error bars of Fish from Llanquanelo and Nihuil (all from Patagonian Desert).

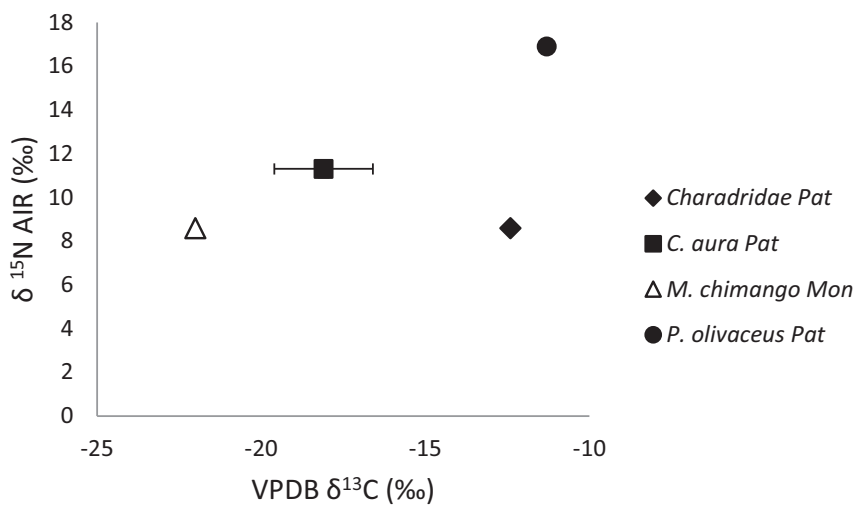


Fig. 6. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and one standard deviation error bars of carnivorous bird species from Patagonian and Monte Deserts.

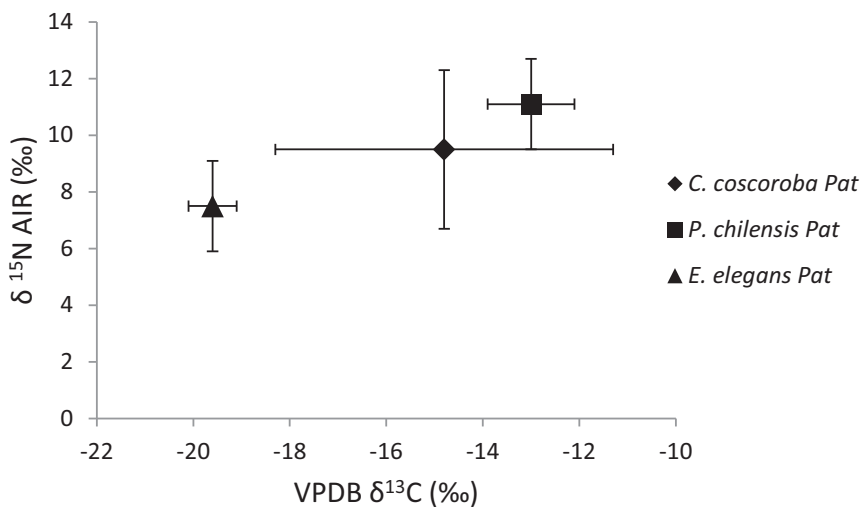


Fig. 7. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and one standard deviation error bars of omnivorous bird species from Patagonian Deserts.

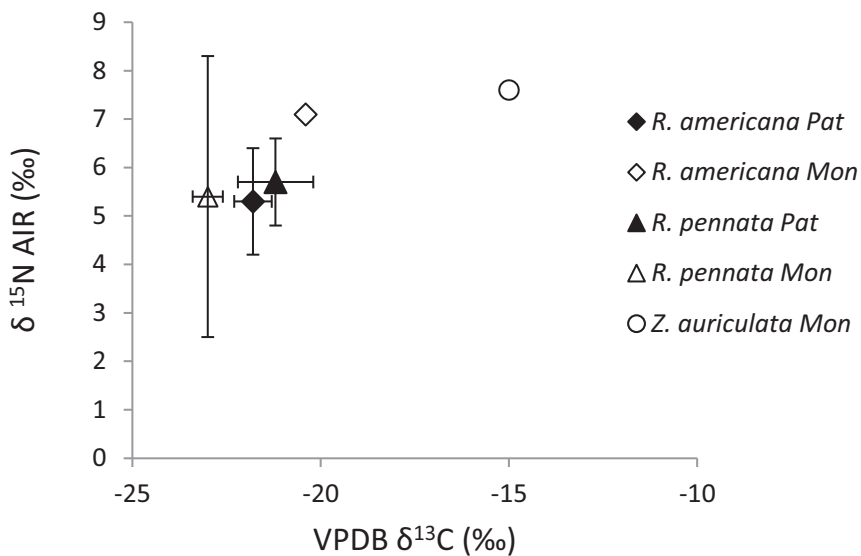


Fig. 8. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and one standard deviation error bars of herbivorous bird species from Patagonian and Monte Deserts.

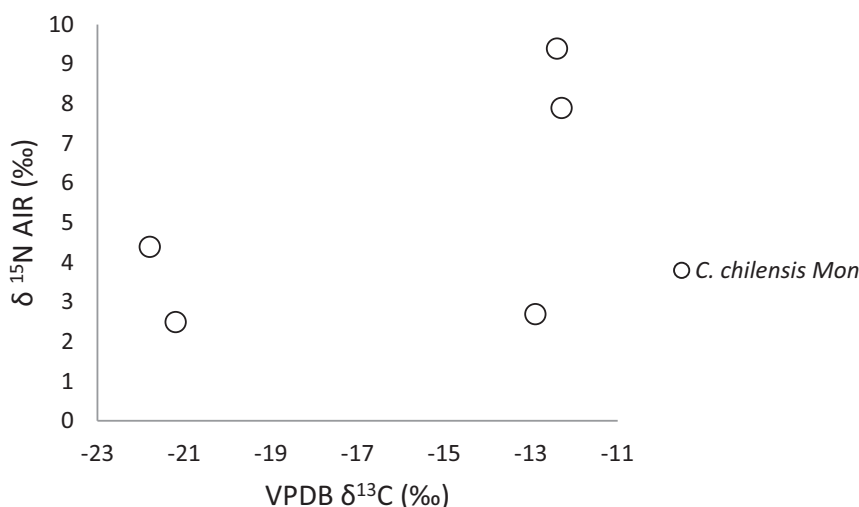


Fig. 9. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of reptile samples (*Chelonoidis chilensis*), all from the Monte Desert.

The very positive samples correspond well with the known distribution and diet of these animals, which occupy lowland deserts and consume a variety of C_4 and CAMS plants, including South American saltbush (*Atriplex lampa*) and various cacti. These positive carbon values are also associated with the two most positive nitrogen values, which are also often elevated in desert settings. The two much more negative $\delta^{13}\text{C}$ values suggest those samples may have been transported from different environments, perhaps from higher elevation areas of Cerro Nevado where Patagonian vegetation dominates (Fig. 9).

6.5. Comparison of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values by desert

To examine differences by region, we contrasted mammal samples from the two deserts after grouping by feeding behavior (Table 3, Fig. 10). These were the only set of samples large enough to provide a meaningful comparison. Among the mammals, only nitrogen values were more positive in the Monte Desert. All mammalian groups exhibited higher $\delta^{15}\text{N}$ values in Monte settings, both means and medians (Table 2 and Fig. 10). These differences are also all statistically significant (Mann-Whitney test; carnivorous mammals: $u = 32.5$, $p = 0.019$; herbivorous mammals $u = 310$, $p = 0.007$; and omnivorous mammals $u = 97$, $p = 0.025$).

The $\delta^{13}\text{C}$ values, in contrast, did not meet our expectations. Carnivorous and herbivorous mammals from the Monte Desert have only slightly more positive $\delta^{13}\text{C}$ values than those from Patagonia (Table 2, Fig. 10), while omnivorous mammals from the Monte are actually more negative than their Patagonian Desert counterparts. None of these differences are statistically significant (Mann-Whitney test: carnivorous mammals $u = 61$, $p = 0.452$; herbivorous mammals $u = 441$, $p = 0.324$ and omnivorous mammals $u = 115.5$, $p = 0.094$).

One potential reason for this discrepancy may be that within the

Patagonian Desert, the area around Laguna Llananelo possesses a qualitatively different vegetation (Roig et al., 2000). The area is an endorheic basin containing a semi-saline to saline lake and halophytic vegetation, which should produce more positive $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values due to elevated soil salinity. Out of a total of 142 samples from Patagonia, 63 (44%) of them come from the Llananelo subregion.

We hypothesized that samples from this area will have higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic values than either Patagonian or Monte samples due to the mentioned effect of salinity on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in plants. In order to check this, we reanalyzed the data after segregating samples into three spatial units: Monte, Patagonia, and Saline (following the vegetation map of Roig et al., 2000). As expected, herbivorous and omnivorous mammals from saline areas have the highest median and mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, while carnivores remain intermediate between the Monte and Patagonian samples (Table 3, Fig. 11). A Kruskal-Wallis test and a Mann-Whitney pairwise comparison test for differences between the three areas further show that the only statistically significant differences are for $\delta^{15}\text{N}$ signatures. Carnivorous mammals from Llananelo are intermediate between, and indistinguishable from, either Monte or Patagonian samples. Those two regions continue to remain different from each other, however, with $\delta^{15}\text{N}$ values of Monte carnivores most positive. Omnivores (mostly armadillos) and herbivores (mostly rodents) from the Llananelo region have the most elevated $\delta^{15}\text{N}$ signatures, as predicted (Table 4). Interestingly, the remaining Patagonian samples continue to exhibit highly elevated nitrogen signals—higher than those from the Monte.

7. Discussion

In a recent investigation focused on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signals from camelids such as *Lama guanicoe* and *Vicugna vicugna*, it was found that

Table 3
Descriptive statistics for taxonomic groups from Patagonia, Saline and Monte environment.

Taxonomic group	Monte				Patagonia				Saline			
	n	Median	Mean	SD	n	Median	Mean	SD	n	Median	Mean	SD
$\delta^{13}\text{C}$												
Carnivorous mammals	15	-17.9	-17.8	0.9	7	-19.5	-18.6	1.9	4	-18.6	-18.7	1.64
Herbivorous mammals	23	-21.6	-19.6	3.8	33	-20.5	-20.1	1.7	12	-19	-19.1	3.05
Omnivorous mammals	18	-19.4	-19.0	1.4	17	-18.1	-18.5	1.4	2	-17.3	-17.3	1.69
$\delta^{15}\text{N}$												
Carnivorous mammals	15	8.1	8.1	1.1	7	6.8	6.70	0.7	4	7.4	7.3	1.0
Herbivorous mammals	23	5.0	4.9	1.3	33	3.2	3.1	1.1	12	6.4	6.4	2.5
Omnivorous mammals	18	6.6	7.2	1.9	17	5.3	5.4	0.9	2	10.3	10.3	0.6

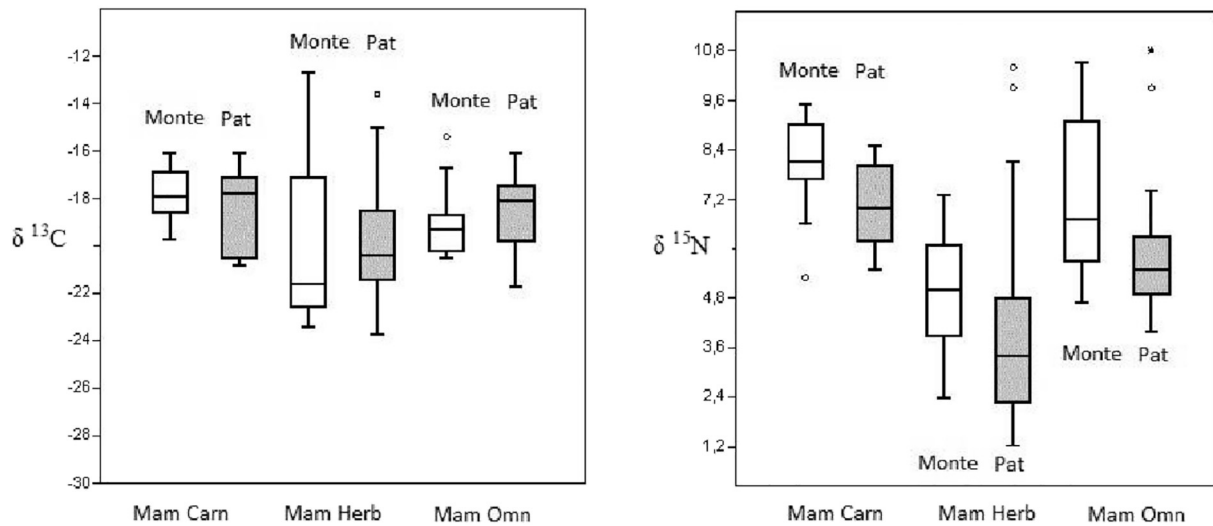


Fig. 10. Box plot on $\delta^{13}\text{C}$ (left) and $\delta^{15}\text{N}$ (right) for each taxonomic group from Patagonia and Monte Deserts.

isotope values differed across Monte and Patagonian Deserts. Both carbon and nitrogen values were more positive in Monte than in Patagonian settings ($\delta^{13}\text{C}$ -16.3‰ vs. -19.2‰ and $\delta^{15}\text{N}$ 6.4‰ vs. 5.0‰ ; Gil et al., 2016:14). Another study of caviomorph rodents from the same region also showed significant differences in $\delta^{13}\text{C}$ between Monte and Patagonia samples (-16.7‰ vs. -18.3‰), though $\delta^{15}\text{N}$ values were indistinguishable (Fernández et al., 2016:48). Each paper, both of which incorporated archaeological and modern samples, interpreted differences in $\delta^{13}\text{C}$ values to be a reflection of the greater diversity and abundance of C_4 photosynthetic plants in Monte environments and consistent with a general trend for a greater abundance of C_4 plants in environments with high mean annual temperatures and summer precipitations (Cavagnaro, 1988). A third study of rhea eggshell also found a statistically significant positive difference in $\delta^{13}\text{C}$ values between deserts ($\delta^{13}\text{C}_{\text{carbonate}}$ -8.9‰ vs. -10.5‰ ; Giardina et al., 2014a:13). This was also attributed to the greater quantity of C_4 plants in the Monte Desert, even though C_3 plants are the most significant part of rheid diets (Paoletti and Puig, 2007; Giardina et al., 2014a).

The results presented here, based on modern bone samples, differ from the patterns found in previous studies of camelids, rodents, and rheas. Of the 13 species for which we have data, nine exhibit significantly higher $\delta^{15}\text{N}$ values in the Monte Desert. Of those four that

don't, the difference is $< 0.3\text{‰}$ and the sample size is in each case less than three individuals. If we aggregate by feeding behavior within class (Table 2), all groups show higher $\delta^{15}\text{N}$ values in Monte settings, though the sample size is very small in herbivorous birds ($N_{\text{Monte}} = 5$). "All groups" in this case means carnivorous, omnivorous, and herbivorous mammals, plus herbivorous birds; essentially carnivores, armadillos, rodents, and rheas. Limiting ourselves to just the mammalian groups and breaking out samples from saline habitats such as Laguna Llanquanelo (Table 3), we find that Patagonian samples have the most negative $\delta^{15}\text{N}$ values in all cases, while with the exception of carnivorous mammals, samples from saline areas are the most positive. The sample of saline carnivores amounts to just four individuals, however, and the difference between those and carnivores from the Monte is not statistically significant.

While human activities such as fires, grazing and agriculture can alter the nitrogen isotope distribution of terrestrial ecosystems (Aranibar et al., 2003, 2008, 2011; Cook, 2001) and urban development and human waste water disposal that of aquatic ecosystems (Lake et al., 2001), none of the differences observed here are likely to be anthropogenic in nature. Overall population density outside of the urban centers of San Rafael and Malargüe is very low. The samples from Monte Desert were collected from places with low, if any, agricultural and livestock activity, while the saline areas considered in this paper

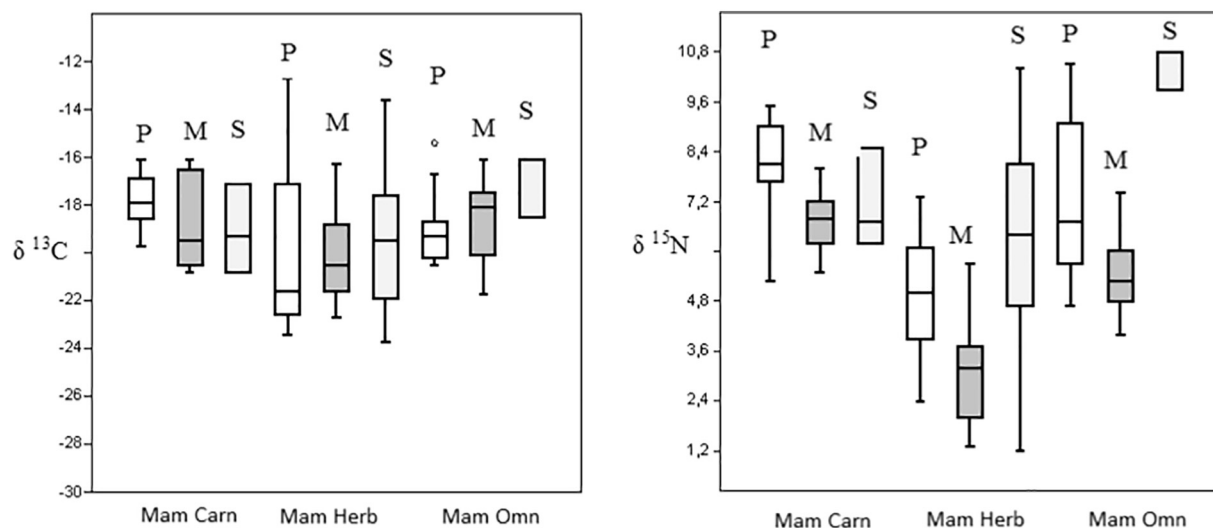


Fig. 11. Box plot on $\delta^{13}\text{C}$ (left) and $\delta^{15}\text{N}$ (right) for each taxonomic group from Patagonia (P), Monte (M), and Saline (S) areas.

Table 4Kruskal-Wallis and Mann-Whitney post-hoc pairwise comparisons for median $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the taxonomic groups. Bold values indicate significance.

Taxonomic group	$\delta^{13}\text{C}$				$\delta^{15}\text{N}$			
	Kruskal-Wallis		Mann-Whitney pairwise comparison		Kruskal-Wallis		Mann-Whitney pairwise comparison	
	H (p-value)	Monte-Pat	Monte-Saline	Pat-Saline	H (p-value)	Monte-Pat	Monte-Saline	Pat-Saline
Carnivorous mammals	1.17; p = 0.554	p = 0.457	p = 0.365	p = 1	7.11; 0.02	0.009	0.270	0.448
Herbivorous mammals	1.53; p = 0.463	p = 0.329	p = 0.554	p = 0.235	29.43; p < 0.001	< 0.001	< 0.001	< 0.001
Omnivorous mammals	3.80; p = 0.148	p = 0.165	p = 0.114	p = 0.387	12.99; p < 0.001	0.003	0.050	0.028

fall largely within a National Park where agriculture and herding activities are reduced. Grazing of goats and cattle does occur in Patagonian settings outside of the National Parks, and its effect cannot be completely excluded. However samples from these areas tend to have the lowest average stable nitrogen values, even though we would expect grazing to increase rather than decrease them.

The observed regional differences in $\delta^{15}\text{N}$ signals are significant. Differences in nitrogen isotope values are often used to define trophic relationships between taxa. In our case study, for example, we found that herbivorous mammals from Patagonian and saltmarsh contexts exhibited a difference of ca. 3.2‰ in their stable nitrogen values. This is close to the difference typically accepted in the literature to reflect a full step in trophic level. A failure to account for geographic variation in nitrogen values might potentially confound estimates of trophic relationships.

Looking at carbon isotope values, only five of the 13 species (38%) have more positive values in Monte settings (Table 2). Aggregating by feeding behavior and class increases this to 3 out of 4 groups, with omnivorous mammals the negative case and carnivorous mammals only weakly positive. Breaking out the saline mammals, we find no clear patterning. In two of the three groups Patagonian samples produce the most negative $\delta^{13}\text{C}$ values and saline samples the most positive ones, but the groups differ in each case. Moreover none of the observed contrasts in $\delta^{13}\text{C}$ values are significant (Table 4).

This inconsistent patterning in animal $\delta^{13}\text{C}$ values echoes the results of a recent study of isotope patterns in plants conducted by Gatica et al. (2016). That study systematically sampled three woody plant species (*Larrea* sp., *B. retama* and *P. flexuosa*) at three precipitation levels in Central-western Argentina in order to analyze covariation between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and rainfall. Their expectation was an increase in plant $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with decreasing mean annual precipitations due to a reduction in stomatal conductance and soil enrichment in ^{15}N respectively. However their results did not show the expected trend in carbon values.

Gatica et al. (2016) present two explanations for their results. One is that rainfall recorded at the wettest sites was markedly below the historical average during the year of their study (Gatica et al., 2016:9). The other explanation is that biotic control of plants might be more important than spatial variation in precipitation, which may not be strong enough to produce differences in the plants collected at different precipitations levels. The researchers point out that drought tolerant species are generally characterized by foliar and root functional traits that allow photosynthesis at low and constant stomatal conductance, being less sensitive to changes in water availability than other species. They also found that $\delta^{15}\text{N}$ does not always vary linearly with precipitation gradients, which may reflect that fact that N losses are partially independent of annual rainfall pattern (Gatica et al., 2016). These findings suggest that we should consider the possibility that some of the floral taxa composing the diet of herbivorous faunas sampled here might not exhibit clear differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ across the landscape, with similar implications for their animal consumers.

Regarding the isotopic values observed in faunal samples from salt marshes, our findings are in agreement with isotopic analyses from other parts of the world. The $\delta^{15}\text{N}$ values of plants and animals are

often more positive in saline regions (Ambrose, 1991; Heaton, 1987; Britton et al., 2008; Ugan and Coltrain, 2011; Kammerdiener, 2004), and the $\delta^{15}\text{N}$ values of coscoroba swan, Chilean flamingo, and olive cormorant located in Laguna Llanquanelo are remarkably high. Ugan and Coltrain (2011) analyzed nitrogen isotopic variation at a relatively small geographic scale while extensively sampling one taxa: *Lepus californicus* (black-tailed jack rabbits). They compare $\delta^{15}\text{N}$ values of that animal with environmental parameters (temperature, precipitations pH, soil salinity) from five different locales. They found no correlation with temperature and rainfall, but a significant and positive relation with soil salinity (Ugan and Coltrain, 2011:1420). In the research presented in this paper, when samples were segregated in three different spatial units (Monte, Patagonia and saltmarshes areas) the highest $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of herbivorous and omnivorous mammals were recorded in saline areas.

7.1. Implications for archaeology and human dietary reconstruction

This initial look at the faunal baseline stable isotope data has significant implications for the archaeology of mid-latitude deserts in general and Central-western Argentina in particular. Until recently, most human dietary reconstructions were based on stable isotope values from just a few resources, without fine-grained or explicit geographic provenience and generally without temporal assignment. Just eleven bones specimens from six taxa were used as an initial reference in interpreting human diets (Gil et al., 2006). This was useful as a first step, but insofar as Central-western deserts are highly variable at both temporal and spatial scales it is necessary to check the validity of these first values. The 209 modern samples from 26 native taxa provided here improve our sense of the range of variation that can be expected. Substantial intrataxonomic variation in faunal isotope values is clearly confirmed in this paper and calls attention to the need for accounting for it when applying mixing models to reconstruct human diets.

The $\delta^{15}\text{N}$ data provided here show that faunas from the Monte Desert generally exhibit higher values than those from the Patagonian Desert. Differences in $\delta^{15}\text{N}$ become more evident when samples are segregated into Monte, Patagonian, and saltmarsh contexts, with samples from saline/saltmarsh contexts often producing $\delta^{15}\text{N}$ values even higher than those from the Monte. These differences suggest that nitrogen values may have some utility as a geographic marker. If human populations from central-western Argentina were highly mobile, with home ranges that included both deserts, we might not expect any isotopic differentiation. But if human ranges were smaller, with sporadic connections among Monte and Patagonia environments, then differentiation in $\delta^{15}\text{N}$ might be expected. This could occur even if human diets included many of the same prey taxa. Clearly, spatial differences in animal $\delta^{15}\text{N}$ values underline the need to build a strong and biogeographically sound baseline in order to accurately reconstruct human diets.

Differences in $\delta^{13}\text{C}$ values between the two regions (Monte and Patagonia) are low and non-significant. This isotopic similarity implies that geographic differences in human $\delta^{13}\text{C}$ signals are likely to be muted, even if prehistorically mobility was low enough to constrain foragers to a particular desert. These results point out to the necessity of

develop more specific research in smaller spatial scale as illustrated when saltmarsh areas were considered separately in our comparison.

7.2. Other concerns and caveats

This study is based on modern animal samples and allows us to control for temporal variation while evaluating the geographic and ecological relationships in stable isotope signals among the various taxa. Two issues that can affect our results need to be considered. First, while most of the study area exhibits low human economic activity, it is not “pristine” and remains situated in a world ecosystem substantially modified by people in the last few centuries. There remains the possibility that the trends observed here are in some ways indirectly impacted by modern human activities (Hofman-Kamińska et al., 2018), something for which we have no control. At the same time, there is also an archaeological record from this region. That record lacks the fine-grained temporal control seen here, but is also free from biases introduced by modern human economic activity. Using both records should allow us to better refine our understanding.

The second issue at hand is simply the need for additional samples. While we looked at hundreds of modern animal samples, these samples traded depth for breadth. Few taxa can be considered well-sampled, and the samples are not balanced across taxa or regions. This simply reflects limitations on sample access, particularly where animals are rare, regulated, or otherwise difficult to acquire. Given the substantial individual variation observed even with small samples, the need for additional sampling and data is clear.

8. Concluding remarks

In this paper, we provide bone collagen stable isotope data for various dietary resources and discuss spatial variation in their values. The differences observed in $\delta^{15}\text{N}$ and the lacks of differences in $\delta^{13}\text{C}$ have implications for the understanding of past human diets in Central-western Argentina. An isotopic pattern showing a clear relation between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of animals and altitude and the percentage of C_3 and C_4 plants observed in previous studies in other places (Samec et al., 2017; Goude and Fontugne, 2016) and on camelids, rodents and Rhea eggshell in our own area of study (Gil et al., 2006; Fernández et al., 2016; Giardina et al., 2014a), was not fully met among the species considered in this paper. No statistical differences were seen among the $\delta^{13}\text{C}$ values of animals from the two deserts. This lack of differentiation is evident among broader taxonomic groups and at the species level, although comparisons at the species level are limited by small sample sizes. Where adequate samples from both deserts allowed a Mann-Whitney test (Patagonian mara, Plains viscacha, puma, greyfox, pichi armadillo and two species of rheidae family), no statistical differences were found. As a hypothesis, we propose that this might be due to the generally arid conditions characteristic of both deserts (both arid, the Monte just slightly more so) and the biotic control of plants, which could make less of a difference in the stable isotope signals of the same plants of the different deserts, as observed by Gatica et al. (2016). Regarding $\delta^{15}\text{N}$ values, all mammal taxonomic groups are more positive in Monte than in Patagonian Desert, as expected, and statistical differences were found. When samples from saltmarsh areas like Laguna Llanacanelo were segregated, differences become significant in both stable isotopes, suggesting that salinity could be a determinant factor in determining $\delta^{15}\text{N}$ isotopic composition. This results show that there might exist small-scale differences in nitrogen values which could be influenced by soil salinity.

Clearly the results confirm the high variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ within and between taxonomic groups. Our results do not confirm the expected differences in $\delta^{13}\text{C}$ between deserts, but do that for $\delta^{15}\text{N}$. This significant intra- and inter-taxonomic difference, even though not fully explained by desert environment structure, needs to be considered in human isotopic diet interpretation.

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Appendix A. Supplementary data

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