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SPECIAL ISSUE PAPER

$\delta^{13}C$ and $\delta^{15}N$ Characterization of Modern Huemul (*Hippocamelus bisulcus*) from the Patagonian Andean Forest. Scope and Limitations of Their Use as a Geographical Marker

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ABSTRACT This paper presents an isotopic characterization ($\delta^{13}C$ and $\delta^{15}N$) of modern huemul from Patagonian Andean forest. This deer is considered an endemic species, now inhabiting the sub-Antarctic forest of Chile and Argentina. We analyse if the isotopic signals of the modern huemuls can be used as geographic markers on two distinct spatial scales. Firstly, on the intra-forest level, we analyse the relation between the $\delta^{13}C$ and $\delta^{15}N$ of the huemul and the annual precipitation in the place in which the sample was collected. Secondly, on the inter-environmental level, we evaluate to what extent the huemul's isotopic signal differs from that of the guanaco (*Lama guanicoe*), an herbivore that occupies Patagonia's continental steppe. The results reveal that, on the one hand, there is no relation between the isotopic values of modern huemules and precipitation levels, whereas on the other hand, the modern huemul is different from the guanaco in both isotopes. We believe that this difference between the herbivores is associated with the isotopic signals at the base trophic chain, which is influenced by the precipitation gradient. In this way, even though for now, these isotopic markers turn out not to be useful for differentiating between huemuls coming from sectors of the forest with marked differences in precipitation, it is possible to distinguish herbivores coming from the forest and steppe of continental Patagonia, enabling the use of $\delta^{13}C$ and $\delta^{15}N$ as geographic markers. The isotopic characterization of $\delta^{13}C$ and $\delta^{15}N$ of the modern huemuls and its relation to the Patagonian Andean forest has strong implications for paleoecological and archaeological aspects of this environment, including the biogeographical history of the huemul, and in order to the test the models of use and exploitation of the forest by hunter-gatherers in the past. Copyright © 2013 John Wiley & Sons, Ltd.

Key words: carbon; *Hippocamelus bisulcus*; Holocene; hunter-gatherer; *Lama guanicoe*; nitrogen; Patagonian Andean forest; steppe

Introduction

Environmental–climatic factors determine the variations in the natural distribution of carbon and nitrogen stable isotopes. The stable isotopes of ^{13}C and ^{15}N exhibit variations according to environmental and climatic parameters such as precipitation, temperature, relative humidity, latitude, altitude, soil pH and soil salinity, as well as, the perturbations of the ecosystem such as grazing and fires (Tieszen, 1991; Schulze *et al.*, 1998; Austin & Sala, 1999; Handley *et al.*, 1999; Heaton, 1999; Schulze *et al.*, 1999; Cook, 2001; Amundson *et al.*, 2003; Murphy & Bowman, 2006; Hartman, 2011). Among these factors, the variables related to the availability of water (annual precipitation, evapotranspiration index and water balance) are among the most relevant for explaining the foliar and soils $\delta^{13}C$ and $\delta^{15}N$ variation (Handley *et al.*, 1999; Amundson *et al.*, 2003; Hartman, 2011). With respect to stable carbon isotopes ($^{13}C/^{12}C$), plants fix atmospheric CO_2 via three different

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photosynthetic pathways: C_3, C_4 and crassulacean acid metabolism. The most frequent photosynthetic pathway in terrestrial environments is C_3, through the Calvin cycle. Patagonia is dominated by this photosynthetic pathway (Paruelo *et al.*, 1998; Epstein *et al.*, 2002). The $\delta^{13}C$ distribution in C_3 plants is between −34 and −22‰ with a modal value of −27‰ (Heaton, 1999). This wide range registered in the distribution of values is due to diverse environmental variables that influence the synthesis of carbon by the plant (Tieszen, 1991; Heaton, 1999). For example, water stress or saline environments cause an increase of the $\delta^{13}C$ in plants, whereas an increase in precipitation translated into a decrease of the $\delta^{13}C$ (Tieszen, 1991). Also, in dense forests, a decrease in solar irradiation and the low circulation and recycling of CO_2 contributes to the depletion of the $\delta^{13}C$ in plants. The combination of these processes has been called a canopy effect, which implies a variation in the vertical gradient of $\delta^{13}C$, with depleted values at lower parts of the forest and increased values at higher parts (van der Merwe & Medina, 1991; Drucker *et al.*, 2008). Although this effect has been used to explain the depletion of the isotopic signal in tropical forests (van der Merwe & Medina, 1991; Cerling *et al.*, 2004), it has also been registered in forests in high latitudes with less developed canopies (France, 1996; Drucker *et al.*, 2003).

Initially, the effect of the aridity or water stress in the natural distribution of $\delta^{15}N$ was considered stronger in animals than in plants (Ambrose & De Niro, 1986; Heaton *et al.*, 1986; Heaton, 1987; Sealy *et al.*, 1987). Consequently, diverse models related to the metabolism and physiology of animal species have been proposed (Ambrose & De Niro, 1986; Sealy *et al.*, 1987; Ambrose, 2000; Balter *et al.*, 2006; Sponheimer *et al.*, 2003; Hartman, 2011). These models have not, however, been positively proved either by field (Cormie & Schwarcz, 1996; Gröcke *et al.*, 1997; Murphy & Bowman, 2006; Hartman, 2011) or experimental studies (Ambrose, 2000; Sponheimer *et al.*, 2003). In this regard, recent studies conclude that the $\delta^{15}N$ present in the collagen of the animal species records the variation of the $\delta^{15}N$ in soil and plants, without detecting any effect related to the previously cited metabolic–physiological factors (Murphy & Bowman, 2006; Hartman, 2011). Although the processes involved are not entirely clear, these variations in $\delta^{15}N$ plants are explained by a greater opening of the nitrogen cycle as precipitation decreases, generating greater losses in the cycle (Austin & Sala, 1999; Handley *et al.*, 1999; Schulze *et al.*, 1999; Cook, 2001; Amundson *et al.*, 2003; Hartman & Danin, 2010). The spatial arrangement of the natural distribution of $\delta^{13}C$ and $\delta^{15}N$ enables these stable isotopes to be used as geographical markers in ecological, paleoecological and archaeological studies. In archaeology context, spatial variability in the natural distribution of the stable isotopes is employed in order to characterise the use of a specific environment by animal species and human populations (Barberena, 2002; Drucker *et al.*, 2003; Murphy & Bowman, 2006; Pate & Anson, 2008; Hartman & Danin, 2010). In Patagonia, isotopic studies applied to archaeological issues have considered the terrestrial environment as a single unit, interpreting human paleodiets according to the relative importance of the terrestrial and marine resources in the diet (Yesner *et al.*, 1991; Barberena, 2002; Zangrando *et al.*, 2004; Panarello *et al.*, 2006; Favier Dubois *et al.*, 2009; Moreno *et al.*, 2011). However, the terrestrial environment in continental Patagonia presents marked differences according to the availability of water. The Andes, in combination with the prevailing westerly winds, produce a rain shadow effect, a west-east variation in precipitation that translates into a gradient of vegetation types. In sectors with greater humidity, to the west, a temperate forest develops, dominated by species of the Nothofagus genus (Soriano, 1956; León *et al.*, 1998). This forest stretches between latitudes 39ºS and 53ºS in a narrow strip, 2000 km in length with an average width of 120 km (Armesto *et al.*, 1995). In continental Argentina, steppe succeeds the Patagonian Andean forest after a few kilometres. The highest precipitation is found in the Andean region, with sectors that experience more than 2000 mm annually, and the lowest levels −125 mm annually− are found in the centre-east zone. Below *ca.* 500 mm of annual precipitation various steppe formations (grassy, shrubby-grassy and shrubby) and wastelands is recorded (León *et al.*, 1998).

The correlation between the $\delta^{13}C$ and $\delta^{15}N$ values of soils and plants and annual precipitation indicate the importance of water availability in structuring the natural distribution of these isotopes in Patagonia (Austin & Sala, 1999: 294; Peri *et al.*, 2012). Thus this relationship should be expected in herbivores, allowing the analysis of habitat use and dietary preferences of animal species. One of these is the huemul, the Andean-Patagonian continental forest's largest-bodied herbivore, which formed part of the hunter-gatherer's diet during the Holocene (De Nigris, 2004; Fernández, 2008). This deer lives in southwestern South America and is considered an endemic species in the sub-Antarctic forests of Chile and Argentina (Redford & Eisenberg, 1992). Currently, its distribution has contracted notably and is now restricted to areas of difficult access in the mountainous forests. Before the 19th century in Argentina, the huemul was seen from the south of Mendoza (36º S) to Santa Cruz Province (52º S) (Díaz, 1990, 2000; Serret, 2001; Vila *et al.*, 2004).

Classified as 'endangered' on the Red List of the International Union for the Conservation of Nature, it is protected by national and provincial laws (Serret, 2001). There is broad agreement that huemuls have suffered changes in their distribution as a result of the influence of anthropogenic perturbations because the colonisation of Argentina and Chile (Povilitis, 1978; Díaz, 2000; Serret, 2001). According to historical records, Díaz (1990, 2000) and Flueck & Smith-Flueck (2012) argue that huemuls had occupied parts of the steppe in Patagonia including the central and eastern plains, even reaching the Atlantic coast. Moreover, for Serret (2001) the huemul's optimum habitat was the forest-steppe ecotone, which the deer progressively abandoned with the development of animal husbandry and urbanisation. Recently, on the basis of $\delta^{15}N$ and $\delta^{13}C$ collagen values of 12 huemul samples –two modern and ten archaeological[1] – from Chilean Patagonia (Aisén Region, 43–48° S) Barberena *et al.* (2011) proposed that in the past, huemul regularly consumed plants that grow in open spaces. However, there is a lack of zooarchaeological records to support the proposition that huemul ever occupied the steppe (Barberena *et al.*, 2011: 2319).

We agree with Barberena *et al.* (2011) regarding the potential that isotopic analyses have for evaluating the geographic distribution of the huemul in the past, and the implications such analyses have for the reconstruction of the hunter-gatherer diet in Patagonia throughout the Holocene. Nevertheless, we consider that in order to establish the scope of the $\delta^{13}C$ and $\delta^{15}N$ as geographic markers, it is necessary to employ modern samples of huemul with known ecological habits. As a result, the goals of this study are to offer an isotopic characterization of modern individual huemuls recovered from the forest environment, analysing the relation between the $\delta^{13}C$ and $\delta^{15}N$ isotopic signals and the average annual precipitation at the place in which the sample was recovered. In addition, we will evaluate the suggestion that huemul $\delta^{15}N$ and $\delta^{13}C$ values provide an isotopic marker of ecological association with cold-forest ecosystems (Barberena *et al.*, 2011: 2320). Thus, we provide a comparison of those values and the isotopic values of the guanaco, a camelid that inhabited Patagonia's continental steppe throughout all of the Holocene. We expect modern huemuls, currently restricted to the Patagonian Andean forest, to register isotopic values of carbon and nitrogen more depleted than those of guanacos because of their more closed and humid habitat (Barberena *et al.*, 2011). In sum, we seek to determine if the isotopic signals of modern huemuls can be used as geographic markers on two spatial scales: intra-forest, starting from a consideration of variations in precipitation and inter-environmental, comparing the most important herbivores of the forest and steppe –Argentine Patagonia's two terrestrial continental environments.

[1] One of the samples comes from the early Holocene, one from the mid-Holocene, eight from the late Holocene, and two are modern (Barberena *et al.*, 2011).

Materials

Modern huemul bones were recovered between 41° 20′ S and 49° 39′ S along a north–south axis (Figure 1). The behaviour and demographics of this species make it difficult to obtain biological samples. In fact, over several years, researchers and park rangers of the Administración de Parques Nacionales (APN) collected bone fragments representing 30 huemul individuals. From the APN collection, 15 individuals (50%) were analysed.[2] Three samples come from Río Negro Province, two from the Ñirihuau sector of the Nahuel Huapi NP, an ecotonal area (Eduardo Ramilo, pers. com. December 2007) and one from Cerro Ventisquero, in a coihue (*Nothofagus dombeyi*) forest environment (Pastore, 2006). From Chubut Province, also from a forest environment, two samples came from Los Alerces NP and one from La Plata Lake (Smith-Flueck & Flueck, 2001). Lastly, from Santa Cruz Province, seven samples come from Perito Moreno NP (Serret & Borghiani, 1998) and two from Moyano Channel in the Los Glaciares NP (Serret, 1995). Precipitation associated with the samples ranged from *ca*. 1800 to 445 mm, reflecting the abovementioned gradient (Table 1). Guanaco samples came from northern Patagonia, one from Nahuel Huapi NP (Limay area) and another from Tecka (Chubut province, Figure 1, Table 1). These samples were supplemented with the isotopic values of 70 guanacos from the centre-west of Santa Cruz Province reported by Tessone (2010), corresponding from the last 8000 years. Together, guanaco samples cover a latitudinal range comparable to the huemul samples.

Methods

Estimating precipitation

The precipitation values at the points in which the samples were collected are listed in Table 1 and correspond mainly with the 1993–2008 average of the records of

[2] At the time of our analysis, the APN's huemul collection comprised 30 individuals. Since then, the sample has increased to a total of 42 individuals (H. Pastore, personal communication, March 2013).

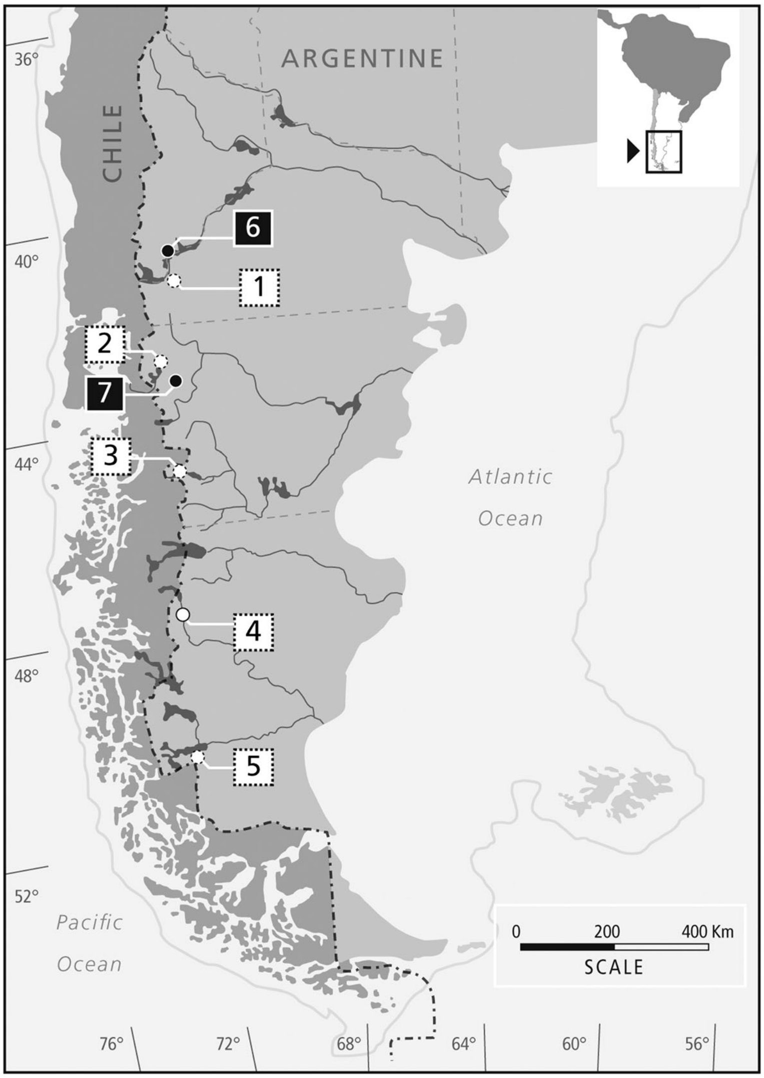

Figure 1. Map of Patagonia with the provenance of analysed samples. Huemul deer (1) Nahuel Huapi NP, Ñirihuau sector, and Cerro Ventisquero; (2) Los Alerces NP; (3) lake La Plata; (4) Perito Moreno NP and (5) Los Glaciares NP. Guanaco: (6) Nahuel Huapi NP, Limay area, and (7) Tecka.

hydrometeorological stations monitored by the subsecretary of water resourses of the nation (Secretaría de Obras Públicas, 2010). In some cases, estimating annual precipitation was complicated by (i) the lack of precise provenance of the huemul samples ($N = 4$) and (ii) the absence of precipitation records for certain sectors of Patagonia, which influences the precision of the estimates associated with each bone sample. For the samples from Río Negro and Chubut that are close to any stations, we used the value of the longitudinally closest meteorological station, taking into account the strong correlation exhibited between precipitation and longitude in these provinces ($r_s = 0{,}97$ $p < 0{,}01$, n=18; see also Jobbágy *et al.*, 1995). Other sources included in the study are the values provided by the investigators who collected the sample from La Plata lake (LPUB, Smith-Flueck & Flueck, 2001). For the samples from the Perito Moreno NP, we used the average for the Entre Ríos Estancia's hydrometeorological station and measurements taken by the APN between 2006 and 2010 (Eduardo Ramilo, Delegación Regional Patagonia APN com. pers. 2011). A similar strategy was used for the Los Glaciares NP samples, averaging the data from the year 2007–2009 gathered at the Los Huemules Estancia (Alejandro Serret, Cielos Patagónicos, personal communication, April 2011) with the 2006–2008 record of Las Vueltas river hydrometeorological station.

Isotope analysis

The samples were processed in the Instituto de Geocronología y Geología Isotópica (INGEIS,

Table 1. Results of the isotopic analysis of the collagen extracted from modern huemul and guanaco of the Patagonia. It also records the site of recovery and annual precipitation associated

Species	Sample	Locality	Province	Coord (approx)	Laboratory Code	Part / element analysed	%C	%N	C/N	$\delta^{13}C$	$\delta^{15}N$	Precipitation (mm annual)
Hippocamelus bisulcus (huemul)	NH72	Nahuel Huapi NP, Ñirihuau	Río Negro	41º 20′ S 71º 21′ W	EILAB 195961	Phalanx	43.1	15.9	3.1	−21.2	0.8	884
H. bisulcus	NH38	Nahuel Huapi NP, Ñirihuau	Río Negro	41º 20′ S 71º 21′ W	EILAB 195963	Thoracic vertebra	41.5	15.4	3.1	−20,7	1.3	884
H. bisulcus	CMHP 345	Cerro Ventisquero	Río Negro	41º 41′ S 71º 40′ W	EILAB 195959	Rib	43.2	12.9	3.8	−23.5	0.7	1608
H. bisulcus	LA69	Los Alerces NP	Chubut	42º 50′ S 71º 42′ W	EILAB 195960	Thoracic vertebra	43.6	15.5	3.2	−20.8	1.2	1818
H. bisulcus	LA71	Los Alerces NP	Chubut	42º 50′ S 71º 42′ W	EILAB 195958	Vertebra	42.1	14.9	3.2	−22.8	2.0	1818
H. bisulcus	LPUB	La Plata lake	Chubut	44º 52′ S 71º 50′ W	EILAB 213596	Lumbar vertebra	39.6	14.9	3.0	−22.7	−0.7	1000
H. bisulcus	SPM8	Perito Moreno NP	Santa Cruz	47º 46′ S 72º 21′ W	EILAB 195957	Skull	44.1	16.0	3.2	−19.5	3.1	483
H. bisulcus	CNB	Perito Moreno NP	Santa Cruz	47º 57′ S 72º 09′ W	EILAB 213591	Metatarsal	43.9	16.8	3.0	−20.2	0.3	445
H. bisulcus	H1PNPM	Perito Moreno NP	Santa Cruz	47º 41′ S 72º 10′ W	EILAB 213585	Skull	41.6	15.0	3.2	−18.6	2.5	445
H. bisulcus	H2PNPM	Perito Moreno NP	Santa Cruz	47º 46′ S 72º 20′ W	EILAB 213586	Skull	43.8	15.6	3.2	−21.0	2.7	483
H. bisulcus	H3PNPM	Perito Moreno NP	Santa Cruz	47º 58′ S 72º 07′ W	EILAB 213587	Skull	43.4	15.9	3.1	−19.7	2.7	445
H. bisulcus	H4PNPM	Perito Moreno NP	Santa Cruz	Sin datos	EILAB 213588	Skull	43.5	16.5	3.0	−20.0	2.4	445
H. bisulcus	H5PNPM	Perito Moreno NP	Santa Cruz	Sin datos	EILAB 213589	Skull	42.4	15.5	3.1	−22.1	0.7	445
H. bisulcus	SLGC3	Los Glaciares NP	Santa Cruz	49º 39′ S 72º 37′ W	EILAB 195962	Skull	41.5	15.4	3.1	−20.6	2.6	674
H. bisulcus	SLGC1	Los Glaciares NP	Santa Cruz	49º 37′ S 72º 55′ W	EILAB 195964	Mandible	43.0	15.7	3.1	−20.5	2.9	674
Lama guanicoe (guanaco)	Nahuel Huapi	Nahuel Huapi NP, Limay area	Neuquen	40º 56′ S 71º 03′ W	EILAB 213592	Tibia	41.7	14.7	3.3	−20.5	5.9	sd
Lama guanicoe	Tecka	Tecka	Chubut	43º 29′ S 70º 48′ W	EILAB 213593	Tibia	43.3	15.5	3.2	−19.0	5.0	sd

CONICET-UBA) laboratories. Bone fragments were cleaned with abrasive elements and an ultrasonic bath. Collagen was extracted by demineralization using 2% hydrochloric acid (HCl 2%) over 72 h, replacing the acid every 24 h. Twenty-four hours before and after the demineralization, the bone material was treated with sodium hydroxide 0.1M (NaOH 0.1M). The whole process was performed at room temperature; the material was then dried in an oven at a temperature less than 60ºC (Tykot, 2004). The measurements of the isotopic relations were performed in the Environmental Isotope Laboratory of the University of Waterloo, Canada. Stable isotopes results are measured as the ratio of the heavier isotope to the lighter isotope ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) and reported as δ values in parts per thousand (‰) relative to internationally defined standards for carbon and nitrogen. The standard deviation reported for the values of $\delta^{13}C$ and $\delta^{15}N$ was ± 0.3‰.

A correction factor was applied to modern samples with the purpose of compensating for the so-called 'industrial effect' that produces a decrease in the values of atmospheric $\delta^{13}C$. The methodology employed is proposed by Long *et al.* (2005), in which it is necessary to consider the date of death of the organism. It's considered that the atmospheric CO_2 $\delta^{13}C$ value for periods prior to the industrial revolution is 6.5‰. The year of death of the two guanacos is in 2008, whereas the huemul CMHP 345 died in 2003. For the rest of the samples, only the collection date is recorded (between 1979 and 2009), except in three cases for which no date is recorded. For the samples with a collection date, given that it is difficult to know how long the sample was exposed because the moment of death, it was decided to establish a correction value of 5 years. Taking into account the ages of the recorded collections, a correction factor from 1975–2005 was established. An earlier presumed date of death was assigned to each sample; for example, a 1975 date of death was assigned to the sample collected in 1979. The three samples that had no recorded collection date were assigned in 1994 as the date of death, that being the mean date of the collections. Although the application of Long *et al.*'s (2005) methodology required establishing a presumed date of death in most of the cases, in this way, we arrived to a more accurate factor of correction of the atmospheric $\delta^{13}C$ value.

Results and discussion

The $\delta^{13}C$ and $\delta^{15}N$ results are presented in Table 1 along with the data for the samples' origins and the corresponding precipitation records. The sample CMHP 345 was eliminated from the analysis because it exhibits a C/N of 3.89 ratio outside the normal range (2.9–3.6; De Niro, 1985). This sample could be contaminated by lipids considering it is a modern sample and it shows the most negative $\delta^{13}C$ value (−23.5‰; van Klinken, 1999). The rest of the samples have a C/N ratio within the normal range, with a mean of 3.1 ± 0.07. Similarly exhibit a %C between 41.5 and 44.1%, with an average of 42.9% ± 0.9% and a %N between 14.7 and 16.8% with an average of 15.5% ± 0.5%. These values are found within the normal ranges for modern non-human mammals samples (Ambrose, 1990; Jørkov *et al.*, 2007). We did not observe a correlation between the $\delta^{13}C$ and the C/N relation ($r = 0.06$ $p = 0.8$) or between the $\delta^{13}C$ and the %C ($r = 0.15$ $p = 0.6$).

Table 2 presents the descriptive statistics of the huemul, along with the guanaco sample. The huemul $\delta^{13}C$ ranges from −22.8 to −18.6‰ with a mean value of −20.7‰ ± 1.2‰ and $\delta^{15}N$ shows a mean value of 1.7‰ ± 1.1‰ with a distribution between −0.7 and 3.1‰. The statistically significant correlation between $\delta^{13}C$ and $\delta^{15}N$ huemul ($r = 0{,}59$ $p = 0{,}025$, Figure 2) may be interpreted as a product of variable consumption from two sources with different isotopic signals (Schwarcz, 1991). There are huemuls with isotopic values that can be associated with the most depleted values of the plants of the forest, whereas other individuals are associated with the ecotonal or enriched forest plants (Peri *et al.*, 2012). The first correspond to huemuls recovered in closed forest, that for geographical (LA71, LA69, NH72 and NH38) or anthropogenic reasons (LPUB, Smith-Flueck & Flueck, 2001) did not have access to the ecotone. Conversely, most of the Santa Cruz samples have enriched values, from huemul populations with free access to the ecotone. The exceptions from this pattern are the H5PNPM and CNB samples, which though they come from Santa Cruz are grouped in the most depleted area of the distribution. These results are coherent with those

Table 2. $\delta^{13}C$ and $\delta^{15}N$ descriptive statistics of the isotopic analysis of huemul and guanaco from Patagonia

	Huemul		Guanaco	
	$\delta^{13}C$‰	$\delta^{15}N$‰	$\delta^{13}C$‰	$\delta^{15}N$‰
N	14	14	72	72
Mean	−20.7	1.7	−19.4	6.2
Median	−20.7	2.2	−19.6	6.1
Standard deviation	1.2	1.1	0.9	1.4
Minimum	−22.8	−0.7	−21.2	3.6
Maximum	−18.6	3.1	−16.7	11.5

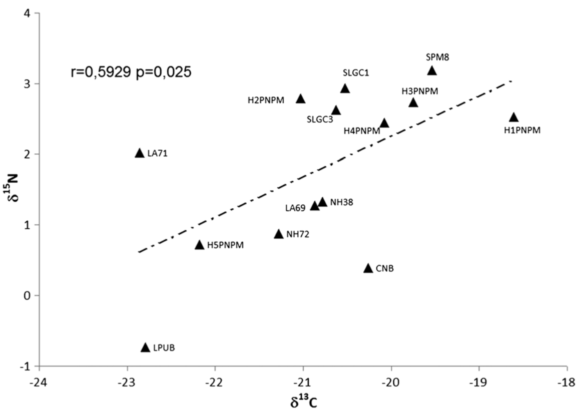

Figure 2. Distribution of $\delta^{13}C$ and $\delta^{15}N$ in huemul deer.

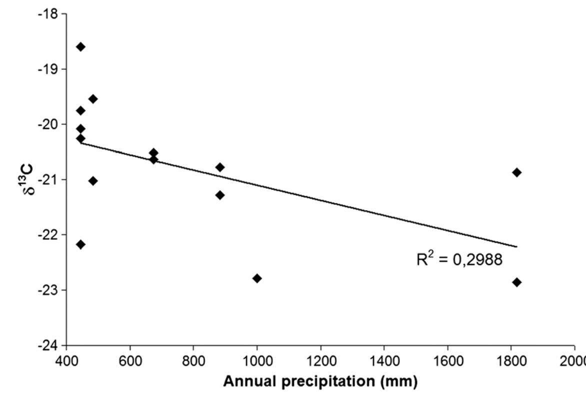

Figure 4. $\delta^{13}C$ values plotted against annual precipitation (mm) for huemul deer analysed.

obtained by Barberena *et al*. 2011 (Figure 3) that show more negative values in those samples associated with closed forest; even so, statistically significant differences are not recorded between the samples grouped according to closed versus open forest (Barberena *et al*., 2011: 2317).

Huemuls' $\delta^{13}C$ and $\delta^{15}N$ have a negative trend line relative to annual precipitation, with the highest values in the spaces with the lowest precipitation (400–500 mm annually, Figures 2 and 3). Although this result is to be expected for terrestrial herbivores in Patagonia –unlike for soils and plants (Austin & Sala, 1999; Peri *et al*., 2012)– there is no correlation between the huemul $\delta^{15}N$ and precipitation ($r^2 = 0.06$), whereas the relation is weak ($r^2 = 0.2988$) between huemuls' $\delta^{13}C$ and precipitation (Figures 3 and 4).

We believe that the lack of a correlation between huemul isotopic values and precipitation could be related to three factors. The first refers to a sampling problem, similar to that documented in other cases that evaluate the relation between isotopes and precipitation (Murphy & Bowman, 2006:1067). In the sample that we analysed, the geographic areas with the greatest precipitation are less represented, and 50% of the huemuls come from areas with precipitation between 445 and 483 mm (Table 1). This problem is difficult to overcome because the sampling was dependent on the availability of modern huemul remains in the APN collection, which in turn is limited by the difficulties of obtaining biological samples from this species. The second factor is related to the precipitation range in which the huemul samples are distributed (445–1818 mm, Table 1). Various studies record nonlinear correlations of herbivores' $\delta^{15}N$ and precipitation; above a certain value —200 to 500 mm annually, depending on the species and the geographic area being considered– linearity are not recorded (Heaton *et al*., 1986; Sealy *et al*., 1987; Gröcke *et al*., 1997; Pate & Anson, 2008; Murphy & Bowman, 2006). Nevertheless, the linear relation between precipitation (300–900 mm annually) and foliar $\delta^{15}N$ and $\delta^{13}C$ (Peri *et al*., 2012), suggest that there is no critical mean annual rainfall value in Patagonia. Third, there is a possible lack of correspondence between the *locus* of recovery of the sample and the total feeding area of the huemul. This factor arises from the interrelation of two variables: the huemul's home range and the magnitude of the isotopic variations of the plants in the area. The former has been characterised as small, based on the study of three populations in Chile (Colomes Gonzáles, 1978; Bahamondes, 1997; Gill *et al*., 2008). It is possible that under different conditions of human disturbance, the home range might be bigger, given the important human presence has as a limiting factor for huemul home range (Gill *et al*., 2008: 259). In our study, the sampled populations are located in protected areas that are much larger than the populations studied in Chile, so it is reasonable to expect the impact of the anthropogenic factor to be less. Beyond the variability of the size of the

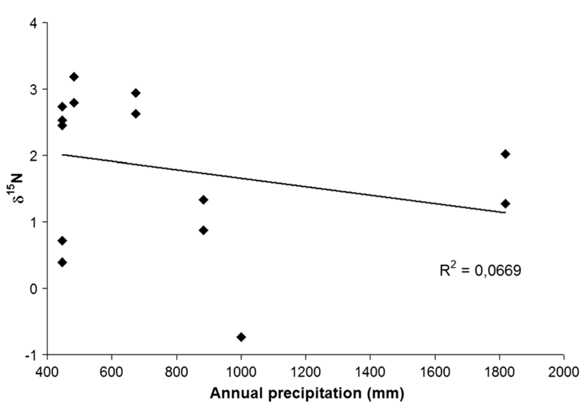

Figure 3. $\delta^{15}N$ values plotted against annual precipitation (mm) for huemul deer analysed.

huemuls' home range, the magnitude of the variation in plant isotopic signals over only a few kilometres in the ecotone should be considered as the principal factor that could explain the lack of correlation between the huemul isotopic signals and precipitation. That is to say, in a few kilometres, the huemul would have access to spaces with plants whose isotopic signals display marked variations.

The comparison of the isotopic signals of huemuls and guanacos, the secondary goal of this study, was expected that $\delta^{15}N$ and $\delta^{13}C$ of modern huemules recorded isotopic signals more depleted than the guanaco. Guanaco collected in the Nahuel Huapi NP (Limay area) had $\delta^{13}C$ −20.5‰ and $\delta^{15}N$ 5.9‰, and those from Tecka showed a $\delta^{13}C$ −19.1‰, and a $\delta^{15}N$ 5.0‰ (Table 1). These results are similar to the sample of 70 guanacos from the centre-west of Santa Cruz (Tessone, 2010; Tessone *et al.*, 2013). All together, these samples have a mean $\delta^{13}C$ of −19.4‰ ± 0.9‰ and $\delta^{15}N$ of 6.2‰ ± 1.4‰ (Table 2), with a non-outlier range between −21.2‰/−18.0‰ and 3.8‰/8.0‰, respectively. The difference between guanacos and huemuls is 1.4‰ for $\delta^{13}C$ and 3.3‰ for $\delta^{15}N$. The $\delta^{13}C$ exhibit an overlap in a large part of the distributions, whereas $\delta^{15}N$ values do not overlap (Figures 5 and 6). In both isotopes, the differences are statistically significant (one-way analysis of variance $\delta^{13}C$ F: 21.68 $p < 0.01$/$\delta^{15}N$ F: 120.1 $p < 0.01$), and the magnitude of the difference is higher for $\delta^{15}N$.

Conversely, Barberena *et al.* (2011) only found significant differences between huemuls and guanacos of the steppe in the $\delta^{15}N$. According to the authors, the lack of significant differences in the $\delta^{13}C$ values of huemuls and guanacos could be because the huemuls are not regularly consuming plants that are subject the canopy effect, highlighting that living in the forest does not necessarily mean eating there (Barberena *et al.*, 2011: 2319). The differences from our results may be

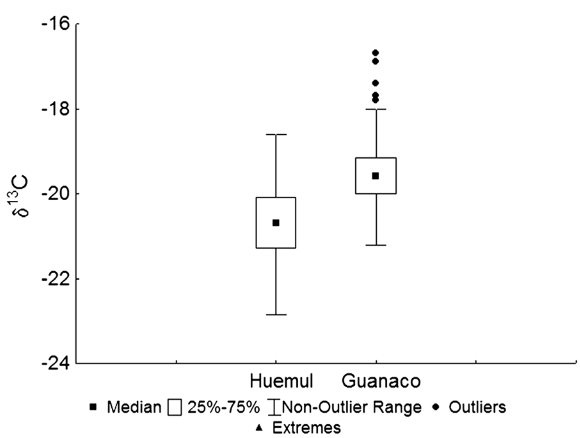

Figure 5. $\delta^{13}C$ comparison of huemul deer and guanaco.

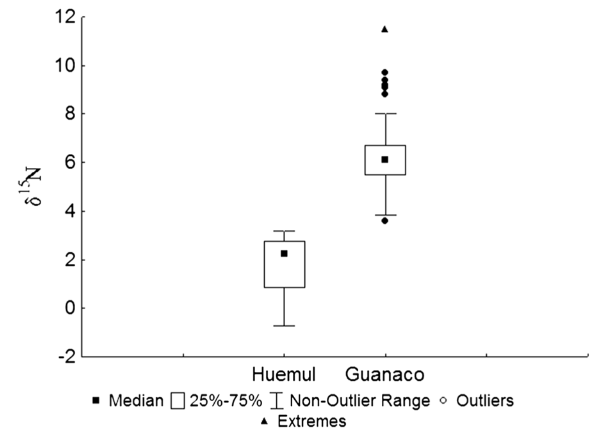

Figure 6. $\delta^{15}N$ comparison of huemul deer and guanaco.

mainly due to the huemul samples in Argentina being lower ($\delta^{13}C$ 0.6‰) than to those of Barberena *et al.* (2011), whereas at the same time, our guanacos have higher values ($\delta^{13}C$ 0.4‰).

In order to give greater strength to the contrast between herbivores, we include the huemul values published by Barberena *et al.* (2011) that correspond mainly to late Holocene archaeological samples. By including them, the huemul sample is composed of 24 individuals[3] with a mean $\delta^{13}C$ of −20.2‰ ± 1‰ and $\delta^{15}N$ of 2.0‰ ± 1.8‰. In both isotopes, when compared with the guanaco, the differences remains statistically significant (one-way analysis of variance $\delta^{13}C$ F: 18.11 $p < 0.01$/$\delta^{15}N$ F: 133.2 $p < 0.01$), reinforcing the isotopic differentiation of both species. The differences between the huemuls and the guanacos $\delta^{13}C$ are so small that it is difficult to think that the cause of the depletion of the huemul signals is due to the canopy effect. Nevertheless, we do believe that the depletion coincides with the consumption of plants that grow in environments with higher levels of precipitation.

In sum, regarding the isotopic characterization of the modern huemul and the possibility of establishing a particular isotopic marker for the Patagonian Andean forest, the results show, in the first place, that there is no relation between the isotopic values of modern huemuls and precipitation, even though previous studies have underlined the relation between these and the foliar $\delta^{13}C$ and $\delta^{15}N$ in Patagonia (Austin & Sala, 1999; Peri *et al.*, 2012). We believe that the great variation of the plants isotopic values in a limited spatial scale would be a relevant factor for the lack of correspondence between huemul recovery site and the precipitation

[3] This group does not include the two samples, one corresponding to the Early Holocene (UGAMS 6673) and the other to the Mid Holocene (UGAMS 8191) (Barberena *et al.*, 2011).

associated with that place. For that reason, for the time being, these isotopic markers are not useful for differentiating between huemuls from various forest sectors along the precipitation gradient. In the second place, as we expected the modern huemul differs in both isotopes from the guanaco, an herbivore that occupies open environment of marked aridity. We believe that this difference is associated with isotopic signals at the base of the trophic chain, which is influenced by the precipitation gradient (Austin & Sala, 1999; Peri *et al.*, 2012). For that reason, the results make it possible to separate these two herbivores associated with strongly contrasting environments, allowing the use of $\delta^{13}C$ and $\delta^{15}N$ as geographic markers for continental Patagonia.

Implications

The characterization of the forest isotopic signal has implications for assessing two relevant aspects of Andean forest history. Firstly, the past distribution of the huemul, an endangered species, could be evaluated. Based on the results found for modern huemuls, the aforementioned hypotheses regarding increased use of the forest-steppe ecotone (Serret, 2001) or of the steppe (Díaz, 2000; Flueck & Smith-Flueck, 2012) can be tested because in the moments prior to the change in the distribution of this ungulate, the isotopic values should be higher in comparison with the modern huemuls. Nevertheless, the heterogeneity of forest types currently occupied by the huemul (Povilitis, 1978; Serret, 2001; Vila *et al.*, 2004) makes it difficult to believe the recent biological history of the huemul has been the same throughout all of continental Patagonia. Thus, we consider that more modern huemul samples with known ecological habits are needed to evaluate these hypotheses (Drucker *et al.*, 2001). These samples should be the representative of the variability of all ecological contexts in which the huemul is currently distributed. In addition, we believe that the evaluation of these hypotheses should be based on the development of analyses that employ a narrower spatial scale than that used in our study. Secondly, how hunter-gatherers in the Holocene used and exploited the forest faunal resources could be better understood. Until now, human paleo diets in Patagonia have been interpreted in relation to the relative importance of the resources of the steppe and marine environments (Yesner *et al.*, 1991; Barberena, 2002; Zangrando *et al.*, 2004; Panarello *et al.*, 2006; Favier Dubois *et al.*, 2009; Moreno *et al.*, 2011). The characterization of the isotopic signal of modern huemuls contributes to this discussion by introducing a new environment to the paleodietary interpretation. Starting from various lines of evidence, it has been proposed that there was an increase in the use and exploitation of forest resources in northwestern Patagonia during the late Holocene (Bellelli *et al.*, 2003; Pérez & Batres, 2008; Lezcano *et al.*, 2010; Fernández *et al.*, 2013). The results of this study suggest that $\delta^{13}C$ and $\delta^{15}N$ are an independent line of evidence that add to the evaluation of hypotheses and models concerning human use of the Patagonian Andean forest in the past.

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