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Isotopic Ecology and Human Diets in the Forest–Steppe Ecotone, Aisén Region, Central-Western Patagonia, Chile

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ABSTRACT This work aims to build a comprehensive isotopic ecology with the ultimate purpose of assessing long-term human diet decision-making by means of stable isotope analysis. We present a set of $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{15}\text{N}_{\text{collagen}}$ isotopic values on the main faunal resources from the forest and steppe areas of the Aisén region (Central-Western Patagonia, Chile), in order to characterise their isotopic ranges and assess their consumption by past hunter–gatherer populations. Two sets of bioarchaeological remains are used for this comparison; a 10 200–9700 cal year BP assemblage from Baño Nuevo cave and a 1600–300 cal year BP assemblage gathered at different locations throughout Aisén. Isotopic signals from both assemblages indicate diets based on the consumption of protein provided by terrestrial mammals from steppe environments and no long-term signature of forest-resource consumption. On the other hand, the earlier group shows values that may indicate a wider dietary breadth, although this observation is preliminary. These results further suggest that the use of forests and the resources they provided, although visible through the zooarchaeological record (i.e. taxa represented at sites), must have been discontinuous and, perhaps, marginal in comparison with steppe regions. Copyright © 2013 John Wiley & Sons, Ltd.

Key words: carbon and nitrogen isotopes; forest/steppe ecotone; human diets; isotopic ecology; Western Patagonia

Introduction

Building a local isotopic ecology is a crucial step for assessing the role of different food resources in the diet of past human populations and as means of establishing the relative importance of specific environments in the evaluation of past settlement choices (Vogel, 1978; Sealy *et al.*, 1987; Bocherens *et al.*, 1995; Schwarcz & Schoeninger, 2011; Weber *et al.*, 2011; Barberena, 2012). Aisén (Chile) extends from 43°38' to 49°16' S, and it is an area characterised by notable environmental contrasts where forest coverage and food resources vary within tens of

kilometres in a west-to-east gradient. These differences are most evident in the area where the forest–steppe transition occurs. Variation in precipitation regimes generates sharply contrasting forested and open-steppe environments, characterised by different assemblages of floral and faunal taxa. These differences imply diverse scenarios for human dwelling, with open-steppe and closed-forest settings forming the ends of an ecological continuum. Cultural decisions within these two contrasting environments were presumably different, and thus, hunter–gatherer populations occupying the area must have had different dietary and mobility choices. In this perspective, learning about the isotopic values of the resources consumed and comparing them to the results for human remains play a key role in the interpretation of long-term human dietary choices. On this basis, the timing and patterns of the human use of particular environments can be assessed.

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A significant amount of isotopic data from southern Patagonia and from the island of Tierra del Fuego has aided in identifying a continuum of isotopic variation between 'marine' and 'terrestrial' human diets (Barberena, 2002; Yesner *et al.*, 2003; Zangrando *et al.*, 2004; Borrero & Barberena, 2006; Borrero *et al.*, 2009; Tessone *et al.*, 2009; Tessone 2010; Moreno *et al.*, 2011). As the former are characteristic of the Pacific coastline and the central-western areas of the Magellan Strait, the latter are predominant in the hinterland of continental Patagonia. The isotopic evidence of systematic marine protein consumption discussed as a proxy for the movement of individuals away from the coastlines is suggestive of restricted levels of mobility (Barberena, 2002; Borrero *et al.*, 2009). This information, however, does not support traditional historically based accounts depicting late hunter-gatherer societies with very large territories extending from the Atlantic coast to the Andes (i.e. Casamiquela, 1991). On the other hand, resources from the Patagonian forests have received very limited isotopic research effort until recently (Tessone, 2010; Barberena *et al.*, 2011; Tessone *et al.*, 2013). Forest-steppe ecotones are particular in that they share resources from different vegetational and faunal communities. The role of these ecosystems in human subsistence can be quantitatively assessed through isotopic studies; however, in the case of Aisén, systematic isotopic values have been presented so far only for the cervid huemul (*Hippocamelus bisulcus*, Barberena *et al.*, 2011). On the other hand, the scarce bioarchaeological evidence available has also hampered isotopic analyses on human remains. Using stable isotopes as means of assessing human paleodiets in Aisén is also motivated by the uneven availability of archaeofaunal assemblages, which are only limited to some caves with good bone preservation (i.e. Mena *et al.*, 2004; Velásquez & Mena, 2006) and do not represent the whole spatial and temporal extent of human occupation. Regional archaeological data extend from 11 500 calibrated years before present (cal year BP) onwards (Méndez & Reyes, 2008) and are unevenly distributed in space and intermittent throughout the Holocene (Mena, 2000; Méndez *et al.*, 2011). Bioarchaeological evidence suitable for stable isotope analysis is only available for two separate time ranges: (i) a 10-individual group recovered from Baño Nuevo 1 site (upper Ñirehuao basin) dated between 10 200 and 9700 cal year BP (Mena & Stafford, 2006; Reyes *et al.*, 2012) and (ii) human remains from several widely distributed sites framed within 1600 and 300 cal year BP, attributed to the latest indigenous human presence in the region (Reyes, 2002).

In this paper, we expand on results previously published, contributing to build a stronger isotopic database by providing $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{15}\text{N}_{\text{collagen}}$ values on a wider faunal assemblage, which includes

archaeological and recent samples from the forest-steppe ecotone. New information on human remains is also presented and discussed in the context of previous results (Reyes & Méndez, 2010; Reyes *et al.*, 2012). This information is employed as means of assessing the dietary role of foods from the forest and steppe among human groups since the Early Holocene, targeting specific periods represented in the bioarchaeological record. On this basis and by integrating recently published data for the neighbour Argentinean steppes (Tessone *et al.*, 2009, 2013; Tessone, 2010), the importance of different ecosystems for past hunter-gatherers can be evaluated.

The study area: climate and ecology

Aisén is characterised by a strong west-east precipitation gradient due to the forced subsidence of the Westerly winds and the barrier effect of the Andes (Garreaud, 2009). Precipitation values are 4300–3000 mm/year in the western archipelagic and coastal mountainous margin, 835 mm/year within the forest (city of Coyhaique) and 400–100 mm/year in the eastern open steppes (Plissock, 2003; SERPLAC, 2005). As a result of this large rainfall gradient, evergreen forests occur in the mountainous west, whereas open areas to the east are characterised by a cold-dry semiarid climate with steppe vegetation (Figure 1). The main vegetal communities are dominated by *Nothofagus betuloides*, *Desfontainia* and *Chusquea* in the evergreen forests, *Nothofagus pumilio*, *Nothofagus antarctica* and *Berberis* in the deciduous forests and forest/steppe transition, and *Festuca* and *Mulinum* in the steppe (Luebert & Plissock, 2006). As most of the region is largely characterised by a rugged mountainous geology, east of the Andes the landscape is composed of extensive sedimentary plains, large lakes and several other landforms of glacial and volcanic origin. The available palaeoenvironmental records for the continental area suggest that the most significant climate and landscape changes occurred during the Pleistocene/Holocene transition. Harsh periglacial environments gave way to today's similar vegetation distribution, which did not vary substantially since ca. 8000 cal year BP, except for fluctuations in the location of the forest-steppe margins (de Porras *et al.*, 2012; Villa-Martínez *et al.*, 2012). The easternmost position of the forest-steppe ecotone in Aisén is documented for the period between 8000 and 3000 cal year BP suggesting an increase in effective moisture, followed by its retraction at 1200 cal year BP when the current vegetation distribution was established (de Porras *et al.*, 2012).

Among the main faunal species from the forest and the steppe Aisén (Table 1), the guanaco (*Lama guanicoe*) stands out. It is the largest terrestrial mammal from

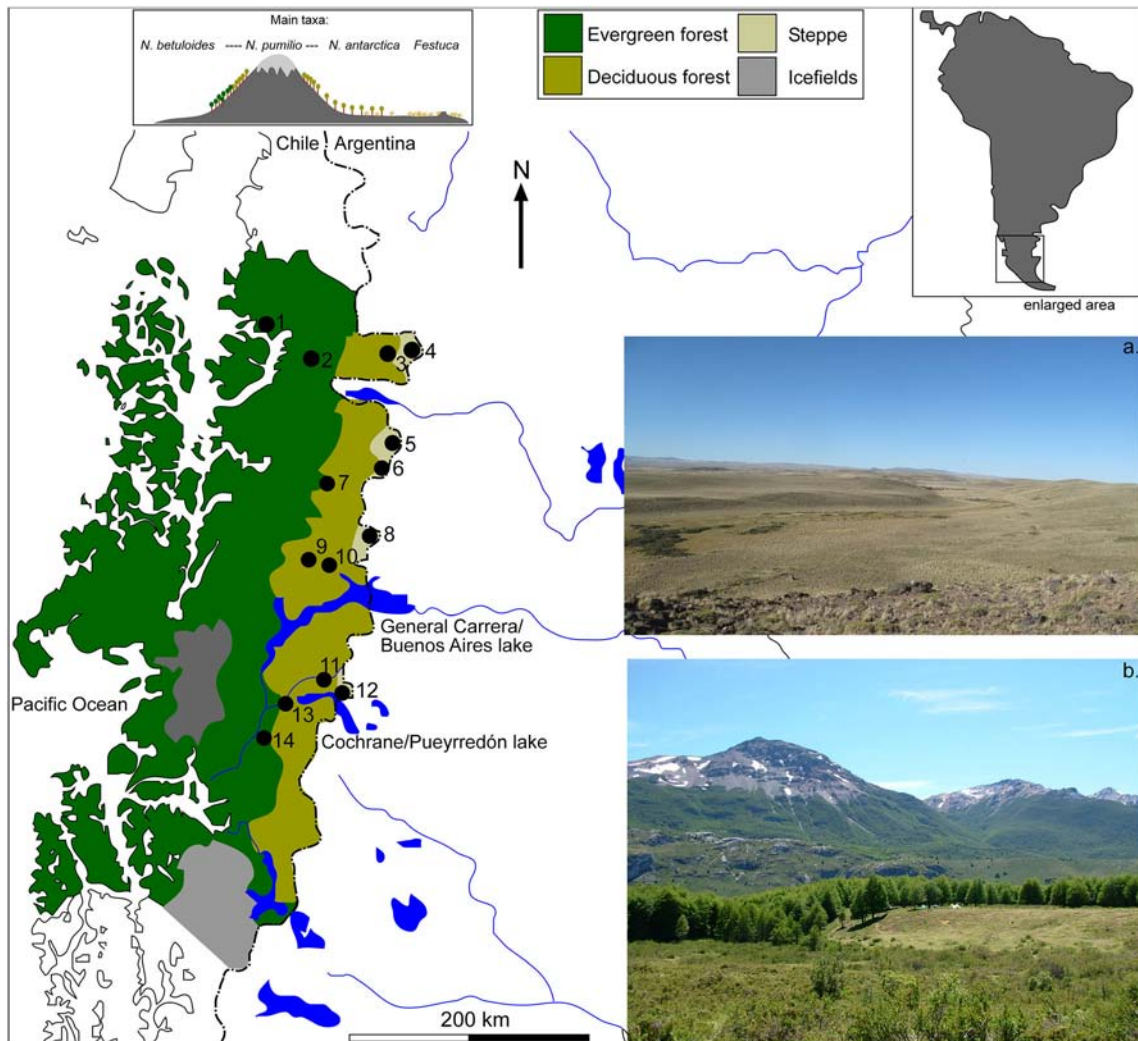


Figure 1. Map of the study area depicting vegetation differences and localities (archaeological sites) mentioned in the text. 1. Gala (Seno Gala 1), 2. Lower Cisnes (Alero El Toro), 3. Middle Cisnes (Chenque Cisnes), 4. Upper Cisnes (El Chueco 1), 5. Upper Nirehuao (Baño Nuevo 1 and 9), 6. Coyhaique Alto (Punta del Monte 2), 7. Coyhaique (Lomo de Dragón bajo), 8. Upper Simpson, 9. Middle Ibáñez (Las Guanacas, Alero Fontana, RI18), 10. Lower Ibáñez (Cementerio Puerto Ibáñez), 11. Middle Chacabuco (Alero Gianella), 12. Upper Chacabuco (Alero Entrada Baker), 13. Cerro Tamango, 14. Los Nadis; (a) open-steppe environment and (b) forest–steppe ecotone. This figure is available in colour online at wileyonlinelibrary.com/journal/oa.

Patagonia and the most widely distributed camelid in South America (from the equator to 54°45' S). It inhabits preferably open grasslands, flat terrains with low hiding cover, although they are known to occupy forested environments in the island of Tierra del Fuego (Raedeke, 1978; González *et al.*, 2006). This species typically feeds on the herbaceous stratum, but it has the ability to alternate seasonally between grazing and browsing with the capacity to digest low quality forage (Puig *et al.*, 2001; González *et al.*, 2009).

The huemul (*Hippocamelus bisulcus*) is a medium-sized cervid that currently inhabits the Andean forests between 45° and 49° S, including mountainous settings

over the forest upper limit. It is in a drastic process of population retraction and genetic impoverishment within its area of distribution (Corti *et al.*, 2011). The huemul feeds primarily on buds, twigs, flowers and other parts of woody plants (González *et al.*, 2009). The second cervid sampled is the pudú (*Pudu pudu*), the smallest in the world and inhabitant of the Andean evergreen forests between 35° and 46°45' S in altitudes below 1700 masl. The pudú has solitary habits, prefers the dim understory and feeds on moss, shrubs and fruits (González *et al.*, 2009).

Two extant foxes are referred in this paper: *Lycalopex culpaeus*, the larger red fox, and *Lycalopex griseus*, the

Table 1. Faunal species sampled for isotopic analysis in the forest/steppe and steppe of the Aisén region

Order	Species	Common name	Habitat	Dietary preferences	Selected references
Artiodactyla	<i>Hippocamelus bisulcus</i>	Huemul (deer)	Forest	Herbivore	González et al. (2009)
	<i>Pudu pudu</i>	Pudu (small deer)	Forest	Herbivore	González et al. (2009)
Bird	<i>Lama guanicoe</i>	Guanaco	Steppe	Herbivore	Puig et al. (2001); González et al. (2009)
	<i>Rhea pennata</i>	Choique (flightless bird)	Steppe	Omnivore (herbivore)	Bonino et al. (1986); Kusch & Henríquez (2011)
	<i>Lycalopex culpaeus</i>	Red fox	Forest & steppe	Carnivore (opportunistic)	Jaksic et al., 1980; Quintana et al., 2009
	<i>Lycalopex griseus</i>	Grey fox	Forest & steppe	Carnivore (opportunistic)	
Carnivora	<i>Dusicyon avus</i>	Extinct fox	Steppe (?) ^a	Carnivore/omnivore (?)	Berman & Tonni (1987); Prevosti & Vizcaino (2006); Prevosti et al. (2011)
	<i>Conepatus humboldtii</i>	Chingue (skunk)	Forest & steppe	Omnivore	Quintana et al. (2009)
	<i>Zaedyus pichiy</i>	Piche (armadillo)	Steppe	Omnivore (opportunistic)	Superina et al. (2009); Tamayo (2009)

^aHabitat reconstruction based on occurrences in the zooarchaeological record.

smaller grey fox. As *L. culpaeus* has a wide distribution from 1°40' N to 53° S, *L. griseus* geographical distribution ranges from 18° to 53° S (Jaksic et al., 1980; Quintana et al., 2009). Foxes are more common in the open steppe, but they also inhabit forested areas of Aisén (Figuerola et al., 2000). Both species are opportunistic carnivores of crepuscular/nocturnal habits which feed largely on rodents, birds and other larger prey, and occasionally plants and fruits, varying their diets according to the seasonal vulnerability of prey (Quintana et al., 2009). We also refer to *Dusicyon avus*, an extinct fox, originally distributed throughout the southern cone from 32° to 54° S and with taxon dates ranging from 12 500 to 3100 cal year BP (Prevosti et al., 2011). Skeletal comparisons indicate that it was slightly larger than the extant species of *Lycalopex*, and teeth morphology suggests a diet with greater carnivorous habits (Prevosti & Vizcaino, 2006).

The chingue or Patagonian hognosed skunk (*Conepatus humboldtii*) is a nocturnal carnivore which inhabits mainly open grasslands and shrublands from 38° to 53° S, although it may also live in closed forests. It is characterised as an omnivore and generalist, which feeds basically on insects, beetles, amphibians, small rodents, eggs and bulbs (Quintana et al., 2009).

The last mammal sampled was the dasypod *Zaedyus pichiy* or piche. This armadillo of solitary, diurnal/nocturnal and semi-fossorial habits lives in open grasslands of arid and semiarid environments on scattered locations between 33° and 44° S and continuously from 44° to 53° S (Tamayo, 2009). It is an opportunistic omnivore whose diet includes insects, small vertebrates such as lizards and rodents, arachnids, moss and roots (Superina et al., 2009; Tamayo, 2009).

The flightless bird *Rhea pennata* or choique is the largest bird living in the open steppes of Patagonia and reaching 53° S. It prefers areas with grasses and floral diversity (Kusch & Henríquez, 2011) and is described as an omnivore feeding mainly on shrubs, leaves, stems and roots of various grasses (Bonino et al., 1986).

Materials and methods

We selected the forest–steppe transition and steppe areas for archaeological survey because they provide information on human locational choices by comparing contrasting environments and their resources and because these are the areas with the largest amount of available archaeological evidences.

The samples analysed in this paper were recovered both from archaeological sites (65.31%, either surface or stratigraphic) and surface findings of animal carcasses

(34.69%) with various degrees of disarticulation. The sites and surface samples are unevenly distributed throughout the region and are biased in favour of the Ñirehuao river basin. The selection of samples was intended to represent those species most common in the archaeological record within the study area (i.e. Mena *et al.*, 2004) and the immediate vicinity (Tessone & Panarello, 2008/2010). In the case of archaeological samples, taxonomical identification was performed by observation of key anatomical features by comparison to reference material. Taxonomic discrimination of modern samples was easier and is followed by an ongoing programme of carcass monitoring, decomposition and bone retrieval.

Sample selection favoured open-steppe settings (67.3%) because they comprise the majority of research efforts and yield the highest frequency of archaeological sites based on comparative studies (Reyes *et al.*, 2009). Samples recovered at the forest–steppe transition (16.3%) and within the forest (deciduous: 4.1%; evergreen 12.2%) were less and mainly focused on the two available deer species (Barberena *et al.*, 2011). Whenever available, sampling also sought to consider temporal variation; however, changes in temporal trends have proven not to be significant, at least for *Hippocamelus bisulcus* (Barberena *et al.*, 2011) and *Lama guanicoe* (Barberena *et al.*, 2009). This information is fundamental to evaluate changes in human dietary choices through time. All age determinations discussed here were performed by direct ^{14}C analyses on bones. They are expressed in cal year BP and were calibrated with the OxCal 4.1 programme (Bronk Ramsey, 2009) utilising the ShCal04 curve (McCormac *et al.*, 2004). Although Early Holocene samples recovered at Baño Nuevo 1 cave were in an excellent state of preservation because of the dry conditions within the cave (Reyes *et al.*, 2012), Late Holocene open-air burials have diagenetic consequences resulting in poor bone preservation, and thus, samples only occasionally provide enough collagen for ^{14}C and stable isotope analyses.

Most of the samples were processed at the Center for Applied Isotope Studies, University of Georgia (USA). The crushed bone samples were treated with diluted 1 N acetic acid to remove surface absorbed and secondary carbonates. Periodic evacuation insured that evolved carbon dioxide was removed from the interior of the sample fragments and that fresh acid was allowed to reach even the interior micro-surfaces. The chemically cleaned sample was then reacted under vacuum with 100% H_3PO_4 to dissolve the bone mineral and release carbon dioxide from bioapatite for carbon isotope ratio analysis. The residue was filtered, rinsed with deionized water and under slightly acid condition (pH 3) heated at 80° C for 6 h to dissolve collagen and leave humic substances in the precipitate.

The collagen solution was then filtered to isolate pure collages and dried out. The dried collagen was combusted at 575° C in evacuated/sealed Pyrex ampoule in the presence of CuO . The carbon dioxide and nitrogen were cryogenically separated. The isotopic ratios of carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) were measured separately, using a Finnigan MAT 252 Isotope Ratio Mass Spectrometer following off-line sample preparation. The dual-inlet rationing system alternately measures unknown sample and known reference gas to achieve a high-precision stable isotope measurement. Calibration is made using National Institute of Standards and Technology (NIST) standard hydrocarbon oil, NBS-22 (Noakes *et al.*, 2006). The ratios are expressed in per thousand (‰) using the δ notation and are measured with respect to the limestone Vienna Pee Dee Belemnite, in the case of $\delta^{13}\text{C}_{\text{collagen}}$, and to atmospheric air nitrogen, in the case of $\delta^{15}\text{N}$ (Schwarcz & Schoeninger, 2011). Error is less than 0.1‰ for $\delta^{13}\text{C}$ and less than 0.2‰ for $\delta^{15}\text{N}$.

Two $\delta^{13}\text{C}_{\text{collagen}}$ values presented in this paper are product of ^{14}C AMS dates (UCIAMS 19487 and BETA 230515). Available information suggests that these values can be confidently used for stable isotopic research (van Klinken *et al.*, 2000). A +1.5‰ correction factor was applied to the $\delta^{13}\text{C}$ values of modern samples in order to deal with the 'Suess' effect associated with the injection of ^{13}C -depleted carbon to the atmosphere due to the burning of fossil fuels. This produces lower $\delta^{13}\text{C}$ values in organisms post-dating the XIX Century (Marino & McElroy, 1991).

Results

In this paper, we present isotopic results for 22 new faunal samples (Table 2) and 3 new samples on human remains (Table 3). This information adds to 13 previous determinations for faunal samples of huemul and pudú (Barberena *et al.*, 2011), and 7 samples from human remains (Reyes & Méndez, 2010; Reyes *et al.*, 2012).

Isotopic ecology of faunal species

Descriptive statistics for isotopic values of the faunal species analysed are presented in Table 4. The isotopic ecology of *Hippocamelus bisulcus* has been well characterised for Aisén. The results presented here indicate a $\delta^{13}\text{C}$ average of -20.2‰ with a standard deviation of 0.8‰ (Figure 2). As suggested previously (Barberena *et al.*, 2011), the huemul does not show a significant incidence of the canopy effect (van der Merwe & Medina, 1991; Drucker *et al.*, 2008), which would produce low $\delta^{13}\text{C}$

Table 2. Isotopic values of resources discussed in the text

Species	Environment	Locality/river basin	Site	#LAB	$\delta^{13}\text{C}$ _{1uncorrected}	$\delta^{13}\text{C}$ _{corrected}	$\delta^{15}\text{N}$	Context
<i>Conepatus humboldtii</i>	Steppe	Upper Nirehuao		UGAMS 10667	-21.4	-19.9	8.9	Surface
<i>Conepatus humboldtii</i>	Steppe	Upper Simpson		UGAMS 10668	-20.4	-18.9	9.2	Surface
<i>Conepatus humboldtii</i>	Steppe	Upper Simpson		UGAMS 8186	-21.4	-19.9	7.3	Surface
<i>Dusicyon avus</i>	Steppe	Upper Cisnes	El Chueco 1	UGAMS 6583	-19.9		10.9	Stratigraphic
<i>Hippocamelus bisulcus</i>	Deciduous forest	Middle Ibañez	Alero Fontana	UGAMS 6677 ^c	-20.4		1.5	Stratigraphic
<i>Hippocamelus bisulcus</i>	Deciduous forest	Middle Ibañez	Alero Fontana	UGAMS 6678 ^c	-20.5		0.9	Stratigraphic
<i>Hippocamelus bisulcus</i>	Evergreen forest	Lower Cisnes	Alero El Toro	UGAMS 6671 ^c	-20.8		0.7	Stratigraphic
<i>Hippocamelus bisulcus</i>	Evergreen forest	Lower Cisnes	Alero El Toro	UGAMS 6672 ^c	-20.6		-0.6	Stratigraphic
<i>Hippocamelus bisulcus</i>	Evergreen forest	Coyhaique	Lomo de Dragón bajo	UGAMS 8191 ^c	-21.7		3.5	Stratigraphic
<i>Hippocamelus bisulcus</i>	Evergreen forest	Los Ñadis		UGAMS 6676 ^c	-21	-19.5	1.3	Surface
<i>Hippocamelus bisulcus</i>	Steppe	Upper Nirehuao	Baño Nuevo 1	UGAMS 6673 ^c	-20.6		2.2	Stratigraphic
<i>Hippocamelus bisulcus</i>	Steppe	Upper Nirehuao	Baño Nuevo 1	UCIAMS 19487 ^d	-20.5			Stratigraphic
<i>Hippocamelus bisulcus</i>	Steppe	Upper Chacabuco	Alero Entrada Baker	UGAMS 6674 ^c	-19.8		5.3	Stratigraphic
<i>Hippocamelus bisulcus</i>	Steppe forest transition	Lower Ibañez	Las Guanacas	UGAMS 6680 ^c	-18.8		4.4	Stratigraphic
<i>Hippocamelus bisulcus</i>	Steppe forest transition	Lower Ibañez	Las Guanacas	UGAMS 6679 ^c	-18.8		2.6	Stratigraphic
<i>Hippocamelus bisulcus</i>	Steppe forest transition	Middle Chacabuco	Alero Gianella	UGAMS 6675 ^c	-19.9		5.3	Stratigraphic
<i>Hippocamelus bisulcus</i>	Steppe forest transition	Cerro Tamango		UGAMS 05218 ^c	-22.1	-20.6	5.4	Surface
<i>Lama guanicoe</i>	Steppe	Upper Cisnes	El Chueco 1	UGAMS 06106	-20.2		6.1	Stratigraphic
<i>Lama guanicoe</i>	Steppe	Upper Cisnes	El Chueco 1	UGAMS 06107	-20.1		4.5	Stratigraphic
<i>Lama guanicoe</i>	Steppe	Upper Nirehuao	Baño Nuevo 9	UGAMS 10662	-18.8		7.1	Surface
<i>Lama guanicoe</i>	Steppe	Upper Nirehuao		UGAMS 10665	-19.1		7.6	Surface
<i>Lycalopex culpaeus</i>	Steppe	Upper Nirehuao	Punta del Monte 2	BETA 297426	-20.1		6	Surface
<i>Lycalopex griseus</i>	Steppe	Coyhaique Alto		UGAMS 10660	-21	-19.5	8.6	Surface
<i>Lycalopex sp.</i>	Steppe	Upper Nirehuao		UGAMS 10663	-21.2	-19.7	11	Surface
<i>Pudu pudu</i>	Steppe	Upper Nirehuao		UGAMS 10666	-21.2	-19.7	9.4	Surface
<i>Pudu pudu</i>	Evergreen forest	Gala	Seno Gala 1	BETA 230515 ^a	-23.6			Surface
<i>Rhea pennata</i>	Evergreen forest	Lower Cisnes	Alero El Toro	UGAMS 6670 ^c	-21.6	-19.2	1.8	Stratigraphic
<i>Rhea pennata</i>	Steppe	Upper Nirehuao		UGAMS 10656	-20.7	-14	10	Surface
<i>Rhea pennata</i>	Steppe	Upper Nirehuao		UGAMS 10657 ^b	-15.5	-14	9.4	Surface
<i>Rhea pennata</i>	Steppe	Upper Nirehuao		UGAMS 10658	-22	-20.5	6.2	Surface
<i>Rhea pennata</i>	Steppe	Upper Nirehuao		UGAMS 10664	-22.3	-20.8	8.1	Surface
<i>Zaedyus pichiy</i>	Steppe	Upper Nirehuao		UGAMS 10659	-20.8	-19.3	9.5	Surface
<i>Zaedyus pichiy</i>	Steppe	Upper Simpson		UGAMS 8187	-22.5	-21	9.1	Surface
<i>Zaedyus pichiy</i>	Steppe	Upper Simpson		UGAMS 8188	-21.7	-20.2	7.8	Surface
<i>Zaedyus pichiy</i>	Steppe	Lower Ibañez		UGAMS 10669	-18.7	-17.2	9.4	Surface

All material analysed is bone collagen, except ^atooth; ^begg shell; ^c $\delta^{13}\text{C}_{\text{collagen}}$ in contemporary samples was corrected for Suess effect. Isotopic values were previously reported by ^dBarberena et al. (2011) and ^eStafford (2005).

Table 3. Isotopic values of human beings discussed in the text

Locality/river basin	Site	#LAB	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	^{14}C age	Environment	Reference
Middle Cisnes	Chenque Cisnes	UGAMS 5963	−19.6	10.7	1590 ± 25 BP	Steppe forest transition	Reyes & Méndez (2010)
Upper Ñirehuao	Baño Nuevo 1 (ind. 1)	CAMS 79933	−19	10.3	8950 ± 50 BP ^a	Steppe	Reyes <i>et al.</i> (2012)
Upper Ñirehuao	Baño Nuevo 1 (ind. 2)	UGAMS 5924	−21	11.5	8850 ± 50 BP (CAMS 36633) ^a	Steppe	Reyes <i>et al.</i> (2012)
Upper Ñirehuao	Baño Nuevo 1 (ind. 3)	UGAMS 5925	−18.5	10.4	8950 ± 60 BP (CAMS 101893) ^a	Steppe	Reyes <i>et al.</i> (2012)
Upper Ñirehuao	Baño Nuevo 1 (ind. 4)	CAMS 101894	−19.4	11.7	8945 ± 40 BP ^a	Steppe	Reyes <i>et al.</i> (2012)
Upper Ñirehuao	Baño Nuevo 1 (ind. 6)	UGAMS 5926	−21.2	7.3	Undated	Steppe	Reyes <i>et al.</i> (2012)
Upper Ñirehuao	Baño Nuevo 1 (ind. 10)	UGAMS 5002	−19	12.6	8960 ± 40 BP	Steppe	Reyes <i>et al.</i> (2012)
Middle Ibáñez	R118	UGAMS 8192	−19.6	10	410 ± 40 BP (CAMS 71701) ^b	Steppe forest transition	This paper
Lower Ibáñez	Cementerio P. Ibáñez (ind. 1)	UGAMS 8189	−20.6	9.6	570 ± 40 BP (CAMS 79934) ^b	Steppe forest transition	This paper
Lower Ibáñez	Cementerio P. Ibáñez (ind. 7)	UGAMS 8190	−23	9.4	370 ± 40 BP (BETA 160305) ^b	Steppe forest transition	This paper

ind. = individual; ¹⁴C dates are expressed in years BP and provided in the reference, except when noted by ^aMena & Stafford (2006) and ^bReyes (2002).

values. This was originally expected given huemul's preference towards inhabiting closed-forest settings. Considering that guanacos from forest and ecotone settings do show an influence of the canopy effect in southern Patagonia (Barberena *et al.*, 2009; Tessone, 2010), it is suggested that these relatively higher isotopic values reflect a specialised feeding behaviour focusing in open patches within the forest (Barberena *et al.*, 2011), which are characteristic of high areas of Aisén.

On the other hand, the huemul presents significantly low $\delta^{15}\text{N}$ values with a large range extending from 5.4‰ to −0.6‰ (Figure 3). This can be interpreted in the light of global studies in soil isotopic ecology and plant communities from cold-forested environments, which indicate lower $\delta^{15}\text{N}$ values due to the limited availability of N in these ecosystems (Craine *et al.*, 2009). The existence of nitrogen-fixing bacteria could also contribute to produce these low values. This would explain the low $\delta^{15}\text{N}$ values recorded for huemul from Aisén, as well as for other cervid species around the world (Bocherens, 2000; Drucker *et al.*, 2008). Thus, the $\delta^{15}\text{N}$ signature may constitute an isotopic marker of forest use by huemul (Barberena *et al.*, 2011) and, as discussed later, can also be used for distinguishing systematic huemul consumption by humans. Variation recorded in $\delta^{15}\text{N}$ values and to a lesser degree in $\delta^{13}\text{C}$ values may be associated with the access to closed settings and open or semi open grasslands, which may be reached not only towards the eastern ecotone but also along the large altitudinal gradient of Aisén. These results for huemul are in agreement with others obtained at similar regions in Argentinean Patagonia (Tessone, 2010; Tessone *et al.*, 2012), which indicate that the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ patterns recorded have a macro-regional expression.

Regarding the smaller cervid (*Pudu pudu*), the two analysed samples present low $\delta^{13}\text{C}$ values with respect to both huemul and guanacos from open environments, falling within the range of values for the guanacos from forested environments (Barberena *et al.*, 2011). This is consistent with the influence of the canopy effect in this species, as well as with the available ecological information (González *et al.*, 2009). However, because of the small size of our sample, this is only tentative. The only $\delta^{15}\text{N}$ value available is low, which is further in agreement with the depleted signature of forest herbivores already discussed for huemul.

Lama guanicoe was the main protein staple for the Patagonian macro-region at large (Borrero, 1990; Mengoni Goñalons, 1999; Velásquez & Mena, 2006, among many others). Here, we present five values for Aisén. $\delta^{13}\text{C}$ results have an average of −19.66‰ with a small standard deviation and are consistent with the C₃-dominated southern Patagonian environment. The mean for guanaco cannot be statistically differentiated from that for huemul

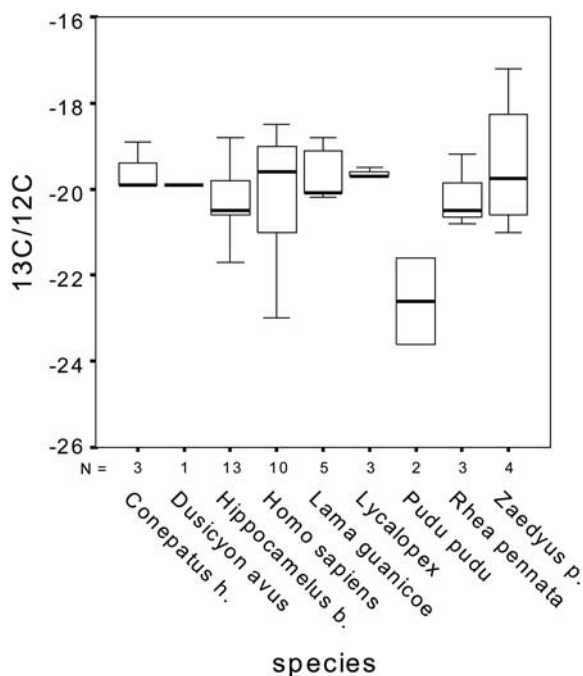
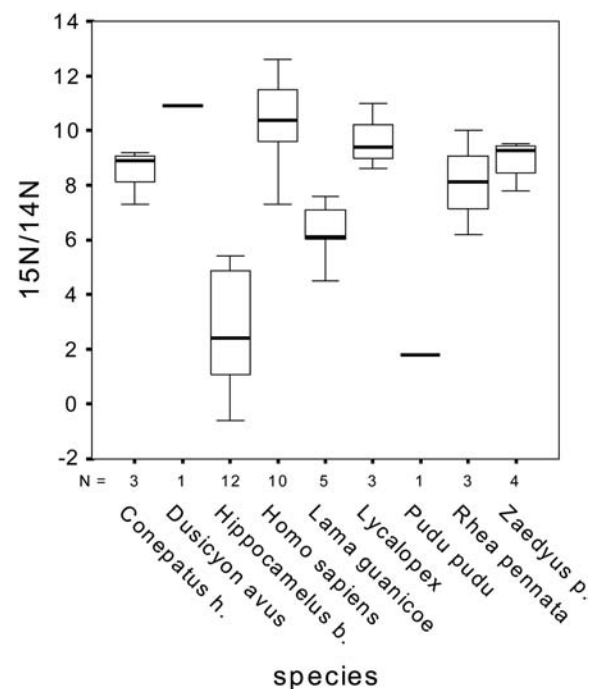
Table 4. Descriptive statistics for $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{15}\text{N}_{\text{collagen}}$ data on Aisé'n's faunas discussed in the text

Faunal resources	Isotope ratio	N	Average	Maximum value	Minimum value	Standard deviation
Foxes	$\delta^{13}\text{C}$	4	-19.6	-19.5	-19.9	0.1
	$\delta^{15}\text{N}$	4	10	11	8.6	1.2
<i>Conepatus humboldtii</i>	$\delta^{13}\text{C}$	3	-19.6	-18.9	-19.9	0.6
	$\delta^{15}\text{N}$	3	8.5	9.2	7.3	1
<i>Zaedyus pichiy</i>	$\delta^{13}\text{C}$	4	-19.4	-17.2	-21	1.6
	$\delta^{15}\text{N}$	4	9	9.5	7.8	0.8
<i>Rhea pennata</i>	$\delta^{13}\text{C}$	3	-20.2	-19.2	-20.8	0.9
	$\delta^{15}\text{N}$	3	8.1	10	6.2	1.9
<i>Lama guanicoe</i>	$\delta^{13}\text{C}$	5	-19.7	-18.8	-20.2	0.7
	$\delta^{15}\text{N}$	5	6.3	7.6	4.5	1.2
<i>Hippocamelus bisulcus</i>	$\delta^{13}\text{C}$	13	-20.2	-18.8	-21.7	0.8
	$\delta^{15}\text{N}$	12	2.7	5.4	-0.6	2.1
<i>Pudu pudu</i>	$\delta^{15}\text{N}$	2				
	$\delta^{13}\text{C}$	2		-21.6	-23.6	

($t = 1.2991$, $p = 0.212$, normality tested by Shapiro–Wilk). The $\delta^{15}\text{N}$ values have an average of 6.3‰. The $\delta^{15}\text{N}$ range for guanaco does not overlap at one standard deviation with that recorded for huemul and can be statistically differentiated ($t = 3.5898$, $p = 0.002$, normality tested by Shapiro–Wilk). This is important because it lends support to the possibility of discriminating human consumption of meat protein from artiodactyls from forest versus steppe environments. Beyond Aisé'n, guanaco has been thoroughly characterised isotopically, and although there are regional variations, the values presented here are contained within the known ranges for the species (Barberena *et al.*, 2009; Tessone, 2010; Tessone & Belardi, 2010).

Different carnivore species are analysed here: *L. culpaeus*, *L. griseus*, *Dusycion avus* and *Conepatus humboldtii*. There are few values for each species, allowing only a preliminary characterization. The $\delta^{13}\text{C}$ values for the two species of *Lycalopex* and one for *Dusycion avus* are similar and consistent with a high trophic position. Variability is larger for $\delta^{15}\text{N}$ and may be associated to the large dietary breadth characteristic of these species, including rodents, insects and also small fruits (Jaksić *et al.*, 1980; Johnson & Franklin, 1994; Prevosti & Vizcaino, 2006; Quintana *et al.*, 2009).

The four samples of the opportunistic omnivore *Zaedyus pichiy* analysed here are consistent with

Figure 2. Boxplots for $\delta^{13}\text{C}_{\text{collagen}}$ values for faunal resources and human beings from Aisé'n.Figure 3. Boxplots for $\delta^{15}\text{N}_{\text{collagen}}$ values for faunal resources and human beings from Aisé'n.

ecological data, indicating an important variability and higher $\delta^{15}\text{N}$ values overlapping with *Lycalopex* (see also Martínez *et al.*, 2009). The fact that *Zaedyus pichiy* and *Conepatus humboldtii* show very similar averages and ranges for both chemical elements reinforces the similarities in diets indicating a high degree of opportunistic omnivory.

Three samples of the flightless bird *Rhea pennata* indicate a very well-defined C_3 diet with an average of -20.2‰ and a larger variability in $\delta^{15}\text{N}$ values with a range that overlaps partially with that for carnivores. This may indicate some degree of omnivory, as well as differences due to digestive systems (see discussion in Gómez Otero, 2007; Tessone & Panarello, 2008/2010; Tessone, 2010). Importantly, these results and the larger database presented by Tessone (2010) suggest the possibility of discriminating the consumption of choique and guanaco on the basis of $\delta^{15}\text{N}$ values. One value on choique eggshell is presented in Table 2 but not discussed further because of the lack of additional data.

The information presented for the isotopic ecology provides a frame of reference for reconstructing human paleodiets. In some respects, the tendencies described are exploratory because of small sample sizes. In other respects and by integrating data generated by Tessone (2010) for Santa Cruz Province in Argentina, two well-based conclusions can be presented for the forest–steppe ecotone of Aisén:

- (a) The human consumption of the main meat protein sources from the forest (huemul and pudú) can be differentiated from those from the steppe (guanaco) by means of $\delta^{15}\text{N}$ values, because the sustained consumption of the first should result in lower signatures. Huemul presents an average $\delta^{15}\text{N}$ value of $\sim 3\text{‰}$ (range between -0.6 and 5.4‰). Considering an isotopic fractionation of 3‰ (Ambrose, 1991; Schwarcz & Schoeninger, 2011; although see Hedges & Reynard, 2007), a human diet fully based on the consumption of cervid protein would produce $\delta^{15}\text{N}$ values of $\sim 6/7\text{‰}$, whereas a diet based on guanaco would produce values of $\sim 9/10\text{‰}$. Values arising from diets mixing both protein sources would be around $7/8\text{‰}$. On the contrary, $\delta^{13}\text{C}$ results would be similar for diets based on protein from the forest and steppe.
- (b) Diets based on the consumption of protein from guanaco would produce lower $\delta^{15}\text{N}$ values than diets including a wider diversity of taxa, such as *Zaedyus*, *Conepatus*, foxes and *Rhea*.

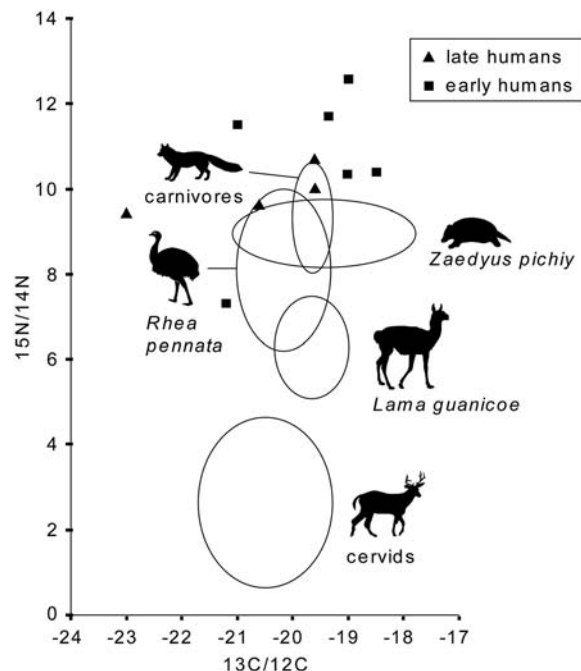


Figure 4. $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{15}\text{N}_{\text{collagen}}$ values for faunal resources and human beings from Aisén. Fields defined by the ellipses stand for 1-sigma errors.

Human beings

The human sample is composed by six individuals from the Early Holocene and four samples from the Late Holocene (Table 3). With one exception, all the samples are directly dated by ^{14}C AMS. The individual 6 from Baño Nuevo 1, which is the only undated sample, can be confidently included in the Early Holocene temporal set because it groups with the rest in terms of stratigraphic position. This bioarchaeological assemblage provides the largest isotopic dataset for Early Holocene Patagonian human remains.¹

The complete human sample has average values of $-20.1 \pm 1.4\text{‰}$ for $\delta^{13}\text{C}$ and $10.4 \pm 1.5\text{‰}$ for $\delta^{15}\text{N}$. Figure 4 shows human values in the context of the isotopic ecology, indicating that $\delta^{13}\text{C}$ values for humans could result from the consumption of several species, such as guanaco, choique, small mammals and cervids, in varying combinations. This is due to the existence of relatively small interspecific spacing in the currently available isotopic ecology set of samples. On the other hand, $\delta^{15}\text{N}$ values indicate an average spacing of $\sim 5\text{‰}$ between human samples and cervids, and closer association with species from the steppe. The individual 6 from Baño Nuevo 1 site, with values of -21.2‰ for $\delta^{13}\text{C}$ and 7.3‰ for $\delta^{15}\text{N}$,

¹ The signal for one individual from Baño Nuevo 1 was previously considered anomalous (Reyes *et al.*, 2012) and is therefore not included here.

constitutes an exception indicating a diet including N and C-depleted resources, probably from the forest.

A comparison of the Early Holocene (average values of $-19.7 \pm 1.1\text{‰}$ for $\delta^{13}\text{C}$ and $10.6 \pm 1.9\text{‰}$ for $\delta^{15}\text{N}$) and Late Holocene (average values of $-20.7 \pm 1.6\text{‰}$ for $\delta^{13}\text{C}$ and $9.9 \pm 0.6\text{‰}$ for $\delta^{15}\text{N}$) assemblages indicates that $\delta^{13}\text{C}$ values overlap and cannot be statistically differentiated ($t = 1.1889$, $p = 0.268$, normality tested by Shapiro–Wilk). $\delta^{15}\text{N}$ values show higher values for the Early Holocene human remains. Although the samples cannot be statistically differentiated on the basis of their means ($t = 0.737$, $p = 0.481$, normality tested by Shapiro–Wilk), variance analysis indicates the possible existence of differences ($F = 10.351$, $p = 0.08$). Samples are small, hampering the strength of these tendencies, which are nonetheless valuable for exploratory analysis, because the low p -value points in the line of the differences perceived in the graphic analysis.

Discussion

With one exception, the values presented for human samples are consistent with diets based on the consumption of protein from mammals from the steppe, which in Aisén are dominated by species displaying the C_3 photosynthetic pathway, better adapted to cold and humid conditions (Ehleringer & Cerling, 2001). Data published for southern Patagonian marine animal species, mainly mammals and birds (Zangrando *et al.*, 2004; Borrero *et al.*, 2009), indicate higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than the human samples reported here, lending support to the suggestion of terrestrially based human diets in Aisén. This is consistent with the geographical setting of eastern Aisén, separated from the coast by 100–140 km of rugged mountainous landscape, and consistent with the main circulation routes defined by other datasets (Méndez & Reyes, 2008; Méndez *et al.*, 2012).

Results presented here and elsewhere (Barberena *et al.*, 2011) indicate that in the context of terrestrial food webs in Aisén, the recurrent consumption of huemul and pudú would produce a low $\delta^{15}\text{N}$ signature. On the other hand, huemul consumption would not be recognised in $\delta^{13}\text{C}$ values because they are indistinguishable from other more commonly preyed terrestrial resources from the steppe, such as guanaco. The data presented for the isotopic ecology and human remains from Aisén allow an estimation of the importance of proteins from the steppe versus forest in human diets from the Early and Late Holocene. The spacing recorded in $\delta^{15}\text{N}$ values between forest mammals (i.e. cervids) and humans is almost in the order of two trophic levels

(Ambrose, 1991; Szpak *et al.*, 2009). This is conclusive evidence that neither huemul nor pudú provided a substantial part of the protein consumed by the early and late individuals sampled in this study (with the exception previously noted). This does not imply that they did not consume these resources to any extent, because stable isotopes do not provide a record of unusual or rare feeding events (Ambrose, 1993). This implies that these foods were not a staple, providing geographical information on the role of different environments in human settlement.

The main issue dealt with here is the role of forest environments in human subsistence and spatial organisation, especially considering that a significant proportion of Patagonian forests are located within Aisén. The zooarchaeological record from forests of the eastern flank of western Patagonia is characterised by assemblages including huemul and pudú in different proportions (Mena, 1983; Belardi & Gómez Otero, 1998; De Nigris, 2004; Mena *et al.*, 2004; Fernández, 2010). These assemblages indicate that at least during some periods, cervids (especially huemul) were targeted as prey and that forested environments were regularly visited for hunting activities, if not for year-round occupations in particular cases. In Aisén, systematic huemul hunting is documented from 5500 cal year BP onwards (Mena, 1983, 1992; Fuentes & Mena, 2010) in several forest sites (Table 5), although it appears exceptionally in the Early Holocene component of Baño Nuevo 1, located in the steppe (Velásquez & Mena, 2006). On the other hand, pudú archaeological occurrences are much less documented and almost exclusively restricted to closed settings.

At face value, these zooarchaeological evidences could be seen as contradictory with the isotopic results presented here. It could be argued that the human samples only date to particular moments in time and that the Early Holocene (Baño Nuevo 1) subsample predates the establishment suggested for forest adaptations (Mena, 1998). In fact, there is no bioarchaeological record in Aisén for the 8800–1600 cal year BP time span, a crucial period for understanding the incorporation of forests and their resources by Patagonian hunter-gatherers. However, the Late Holocene human sample, although admittedly small, also fails to show a $\delta^{15}\text{N}$ forest signature. There is an important difference in the character of subsistence information provided by the zooarchaeological record and isotopic analysis, enhancing their complementarity (Barberena & Borrero, 2005). Faunal assemblages provide information at the scale of the archaeological site and may not be representative of human subsistence at larger scales. Assemblages from forest settings may be biased towards locally available resources, leading to an over-representation of cervids in the zooarchaeological record of Aisén forests. On

Table 5. Presence (absence) of selected taxa in the zooarchaeological record from the forest/steppe transition and steppe of the Aisén region

Sites/taxa	Early Holocene	Middle Holocene			Mid-to-late Holocene	Late Holocene				
	Baño Nuevo 1	Baño Nuevo 1	El Chueco 1	Las Guanacas	Fontana	Baño Nuevo 1	El Chueco 1	El Toro	Las Guanacas	Entrada Baker
<i>Hippocamelus bisulcus</i>	X	X		X	X	X		X	X	X
<i>Pudu pudu</i>					X			X	X	X
<i>Lama guanicoe</i>	X	X	X	X		X	X		X	X
<i>Rhea pennata</i>		X		X						X
<i>Lycalopex</i>	X				X	X	X	X		X
<i>Dusicyon avus</i>		X	X			X				
<i>Conepatus humboldtii</i>							X			
<i>Zaedyus pichiy</i>					X		X			X

Data are based on the works of Mena (1983, 1992); Mena *et al.* (2004); Méndez & Velásquez (2005); Velásquez & Mena (2006); Fuentes & Mena (2010); Méndez *et al.* (2011).

the other hand, isotopic data average foods consumed in different areas, thus constituting appropriate indicators of human home ranges and suitable for revealing inter-individual variation. The isotopic information presented here is consistent with suggestions indicating the use of the forest from demographical nodes located in the eastern steppes (Borrero, 2004). As a matter of fact, contemporary individuals from the neighbouring Santa Cruz region in Argentina show primary consumption of steppe resources as well (Tessone *et al.*, 2009).

The temporal analysis indicates that $\delta^{13}\text{C}$ values are similar in the Early and Late Holocene samples. On the other hand, $\delta^{15}\text{N}$ values are higher in average in the Early Holocene set. Statistical analysis of variances is not significant but indicates the need to explore the issue in depth. We suggest these tendencies could be consistent with the existence of broader Early Holocene diets, including a wide array of terrestrial animal resources with higher $\delta^{15}\text{N}$ values, such as small mammals. This is in agreement with the idea that guanaco was not the solely dietary preference as reflected in the initial occupations of sites in northern Patagonia (Borrero, 2008). The individual 6 from Baño Nuevo constitutes an exception, displaying low values and highlighting dietary variation in the Early Holocene set. Other resources potentially contributing to high $\delta^{15}\text{N}$ values, such as birds, should be further explored because of their significance in the Baño Nuevo 1 faunal assemblage (Mena, 2009). Plant foods can also account for some variability in $\delta^{15}\text{N}$. However, experimental studies suggest that collagen would be basically synthesised from animal protein in diets primarily relying on it (Ambrose & Norr, 1993), such as those from southern Patagonia. On the other hand, the Late Holocene values are consistent with a diet

focused in the consumption of guanaco, which is also in agreement with ethnographic information on plant use in this region (Musters, 1871).

Conclusions

The set of isotopic values on faunal resources presented here provides a framework for assessing long-term human dietary choices and spatial organisation in Aisén. These data were used to interpret the isotopic signatures recovered from all the available bioarchaeological remains from the region: the Early Holocene sample from Baño Nuevo 1 located in the steppe and a dispersed assemblage of Late Holocene human remains from the forest–steppe ecotone. The analysis suggests two main conclusions: (i) dietary choices were preferentially focused on protein provided by terrestrial mammals from steppe environments, and (ii) the Early Holocene groups may have had a wider dietary breadth including small carnivores and omnivores as well as birds. Although the first conclusion is solid grounded, the second remains hypothetical and in need of further testing.

The main issue pursued in this paper was to use isotope data as means of establishing the role of forest and steppe ecosystems in the subsistence of past human societies. In average, the isotopic data do not show a long-term signature of forest-resource consumption. These results have a twofold implication: (i) isotope studies are significant in the calibration of inferences based on the zooarchaeological record, which in the case of Aisén forest may be biased towards the representation of local resources (i.e. cervids), and (ii) isotope studies may suggest a wider variability in hunter–gatherer decision-making (i.e. diets and settlement choices) and

not just relying on local environment extrapolation. We consider that the trends exhibited here are the results of the forest of Aisén being occupied as a marginal area (Borrero, 2004) and that, at least during some periods, human groups expended longer seasons dwelling on open-steppe areas.

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