

Ecological conditions and isotopic diet (^{13}C and ^{15}N) of Holocene caviomorph rodents in Northern Patagonia



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ABSTRACT

This work improves our knowledge about the relationship between diet and environment among Northern Patagonian caviomorph rodents. In order to characterize long-term individual diets, we present $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data from osteological remains of the caviomorph rodents *Dolichotis patagonum*, *Myocastor coypus*, *Lagostomus maximus*, *Lagidium viscacia*, *Microcavia australis*, *Galea leucoblephara* and *Ctenomys* sp., recovered from archaeological and recent contexts. These data are analyzed by temporal and geographic context and compared with the previous dietary studies based on macrorremains and microhistological analysis. Significant differences were found between rodents from Monte and Patagonian phytogeographic provinces, as well as between archaeological and modern members of the genus *Ctenomys*, indicating diet changes between Late Holocene and recent times individuals, that could confirm the climatic variations and/or the recent overgrazing effect. The results indicate trends in rodent diets of 20th and 21st centuries were different to those of the Late Holocene, suggesting a decrease in precipitation and/or an increase of the summer pattern of the same, and/or an increase of mean annual temperature. In addition, this work confirms the generalist strategy of several taxa, although mainly in *Ctenomys*, which its diet co-varies with these environments.

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1. Introduction

The relationship between diet and resource structure is central for understanding evolutionary, ecological and paleoecological processes, particularly at the community level. Most organisms depend on other living creatures for food, whether directly or indirectly. Even where they do not, as with primary producers, they still serve as a source of food for others. These consumer–resource interactions play a critical role in determining both the development of community structure and the evolutionary trajectories of community members. Rodents form a key link in this chain owing to their small size, high numbers, high reproductive rates, and low trophic position. They play important roles in plant dispersal (Van der Waal, 2003), alter vegetation and landscape characteristics via herbivory and burrowing (e.g. Zhang et al., 2003), serve as hosts for parasites and as vectors for pathogens (Meerburg et al., 2009), and constitute the primary dietary components of many small to large

sized reptilian, avian, and mammalian predators. While less well studied than in other parts of the world, a growing number of investigations from arid western Argentina have focused on many of these key issues in rodent ecology, including their diets (e.g. Albanese et al., 2010; Borrueal et al., 1998; Campos, 1997; Galende and Grijera, 1998; Galende and Raffaele, 2012; Galende et al., 1998, 2013; Kufner and Pelliza De Sbriller, 1987; Puig et al., 1998, 2010), habitat use and conservation (Gonnet and Ojeda, 1998; Rodriguez, 2009; Tabeni et al., 2012, 2013), and role as prey (Bisceglia et al., 2008, 2011; Nabte et al., 2008).

Here we are concerned with the diets of seven taxa belonging to four representative families of caviomorph rodents from northern Patagonia and Monte Desert of western Argentina. Our particular interest is in identifying spatial and temporal variation in the diet using stable isotope signatures. Ultimately we want to identify the extent to which a given taxon can be used as an indicator of particular habitats or climatic regimes. In the process we hope to contribute data useful to the broader ecological debates just cited.

In order to do this, we employ stable carbon and nitrogen isotopes to infer or confirm the diets of the caviomorph rodents *Dolichotis patagonum*, *Myocastor coypus*, *Lagostomus maximus*,

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Lagidium viscacia, *Microcavia australis*, *Galea leucoblephara* and *Ctenomys* sp. recovered from archaeological and recent contexts in arid and semi-arid regions of North Patagonia. These include specimens from both Monte Desert and northern Patagonian environments of southern Mendoza and the extreme north of Neuquén. Our results 1) demonstrate broad agreement between the observed isotope values of many, but not all, rodents and the values expected given existing histological studies for those same species, 2) highlight geographic differences in diets of rodents inhabiting Monte and Patagonian phytogeographic regions, and 3) identify temporal changes in isotope values and inferred diet among the genus *Ctenomys*, the best represented taxon. The latter appear related to vegetation changes, recent warming trends, and overgrazing by cattle during the last century.

2. Materials and methods

2.1. Study area

The study area is located in western Argentina between 34°30'–37°30'S and 70°30'–67°W (Fig. 1). The region is environmentally heterogeneous, owing in large part to the presence of the Andean cordillera, which reaches heights of up to 5000 m asl. The high mountains impede the Westerlies generated by the Pacific anticyclone, casting a substantial rain shadow and producing arid

to semi-arid climatic conditions (Polanski, 1954). A piedmont fringe composed of numerous alluvial fans with heights between 1800 and 1000 m asl extends along the mountains, while a large, lowland plain averaging 200 m asl extends eastward from the piedmont to the Desaguadero river. These plains are formed by alluvial sediments deposited by the Atuel and Diamante rivers, and in certain sectors form extensive aeolian dune fields (Polanski, 1954). Finally, there is the volcanic region of La Payunia, a large area of volcanic badlands and ephemeral fluvial systems covering much of the south portion of the province of Mendoza east of the Andes and south of Cerro Nevado (Polanski, 1954).

Vegetation within these various regions is grouped into three basic phytogeographic units (Cabrera, 1976). From west to east these are the High Andean, Patagonian and Monte vegetation zones (Fig. 1). The High Andean unit comprises the Andean cordillera above 3000 m. It is characterized by cold, windy climatic conditions and winter dominant precipitation (300–800 mm). The shrubby and herbaceous steppes of this unit are composed mostly of C₃ photosynthetic bunch grasses and shrubs such as *Adesmia* spp., *Oxalis muscoides* and *Mulinum spinosum* (Cabrera, 1976; Cavagnaro, 1988; Llano, 2009). The Patagonian unit is located from the piedmont fringe to sectors of the eastern plain and western La Payunia region. It is defined by a cold and semi-arid climate with winter precipitations (200–500 mm). The steppe community is mainly dominated by C₃ plants such as *M. spinosum*, *Ephedra ochreata*,

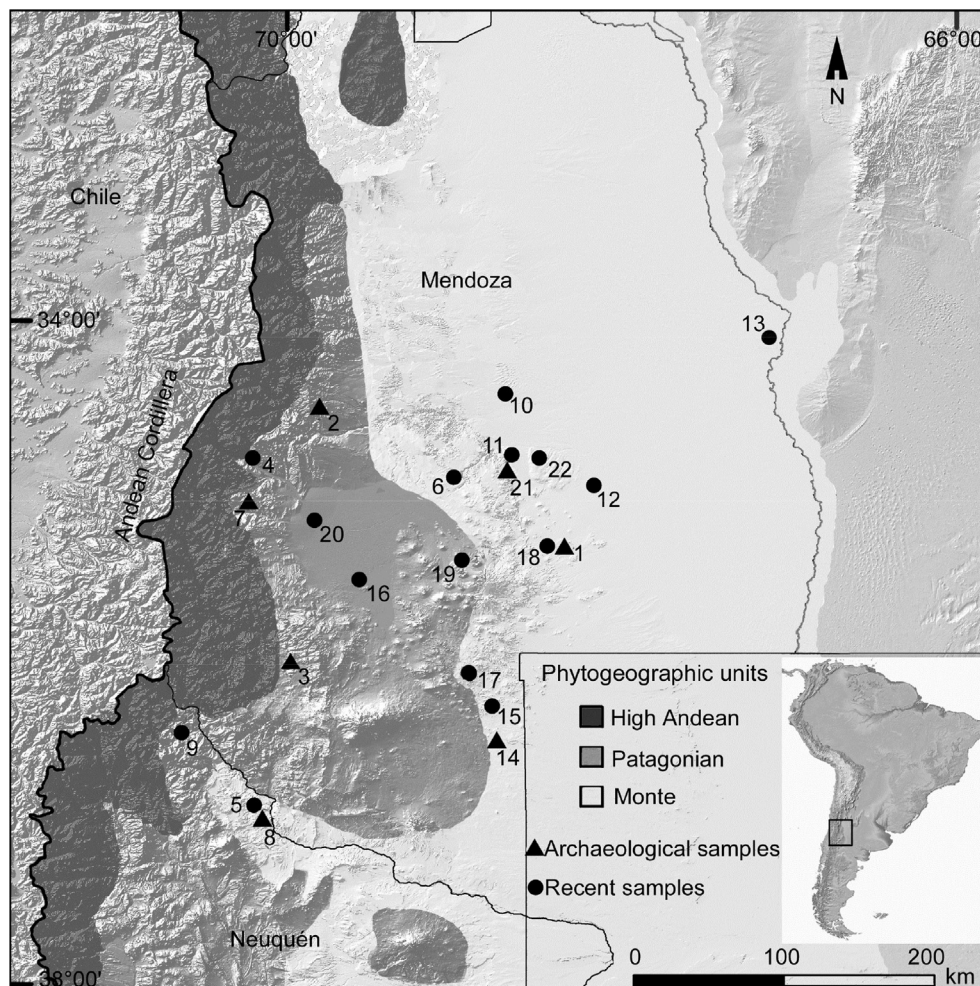


Fig. 1. Map of the study area, including Mendoza and northern Neuquén Provinces, Argentina. The map shows the locations of archaeological and recent samples superimposed on the main phytogeographic units (according to Cabrera, 1976). Numbers are those used in Supplementary material.

Chiquiraga rotulata, *Adesmia* spp., *Poa lanuginosa*, *Stipa chrysophylla* and *Senecio filagenoides* (Cabrera, 1976; Cavagnaro, 1988; Llano, 2009). Finally, the Monte unit covers the majority of the study area, being a wide fringe containing the eastern plains and eastern part of La Payunia. It is characterized by an arid climate with summer-dominant precipitation (150–350 mm). The shrubby and herbaceous steppes are composed by numerous C₄ plants, such as *Atriplex lampa*, *Aristida subulata*, *Bouteloua curtipendula*, *Distichlis scoparia*, *Sporobolus rigens*, *Panicum urvilleanum*, *Trichloris crinita* and *Setaria leucopila*, various cacti with Crassulacean acid metabolism (CAM) (*Opuntia sulphurea* and *Trichocereus candicans*), and C₃ plants such as *Larrea* spp., *Prosopis* spp., *Cercidium praecox*, *Chiquiraga erinacea*, *Lycium chilense*, and *Geophroea decorticans* (Cabrera, 1976; Cavagnaro, 1988; Llano, 2009).

2.2. Stable isotopes and their application to rodent diet

While the diets of some animals can be readily determined through behavioral observation, those of many species are difficult to characterize and can require a more invasive approach. In some animals, this can be through the analysis of regurgitated stomach contents or faecal materials, while in others it is only possible through the post-mortem analysis of digestive contents. The main disadvantage of any of these conventional techniques is that they are dietary snapshots; they provide a measure of immediate feeding habits, but require repeated use in order to develop a long-term picture of diet.

Existing studies of rodent diets in extreme northern Patagonia are based on the analysis of modern specimens and focus on microhistological analyses of scatological remains and stomach and intestinal contents (e.g. Albanese et al., 2010; Campos, 1997; Galende and Grijera, 1998; Galende and Rafaele, 2012; Galende et al., 1998, 2013; Puig et al., 2010). These studies have a short time resolution and limited dietary specificity due to the high fragmentation of dietary remains. Whether these measures are representative of long-term diets has yet to be evaluated. We attempt to address this last issue by providing complementary stable isotope data for many of the same taxa. While lacking the detail of histological studies, stable isotopes analyses have the benefit of integrating diets over longer time periods. They also offer an approach which in most cases is non-destructive and non-invasive (Newton, 2010) and allows researchers to investigate the responses of individuals to environmental conditions (Ben-David and Flaherty, 2012). As a consequence, stable isotope studies have improved our understanding of ecological processes, particularly as they relate to diet, trophic relationships, resource use, and biogeography (e.g. Ambrose, 1993; Clementz, 2012; Michener and Lajtha, 2007; Newton, 2010; Schoeninger and DeNiro, 1984).

The method is based on the observation that chemical processes will often discriminate between isotopes of the same atom due to differences in their weight (Ben-David and Flaherty, 2012; Fry, 2006; Sharp, 2007). Since such differences are usually small, differences are measured as the ratio of heavier to lighter isotopes of a given element (e.g. ¹³C/¹²C, ¹⁵N/¹⁴N) relative to a standard (VPDB belemnite, for carbon; AIR for nitrogen). These are reported in parts per thousand (‰) using delta (δ) notation where:

$$\delta = \left[\left(R_{\text{sample}} / R_{\text{standard}} \right) - 1 \right] 1000$$

In the case of carbon, for example, plants differentially discriminate against heavier ¹³CO₂ depending on their photosynthetic pathway (Calvin–Benson, Hatch–Slack, and CAM; Farquhar et al., 1989). Cool-season grasses and more than 98 percent of dicots (almost all trees and most shrubs and herbaceous plants) use Calvin–Benson (C₃) photosynthesis. This pathway discriminates

heavily against ¹³CO₂ and C₃ plants have an average δ¹³C value of $-26.7 \pm 2.7\text{‰}$ (Cerling et al., 1998). The Hatch–Slack (C₄) photosynthetic pathway is characteristic of a small array of grasses, forbs, and shrubs where daytime growing-season temperature exceeds 22 °C and precipitation exceeds 25 mm (Ehleringer et al., 1997). C₄ photosynthesis discriminates less against ¹³CO₂, resulting in average δ¹³C values of $-12.5 \pm 1.1\text{‰}$ (Cerling et al., 1998). The range of values does not overlap those for C₃ plants. The third pathway, CAM, is a highly flexible system wherein plants partition photosynthetic activity temporally. In Argentina these are primarily succulent plants from arid areas (e.g. Crassulaceae, Cactaceae). CAM plants produce δ¹³C values between -10 and -22‰ , overlapping the ranges of C₃ and C₄ photosynthesizers (Ben-David and Flaherty, 2012). Llano and Ugan (2014) estimated the isotopic signature to north Patagonian cacti. They indicated δ¹³C values for all taxa ranging from -11.8‰ to -14.0‰ , with the exception of *Maihuenia poeppigii* (-21.7‰).

The stable isotope values of foods are passed along to consumers, with some modifications related to digestion, the routing of nutrients to different tissues, and other physiological processes (Ambrose and Katzenberg, 2000; Fry, 2006). As a result, the δ¹³C values of herbivore tissues correlate positively with their diet and provide evidence of the kinds of plants that were consumed (Ambrose, 1992; Ben-David and Flaherty, 2012). Similarly, carnivore tissues reflect the isotopic signature of dietary protein derived from herbivorous animals and, by extension, the kinds of plants those herbivores consumed, while the δ¹³C values of omnivores represents the contribution of both plants and animal protein to diet (Ambrose, 1991). This principle also holds for rodents, and a growing number of studies have used stable carbon isotopes to help approximate rodent diets (e.g. Bergstrom, 2013; DeMots et al., 2010; Grimes et al., 2004; Mauffrey and Catzefflis, 2003).

2.3. Caviomorph rodent ecology

Within the study area there are currently 10 recognized caviomorph rodent species belonging to five major groups; three caviids; two ctenomyids; one myocastorid; two chinchillids; and two octodontids (Carleton and Musser, 2005). In this work, two chinchillids (*L. viscacia* [southern mountain viscacha] and *L. maximus* [plains viscacha]), one myocastorid (*M. coypus* [coypu or nutria]), three caviids (*D. patagonum* [Patagonian cavy], *M. australis* [southern mountain cavy] and *G. leucoblephara* [common yellow-toothed cavy]), and one ctenomyid (*Ctenomys* [tuco-tucos]) species were studied. Their main features are described in Table 1:

2.4. Materials

Stable carbon and nitrogen data were obtained from the bone collagen of 85 rodents sampled from different environments in extreme northeast Patagonia. They include both recent (n = 58) and archaeological samples (n = 27) of small-sized (<1 kg; *M. australis*, *G. leucoblephara* and *Ctenomys* sp.), medium-sized (1–5 kg; *L. viscacia*) and large-sized (>5 kg; *D. patagonum*, *M. coypus* and *L. maximus*) rodents collected from areas characterized by Monte or Patagonian vegetation (Supplementary Material; Fig. 1).

2.5. Methods

Taxonomic identifications were made based exclusively on cranial and mandibular remains by comparison with reference materials from the collection in the Museo de Historia Natural de San Rafael (MHNSR). Since fragmentary remains of tuco-tuco are very difficult to identify to species, they were characterized only to the generic level (*Ctenomys*).

Table 1
Main features of the studied caviomorph rodents.

	Weight	Habitat and geographic distribution	Patagonian phytogeography	Habits	Diet
<i>Lagidium viscacia</i>	1–3 (kg)	Rocky outcrops of the Andean cordillera (700–4800 m), from southern Peru to Chubut	High Andean, Patagonian, Monte	Colonial, diurnal to crepuscular	Herbivore, eating grasses and occasional shrubs
<i>Lagostomus maximus</i>	2.5–9 (kg)	Subtropical, semi-arid, and arid lowland, from southern Bolivia and Paraguay to the northern Río Negro and Neuquén	Monte, Patagonian	Colonial, burrowing, nocturnal	Herbivore, feeds on a wide variety of plants, with preference for grasses
<i>Myocastor coypus</i>	5–10 (kg)	Lagoons, lakes, rivers and wetlands, from central Bolivia, northern Paraguay and southern Brazil to southern Chile and Argentina	Monte, Patagonian	Amphibious, gregarious, nocturnal	Preys on aquatic plants, occasionally insects and molluscs
<i>Dolichotis patagonum</i>	7.73–8.33 (kg)	Arid and semi-arid environments of south-central Argentina	Monte, Patagonian	Cursorial, diurnal to crepuscular	Herbivore, feeds mainly on leaves fruits of grasses and herbs
<i>Microcavia australis</i>	200–326 (g)	Arid and semi-arid valleys and lowlands, from northwestern to southern Argentina	Monte, Patagonian	Colonial, diurnal	Herbivore, eating mostly shrubs
<i>Galea leucoblephara</i>	225 (g)	Lowland deserts, from Bolivia and Paraguay south to Río Negro	Monte	Colonial, diurnal to crepuscular	Herbivore, feeding grasses and occasional shrubs
<i>Ctenomys</i>	108–250 (g)	Arid and semi-arid environments, between central Mendoza and extreme northern Neuquén only occurs <i>C. mendocinus</i> and <i>C. pontifex</i>	High Andean, Patagonian, Monte	Fossorial, diurnal	Herbivore, eating grasses and shrubs

Sources: Campos (1997), Campos et al. (2001), Dunnun et al. (2011), Fernández (2012), Jackson et al. (1996), Parada et al. (2011), Puig et al. (1998), Tognelli et al. (2001), Walker (2001), and Wood et al. (1992).

In order to identify possible changes in rodent diets across time, we compared the stable isotope values of modern and archaeological samples from Monte and Patagonian environments. The recent samples include all those obtained during the last decade and the archaeological samples all those recovered from archaeological sites. These archaeological specimens date to the Late Holocene (and previous to 20th century), mostly the last 2000 yrs (Supplementary Material). The isotopic results were also compared with published information about the rodent's diet from the closest geographic area.

Collagen extraction took place in the archaeological laboratory of MHNSR. Visually the specimens exhibited excellent preservation, without signs of thermal alteration or advanced weathering. Approximately one gram of bone material was taken from each specimen, cleaned, and demineralized in 0.6 N HCL at 4 °C. After demineralization, the collagen pseudomorphs were rinsed repeatedly in distilled water and then treated with 5% KOH to remove humic acids and other base-soluble contaminants (Coltrain et al., 2004). The extracted collagen pseudomorph was once again rinsed to neutrality, then lyophilized and weighed to obtain the yield of collagen.

Approximately 100 mg of lyophilized collagen was gelatinized by heating for 24 h in 5 ml of acidified water (pH 3) at 120 °C. The soluble and insoluble phases were separated by filtration with 10 µm PTFE membrane filter (Millipore), and the soluble phase again lyophilized. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of this filtered collagen were determined by combustion to produce CO_2 and N_2 and passing it through a Finnigan Delta Plus XP mass spectrometer connected to a Costech Elemental Analyzer (EA) 1108 at University of Utah (SIRFER). The measurement of both stable isotopes and the weight percentage of carbon and nitrogen were obtained from a single combustion and measured relative to Vienna Pee Dee Belemnite (C) and AIR (N). Prior to any analysis, the isotope ratio mass spectrometers are checked for several parameters (signal

stability, sample count, peak jumping, etc). Necessary adjustments are performed if the instruments fail to meet minimum tolerances. For EA and Thermo-Chemical Elemental Analyzer (TCEA) analyses, samples are placed in a zero blank autosampler to keep samples dry and avoid atmospheric water vapor changes. SIRFER uses a two-point normalization routine to correct raw instrument data. The normalization is based on the analysis of two primary laboratory reference materials (PLRM) with very different delta values. These primary laboratory reference materials are calibrated annually against National Institute of Standards and Technology (NIST) and International Atomic Energy Agency (IAEA) certified reference materials. For quality control, SIRFER uses a secondary laboratory reference material (SLRM). The SLRM are chosen to have a similar elemental composition as the samples. To minimize linearity issues, the amount of each sample, PLRM, and SLRM is selected to yield signals of approximately the same peak area.

Collagen production was high and in all samples, with C:N ratios ranging from 2.9 to 3.6. These values suggest very good collagen preservation (Ambrose, 1990), consistent with the visual characterization of the specimens. These isotopic data are provided in the Supplementary Material. Because modern $\delta^{13}\text{C}$ values are approximately 1.5–2‰ more negative than those obtained before widespread burning of fossil fuels (the Suess effect; e.g. Keeling et al., 2010; Suess, 1955), 2‰ were added to modern $\delta^{13}\text{C}$ values before comparing them with archaeological specimens. The values shown in the Supplementary Material, however, are the original, unmodified data.

The stable isotopes information generated from the rodent materials was analyzed using one-way ANOVA analyses to compare averages between the rodent samples. There are several studies using ANOVA to make comparison in stable isotope values (e.g. Bodin et al., 2007; Dalu et al., 2014). In addition, a box plot was used to graph the median and interquartile range of the samples. Statistical analyses were made with the program PAST

(PALEontological STatistics) version 2.07.

In order to compare the isotope data to dietary estimates based on macrorremains and microhistological analysis, stable carbon ratios were first estimated for the latter based on the available published data (see references Table 2). These diets were segregated by species, and when possible by phytogeographic unit and season. First, we identified the photosynthetic mechanism for each taxon consumed (C₃, C₄, or unknown). The published data were mostly presented in qualitative mode, in order to make a comparative framework and a heuristic scale was employed to translate in a quantitative scale. In this attempt, next we assessed how frequently these resources were consumed translating the qualitative information using in an ordinal scale of high, medium or low frequency. For each diet an associated $\delta^{13}\text{C}$ value was calculated by averaging the isotopic value of C₃ (−24‰) and C₄ (−12‰) plants within each frequency category and then weighting those values by a frequency coefficient. This coefficient was 0.55 for high frequency plants, 0.30 for medium frequency plants, and 0.15 for low frequency plants. Plants whose photosynthetic pathway are unknown are excluded.

As an example, published information on *M. australis* foraging during the fall and winter identifies three C₃ plant taxa that were consumed at high frequencies, one C₃ taxon consumed at moderate frequencies, and one C₄ taxon consumed at low frequencies. An expected dietary isotope value was calculated as $(-72/3) * 0.55 + (-24 * 0.30) + (-12 * 0.15)$, for an expected average dietary value of −22.2‰. If the frequently consumed plants had included one C₄ and two C₃ plants, the weighted contribution would have been $(-60/3 * 0.55)$, etc. These expected dietary isotope values were then compared with the isotopic value obtained from bone collagen analysis, assuming that collagen is enriched +5‰ relative to actual diet.

3. Results and discussion

3.1. Rodents, isotopic diets and environmental structure: taxonomic and spatial trends in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

Fig. 2 shows the wide isotopic variability seen in the various

Table 2

Number and frequency of C₃, C₄, and indeterminate plant taxa consumed by rodents in different phytogeographic units and seasons. Information taken from the following microhistological studies: *Lagidium viscacia* (Galende and Grijera, 1998; Galende and Raffaele, 2012; Galende et al., 1998), *Lagostomus maximus* (Campos, 1997; Puig et al., 1998), *Myocastor coypus* (Galende et al., 2013), *Dolichotis patagonum* (Campos, 1997; Puig et al., 2010), *Microcavia australis* (Campos, 1997), *Galea leucoblephara* (Campos, 1997) and *Ctenomys* (Albanese et al., 2010). Phytogeographic units: M: Monte, P: Patagonian. Seasons: F/W: fall/winter; Sp/Su: spring/summer.

	Unit	Season	C ₃ (n)	%	C ₄ (n)	%	Indet	%
<i>Lagidium</i>	P1	F/W	11	90.4	1	0.5	5	8.1
	P1	Sp/Su	12	96	–	–	5	3.9
	P2	F/W	16	93.8	–	–	3	4.75
	P2	Sp/Su	15	90.1	–	–	4	7.8
	P3	W	14	78.9	–	–	4	11.8
<i>Lagostomus</i>	P3	Su	14	78.7	–	–	4	7.6
	M1	F/W	7	73.4	10	20.4	3	3.2
	M1	Sp/Su	6	72.3	12	23.8	4	1.3
<i>Myocastor</i>	P	W	15	61.1	6	36	6	2.9
	P	Sp	12	83.6	2	16.1	–	–
<i>Dolichotis</i>	M		4	18	4	59	–	–
	P		6	78.2	2	17.4	–	–
<i>Microcavia</i>	M	F/W	4	78.1	1	0.1	1	20
	M	Sp/Su	7	70.1	5	1.6	2	21.9
<i>Galea</i>	M	F/W	4	15.7	8	76.6	–	–
	M	Sp/Su	3	2.5	7	91.3	1	0.1
<i>Ctenomys</i>	M		11	34.8	5	53.2	3	7.8

caviomorph rodents. The $\delta^{13}\text{C}$ values range from −22 to −10‰, and $\delta^{15}\text{N}$ values from 1‰ to 10‰. These data generally cluster into two groups based on $\delta^{13}\text{C}$ values: a more negative group with $\delta^{13}\text{C}$ values between −21‰ and −19‰ and a more positive group with $\delta^{13}\text{C}$ values between −17‰ and −15‰.

Comparing rodents from different phytogeographic units (Fig. 3), we see a significant difference between Monte and Patagonian groups (one-way ANOVA $p = 0.014$, $F = 6.238$), with a greater proportion of C₄ plants in rodent from the Monte habitats (average −16.70‰) than Patagonian ones (average −18.28‰). These differences reflect the greater diversity and abundance of C₄ photosynthetic plants within the Monte phytogeographic unit (Cavagnaro, 1988) and a more general pattern of greater C₄ abundance in environments with high annual mean temperatures and summer precipitation (Latorre et al., 1997). Similar differences were also found in comparisons of camelids (Barberena et al., 2009) and ratite birds eggshell (Giardina et al., 2014) from the same regions. $\delta^{15}\text{N}$ values show no significant differences. They average 4‰, consistent with the low trophic position and generally herbivorous diet of the rodents studied here.

Four analyzed taxa were collected from both Monte and Patagonian phytogeographic units. When comparing intra-taxonomic differences in diets for each ecosystem, we found a significant difference in *Ctenomys* (one-way ANOVA $p = 0.0029$; $F = 10.53$) and *D. patagonum* (one-way ANOVA $p = 0.02$, $F = 17.1$). As one would expect, *Ctenomys* specimens from Monte environments show a diet significantly more enriched in ^{13}C than those from Patagonian ones (averages $\delta^{13}\text{C}$ −16.1‰ and −19.7‰, respectively). In contrast, *D. patagonum* in the Monte unit shows a diet more biased toward C₃ plants than their Patagonian counterparts. Why is unclear, but the small size of the Patagonian sample ($n = 5$) and their proximity to the Monte unit boundary may be partly to blame.

Table 2 shows the estimated isotopic values of various diets based on studies of macrorremains and microhistological taken from the study area and surrounding sectors.

In an area of central-east of Mendoza Province (Biosphere Reserve of Ñacuñán) containing Monte vegetation, diets of *L. maximus*, *D. patagonum*, *G. leucoblephara*, and *Ctenomys mendocinus* were studied. *L. maximus* consumed C₄ gramineae [mainly *Chloris castilloniana*, *Pappophorum caespitosum*, *Sporobolus cryptandrus* and *T. crinita*], C₄ shrubs (mostly *A. lampa*), C₃ herbs (scarce *Che-nopodium papalosum*), and C₄ trees (mainly *Prosopis*) (Campos, 1997). Several authors report a high consumption of monocots in *D. patagonum* diets, mainly perennial C₄ grasses (*Chloris*, *Pappophorum*, and *Trichloris*), while among the C₃ and C₄ perennial dicots it focuses on *A. lampa*, *Lycium* and *Prosopis* (Campos, 1997; Kufner and Pelliza De Sbriller, 1987). *M. australis* largely feeds on C₃ plants such as *Prosopis* spp., *Larrea* spp. and *G. decorticans* (e.g. Borrueal et al., 1998; Campos, 1997), even though C₄ plants predominate in the area (Cavagnaro, 1988). *G. leucoblephara* diet is composed of numerous C₄ species such as *Pappophorum*, *Chloris*, *Trichloris*, *Sporobolus* and *Aristida*. C₃ species, mainly *Prosopis flexuosa* and *Larrea cuneifolia*, are consumed more rarely (Campos, 1997). *C. mendocinus* diet includes various C₃ species (mainly *P. flexuosa*), and several C₄ species such as *P. urvilleanum*, *Setaria*, *Digitaria californica*, *Pappophorum*, *C. castilloniana* and *A. lampa* (e.g. Albanese et al., 2010; Borrueal et al., 1998; Campos, 1997).

In La Payunia region of southern Mendoza associated with Patagonian vegetation, the diet of *L. maximus* is dominated by C₃ and C₄ grasses, mostly *Poa* and *Panicum* complemented with lesser amounts of *Stipa*, *Digitaria*, *Hordeum* and *Bromus* (Puig et al., 1998). In the same region, the diet of *D. patagonum* is dominated by C₃ and C₄ grasses (mainly *Panicum* and *Poa*, followed by *Bromus* and *Stipa*). These are complemented by C₃ shrubs such as *Lycium* and *Prosopis* in times of major drought, when grasses are scarce (Puig et al., 2010).

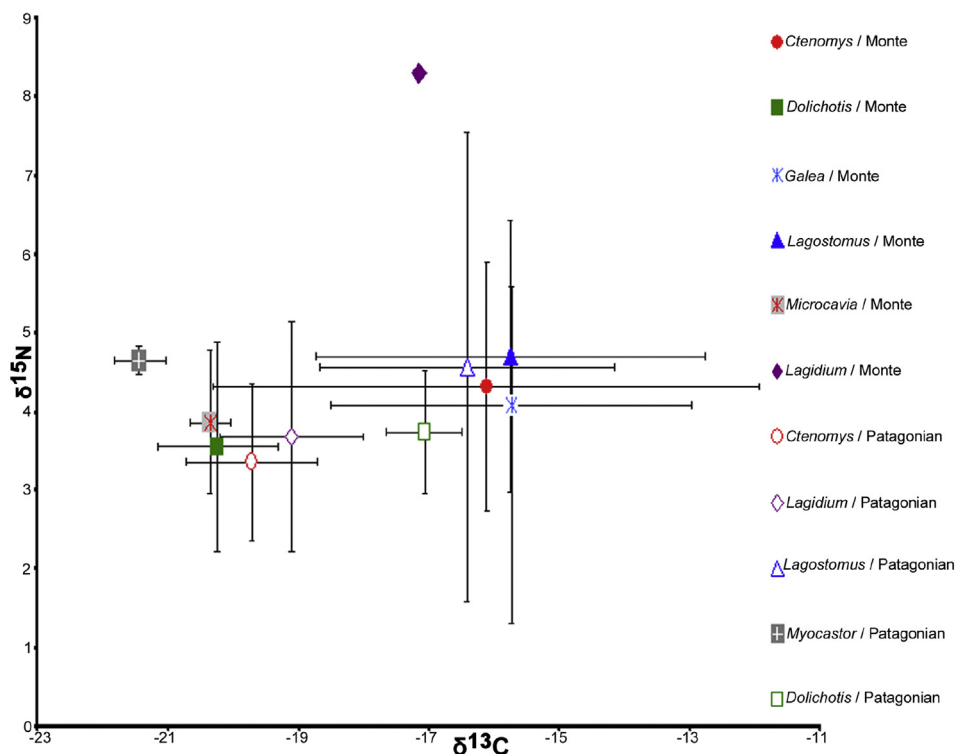


Fig. 2. Stable isotope means and standard deviations by taxon and phytogeographic unit.

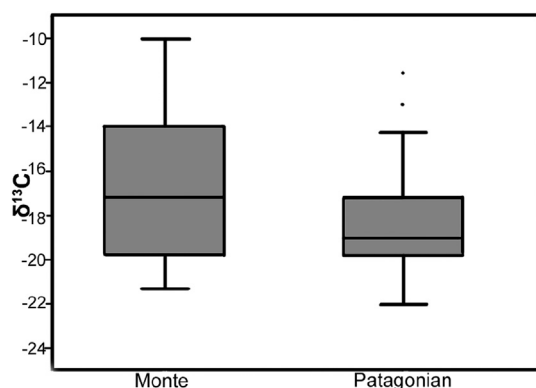


Fig. 3. Comparison of $\delta^{13}\text{C}$ values for Monte and Patagonian phytogeographic units.

In studies from extreme southwest of Neuquén Province, *L. viscacia* diets include the C_3 grasses *Stipa*, *Poa*, and *Festuca* (the most dominant), and the C_3 shrubs *Mulinum*, *Schinus*, *Senecio*, *Berberis*, and *Adesmia* (Galende and Grijera, 1998; Galende et al., 1998; Galende and Raffaele, 2012). In a study from Río Negro Province (Wildlife Refuge Laguna los Juncos), the aquatic C_3 plants *Myriophyllum* and *Schoenoplectus californicus* dominated *M. coypus* diets, complemented by lesser amount of C_3 plants such as *Juncus*, *Bromus* and *Poa* (Galende et al., 2013).

Table 3 compares these predicted dietary values with the actual $\delta^{13}\text{C}$ values of particular rodent groups. A relationship of $r = 0.67$ was found between the expected isotopic values for particular diets and those of rodents obtained from the same areas and presented here. The differences between the expected and observed values in *L. viscacia*, *L. maximus*, *M. coypus*, *M. australis*, *Ctenomys* (further than season and environment) and *D. patagonum* (from Patagonian), ranging from ca. 0.1‰–8.6‰ (Table 3). The estimated dietary

$\delta^{13}\text{C}$ values of *L. viscacia*, *L. maximus*, *D. patagonum* and *Ctenomys* (Monte) all fall within two standard deviations of their observed collagen values, suggesting that the sampled rodents were eating a range of plants similar to those identified elsewhere (Albanese et al., 2010; Campos, 1997; Galende and Grijera, 1998; Galende and Raffaele, 2012; Galende et al., 1998, 2013; Puig et al., 1998, 2010).

On the other hand, *D. patagonum*, *G. leucoblephara*, and *M. australis* from the Monte desert and *M. coypus* from Patagonian habitats all have collagen $\delta^{13}\text{C}$ values that are much more negative than would be predicted given what is known about their diet (Table 3). This trend is contrary to the pattern found, if the macroremains and microhistological information were a reflection of the average diet for each taxon. It is interesting to note that the most extreme deviations occur among Monte taxa thought to consume a high number of C_4 plant taxa (*G. leucoblephara*, *L. viscacia*, and *D. patagonum*). C_4 plants often have thicker cell walls, rigid leaves, and more rapid lignification (Van Soest, 1994). These traits make them less preferable forage, and it may be that even though they were certainly eaten, that their contributions or relative importance is less than microhistological studies or studies of macroremains would suggest. Additional studies of both macroremains and rodent isotope signatures should be able to help clarify this possibility.

3.2. Rodents, isotopic diets and environmental structure: temporal trends in $\delta^{13}\text{C}$

In order to evaluate temporal variability in the diet of rodents, we also compared archaeological and recent samples. Due to the isotopic variability between phytogeographic units and among different taxa, this comparison only makes sense if both are controlled for. Here we are only able to look at *Ctenomys*, which fortunately happens to represent the largest sample ($n = 33$).

Table 3
Comparative analysis between isotopic diet expected and isotopic diet calculated.

	Phytogeographic Unit	Season	Estimated dietary values	Expected collagen values (est. diet +5‰)	Observed collagen values	Difference (exp-obs)
<i>Lagidium</i>	P1	F/W	-23.8	-18.8	-19.1 ± 1.1	-0.3
	P1	Sp/Su	-24.0	-19		-0.1
	P2	F/W	-24.0	-19		-0.1
	P2	Sp/Su	-24.0	-19		-0.1
	P3	W	-24.0	-19		-0.1
	P3	Su	-24.0	-19		-0.1
<i>Lagostomus</i>	M1	F/W	-19.3	-14.3	-15.7 ± 2.9	-1.4
	M1	Sp/Su	-19.2	-14.2	-15.7 ± 2.9	-1.5
	P		-20.2	-15.2	-16.4 ± 2.2	-1.2
<i>Myocastor</i>	P	W	-23.6	-18.6	-21.4 ± 0.4	-2.8
	P	Su	-22.9	-17.9		-3.5
<i>Dolichotis</i>	M		-16.6	-11.6	-20.2 ± 0.9	-8.6
	P		-21.4	-16.4	-17.1 ± 0.6	-0.7
<i>Microcavia</i>	M	F/W	-22.2	-17.2	-20.3 ± 0.3	-3.1
	M	Sp/Su	-23.0	-18		-2.3
<i>Galea</i>	M	F/W	-13.8	-8.8	-15.7 ± 2.8	-6.9
	M	Sp/Su	-12.6	-7.6		-8.1
<i>Ctenomys</i>	M		-16.8	-11.8	-16.1 ± 4.2	-4.3

P: Patagonia; M: Monte. F/W: fall/winter; Sp/Su: spring/summer.

Fig. 4 shows the comparison between recent and archaeological specimens of *Ctenomys* segregated by geographic unit (Monte and Patagonian). The results indicate a significant difference, with recent individuals exhibiting more positive $\delta^{13}\text{C}$ values than archaeological ones (one-way ANOVA; Monte $p = 0.028$, Patagonian $p = 0.003$). This suggests a change in dietary preferences, or that vegetation in areas surrounding the archaeological sites has changed in recent times, with greater availability of C_3 plants in the past than at present. This is particularly true in the Monte, where the differences are most stark.

Climate studies also indicate an increase of mean temperature and a change in the precipitation patterns during the 20th century (see Labraga and Villalba, 2009) that might explain the increase of C_4 plants. Other substantial impact is likely to have been historic grazing, which has been well established since the 19th century (e.g. Gil et al., 2006). *Ctenomys* populations from southern Mendoza have declined markedly due to extensive overgrazing by goats (*Capra hircus*) and sheep (*Ovis aries*) (e.g. Fernández, 2012).

4. Conclusions

Several taxa, notably *Ctenomys* sp., *G. leucoblephara*, and *L.*

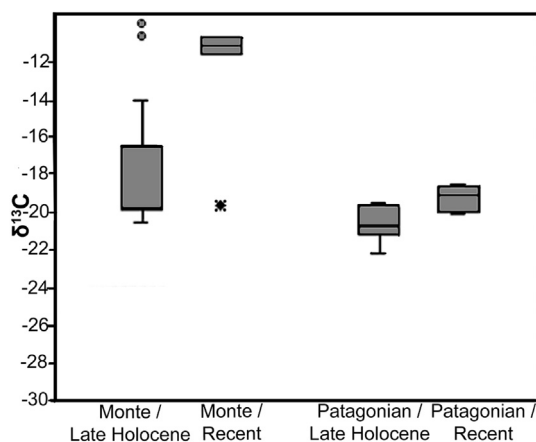


Fig. 4. Comparison of $\delta^{13}\text{C}$ values between archaeological (Late Holocene) and recent samples of *Ctenomys* from Monte and Patagonian phytogeographic units. Differences in both cases are statistically significant.

maximus, show positive and highly variable collagen $\delta^{13}\text{C}$ values consistent with their presence in Monte environments and their reliance on a range of C_3 and C_4 plants. Taxa found in Patagonian environments, in contrast, tend toward more negative and less variable collagen $\delta^{13}\text{C}$ values. These results coincide with previous studies of these rodents in Monte environments from central-eastern Mendoza and northern Patagonia. The noteworthy exception is *D. patagonum*, in which specimens from Monte habitats have more negative $\delta^{13}\text{C}$ values than those from Patagonian ones. The small size of this sample ($n = 5$), or their spatial proximity with the Monte unit boundary could be explanations for this pattern. Confirmation requires future studies.

Stable isotope data, currently limited to data from the genus *Ctenomys*, also indicate that rodent diets of the 20th and 21st centuries differ from those of the Late Holocene. Recent isotopic values are more enriched in $\delta^{13}\text{C}$ than archaeological ones even after accounting for the Suess effect. This could reflect climatic variations, with some combination of declining overall precipitation, increasing summer precipitation, and increasing mean annual temperature leading to a strengthening of Monte vegetation in the last one to two hundred years. It may also reflect intensive overgrazing during the last two centuries, with the preferential exploitation of C_3 plants by introduced goats, sheep, and cattle leading to a change in vegetation structure relative to that which existed prehistorically. Regardless, significant differences in the isotopic ecology of both Monte and Patagonian phytogeographic units are indicated.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jaridenv.2015.10.019>.

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