Dietary ecology of extant guanaco (*Lama guanicoe*) from Southern Patagonia: seasonal leaf browsing and its archaeological implications

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ABSTRACT

The analysis of dietary traits of ungulates through tooth microwear and mesowear has been applied to archaeological sites to investigate seasonal changes in settlements by hunter–gatherers. In this paper we propose to test the hypothesis that tooth microwear (combined to mesowear) is able to indicate seasonality in the diet of extant ungulates in arid habitats (semi-deserts or steppe). The material analyzed comes from six faunal monospecific assemblages of guanaco (*Lama guanicoe*) resulting from a mass mortality event in winter 2000 near the Cardiel Lake in Southern Patagonia (Province of Santa Cruz, Argentina). Mesowear results indicate that the guanacos from the Cardiel Lake area are mixed feeders, and thus, have a diet that shifts seasonally. Moreover, microwear analysis supports the hypothesis that tooth microwear is able to indicate seasonality in the diet of extant guanaco in arid habitats. The pattern is clear for the winter sample and needs to be confirmed for a summer sample. Consequently, tooth microwear is proposed as a new potential proxy for detecting seasonal occupation in archaeological sites in Patagonia and other arid environments.

1. Introduction

The assessment of the season of capture of large mammals and, as consequence, the seasonality of human occupations in Pleistocene and Holocene archaeological sites is studied through various proxies such as tooth eruption and replacement (e.g. Carter, 1998, 2001; Oetelaar, 1981; Kaufmann, 2009), skeletochronology (e.g. Burke and Castanet, 1995; Pike-Tay et al., 1999), tooth microwear (e.g. Mainland, 2000; Merceron et al., 2004; Rivals and Deniaux, 2005), stable isotopes (e.g. Balasse et al., 2002; Blaise and Balasse, 2011; Julien et al., 2012), or enamel hypoplasias (e.g. Niven, 2000; Upex and Dobney, 2012). Among these analytical techniques, the interest for tooth microwear (i.e., the observation of microscopic scar left by food item on the surface of the teeth) and mesowear (i.e., the observation of tooth cusps relief and shape) increased significantly in the past decade. Analysis of dietary habits through

microwear analysis has been reported to be able to detect seasonal changes in diets of extant ungulates in temperate and boreal forested areas of the Northern hemisphere (Merceron et al., 2004; Rivals and Solounias, 2007). Tooth wear analysis was also applied to archaeological sites to test for seasonal changes in settlements by hunter–gatherers (Rivals and Deniaux, 2005) as well as for deciphering the duration of occupations in Late Pleistocene sites (Moncel and Rivals, 2011; Rivals et al., 2009a, 2009b; Rivals and Semprebon, 2012). Moreover, sampling for tooth microwear and mesowear analysis is non destructive and it offers the opportunity to analyze large samples.

In this paper we propose to test the hypothesis that tooth microwear (combined to mesowear) is also able to indicate seasonality in the diet of extant ungulates in arid habitats (semi-deserts or steppe). The sample to be analyzed to test our hypothesis has to meet the following criteria: (1) large number of remains available, (2) well preserved specimens, (3) animals coming from the same population and whose season of death is known, and (4) interest of the species in hunter-gatherer subsistence and diet. We located a sample which corresponds to these criteria: a large sample of guanaco (*Lama guanicoe*) from Southern Patagonia resulting from a catastrophic mortality event in the winter 2000

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(Belardi and Rindel, 2008; Rindel and Belardi, 2006). The guanacos from the Lake Cardiel area will be compared with other extant samples of South American camelids: (1) other guanacos collected in museums, and (2) the vicuña (*Vicugna vicugna*), the latter have a more limited distribution in the high alpine areas of the Andes and inhabit the dry vegetation of the puna ecosystems.

The guanaco is a generalist herbivore, basically a grazer but it can also browse according to the offer of available food and the time of the year. It lives mostly in open places, occupying areas of steppe or prairie, even though it can make use of the forest habitat (Borrero, 2001; Cajal and Ojeda, 1994; Montes et al., 2000). Its behavior may be described as seasonally territorial, though with exceptions related mainly to zones with water availability (Casamiquela, 1983; Oporto, 1983). The guanaco is the dominant large herbivore of Patagonia (González et al., 2006) and in the past it was the main game species for the hunter–gatherer groups in Patagonia (Borrero, 1990; Casamiquela, 1983; Mengoni Goñalons, 1995; among others). This animal has the ability to exploit the structure and the ecological diversity of the region. Indeed, this fact is reflected in the archaeological data, that show a pattern of high representation of the taxon in most of the macroregional records, dominating the NISP (Number of identified specimens) in the majority of zooarchaeological assemblages (Cassidoro et al., 2000; De Nigris, 2001, 2003, 2004; De Nigris and Mengoni Goñalons, 2000, 2002; Gradin and Aguerre, 1994; Herrera, 1988; Mena, 1983; Mena and Jackson, 1991; Mena et al., 2000; Mengoni Goñalons, 1999; Mengoni Goñalons and De Nigris, 1999; Mengoni Goñalons and Silveira, 1976; Miotti, 1996, 1998; Muñoz, 1997, 2000; Rindel, 2003, 2004, 2009; Silveira, 1979; among others).

If the hypothesis that tooth microwear is able to indicate seasonality in the diet of guanaco in arid habitats is verified, tooth microwear would become a potential proxy for seasonal occupation in archaeological sites in Patagonia and other arid environments.

2. Diet and seasonality in extant guanaco populations

The guanaco is classified as an opportunistic mixed feeder or intermediate feeder (Hofmann, 1989) foraging on a highly diverse range of plant resources (Puig and Videla, 2000; Puig et al., 1997, 1996). Guanaco feeds mainly on the herbaceous stratum: grasses, grass-likes (Juncaceae and Cyperaceae), and forbs (Puig and Videla, 2000; Puig et al., 1997). Depending on the location, guanaco has the ability to alternate seasonally between grazing and browsing (according to forage availability) and to digest low quality forage (González et al., 2006; Puig et al., 1996). When the availability of herbaceous strata decreases during winter, the guanaco feed mainly on the shrub or tree strata (Bahamonde et al., 1986; Puig et al., 1997, 1996; Raedeke, 1979). Foraging behavior and digestive adaptations to harsh environments have allowed the guanaco to become the dominant large herbivore of the scrubland and steppes of South America (González et al., 2006). According to the classification of diets in the "*Atlas dietario de herbívoros patagónicos*" (Pelliza et al., 1997), the guanacos from the area considered in this study have a diet based on grass (60–80%) associated to ligneous plants (15–30%). It comprises *Festuca* spp. associated to *Stipa* spp. Poaceae are always dominant but ligneous plant proportion increases in winter.

Most researchers who have worked with wild populations of guanacos emphasize its adaptability, which allows a successful colonization of different environments and a wide range of distribution. Part of this adaptability is related to its dietary flexibility. This point is particularly relevant to the argument developed in this work, which will be discussed in detail. One aspect that most researchers have highlighted is the trend, observed in different

Table 1
Changes in the percentage of green plant tissue during spring and summer in Northern Patagonia. Modified from Baldi et al. (2004).

Vegetation type	Spring (% green plant tissue)	Summer (% green tissue)
Perennial grasses	72	27
Perennial forbs	94	14
Annual grasses	92	3
Annual forbs	87	14
Woody dicots	61	66

populations of these animals, to change their diet seasonally (Baldi et al., 2004 in Chubut; Puig et al., 1996 in Mendoza, La Payunia; Bahamonde et al., 1986 in Neuquén; Acerbes et al., 2010 in San Juan; Bank et al., 2003 in Southern Chilean Patagonia, Torres del Paine; Bonino and Pelliza-Sbriller, 1991 in Tierra del Fuego; Contreras et al., 2006 in Chile region IV; Puig and Videla, 2000 comparing different populations in South America; Raedeke and Simonetti, 1988 in Atacama, Northern Chile; among others).[1] This trend implies that guanacos feed predominantly on grasses and pastures during spring and summer and on shrubs in winter, in most of the populations studied. In this sense, Puig and Videla (2000) made a comparison of different populations in South America whose results are relevant to this work. Their conclusions can be summarized as follows: (1) At most sites the consumption of grass is predominant and secondly shrubs and forbs (Puig, 1995). (2) There is a high percentage of lichens and epiphytes in the diet of the populations from Atacama (Raedeke and Simonetti, 1988) as an adaptation to hyper-arid climate. (3) In most populations the dietary diversity is higher in summer, reflecting an adaptation to arid environments with limited food availability and unpredictable fluctuations in quality and phenology of plants consumed (Puig et al., 1996). (4) In general, habitats dominated by herbaceous layer are used during the summer but abandoned during vegetative recession in winter, while habitats with abundant palatable chamaephytes (ligneous or herbaceous) are occupied all year around. These findings highlight the guanaco dietary flexibility, allowing it to survive where the herbaceous layer is not dominant or where it is affected by significant seasonal changes. Thus, the increased use of alternative resources occurs in winter, when there is a decrease of the herbaceous layer. In that case, lichens are incorporated in the diet of the populations from the Atacama desert, xerophytic shrubs in the province of Monte, and deciduous trees in the Andean forest of southern Patagonia and Tierra del Fuego. These significant seasonal changes in the diet are, as noted previously, linked to changes in the availability and quality of forage. When there is greater availability (in summer) the diet spectrum expands, when there is less (in winter) the dietary diversity shrinks. In winter guanacos are subject to a "forced selectivity" because of the low diversity of species available. It is interesting to note that this is the result of the vegetation phenology used by those camelids. Authors such as Baldi et al. (2004), in the case of the province of Chubut, Patagonia Argentina, have indicated that the percentage live plant tissue, in terms of proportion that was green, was significantly higher in spring for all the functional types forming the herbaceous layer, whereas, at the opposite, among the woody dicots, the green tissue percentage is higher in summer than in spring (Table 1).

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[1] Some populations would no fit to this pattern. For example Cortes et al. (2003) observed a continuity in the consumption of grasses throughout the year in north-central Chile, which is clearly different from all other populations of guanacos. However, the study area is located in high Andean mountains above 4100 m, possibly explaining the food peculiarity of these individuals.

The authors also suggest that in Patagonia the percentage of crude protein in grass *Stipa* and *Poa* (highly consumed by the guanaco in the area) decreases from 6 to 10% in spring to 2–4% in summer. The shrubs show a reverse trend. Also, toward late summer the species richness decreases due to the reduction of annual grasses and the relative reduction of perennial grasses. Consequently, the forage is more limited for herbivores as the season of growth is advanced. Something similar occurs in Australia, where there is an increase in competition between sheep and marsupials during the dry season and an increased consumption of shrubs (Baldi et al., 2004). The explanation for this is ecological and has to do with the way the different types of plants are using water. Thus, the content of nutrients in grasses declines as they mature, while dicotyledonous plants are still producing green leaves after the rains because their roots are much deeper. In this sense, authors such as Sala et al. (1989), working in the province of Chubut, close to the study area, have indicated that grasses take most of the water from the upper soil layers and frequently use short duration pulses of water availability. On the contrary, shrubs get most of the water from the lower soil layers and use infrequent pulses and highly durable water availability. Thus, grasses and, in a greater extent, the bushes show a seasonal pattern in leaf water content potential: the content is higher in winter (with higher rainfall) and decreases from spring to a minimum in mid-summer and autumn. The potential of soil water shows a pattern similar to the leaf water content potential: the whole profile is saturated with water during the winter and spring. Toward summer, the soil dries and reaches a low potential peak in mid summer and early fall. This pattern of water use between grasses and shrubs is also consistent with the pattern of distribution of roots in the soil profile. Grasses have most of the roots located in the upper soil layers, and 54% of the root biomass is found between 0 and 10 cm. The bushes, however, have roots that reach a depth of 100 cm and the highest density of roots is found at 55 cm.

3. Material and methods

3.1. Material

The material analyzed comes from an area at the West of the Cardiel Lake in Southern Patagonia (Province of Santa Cruz, Argentina).

Six faunal assemblages were surveyed: four under rockshelters and two in open air sites. All of them were found on the west bank of the Cardiel Lake, in the area called "Cañadones" (Goñi et al., 2005). This setting is distinguished by wide sandstone canyons that belong to the Cardiel Lake Formation (Ramos, 1982) and that have allowed the formation of several rockshelters in a restricted area (Fig. 1). Arturo Olivero, employee at "La Carlina" farm, knew those guanaco assemblages and pointed out that they were formed during the intense snowfalls of 2000. It is interesting to report that all these guanacos gathered and died on the location of archaeological sites (Belardi and Rindel, 2008; Rindel and Belardi, 2006) (Fig. 2).

3.1.1. Rockshelter locations
3.1.1.1. Alero Los Guanacos 1. The wall that forms the rockshelter faces northwest and in some areas it has a visor that provides some protection against rain and snow. The animals were found gathered against the wall of the rockshelter, distributed along a strip of approximately 50 m long by 6 m wide. The GPS coordinates are 48° 48′ 42.4″ S, 71° 23′ 39.1″ W. In February 2005 thirty six guanaco carcasses were found. The remains of at least 16 more animals were also found in the contiguous walls. The assemblage faces northwest. The distribution of the carcasses is uneven, generally separated by vegetation and topographic characteristics of the rockshelter, like boulders and "steps" in the ground, generating contiguous groups of deaths.
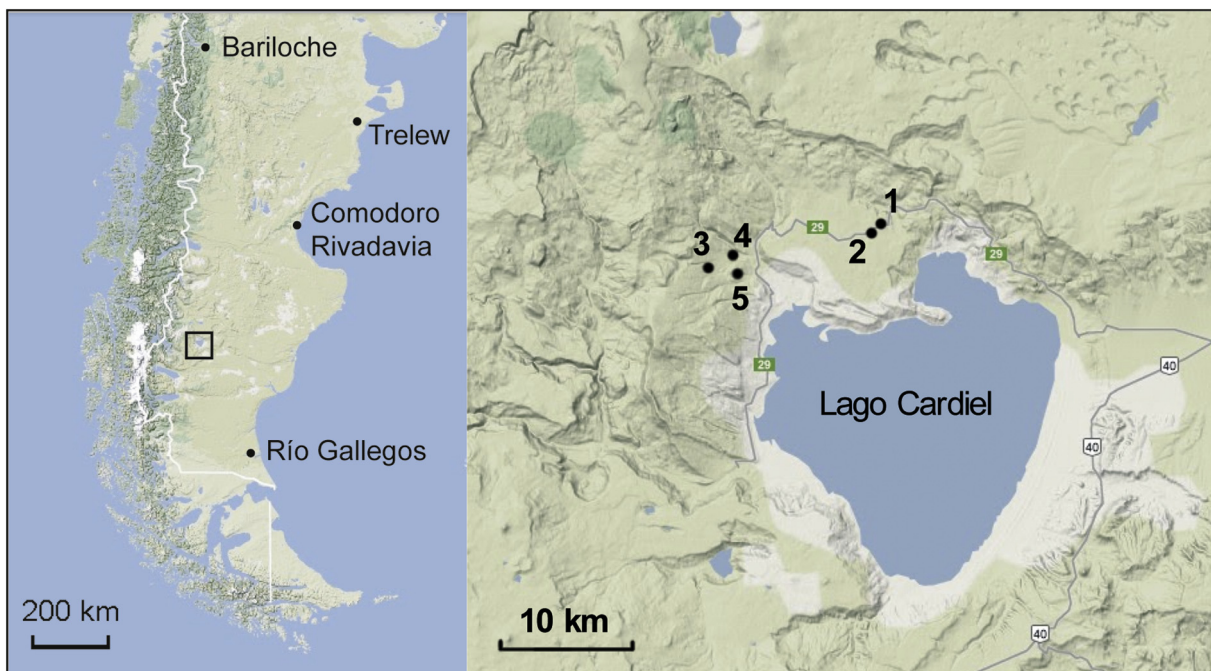
Fig. 1. Map of location of the sites: (1) La Encajada, (2) Olivero, (3) Alero Los Guanacos 3 (ALG 3), (4) ALG 1 and 12, and (5) ALG 4. The exact GPS locations are available as a .kmz file in the supplementary material.
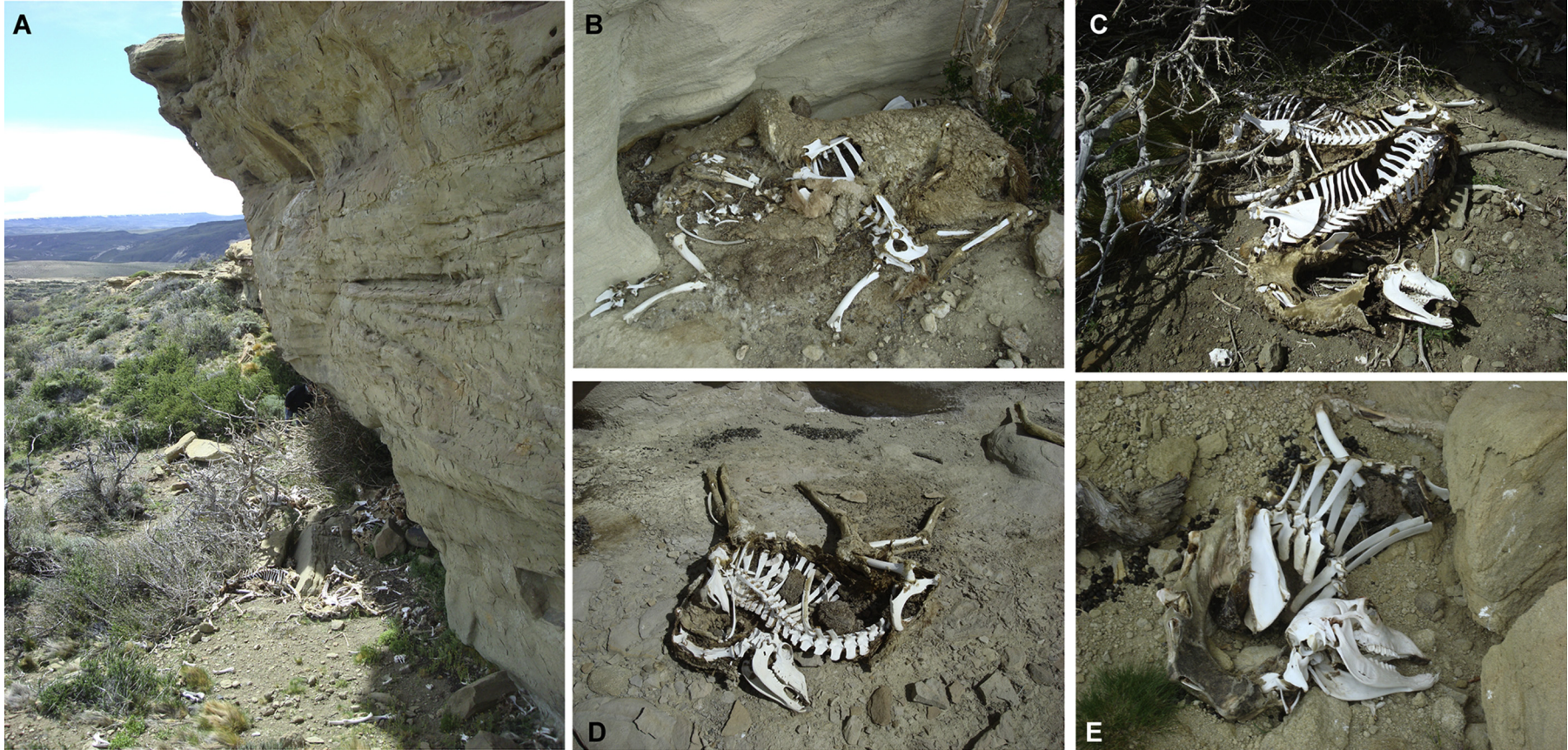
Fig. 2. Assemblages of dead guanacos in November 2011. (A) View of the rock-shelter Alero Los Guanacos 3 (ALG 3). Guanaco skeletons in (B) ALG 1, (C) ALG 12, (D) ALG 4, (E) Detail of a skull in ALG 1.

3.1.1.2. Alero Los Guanacos 3. This rockshelter is conformed by a wall with a northeast-southwest orientation (parallel to Los Guanacos 1 site) and it has important vegetation coverage, mainly "molle" (*Schinus polygamus*) in the front area. The site is between 500 and 700 m south from Los Guanacos 1. The GPS coordinates are 48° 49′ 06″ S and 71° 24′ 25″ W. The elevation is 510 masl. A great concentration of dead guanacos was observed in the place. They showed a better preservation and a higher concentration than Los Guanacos 1. This rockshelter offers a better protection in certain areas due to the presence of a wider roof; it is in those sheltered areas where the guanacos showed a better preservation. The guanaco concentration is 36 m long by 10 m wide.

3.1.1.3. Alero Los Guanacos 4. The site is placed at the beginning of the canyon that is parallel to that of the site Los Guanacos 1, behind Ea. Cerro Bayo. This canyon is 400 m long approximately. The carcasses of 31 animals were observed along this canyon. However, only the concentration found at the beginning of the rockshelter was analyzed in detail, because it is the one that shows the largest density of individuals.

The extension of this rockshelter is approximately 19 m long by 3 m wide. Toward the bottom of the canyon there is an extensive slope in which bones of that concentration, bones of former dead animals (there are remains of guanaco and sheep with weathering stages different from those of the assemblages), and a few lithic artifacts were found. This rockshelter faces west, like Alero Los Guanacos 1 and 3. The site's GPS coordinates are 48° 49.359′ S and 71° 23.495′ W, and is at 385 masl.

3.1.1.4. Alero Los Guanacos 12. This Rockshelter is located in the opposite side of the sandstone outcrop that also forms ALG 1. The rockshelter faces east and does not receive as much solar light as ALG 1. Also, it is possible that it does not accumulate as much snow in winter as the sites facing west. Maybe this explains the better conservation of this assemblage in comparison with ALG 1. The GPS coordinates are 48°48′48.3″ S and 71°23′34.8″ W, with an elevation of 411 masl. The animals are concentrated in a narrow strip of 9 m long by 2 m wide from the rockshelter wall. We included in this analysis the remains of six carcasses because they have crania to make molds, but there are at least three more individuals in the assemblage. Also, we recorded the presence of three sheep carcasses in the assemblage.

3.1.2. Open air locations

3.1.2.1. Olivero. A great amount of guanacos were found in this site, generally associated to molle shrubs, which offers a certain degree of shelter. The GPS coordinates are 48° 47′ 24″ S and 71° 14′ 53″ W. It is 54 m long by 66 m wide. One important aspect of this site is that it is the highest point of the area (460 masl). It is evident that during the winter, the guanacos avoid the lower zones that accumulate snow and try to go to high places, where they finally die. This is similar to the case of the rockshelters. Another important aspect to highlight is the steep slope of this site, approximately 45° in a south−north direction. The preservation of animals in this site, comparing to the rockshelters, is bad. The excellent preservation of the fur in the guanacos of the rockshelters helped the integrity of the carcasses, slowing down the process of disarticulation of the animals. In this case most of the animals have not kept the fur. So, its rate of disarticulation was faster, making it very difficult or impossible to survey and analyzed individual carcasses. The steep slope also contributes to make the process faster, favoring the migration of bones to lower parts of the site. Remarkably, the exceptions to this fur destruction process followed by a fast disarticulation of the skeletal elements are related to carcasses associated to vegetation. In this way, the presence of "molles" seems to act as an efficient barrier against carcasses dispersion. Seven carcasses had fur and were articulated. However, the carcasses in general were more disarticulated than those of the rockshelters.

3.1.2.2. La Encajada. The site is found on a small hill (460 masl), 400 m north of Olivero site approximately. There is a road between both places. The orientation of La Encajada site is northwest− southeast. The coordinates GPS are 18° 47′ 12″ S and 71° 14′ 39″ W. The dispersion surface of this site is 39 m wide by 25.5 m long. The highest bone concentration is found next to a big size "molle" (4 m²). As in the case of Olivero site the preservation of the carcasses is also bad. The process of fur loss and disarticulation of the individuals at La Encajada is even more extreme than in Olivero. The only articulated bones were pieces of the vertebral column. Even though it can not be confirmed this is probably the area where the animals were gathering. From the "molle", the bones are more dispersed and disarticulated throughout the slope and the small body of water behind it.

A total of 100 individuals were sampled. The material analyzed is made of 77 skulls collected by DR and JBB in 2009 and 2010 and curated at the *Instituto Nacional de Antropologia y Pensamiento Latinoamericano* (INAPL) and 23 individuals that were still *in situ* in the Cardiel Lake area and were directly sampled during a field trip in November 2011 (after sampling the skulls were left *in situ*). As we noted before, a total of six sites were studied, two open-air sites and four rock-shelters (or *aleros*). The rock-shelters are located about 12 km away from the open-air sites (Fig. 1). We sampled dental molds on 39 skulls from open-air sites (La Encajada and Olivero) and 61 from rock-shelters (Alero Los Guanacos ALG 1, ALG 3, ALG 4, and ALG 12).

3.2. Methods

The two methods, tooth mesowear and microwear, provide access to very different time frames within the life history of an animal. Tooth mesowear reflects a dietary signal over a "long" temporal scale (months-years). It gives a close approximation of overall diet and more generalized annual ecological conditions. Microwear analysis indicates a signal over a short temporal scale (days−weeks). It will provide information about the diet at time of death and the local or seasonal ecological conditions. Using both methods in reconstructing the diet of fossil ungulates is thus expected to allow us to make inferences regarding seasonal variations in dietary habits of a species.

3.2.1. Mesowear

Mesowear analysis, first introduced by Fortelius and Solounias (2000), is a method of categorizing the gross dental wear of ungulate molars by evaluating the relief and sharpness of cusp apices in ways that are correlated with the relative amounts of attritive and abrasive dental wear. Mesowear is scored macroscopically from the buccal side of upper molars, preferably the paracone of M2 (Fortelius and Solounias, 2000). Among taxa with the appropriate masticatory apparatus, a diet with low levels of abrasion (such as the browsing diet of the moose) maintains sharpened apices on the buccal cusps as the tooth wears. In contrast, high levels of abrasion, associated with a diet of siliceous grass and/or a high rate of soil or dust particle ingestion (such as the coarse grazing diets of African zebra) results in more rounded and blunted buccal cusp apices. Unworn (and marginally worn) teeth, extremely worn teeth, and those with broken or damaged cusp apices are omitted from mesowear analyses. Cusp sharpness is sensitive to ontogenetic age among young individuals (who have not yet developed substantial

wear facets) and among dentally senescent individuals. However, for intermediate age groups, which typically include the majority of individuals in a fossil collection, mesowear was found to be less sensitive to age and more strongly related to diet (Rivals et al., 2007). In this study, the standardized method (mesowear "ruler") introduced by Mihlbachler et al. (2011) is employed. The method is based on seven guanaco cusps (numbered from 0 to 6), ranging in shape from high and sharp (stage 0) to completely blunt with no relief (stage 6) (Fig. 3). The average value of the mesowear data from a single sample of fossil dentitions is the "mesowear score" (Mihlbachler et al., 2011).

3.2.2. Microwear

Microwear features of dental enamel were examined using a Zeiss Stemi 2000C stereomicroscope on high-resolution epoxy casts of teeth following the cleansing, molding, casting, and examination protocol developed by Solounias and Semprebon (2002) and Semprebon et al. (2004). In brief, the occlusal surface was cleaned using acetone and then 96% alcohol. The surface was molded using high-resolution silicone (vinylpolysiloxane). Then casts were created using transparent epoxy resin.

All specimens molded were carefully screened under the stereomicroscope. Those with badly preserved enamel or taphonomic defects (features with unusual morphology and size, or fresh features made during the collecting process or during storage) were removed from the analysis (King et al., 1999).

Casts were observed under incident light with a stereomicroscope at 35 × magnification, using the refractive properties of the transparent cast to reveal microfeatures on the enamel. Microwear scars (i.e., elongated scratches and rounded pits) were quantified on a taphonomically unaltered enamel region on the paracone of the upper second molars. Microwear features were counted in a square area of 0.16 mm^2 using an ocular reticle. We used the classification of features defined by Solounias and Semprebon (2002) and Semprebon et al. (2004). Pits are microwear scars that are circular or sub-circular in outline and thus have approximately similar widths and lengths, while scratches are elongated microfeatures which are not merely longer than they are wide, but they have straight, parallel sides. Scratch (NS) and pit (NP) counts were obtained in two areas of the mold and results averaged. The results were compared to a database constructed from extant ungulate taxa (Solounias and Semprebon, 2002). It is possible to discriminate between the dietary categories of browser (i.e., eating woody and non-woody dicotyledonous plants) versus grazer (i.e., eating grass) using average scratch and pit data.

While it has been standard practice in microwear studies to quantify pits and scratches, significant niche partitioning in extant forms, and habitat differences within each broad trophic group, are discernible by scoring relative pit sizes, scratch textures, and gouges in addition to quantifying the numbers of scratches and pits (Semprebon, 2002; Semprebon et al., 2004; Solounias and Semprebon, 2002). Variations in scratch number ranges, scratch textures, and relative pit sizes are the most useful variables for partitioning living forms into more refined trophic categories such as fruit browser, bark consumer, or dirty browser (browsers ingesting plants that are more abrasive than typical because they are coated with dust, grit, or dirt). Large pits are

deeper, less refractive (always dark), generally at least about twice the diameter of small pits, and often have less regular outlines than do small pits. Gouges are depressions that have ragged, irregular edges and are much larger (2–3 times as large) and deeper than large pits. We noted the presence or absence of large pits, gouges and cross scratches within the 0.16 mm^2 area. Cross scratches are oriented somewhat perpendicularly to the majority of scratches observed on tooth enamel (Solounias and Semprebon, 2002). In addition, scratch textures were assessed as being either fine (i.e., narrow scratches that appear relatively shallow and have low refractivity (are duller) than coarse scratches) or coarse (i.e., wide scratches that are also relatively deep but have high refractivity (relatively shiny)), or a mixture per tooth surface. The scratch width score (SWS) is obtained by giving a score of '0' to teeth with predominantly fine scratches per tooth surface, '1' to those with a mixture of fine and coarse types of textures, and '2' to those with predominantly coarse scratches. Individual scores for a sample are then averaged to get the scratch width score.

3.2.3. Comparison with other samples of guanaco and vicuña

The results on the guanacos from the Lake Cardiel area were compared with other samples of guanacos (*L. guanicoe*) and vicuña (*Vicugna vicugna*). Those samples are made of individuals from collections housed in museums of natural history. They come from various areas of South America and were collected at various time of the year. Consequently they represent a "random" sample of the geographical and temporal (annual) diet for each species.

The random sample of guanacos is housed at the Natural History Museum (London) and specimens come from Argentina, Chile, and Bolivia.

The random sample of vicuña is curated at the Natural History Museum (London) by FR and the American Museum of Natural History (New York) by Nikos Solounias and Gina Semprebon (Fortelius and Solounias, 2000; Solounias and Semprebon, 2002). Specimens originate from Argentina, Peru, and Bolivia.

3.2.4. Statistics

Statistical test were performed on PAST v2.15 (Hammer et al., 2001). Non-parametric Mann–Whitney U test and Kruskal–Wallis H test we used for analyses involving two and three independent samples, respectively. We used the ANOVA to test for differences between the six localities for the mesowear (MWS) and microwear (NP, NS) variables. Finally, the variability in the number of scratches on the enamel, as quantified by the sample-size corrected coefficient of variation (CV*), is used to estimate the diversity and variability in the diet (i.e., the higher the CV*, the more diversified is the diet). The CV* is computed using the following formula: $CV^* = CV(1 + 1/4n)$, where n is the sample size. The method allows to find significant differences between samples of animals that died during a single season versus those that were accumulated over an entire year, or longer periods (Rivals et al., 2009b). We examined CV* estimates for each sample and used the Levene's test to analyze the significance of the differences. To eliminate the influence of scale, the raw data were transformed to the natural log scale.

4. Results

A total of 100 individuals were sampled from sites located in the Cardiel Lake area (Fig. 1), 81 teeth with complete buccal cusps were suitable for mesowear, and 91 with complete protoconid enamel band were suitable for microwear analysis. Results for each site, as well as for the random samples of guanaco and vicuña are summarized in Table 2.
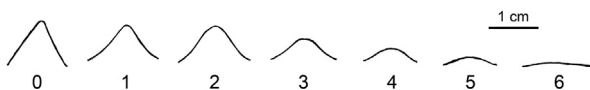

Fig. 3. Scale used to assess mesowear scores on guanaco teeth considering two variables: cusp relief and cusp shape.

Table 2

Mesowear and microwear summary data for the guanaco samples from the Cardiel Lake area and for the extant random samples of guanaco and vicuña (data from Fortelius and Solounias, 2000; Solounias and Semprebon, 2002). Abbreviations: MWS = mesowear score; PIT = average number of pits; SCR = average number of scratches; %LP = percentage of specimens with large pits; %XS = percentage of specimens with cross scratches; SWS = scratches width score (from 0 = fine scratches only to 2 = coarse scratches only); %G = percentage of specimens with gouges.

	Mesowear		Microwear						
	N	MWS	N	PIT	SCR	%LP	%XS	SWS	%G
All 6 localities									
Total	81	1.43	91	32.98	12.73	3.30	7.69	1.15	4.40
CV*		0.54		0.07	0.07				
Open-air	29	1.41	34	33.53	13.19	5.88	2.94	1.21	8.82
Rock-shelter	52	1.44	57	32.66	12.46	1.75	10.53	1.12	1.75
Individual localities									
Encajada	8	1.38	10	31.80	12.40	10.00	0	1.20	10.00
Olivero	21	1.43	24	34.25	13.52	4.17	4.17	1.21	8.33
ALG 1	20	1.65	20	30.20	13.03	0	10.00	1.10	0
ALG 3	21	1.24	23	35.11	11.96	4.35	8.70	1.13	4.35
ALG 4	6	1.67	8	30.94	12.13	0	25.00	1.13	0
ALG 12	5	1.20	6	33.75	12.92	0	0	1.17	0
Random samples									
L. guanicoe	7	1.57	8	41.43	18.19	50.00	12.50	0.75	25.00
CV*		0.34		0.21	0.13				
V. vicugna	19	1.63	14	30.82	18.71	64.30	35.70	1.14	71.40
CV*		0.71		0.59	0.22				

As the samples we analyzed are coming from two type of sites, open-air sites and rock-shelters (or *aleros*), thus we first tested for differences in the mesowear and microwear patterns that could be due to differential preservation of the material. There are no significant differences between the samples from the open-air sites (La Encajada and Olivero) and the rock-shelters (Alero Los Guanacos ALG1, ALG3, ALG4 and ALG 12) either in the mesowear scores ($U = 718.5$; $p = 0.7016$), in the number of pits ($U = 877.5$; $p = 0.4551$), or in the number of scratches ($U = 776.5$; $p = 0.1139$) (Table 3). That comparison suggests that there is no difference between the two types of sites related to differential taphonomic alteration between rock-shelters and open-air sites on the tooth wear patterns. As differences between the 6 sampling areas are not significant, and because all individuals died in winter 2000, we grouped all the individuals in a single sample.

A total of 81 specimens were analyzed using the tooth mesowear method. Second upper molars have predominantly high relief and sharp or round cusps (Fig. 3) indicating high attritive (tooth to tooth contact) and low abrasive (tooth to food contact) masticatory forces. The cusps shapes correspond to the mesowear scores 0, 1 and 2 from the Mihlbachler et al. (2011) scoring scale. The average mesowear score for the Cardiel Lake sample is 1.43 (Table 2; Fig. 4) which indicates leaf browsing or browse dominated mixed feeding habits by comparison to the data on extant free-ranging ungulates from Fortelius and Solounias (2000). Mesowear score is very similar to those observed on random samples of guanaco (MWS = 1.57) or vicuña (MWS = 1.63). Differences between the three samples are not significant ($H = 1.41$, $p = 0.441$). The annual average diet for the guanaco from the Cardiel Lake is to be categorized as a mixed-feeder; it means a diet which shifts according to seasonal changes.

A total of 91 specimens were analyzed through the tooth microwear technique. Occlusal enamel surfaces of the second molars are well preserved as 91% of the teeth sampled were suitable for microwear analysis. The enamel display low numbers of scratches and relatively high numbers of pits (Table 2). On the microwear bivariate plot (Fig. 5), the average for the 91 individuals sampled falls among the leaf browser morphospace.

There are no significant differences in the numbers of pits between the three samples ($H = 1.917$; $p = 0.3832$). However, when

Table 3

ANOVA and Tukey's HSD test results. Abbreviations: df = degrees of freedom; SS = sum of squares; MS = mean square.

Mesowear scores (MWS)

ANOVA results:

Source	df	SS	MS	F-ratio	p
Model	5	2.366	0.473	0.7798	0.5674
Residual	75	45.511	0.607		

Pair-wise comparisons – q values (Tukey's method); $p < 0.05$:

	ENCA	OLIV	ALG1	ALG3	ALG4	ALG12
Encajada	–					
Olivero	0.211	–				
ALG1	1.084	0.873	–			
ALG3	0.539	0.751	1.623	–		
ALG4	1.149	0.938	0.066	1.689	–	
ALG12	0.689	0.901	1.773	0.150	1.839	–

Number of pits (NP)

ANOVA results:

Source	df	SS	MS	F-ratio	p
Model	5	348.353	69.671	1.103	0.365
Residual	85	5369.37	63.169		

Pair-wise comparisons – q values (Tukey's method); $p < 0.05$:

	ENCA	OLIV	ALG1	ALG3	ALG4	ALG12
Encajada	–					
Olivero	1.04	–				
ALG1	0.679	1.72	–			
ALG3	1.405	0.365	2.084	–		
ALG4	0.366	1.407	0.313	1.771	–	
ALG12	0.828	0.212	1.507	0.577	1.194	–

Number of scratches (NS)

ANOVA results:

Source	df	SS	MS	F-ratio	p
Model	5	34.737	6.947	1.408	0.2296
Residual	85	419.417	4.934		

Pair-wise comparisons – q values (Tukey's method); $p < 0.05$:

|	ENCA	OLIV	ALG1	ALG3	ALG4	ALG12
Encajada	–					
Olivero	1.703	–				
ALG1	0.949	0.753	–			
ALG3	0.674	2.377	1.623	–		
ALG4	0.418	2.121	1.367	0.256		
ALG12	0.785	0.918	0.165	1.459	1.203	–

we consider the numbers of scratches some differences can be identified. The vicuña sample differ significantly from the winter and random samples of guanacos ($U = 149.5$; $p = 0.000004$ and $U = 14$; $p = 0.0045$, respectively). The two samples of guanacos (winter and random) are not significantly different ($U = 345.5$; $p = 0.8165$). The winter sample from the Cardiel Lake area has an average number of scratches (and S.E.M.) that falls in the lower part of the range of variation of the random sample of guanaco. This result is consistent with the fact that the winter sample could be considered as a sub-sample of the random sample.

Large pits, cross scratches, and gouges are scarce (3–7%). The low percentages of individuals with large pits or gouges permit to exclude fruit browsers and bark consumers. However the high number of pits in comparison to the other leaf browsers and grazers would suggest the ingestion of high proportion of dust and grit associated to the vegetation (Rivals and Semprebon, 2006; Semprebon and Rivals, 2007, 2010).

The winter sample from the Cardiel Lake area has a coefficient of variation (CV*) significantly lower than the random samples of guanacos (F-ratio = 26.72; $p = 0.0000001$) or vicuñas (F-ratio = 65.75; $p = 0.0004$) (Table 2; Fig. 5). The CV* for the two random samples are not significantly different (F-ratio = 0.2934; $p = 0.1751$).

5. Discussion

The combined analysis of tooth mesowear and microwear indicates browse dominated mixed feeding traits for that population
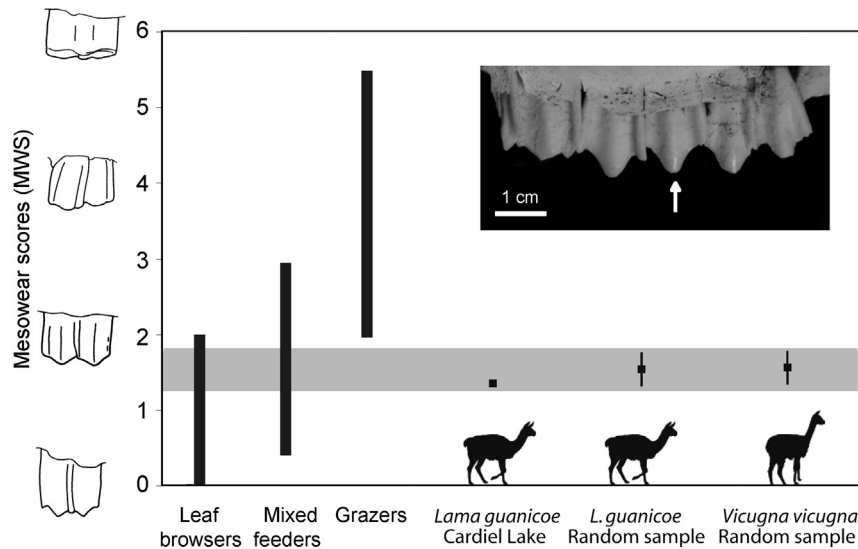
Fig. 4. Mesowear scores based on the extant reference species from Fortelius and Solounias (2000) and the extant samples from the Cardiel Lake and the random samples of guanaco and vicuña. Extant taxa are classified as leaf browsers (**LB**), mixed feeders (**MF**) and grazers (**G**), mesowear scores for extant species calculated from Fortelius and Solounias (2000) see Appendix 2. Error bars = Standard Error of the Mean. The insert illustrate a right maxilla of guanaco from La Encajada (specimen #9). The arrow indicates the paracone of the M2.

resulting from a catastrophic mortality event that occurred during the winter 2000 in the Cardiel Lake area. The results obtained through tooth wear analysis are consistent with data available for guanaco diet and for the vegetation available during winter in semi-desert areas of Southern Patagonia. Results are also consistent with the phenology of the vegetation and the water resources available in the soil (Sala et al., 1989; Baldi et al., 2004). The most widespread plant communities on the Patagonian plateaus are the shrub steppes with tall to medium shrubs such as *Schinus polygamus*, *Nardophyllum obtusifolium*, *Colliguaja integerrima*, *Berberis* spp., *Junellia tridens* and dwarf-shrub steppes represented by cushion plants such as *Nassauvia*, *Ephedra frustillata* and *Azorella* sp. (Bamonte and Mancini, 2011; Mancini et al., 2012). The grass stratum is composed dominantly by *Stipa* and *Poa*. In some areas grasslands are sometimes mixed with some bushes that can form vast areas of shrubland (Mancini, 1993). Considering that extant guanacos in Southern Patagonia shift seasonally their diet, tooth mesowear indicate the average annual diet for that population

(mixed feeding) while microwear captured a snapshot indicating winter diet (browse dominated mixed feeding).

The variability of the number of scratches (reflected in the CV*) for the winter sample from the Cardiel Lake is significantly lower compared to the random samples of guanaco and vicuña. The low CV* indicates here a seasonal signal (Rivals et al., 2009b) and is related to the fact that all individuals belong to the same population (same area), died at the same season (winter) and had access to the same vegetal resources. At the contrary, the random samples are composed of individuals from various populations in South America and died at various seasons of the year. Thus, because they have had access to a large variety of vegetal resources, they have a higher variability in their microwear pattern.

The low CV* thus reflects the low dietary breadth of the guanaco in winter due to a decrease in the diversity of plant resources available in the area. The browsing at this time of the year must be related to a better availability of bushes than grass that would be covered by snow.

The observations made from tooth wear analysis are consistent with data on ecology of the guanaco. In the Mendoza Province – Central Western Argentina–, Puig et al. (2001) reported a summer opportunistic feeding behavior with high dietary diversity that shifts to a more selective behavior during winter with a narrower dietary breadth. Proportions of plant categories in the guanaco diet showed significant seasonal changes and a positive association with changes in food availability. Enlargement of food-niche breadth corresponded to seasonal increases in diversity of available plants (Puig et al., 1996). Enlargement of the food niche when environmental availability increases in diversity can be interpreted as another adaptation to arid environments, where high climatic fluctuations reduce the predictability of phenological and nutritional changes in the vegetation (Miller and Gaud, 1989).

The high food diversity may also reflect the adaptation of this camelid to arid environments, where vegetation generally shows low availability and low quality for most of the year (San Martín, 1991). Quintana et al. (1994) describe a similar situation as 'forced selectivity' by low food diversity in winter.

Comparison with other populations of free-ranging guanacos from a random sample indicates that seasonal changes in diet can be identified. It confirms our hypothesis that tooth microwear is
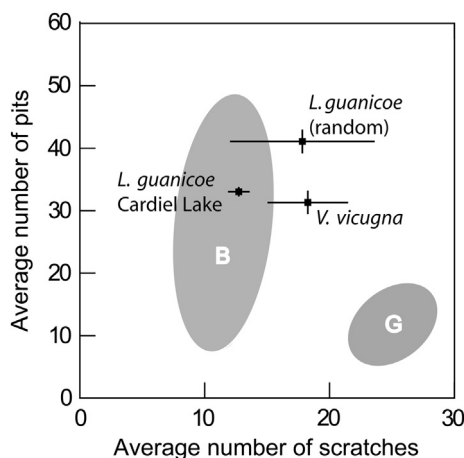
Fig. 5. Bivariate diagram based on microwear signatures of extant reference species from Solounias and Semprebon (2002) and the guanaco and vicuña samples from this paper. Gray areas indicating Gaussian confidence ellipses (p = 0.95) on the centroid of the grazer/browser sample adjusted by sample size.

able to indicate seasonality in the diet of ungulates from arid habitats (semi-deserts or steppe). The next step of the study would be to confirm our hypothesis with the analysis of a random sample and/or a summer sample of guanacos from the same area as the winter sample. This approach would be useful to detect seasonal occupations in archaeological sites in Patagonia and the objective is now to apply the method on archaeological assemblages from the same area in Southern Patagonia.

Besides seasonal patterns, the application of tooth microwear to archaeological assemblages of this region would certainly allow to improve the identification of hunting strategies. Considering that attritional assemblages composed of individuals sequentially accumulated over a long period of time would display higher variability than massive hunting activities where one should observe a higher homogeneity, the method would also permit to characterize hunting strategies on a gradient from communal hunting of a large number of animals to solitary hunting of single individuals. The seasonality of the occupations at each site will be crucial for a better understanding of the group mobility on the different areas of their territory.

Acknowledgments

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jas.2013.03.005.

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