Taphonomic analysis of Plant Remains Contained in Carnivore Scats in Andean South America

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Plant remains contained in carnivore scats from Puna rockshelters in the Argentinean Andean Puna are analysed. Only 31% of the scats (n=16) contained plant remains, all of them corresponding to the Poaceae family. Most of these are leaf and culm parts, and only in one case seeds were identified, possibly also corresponding to the same family. The lack of fleshy fruit seeds suggests a different pattern of plant intake as compared to other areas, possibly just for purging here. Plant anatomical structure has suffered no damage from digestive acids but some softening, and all anatomical features are perfectly recognizable. Plants can thus then enter the fossil record in rockshelters in the region via carnivore scats, and this should be taken into account, especially as these are the same kind of plants most commonly introduced by humans in the past according to the regional archaeological record.

Keywords: CARNIVORE SCATS, PLANT REMAINS, POACEAE, TAPHONOMY, ROCKSHELTERS, ANDES, SOUTH AMERICA

Introduction

This paper is part of a more general research aimed at understanding the taphonomic action of mammalian carnivores in Puna rockshelters (Mondini 2001, 2002, 2003). The research has basically consisted in analysing faunal remains accumulated by carnivores in rockshelters of the region nowadays in the light of the ecology of these mammals, modelling their taphonomic action, and using the inferences so generated to assess the consequences of these taphonomic processes in the archaeofaunal record of the area.

Here we focus on the characteristics of plant remains contained within modern carnivore scats and their implications. Scats
Plant remains in carnivore scats

represent a common way of introduction of bone and other faunal remains into the fossil record—and in the case of the zooarchaeological record in particular, of remains of non-cultural origin—as well as a source of palaeoecological information (Stallibrass 1990; Borroto & Martin 1996; Schmitt & Lupo 1995; Fernández Jalvo et al., 1996; among others). Depending on preservation conditions, they can also represent a way of introduction of plant material into the record, an aspect that has not been as fully studied.

The aim of the study here presented has been to identify the plants consumed by Puna carnivores and study the properties of these remains relative to the digestive processes that affected them, regarding their identifiability and chances of conservation in the fossil record.

The Puna or Altiplano is a high-altitude plateau, over 3500 masl (metres above sea level) East of the Central-Southern Andes (Cabrera 1957; Troll 1958, Cabrera & Willink 1980; Santoro & Núñez 1987, Baied & Wheeler, 1993; among others). It is characterised by high levels of aridity and by a patchy environment and a low, although variable, general productivity. This study is focused in the Eastern flank of the Salty Puna, specifically in Antofagasta de la Sierra, Catamarca, Argentina (Figure 1). This area is an endorreic basin, having the Antofagasta lake (3450 masl) as the bottom, and reaches some 5000 masl in the mountains and volcanoes surrounding it. The drainage net is not well developed, and it depends fundamentally on the summer ice melting. Climate is of the puneño Andean arid type, with mean annual precipitations of 100 mm or even less, concentrated in the hot season, although the pluvial regime is highly unstable. There is high solar radiation and evaporation, and a high thermal amplitude, both daily and annual, the mean annual temperature being <10º C (Cabrera, 1957; Garcia Salemi, 1986; among others).

Phytogeographically, the Antofagasta de la Sierra basin corresponds to the Puna Province of the Andino Patagónico Domain (Cabrera, 1976). Dominant vegetation in this Province is the shrubby steppe, and herbaceous, halophyte, and samophile steppes also develop here (Cabrera & Willink, 1980). In Antofagasta de la Sierra, the tolar can be found up to some 3800 masl, where shrub and sub-shrub species of the genera Parastrephia and Acantholippia are common. Above this altitude, grassland develops in which Festuca, Jarava, Deyexia, and other shrub species of the Adesnia, Baccharis, Parastrephia, and Fabiana genera are abundant, and correspond to the rangeland (pajonal) plant association (Rodríguez & Rúgolo de Agrasar, 1999). Besides the tolar and rangeland, there are different types of vegas, which include species of the Poaceae and Juncaceae families (Haber, 1991).

Regarding the fauna, most herbivore biomass in the area corresponds to artiodactyls, currently represented by ovicaprids and camelids. Rodents are an important component as well. There are different wild carnivores in the Puna and in Antofagasta de la Sierra in particular (Cabrera, 1957; Olrog & Lucero, 1981; Redford & Eisenberg, 1992; Jaksic, 1997; among others). Those most commonly involved in the use of rockshelters are South American foxes, represented by the red one or culpeo (Pseudalopex culpaeus) and the grey one or chilla (Pseudalopex griseus). Several felids also inhabit the region, the puma (Puma concolor) being the largest one, and others being the pampas cat (Lynx colocolo), the Andean mountain cat (Oreailurus jacobita), and Geoffroy’s
cat (*Oncifelis geoffrogi*) in the lower areas. Mustelids that can be found in the area are the hog-nosed skunk (*Conepatus chinga*) and the little grisón (*Galictis cuja*), although as they do not usually live above 3000 or 3500 masl they are more likely to be found in lower areas at the Puna fringe. Except for the puma, a "specialist", these carnivores correspond to the adaptive zone that Berta (1988) defined for small-sized omnivores-carnivores—foxes being the most frugivorous ones—, this region lacking representatives of the large "generalists". Finally, there are also dogs (*Canis familiaris*), their introduction in the area being relatively recent: the earliest records in the whole Andean region date to the Middle Holocene (Wing, 1989).

Regarding diet, pumas and other cats are the most carnivorous species, followed in decreasing order by the grisón, the canids, and finally the skunk, which is the most insectivorous of these carnivores. Foxes, which are the ones most prone to using rockshelters, are highly opportunistic: they tend to adjust to the most abundant items through each annual cycle (Olrog & Lucero, 1981; Erlich de Yoffe et al., 1985; Simonetti, 1986; Meserve et al., 1987; Mares et al., 1989; Ginsberg & Macdonald, 1990; Redford & Eisenberg, 1992; among others). Generally, culpeos have a wide omnivorous diet—although according to some studies it is selective—, which is based principally on small mammals and includes the scavenging of larger ones. The diet of the grey South American fox is similar, though it is usually somewhat wider and includes a higher proportion of invertebrates, fruit and scavenging of vertebrates. The gnawing apparatus of both species is characterised, as in other canids, by large and prominent canines and molars with a small crushing surface. Given their body size and their jaw structure, a low destructive power is to be expected in both cases.

There are several possible contexts in which carnivore scats can be deposited, such as latrines, dens, points of territory demarcation, and feeding sites (Andrews & Evans, 1983; Martin, 1998; Bouchner, 1999; among others). The loci used for these different purposes often coincide with those used by humans, especially in the case of rockshelters, a topographic resource highly appreciated by both kinds of agents. In the Puna, in fact, carnivore scats have been recorded in different archaeological sites, but these remains and their meaning had not been analysed in detail before, and there was no relevant modern analogue available to compare them. This study aims at making a contribution in this regard, and we hope it can be of use to the analysis of other fossil records as well.

**Materials and methods**

During the general actualistic taphonomic research, broad areas were surveyed in different Puna sectors, and a number of taphonomic sites in rockshelters, consisting of carnivore dens and latrines—containing only scats—, as well as the faunal remains contained in them were studied. The results presented here were obtained in the Antofagasta de la Sierra area, where eight dens were surveyed—most in the Paycuqui-Cacao-Curuto area and one, ANSm8, in Laguna Colorada—, located in small shelters in the tolar zone, at 3500-3700 masl (Figure 1). Five of these dens contained scats, three of which also contained bones. Most of the faeces were found on the surface, except for a few in den ANSm7 that were beginning to bury hardly below surface. The scats generally
Plant remains in carnivore scats

presented some dehydration and some presented weathering signs –expressed in their texture and more whitish colour–, which is most certainly due to the arid local conditions.

A total of 148 carnivore scats were collected –although not all the surface of the narrow den ANSm8 could be reached–, and 10% of them were opened for content analyses. Each scat specimen, either complete or fragmented, was considered a unit, and the number of scats originally deposited in not known. The name of each unit has three parts: the number identifying the den of provenance –which were numbered after the abbreviation of Antofagasta de la Sierras: ANS–, the number with which the scat or group of scats were identified when collected in the field –which identifies it on the site map–, and finally subsequent letters for each individual unit (e.g., “7/87/CV” is one of the scats of collection locus No. 87 in the map of den ANSm7).

The scats were first described according to their general properties, and based on these they were then taxonomically determined with the help of guides (e.g., Bouchner, 1999) and the advice of specialists. Morphological criteria were used in these determinations, and hence they are of a probabilistic nature. According to these criteria, the carnivores that would have most commonly used these shelters are foxes (41% specimens average were identified as probable fox scats), especially culpeos. This last inference is based not only on scat size, but also on fox ecology, being culpeos more likely to be present in the high areas where dens ANSm2-7 are located; in the lower area of ANSm8, instead, a grey fox was spotted. Regarding scat identification, foxes are followed by felids (an average of 11% specimens were identified as probable puma and 23% as probable small cat), and perhaps mustelids, with a tiny representation (about 1% on average, although in none of these cases small foxes can be ruled out).

Taking into account the potential error implied in typological determinations based on morphology according to some experimental studies (e.g., Foran et al., 1997, Davison et al., 2002), these identifications were corroborated, whenever it was possible, with the determination of predator hair contained in the scats (Perovic, 2002). This hair would have been ingested during grooming, and it is highly improbable it derives from prey, as it is found in a very low proportion. Culpeo was identified in three scats from ANSm7, Geoffroy’s cat in one scat also from ANSm7, and apparently dog hair was found in one from ANSm3, being these determinations consistent with the morphological ones. It should be noticed that although dog and puma hair are practically indistinguishable, Perovic (2002) considers that the case of ANSm3 probably corresponds to dog due to the size of the scat, its abundant plant content which suggests an omnivore diet, and a high proportion of micromammals according to bone and hair. It should also be noticed that from scat morphology only, no dog scat was identified as such in the region. Even taking into account that this could be partly an identification bias and that dog scats can be highly variable –as this ANSm3 case suggests–, scat morphology in the dens analysed is generally not consistent with dog scats and the specialists asked did not detect their presence either. It is reasonable to conclude that the studied faeces represent mostly wild species.

Ten per cent of the scats at each site (total n=16) were broken open to separate and study their different contents: bones,
Sample selection was made trying to represent, whenever possible, the different variants present at each site, especially with regards to morphology and preservation state. There are two main techniques to open faeces: to previously soak them in water (e.g., Stallibrass, 1990) or in some solution (e.g., Figuerero Torres, 1981), or to dry them (e.g., Meserve et al., 1987). Given that the Puna scats were highly dehydrated, they were just disintegrated, with no previous treatment, with the help of wooden sticks and tweezers. An 850 mm mesh was used to help recover smaller fragments. Bone remains—corresponding basically to small taxa, and highly fragmented but mostly with subtle digestion traces (Mondini, 2000, 2003)—, hair (Perovic, 2002), and plant remains were analyzed.

To create the botanical reference collection used in this study, as well as in the archaeobotanical research carried out in the Antofagasta de la Sierra basin, transects were made in different directions along which plant species were sampled.
### Plant remains in carnivore scats

<table>
<thead>
<tr>
<th>scat</th>
<th>taxon</th>
<th>size (mm)</th>
<th>colour/condition</th>
<th>contents</th>
<th>observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>3/53/F</td>
<td>carnivore indet. - dog (puma?)</td>
<td>F 60 x 10</td>
<td>dark brown</td>
<td>bone - hair - plant remains - clasts - sediment</td>
<td>Most of the matrix consists of plant remains. Abundant hair.</td>
</tr>
<tr>
<td>4bis/58/D</td>
<td>fox/mustelid</td>
<td>F 31 x 11</td>
<td>brown - shiny surface</td>
<td>bone - hair - insects - feather - clasts - sediment</td>
<td>Most of the matrix consists of hair.</td>
</tr>
<tr>
<td>5/70/A</td>
<td>fox/cat</td>
<td>C 39 x 15</td>
<td>very dark</td>
<td>bone - hair - plant remains - clasts - sediment</td>
<td>Abundant plant remains.</td>
</tr>
<tr>
<td>7/87/CS</td>
<td>puma/fox</td>
<td>F 59 x 20</td>
<td>greyish w/dark areas - compact brown - cracked surface</td>
<td>bone - hair - keratin - clasts - sediment</td>
<td>Most of the matrix consists of hair. Abundant clasts.</td>
</tr>
<tr>
<td>7/87/CV</td>
<td>puma/fox</td>
<td>F 69 x 18</td>
<td></td>
<td>bone - hair - plant remains - clasts - sediment</td>
<td></td>
</tr>
<tr>
<td>7/87/CY</td>
<td>carnivore indet. Pseudolapex culpaeus</td>
<td>F 44 x 16</td>
<td>very dark brown - area w/shiny surface</td>
<td>bone - hair - sediment</td>
<td>Several contents look dark.</td>
</tr>
<tr>
<td>7/87/CZ</td>
<td>carnivore indet. Pseudolapex culpaeus</td>
<td>F 83 x 18</td>
<td>dark brown</td>
<td>bone - hair - plant remains? - clasts</td>
<td>Most of the matrix consists of hair.</td>
</tr>
<tr>
<td>7/87/DA</td>
<td>carnivore indet. Oncifelis geoffrogi</td>
<td>F 68 x 17</td>
<td>brown - partially cracked surface - fissures</td>
<td>bone - hair - feather - plant remains - clasts</td>
<td>Most of the matrix consists of hair.</td>
</tr>
<tr>
<td>7/87/DC</td>
<td>carnivore indet.</td>
<td>F 24 x 13</td>
<td>dark brown - shiny surface - partially cracked surface</td>
<td>bone - hair - clast - sediment</td>
<td></td>
</tr>
<tr>
<td>7/87/DE</td>
<td>carnivore indet. Pseudolapex culpaeus</td>
<td>F 66 x 17</td>
<td>brown</td>
<td>bone - hair - sediment</td>
<td>Most of the matrix consists of hair.</td>
</tr>
<tr>
<td>7/87/DI</td>
<td>puma/fox - carnivore indet.</td>
<td>F 15 x 17</td>
<td>brown - very compact</td>
<td>bone - hair - plant remains? - clasts - sediment</td>
<td>Most of the matrix consists of hair.</td>
</tr>
<tr>
<td>7/87/DO</td>
<td>carnivore indet.</td>
<td>F 21 x 10</td>
<td>brown - partially cracked surface</td>
<td>bone - hair - plant remains - clasts - sediment - organic matter</td>
<td>Most of the matrix consists of hair.</td>
</tr>
<tr>
<td>7/91/D</td>
<td>prob. puma</td>
<td>F 19 x 15</td>
<td>white - weathered</td>
<td>bone - hair - plant remains - clasts</td>
<td></td>
</tr>
</tbody>
</table>
The area surveyed covered the margins of the Las Pitas, Punilla, and Miriguaca rivers and those of the Antofagasta lake. Collected specimens were identified and deposited in the Herbarium of the Instituto de Botánica Darwinion, and form part of its reference collection. Reference histological sections of the collected present day species were prepared, and were complemented with material from the Darwinian Institute's Herbarium (SI) (Holmgren et al., 1990).

In this paper, herbaceous species are of concern, since as will be shown below, only this kind of plants were identified in the samples studied. For these species, parts of leaves and of culms of specimens of the Poaceae family were collected. They were boiled for some 15 minutes with some drops of detergent of commercial use, and then histological sections were handmade transversally with a shaving blade. The best sections were selected under magnification and they were stained with diluted safranine. Lastly, they were mounted on gelatin-glycerin (D’Ambrogio de Argüeso 1986). These histological sections were observed and photographed with light microscope (NIKON FX-A). These observations allowed the anatomical analysis of the species, which in turn was used to identify the specimens consumed by the carnivores (Table 2).

For the analysis of the scatological plant remains the same procedure was followed: opened scats were content analyzed. Abbreviations used: indet.: indeterminate; w/: with; prob.: probable. Taxonomic determinations based on morphology followed by hair determinations (if available) after a dash.

Table 1 (opposite page). Sample of scats opened for content analysis. Abbreviations used: indet.: indeterminate; w/: with; prob.: probable. Taxonomic determinations based on morphology followed by hair determinations (if available) after a dash.

<table>
<thead>
<tr>
<th>species</th>
<th>reference specimens’ origin and allocation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deyeuxia crispa Rúgolo et Villav. nov. sp.</td>
<td>Argentina, La Rioja, Dpto. Sarmiento, Quebrada del Río Salado, 4200 masl, 1995, J. Hunziker &amp; O. Caso 4166 (SI)</td>
</tr>
<tr>
<td>Deyeuxia eminens J. Presl var. eminens</td>
<td>Argentina, Catamarca, Dpto. Antofagasta: route 53, Vega de Los Colorados, 3750 masl, 18-II-1980, Cabrera et al. 31818 (SI); Antofagasta de la Sierra, 3400 m s. m., 5-II-1946, Cabrera 8944 (BAA); Paicuqui, over Punilla river, 3300 masl, IV-1958, Vervoorst 717 (LIL)</td>
</tr>
<tr>
<td>Festuca scirpifoila Kunth</td>
<td>Argentina, Catamarca, Dpto. Antofagasta de la Sierra, Antofagasta de la Sierra, 3900 masl, XII – 1998, Rodríguez 9 (SI)</td>
</tr>
</tbody>
</table>
followed, the only difference being a shorter boiling time (no longer than 3 minutes), as the material was already softened by the predators’ digestive acids. The best histological sections were selected under a microscope, and the comparative anatomical analysis was performed to allow species identification.

Results

The identification of plant contents of the Antofagasta de la Sierra carnivore faeces are presented in Table 3. Plant remains could only be identified from one scat from ANSm3 (the single analyzed scat from this den), one from ANSm5 (idem), and 3 of the 12 analyzed scats from den ANSm7. All of the identified specimens correspond to the Poaceae family.

For each identified species, the anatomical characters of the leaf and of the culm that are coincident in the taphonomic and reference material are described in Table 4, which also includes the area where the reference specimens were collected. They can be seen in Figure 2. As mentioned, the only observable damage to these specimens was some softening, but anatomical features were undamaged.

Table 3. Scatological plant remains identified.

<table>
<thead>
<tr>
<th>den</th>
<th>scat</th>
<th>plant sample</th>
<th>vegetative/ reproductive structure</th>
<th>taxon</th>
</tr>
</thead>
<tbody>
<tr>
<td>ANSm3</td>
<td>3/53/F</td>
<td>-</td>
<td>culm</td>
<td><em>Deyeuxia eminens</em> var. <em>eminens</em></td>
</tr>
<tr>
<td>ANSm5</td>
<td>5/70/A</td>
<td>-</td>
<td>culm</td>
<td><em>Puccinellia frigida</em></td>
</tr>
<tr>
<td>ANSm7</td>
<td>7/87/CV</td>
<td>I</td>
<td>leaf plade</td>
<td><em>Festuca scirpifolia</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td>II</td>
<td>leaf plade</td>
<td><em>Festuca scirpifolia</em></td>
</tr>
<tr>
<td></td>
<td>7/87/DA</td>
<td>-</td>
<td>leaf plade</td>
<td><em>Deyeuxia crispa</em></td>
</tr>
<tr>
<td></td>
<td>7/87/DO</td>
<td>-</td>
<td>very small seeds</td>
<td>possibly Poaceae</td>
</tr>
</tbody>
</table>

Discussion and conclusions

The low representation of plants generally—which were identified in only 31% of opened faeces—and that of fruit in particular are novel and significant results to the ecology of these predators and certainly also to the taphonomic history of the archaeobotanical record in the region. Frugivory is very common in the diet of some carnivores in other regions (e.g., Willson, 1993), and in the case of South American foxes fruit seeds can be found in about half of their faeces in central Chile (Silva et al., 2005). The pattern observed in Antofagasta de la Sierra might be related to the scarcity of fleshy fruits in this high-altitude desert. Of the fruits known to be consumed elsewhere (Willson, 1993; Castro et al., 1994), Cactaceae, Solanaceae, Chenopodium, and Trichocereus (Cabrera, 1957, 1976) are present in the study area, and some other families with edible fruits may also be present. However, there is no evidence of their consumption by carnivores in the sample studied.

This result might also be related to the relative abundance of micromammals, as it has been observed elsewhere that frugivory
Table 4. Description of the species identified.

<table>
<thead>
<tr>
<th>species</th>
<th>location of reference specimens</th>
<th>description of cross sections</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Deyeuxia crispa</em> Rúgolo et Villav. nov. sp.</td>
<td>Margins of Las Pitas river (middle-lower course), 3600 masl. Plant association: vega.</td>
<td><em>Leaf</em> (Figure 2.A-B). “U”-shaped cross section. Marked ribs and furrows on adaxial face. Truncated ribs, of similar size; marginal ribs with quite parallel internal faces. Adaxial epidermic cells with outer wall tangentially thickened; conspicuous buliform cells distributed in regular groups in the furrows and absent in the abaxial face. Stomata on the lateral faces of the furrows. Generally 5 vascular bundles, the central one being primary and the lateral 4 ones secondary. Noticeable mestomatic sheath, parenchymatic sheath rather undeveloped, no specialized chloroplasts. Mesophyll with diffuse chlorenchyma. Discontinuous sclerenchyma, forming subepidermic packages in the adaxial face of ribs, unrelated to vascular bundles; scarce subepidermic abaxial sclerenchyma; marginal sclerenchyma formed by 1-2 fibre layers.</td>
</tr>
<tr>
<td><em>Deyeuxia eminens</em> J. Presl var. eminens</td>
<td>Margins of Punilla river, 3400 masl; 16 km from Punta de la Peña and 20 km from Quebrada Seca. Plant association: vega.</td>
<td><em>Culm</em> (Figure 2.E-F). Hollow culm of elliptic contour. Unistratified epidermis, with tangential external wall thickened. Conspicuous abaxial sclerenchyma formed by 5-6 fiber layers. Abundant fundamental parenchyma formed by cells of similar size which gradually increases to the centre. Vascular bundles distributed in 2 series, an internal one composed of primary bundles and an external one with smaller alternate bundles; all of them surrounded by a parenchymatic sheath of thickened walls.</td>
</tr>
<tr>
<td><em>Festuca scirpifolia</em> Kunth.</td>
<td>Area around middle-upper course of Las Pitas river, 3900-4000 masl. Plant association: rangeland.</td>
<td><em>Leaf</em> (Figure 2.C-D). “U”-shaped cross section. Quite marked ribs and furrows on adaxial face. Truncated ribs, both small and large; marginal ribs with quite parallel internal faces. Adaxial epidermic cells with outer wall tangentially very thickened; conspicuous buliform cells distributed in regular groups in the furrows and absent in the abaxial face. Stomata on the lateral faces of the furrows. Generally 7-10 primary and secondary vascular bundles, alternating with the former, and some tertiary ones. Noticeable mestomatic sheath, parenchymatic sheath rather undeveloped, no specialized chloroplasts. Mesophyll with diffuse chlorenchyma. Discontinuous sclerenchyma, forming subepidermic packages in the adaxial face of ribs, unrelated to vascular bundles; subepidermic abaxial sclerenchyma formed by fibre packages alternating with epidermic cells; marginal sclerenchyma formed by 2-3 fibre layers.</td>
</tr>
<tr>
<td><em>Puccinellia frigida</em> (Phil.) I. M. Johns.</td>
<td>Margins of Las Pitas river (middle-upper course), 3800-4000 masl. Plant association: vega.</td>
<td><em>Culm</em> (Figure 2.G-H). Hollow culm of elliptic contour. Unistratified epidermis, with cells with thickened walls. Conspicuous abaxial sclerenchyma formed by 2-3 fibre layers. Abundant fundamental parenchyma formed by cells of similar size. Vascular bundles distributed in 2 series, an internal one composed of primary bundles and an external one with smaller alternate bundles, all of them surrounded by a parenchymatic sheath.</td>
</tr>
</tbody>
</table>
Plant remains in carnivore scats

...tends to increase when the abundance of these prey declines (León-Lobos & Kalin-Arroyo, 1994; Castro et al., 1994; Silva et al., 2005). Furthermore, Silva et al. (2005) hypothesize that during nutritional bottlenecks –low availability of mammalian prey– a mixed diet should yield a positive energy/mass balance for foxes. If the pattern observed in Antofagasta de la Sierra is confirmed, it can be thought that foxes here do not have such a supplement available in the form of fleshy fruits as in arid central Chile, and that such bottlenecks might have more severe effects here, which deserves further investigation in future.

Fox-plant relationships are highly species-specific, and hence not generalisable (Castro et al., 1994), and the study presented here, where only Poaceae plant parts were ingested, seems to be one example of this. Grasses are generally accessory plants in carnivore diets, used for purging (P. Perovic, pers. comm.). It is unlikely that foxes intentionally consume Poaceae seeds, as they are very little and of low palatability, but most probably they entered their digestive tracts while ingesting leaves and/or culms. Castro et al. (1994) also observed some consumption –although little– of indeterminate seeds, possible of gramineae, in spring by culpeos in arid central Chile.

Regarding the incidence of digestion on plant matter, there is not much available information with which to compare our results, except for seeds –there is some evidence that they are not broken unless they are too large for ingestion, and that mastication and enzymatic activity can alter germination rates in some cases but do not affect it otherwise (León-Lobos & Kalin-...
Arroyo, 1994; Castro et al., 1994). Our study suggests only some softening attributable to the action of digestive acids. This implies low levels of damage, at least in this kind of plant remains, which might be related to the relative resistance of the different structures of the grasses represented and maybe also partly to the dominance of small carnivores in the regional predator assemblage. It should be noticed that the bones contained in the scats did not bear very intensive digestive damage either (Mondini, 2000, 2003), and that, as expected given their structure, hair has not been affected by these processes (Perovic, 2002). All of this suggests that remains introduced into rockshelters via carnivore scats in this Puna region, even plants, have some chances of being incorporated into the fossil record, although in the latter case it would be very difficult to identify their scatological origin.

These results also prompt an interesting conclusion regarding the methodology for the identification of plant remains that have undergone some softening due to the chemical alteration by acids during the passage through animal digestive tracts. In spite of such alteration, all the steps followed for the standard identification of species could be followed, and only a shorter boiling period had to be applied. Digestive alteration did not affect the anatomy of leaves or culms of these species at all.

The significance of scatological assemblages relative to the archaeological record has several aspects. One of them is that the very presence of carnivore scats or their contents in a given record is informative of its general integrity. In fact, among the authors that have dealt with the analysis of the contents of predator scats (Binford & Bertram 1977; Walters, 1984, Meserve et al., 1987, Stallibrass, 1990; Andrews, 1990; among others), many of them have done as a way of offsetting the underrepresentation of small bones and bone fragments. This information is in turn useful to other inferences, such as palaeoecological ones (Stallibrass, 1990; Schmitt & Lupo, 1995; Borrero & Martín, 1996). Little attention, however, has been paid to scatological plant contents from a taphonomic viewpoint and to their potential incorporation into the archaeological record in this way.

Here we have shown how macrobotanical remains can be incorporated into rockshelters no just by humans but also by other predators; moreover, the identified species are common in archaeological sites of the region (Rodríguez, 1999, 2004, 2004b; Rodríguez & Rúgolo de Agrasar, 1999; Rodríguez et al., 2003). Other botanical remains such as pollen and phytoliths can also be incorporated in this way (e.g., Carrión et al., 2004). An integral analysis of scats, including their different faunal and plant contents and even mineral ones, may thus provide important taphonomic information not just to archaeology but also to other historical disciplines.

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Plant remains in carnivore scats

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