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Research paper

Palynological analysis of *Lama guanicoe* modern feces and its importance for the study of coprolites from Patagonia, Argentina

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ABSTRACT

The aim of the present study was to develop a seasonality palynological model from modern feces of *Lama guanicoe* for the interpretation of pollen found in coprolites. For this purpose, fecal samples of *L. guanicoe* were collected during a year from dung piles located in the ecotone Subantarctic Forest–Patagonian Steppe, Perito Moreno National Park (PMNP) (NW Santa Cruz province, Argentina). For every season, the food items were characterized and the post-depositional pollen contamination of feces was evaluated. The results showed differences among the pollen sets of feces from every season and no post-depositional pollen contamination of the superficial fecal subsamples. Pollen concentration and percentage values evidenced high pollen abundance of: a) Asteraceae subfam. Asteroideae-*Senecio* type, *Mulinum spinosum* and *Rumex* in summer feces; b) Poaceae in autumn feces; c) *Empetrum rubrum* in winter feces; and d) *Nassauvia*, *Plantago* and Poaceae in spring feces. Seasonality variations in the feces were related to the phenology of plants, to variations in the diet and to the supply of palatable resources for *L. guanicoe*. This seasonal feces model will be useful as an analog in studies on Holocene camelid coprolites found in Cerro Casa de Piedra (PMNP) sites. It will allow clarifying the seasonality in site use. On the other hand, it will contribute data to the *L. guanicoe*'s diet, which represent an important information for the species' regional sustainable management.

1. Introduction

Few studies on modern herbivore feces pollen analysis are reported in the world's literature. King (1977) analyzed the pollen content of modern *Odocoileus hemionius* (mule deer) feces finding that entomophilous and anemophilous pollen types were over and under represented, respectively. Further, the pollen content of a single pellet and other pellets of the same deposition event were similar. Also, Moe (1983) studied the relationship between the pollen spectra of domestic sheep feces, the sheep's fodder and the surface sediments collected in the area of study. Variations in the feces pollen composition attributable to the feeding time of the year were also observed. The author also showed that the feces pollen spectrum reflected the quantitative local vegetation composition in a less degree than the sediment pollen spectrum, and that the anemophilous pollen of trees near the area of study had been consumed together with the fodder, for it should have deposited in parts of the plant consumed before they had been washed by rains.

On the other hand, Bjune (2000) evidenced the potentiality of *Rangifer tarandus platyrhynchus* (Svalbard reindeer) feces pollen analysis as a method for studying diets observing that the feces pollen spectra showed seasonal variations related to the consumed species and to the grazed areas. In the same way, Moe and Bjune (2009) compared the pollen content of plant fragments in *Lagopus lagopus* subsp. *lagopus* L. (grouse) feces, and observed a greater number of pollen taxa than of plant fragment taxa, pointing out that both studies complement each other.

In scatological studies, the analysis of pollen concentration is more important than pollen percentages themselves, because the voluntary consumption of some pollen types cannot be correctly evidenced through percentages. Concentration pollen data are absolute values which have the characteristic of documenting the pollen ingestion magnitude (Reinhard et al., 2006). However, pollen percentage data must be regarded as highly unreliable measures of pollen intake (Chaves and Reinhard, 2006; Dean, 2006; Kelso and Solomon, 2006).

Signs left by animals, such as feces, are important for studying threatened species or animals difficult to observe and trap (Chame, 2003). *Lama guanicoe* (guanaco), of the artiodactyl family Camelidae, is one of such threatened species (IUCN, 2011) inhabiting Patagonia, Argentina. This animal is a pseudo-ruminant herbivore, a generalist of intermediate selection (Raedeke, 1980; Puig et al., 1996); it can take pollen grains as part of its food supply or, accidentally, from

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the ones that adhere to the surrounding vegetation. The distribution range of the guanaco comprises environments with high differences in their vegetation structure: from the Patagonian Steppe to the Subantarctic Forest (Franklin, 1983). Males defecate in clearly defined sites called "dung piles," used as territorial marks. The diet of *L. guanicoe* varies throughout the year (Puig et al., 1996) and a positive relationship between diet and food availability in northwestern Santa Cruz (Pelliza-Sbriller et al., 1997), northern Patagonia (Puig et al., 1996, 2001) and Tierra del Fuego, was confirmed (Raedeke, 1980). Different studies have used methods other than pollen analyses of feces in order to know the diet of guanacos in Argentina (Raedeke, 1980; Puig et al., 1996; 2011; Pelliza-Sbriller et al., 1997); however, this is the first time that pollen from modern fecal material of this herbivore is examined.

The guanaco was the main survival resource and raw material for the hunter-gatherers inhabiting Patagonia (Argentina), as from the late Pleistocene (Miotti and Salemme, 1999). Therefore, the information of its behavior in the past is important to know the population dynamics of native groups.

In the Perito Moreno National Park (PMNP), particularly at the archeological excavations of caves 5 and 7, Cerro Casa de Piedra (CCP), numerous coprolites ascribable to camelids, cervids, *Mylodon* sp., canids, birds and humans, distinguishable from sediments by their morphological characteristics have been found. The ruminant herbivorous coprolites, such as those of camelids, are usually cylindrical and smooth surfaced. Some have a protuberance at an end produced by the anal sphincter contraction at defecation time, and a depression at the opposite end (Harrison, 2011). Particularly, camelid coprolites found at CCP and modern guanaco feces showed a similar morphology, evidence of good remain preservation at the CCP sites.

The coprolites are deposited at CCP sites with attributes (low exposition to solar radiation, relatively constant temperature and humidity) that have permitted preservation of organic remains, such as bone remains, charcoal, fleece and plant litters (De Nigris, 2004), and even coprolites. Studies on palaeoenvironments, paleodiets, resource use seasonality and parasitism status of ancient populations can be performed by means of coprolite microfossil content analyses (Reinhard and Bryant, 1992; Horrocks et al., 2003; Carrión et al., 2004; Velázquez et al., 2010). In particular, paleoparasitological, palynological and microhistological studies of coprolites from the PMNP caves have been done (Fugassa, 2007; Fugassa et al., 2008; Taglioretti, 2008; Sardella et al., 2010; Velázquez et al., 2010; Yagueddú and Arriaga, 2010).

Velázquez et al. (2010) studied coprolites ascribable to camelids found in Cave 7, Cerro Casa de Piedra site, associated to radiocarbon dated layers (9640 ± 190–5610 ± 110 years BP). The authors put forward the pollen analysis results of only the coprolites surface and its comparison with sediment pollen spectra from a profile of the archeological excavation (Mancini, 2007). Similarities were found between the coprolites surface and the sediments, thus reflecting the coprolites pollen analysis potentiality to paleoenvironmental studies. However, some differences between both records, attributable either to the consumed item selection or to the coprolites seasonality, were found.

Chaves (2000) and Alcover et al. (1999) point out that post depositional feces contamination could exist through anemophilous pollen, for the mucus surrounding feces acts as a pollen trap.

In paleoecological studies the modern pollen spectrum is an important reference to interpret the past (Faegri and Iversen, 1989). For this purpose, the information recovered from the examination of modern feces is relevant for comparing with that derived from the analysis of coprolites (Bjune et al., 2005). The aim of the present study was to develop a seasonality palynological model from modern feces of *L. guanicoe* for the interpretation of pollen found in coprolites. The food items were characterized and the post-depositional pollen contamination of the feces was evaluated.

2. Materials and methods

2.1. Study area and field sampling

The studied area is located in the Perito Moreno National Park (PMNP) (northwest of the province of Santa Cruz, Argentina) (47°56′28″S–72°4′16W) (Fig. 1). Perito Moreno National Park is a cool-temperate and semiarid area. It is located at approximately 900 masl, a height where valleys are inhabited. A series of mountain chains follow from east to west and from north to south; the highest peak is at Cerro Heros (2770 masl). The mean annual temperature is below 4 °C (Paruelo et al., 1998) and the precipitation ranges from 600 to 400 mm, decreasing from west to east. Summers are short and western cold winds predominate.

The vegetation is organized into different units: 1) forest, dominated by *Nothofagus pumilio*; 2) woods of *Nothofagus antarctica* and *Nothofagus betuloides*; shrub and herbaceous vegetation associated to the *Nothofagus* forest, like *Escallonia*, *Berberis*, *Fuchsia magellanica* and species belonging to the genera *Osmorrhiza*, *Acaena* and *Perezia*; 3) shrubs *of Chiliotrichium* and *Mulinum spinosum*; 4) *Nardophyllum obtusifolium* steppe with *Festuca pallescens*, accompanied by *Stipa ibari*, *Poa ligularis*, *Carex*, *Cerastium arvense*, *Adesmia lotoides*, *Nassauvia darwinii*, *Acaena pinnatifida* and *M. spinosum*; 5) *F. pallescens* steppe with *P. ligularis*, *Rytidosperma picta*, *Stipa*, *Carex*, *Colobanthus lycopodioides*, *Armeria maritima*, *A. pinnatifida*, *Polygala darwiniana*, *N. darwinii*, *Perezia recurvata*, *Mulinum microphyllum* and shrubs of *N. obtusifolium*, *Senecio filaginoides* and *Berberis heterophylla*; 6) high semi-desert, with dense patches of *Empetrum rubrum*, mostly found in sheltered sites and 7) bogs with *Caltha sagittata*, *Plantago barbata*, *Acaena magellanica* and sedges (Movia et al., 1987; Mermoz, 1998; Ferreyra et al., 2008) (Fig. 1).

During the summer, autumn, and at the ends of winter and spring 2010, four fecal samples of guanaco were collected from a dung pile (Table 1). The dung pile was located in the ecotone Subantarctic Forest–Patagonian Steppe (47°56′28″S–72°4′16″W), close to Cerro Casa de Piedra; it was dominated by Poaceae accompanied by *N. obtusifolium* and *Azorella monanthos* that grow all around the site. Three pools of fresh feces each composed by numerous pellets, assuming that every one belonged to the deposition of a single individual (Bonino and Pelliza-Sbriller, 1991; Puig et al., 1997), were collected at every visit. The feces were stored in plastic bags in order to absorb humidity and to avoid fungi proliferation. In the laboratory they were dried at 35 °C and stored in sterile flasks in the dark.

2.2. Pollen extraction

From a pool of feces, three individual samples for every season were used for pollen analysis (Fig. 2). Samples were weighed. They were measured and observed under a binocular microscope (Chame, 2003). In order to evaluate post-depositional contamination produced by anemophilous pollen, feces were divided into surface and inner subsamples; they were next weighed.

For a reassurance that no part of the subsample is lost during the extraction process and in order to calculate pollen concentration, one tablet of a *Lycopodium clavatum* spore (c. 12.542 spores tablet) (Stockmarr, 1971) was added to each subsample. Subsamples were then treated for 72 h with 0.5% tri-sodium phosphate dodecahydrate at 2°–4 °C. They were subsequently washed with tri-sodium phosphate through a 260 μm sieve. Remains recuperated from the sieves were conservated for macro-botanical examination. Residues <260 μm were selected for pollen and parasitological examination. Pollen extraction was performed by acetolysis (9 parts of acetic anhydride: 1 part of sulfuric acid) to break cellulose into soluble fragments that were successively washed with water (Faegri and Iversen, 1989). Identification and counting of pollen types were carried out following

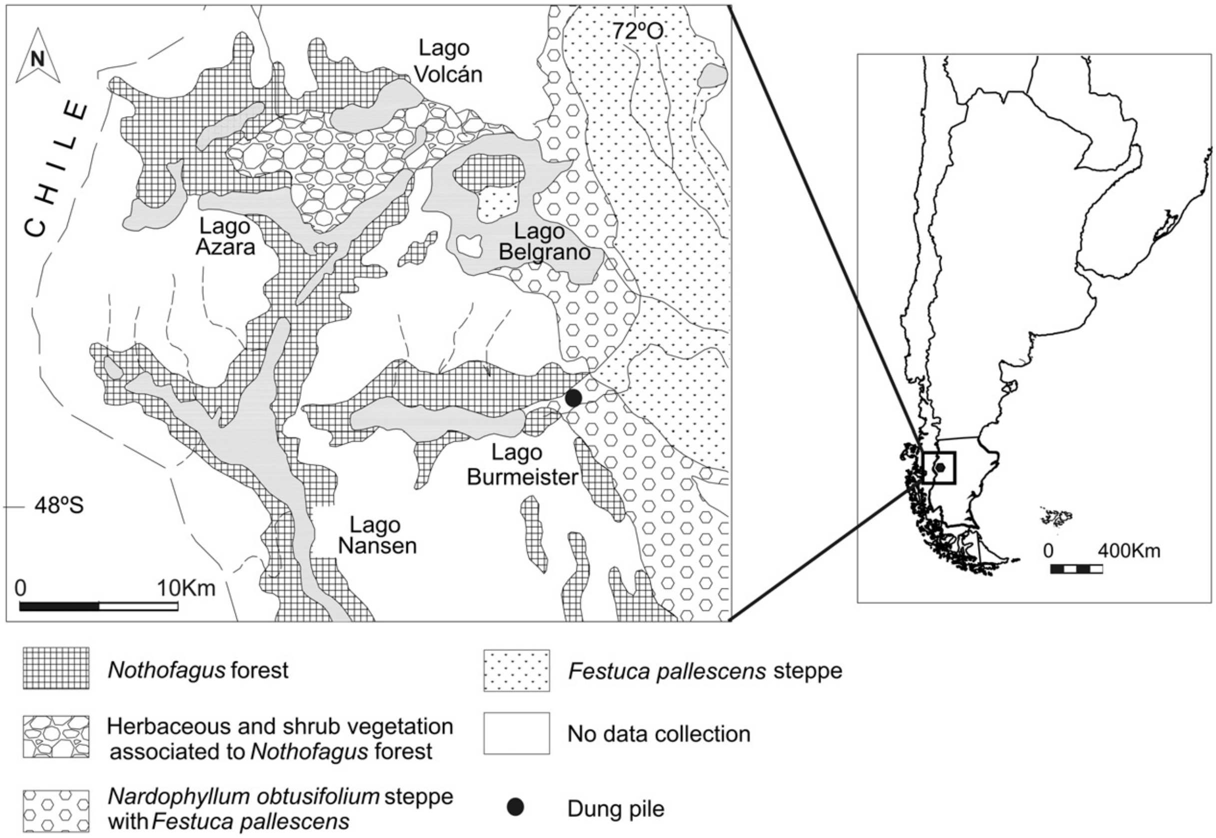

Fig. 1. Map of Perito Moreno National Park (PMNP), Santa Cruz province, showing the main areas of the vegetation units (modified from Movia et al., 1987) and the location of the dung pile.

Heusser (1971), Markgraf and D'Antoni (1978) and Moore et al. (1991). Moreover, a comparison of the new material with that of the pollen collection deposited at the Palynology Laboratory (Universidad Nacional de Mar del Plata, Argentina) was made. Pollen types were counted under 400× and 1000× magnification using an optical microscope.

For each subsample a total of at least 200 pollen grains were counted. Because of low pollen concentrations, it was not possible to reach that minimum count in two cases only. Non-pollen palynomorphs, such as spores of fungi were also registered.

2.3. Statistical analyses

Plotting of pollen percentage and concentration diagrams was carried out using a TILIA 1.7.14 program (Grimm, 2011). Pollen concentration (grains per gram dry weight) was calculated according to:

$$X = a\,b/c\,p$$

where X is the pollen concentration, a is the number of spores of *L. clavatum* added, b is the number of grains of pollen counted, c is the number of spores of *L. clavatum* counted, and p is the weight of the sample (D'Antoni, 1979). Percentages of each pollen type for each subsample were based on a sum of pollen grains that included all pollen types even *Polypodium* spores. Ordination by Detrended Correspondence Analysis (DCA), R program (R Development Core

Table 1
Month and collecting station (Southern Hemisphere) of guanaco feces in Valle del Río Roble (PMNP).

Sample	Collecting month	Collecting station
1–3	March	Summer
4–6	May	Autumn
7–9	September	Winter
10–12	December	Spring

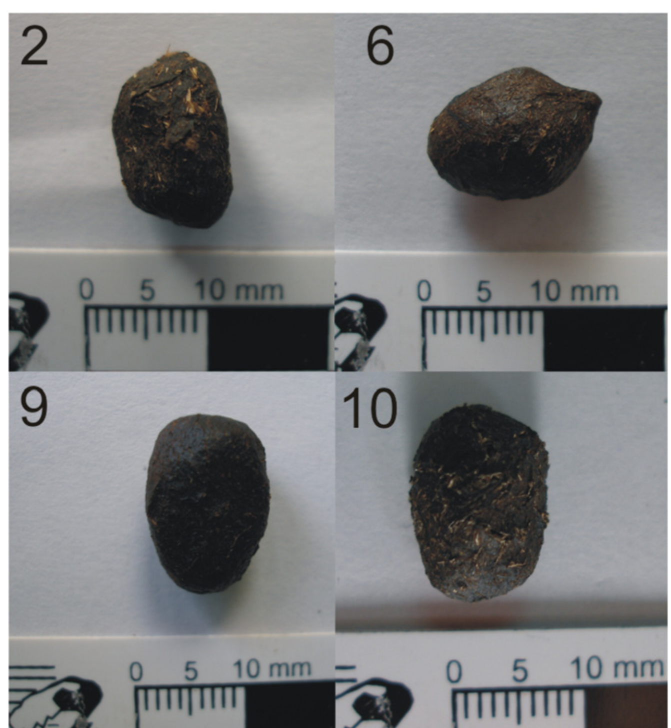

Fig. 2. Guanaco fecal samples, collected from a dung pile located in PMNP. N° 2: summer; 6: autumn; 9: winter and 10: spring.

Table 2
Morphometric description of guanaco feces.

Sample number	Length (mm)	Diameter (mm)	Weight (g)
1	11	12	0.35 (ex: 0.15; in: 0.20)
2	14	10	0.25 (ex: 0.05; in: 0.2)
3	13	10	0.32 (ex: 0.1; in: 0.22)
4	13	10	0.24 (ex: 0.08; in: 0.16)
5	11	9	0.19 (ex: 0.07; in: 0.12)
6	13	8	0.25 (ex: 0.09; in: 0.16)
7	15	10	0.35 (ex: 0.08; in: 0.27)
8	16	10	0.38 (ex: 0.14; in: 0.24)
9	14	10	0.35 (ex: 0.13; in:0.22)
10	14	9	0.27 (ex: 0.12; in: 0.15)
11	13	12	0.31 (ex: 0.13; in: 0.18)
12	13	11	0.28 (ex: 0.11; in: 0.17)

Team, 2011) to detect similarities among samples and subsamples was performed. In order to reduce the statistical noise introduced by minor components of the pollen sum (Howe and Webb, 1983), only pollen types with frequencies ≥2% were considered.

Pollen concentrations of surface and inner subsamples for each pollen type were compared using a Mann–Whitney *U* Test. Percentage and concentration values of every dominant pollen type (Asteraceae subfam. Asteroideae, *Nassauvia*, *Cerastium*, *E. rubrum* y Poaceae) were compared to evaluate the information provided by data expressed as percentage and concentration (i.e. pollen concentration vs. pollen percentage of Asteraceae subfam. Asteroideae, *Nassauvia*, *Cerastium*, *E. rubrum* y Poaceae).

3. Results

3.1. Morphometric descriptions of the guanaco's feces

Feces were small sized. Length, diameter and weight are in Table 2. The weight of the samples ranged from 0.19 g to 0.38 g. All feces were brown-colored and had smooth surfaces with fissures and vegetable inclusions. In general, they were cylindrical to irregular with one acuminate end and the other concave (Fig. 2).

3.2. Pollen analysis

Because of the well-preserved state of the observed pollen grains, reliable pollen identifications were possible and frequencies of undetermined pollen grains fell below 10%. Pollen sums ranged between 116 and 709 pollen grains per subsample. Thirty pollen types were determined as follows: *Nothofagus*, *Podocarpus*, Asteraceae subfam. Asteroideae-*Senecio* type, *Chiliotrichum*, Asteraceae subfam. Mutisioideae, *Nassauvia*, *Perezia*, *Gaultheria*, *E. rubrum*, Apiaceae, *M. spinosum*, *Azorella*, Fabaceae, Caryophyllaceae, *C. arvense*, *Silene*, Poaceae, *Plantago*, Asteraceae subfam. Cichoroideae, Rosaceae, *Acaena*, *A. maritima*, *Loasa bergii*, *Rumex*, *Polygala*, *Gunnera*, Brassicaceae, Iridaceae, Juncaceae, Cyperaceae; and a *Polypodium* spore type (Fig. 3).

The most important pollen types present in modern all-season feces were Asteraceae subfam. Asteroideae-*Senecio* type, *Cerastium* and Poaceae. Collected during summer, subsamples 1e–3i were dominated by Asteraceae subfam. Asteroideae-*Senecio* type (7.6–38.7%), *M. spinosum* (5.5–64%) and Poaceae (3.7–33%). Subsamples 4e–6i (autumn) were represented by Poaceae (35.6–48.9%). *E. rubrum* percentages (44.1–55.3%) were important in winter subsamples 7e–9i. In subsamples 10e–12i (spring), *Nassauvia* (15.3–26%), Poaceae (3.6–56.2%) and *Plantago* (1.3–28.2%) were significant, although subsamples 11e and 11i were represented by *E. rubrum* (69.8–71%).

Ordination of guanaco feces and pollen types by DCA explained 73% of the variance with the first axis and 19% with the second axis (Fig. 4). Because of their lower frequencies, the following taxa were not included in the statistical analyses: *Podocarpus*, Asteraceae subfam. Mutisioideae, *Silene*, Asteraceae subfam. Cichoroideae, Rosaceae, *Polygala*, *Gunnera*, Brassicaceae, Iridaceae, Juncaceae, Cyperaceae and *Polypodium*.

Pollen percentages from both surface and inner subsamples were similar. Pollen sets from modern feces of like seasons showed similarities and those from different seasons were statistically different. The analysis showed an arrangement of modern feces from left to right along the first axis: winter, autumn and spring-summer (Fig. 4). The second axis separated subsamples belonging to spring from subsamples belonging to summer, winter and autumn. Accordingly, the ordination of pollen types showed that the first axis separated the most important variables of each season. According to the pollen diagram,

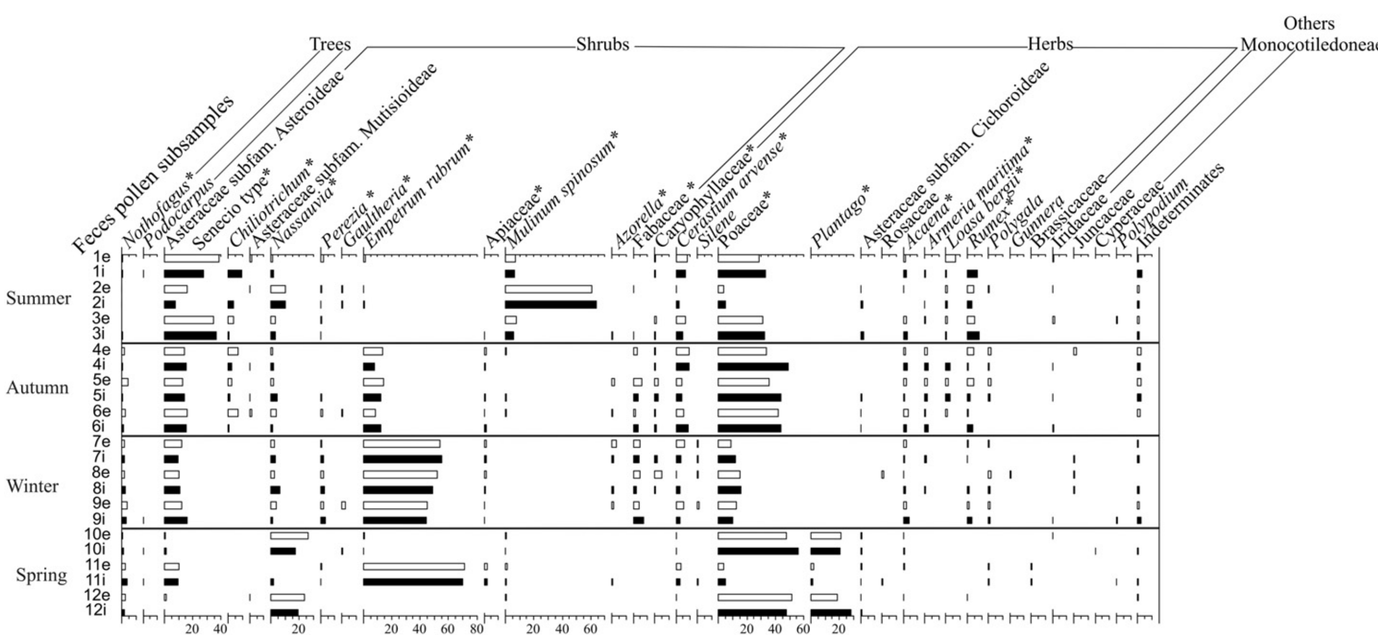

Fig. 3. Summary percentage pollen and spores diagram of guanaco feces for every season: ▭ surface subsamples, ■ inner subsamples; 1e–3i (summer), 4e–6i (autumn), 7e–9i (winter) and 10e–12i (spring). * Pollen types selected for DCA.

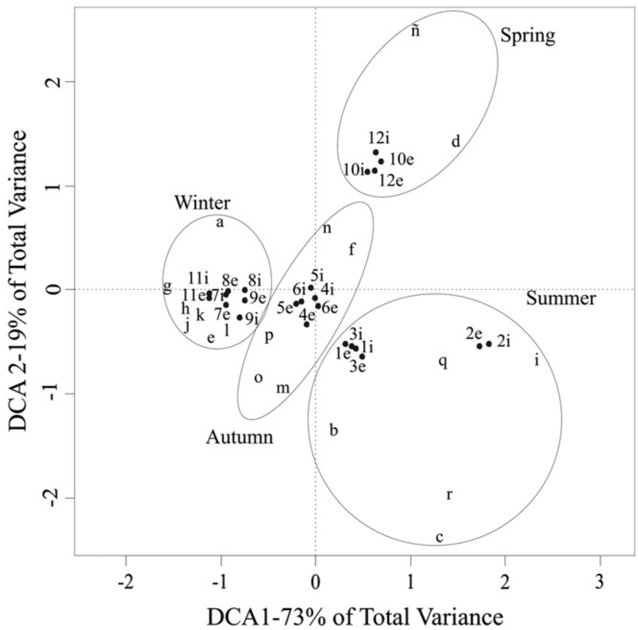

Fig. 4. DCA of pollen percentages of pollen types ≥2% from modern feces of guanaco. Ordination of feces of guanaco (1–12, e: surface subsamples i: inner subsamples) and pollen types: a: *Nothofagus*, b: Asteraceae subfam. Asteroideae-*Senecio* type, c: *Chiliotrichum*, d: *Nassauvia*, e: *Perezia*, f: *Gaultheria*, g: *Empetrum rubrum*, h: Apiaceae, i: *Mulinum spinosum*, j: *Azorella*, k: Fabaceae, l: Caryophyllaceae, m: *Cerastium*, n: Poaceae, ñ: *Plantago*, o: *Acaena*, p: *Armeria maritima*, q: *Loasa bergii* and r: *Rumex*.

Plantago and *Nassauvia* were important in spring samples; Poaceae was outstanding in autumn samples, while *E. rubrum* in winter samples; and Asteraceae subfam. Asteroideae-*Senecio* type and *M. spinosum* were prevalent in summer samples.

The pollen concentration diagram showed variations between the different season's feces of dominant pollen types Asteraceae subfam Asteroideae, *Nassauvia*, *E. rubrum*, *Cerastium* and Poaceae (Fig. 5). Except for the summer feces, no differences between total pollen concentrations of the surface and inner part of each feces were registered. In general, similarities between autumn and winter feces total pollen concentrations (<10,000 grains/gram of subsample) and between spring and summer feces concentration (>10,000 grains/gram of subsample) were observed. The Mann–Whitney *U* test also showed that for every dominant pollen type no significant differences exist between pollen concentrations of both surface and inner subsamples (p-value$>\alpha=0.05$). Accordingly, pollen concentration data (summing the inner and surface part values) were used.

Fig. 6 shows the concentration and percentage bar diagrams for the dominant pollen types present at all seasons. Similarities between pollen concentration and percentage for Asteraceae subfam. Asteroideae, *Nassauvia* and *E. rubrum* were observed. At the same time, differences for *Cerastium* and Poaceae were observed: autumn and winter feces concentrations were lower than those of spring and summer. By contrast, percentages of these pollen types evidenced a greater proportion of autumn–winter feces than of spring–summer feces (Fig. 6).

The results obtained for pollen concentration and percentage data evidenced a high representation in the pollen spectrum of: a) Asteraceae subfam. Asteroideae-*Senecio* type, *M. spinosum* and *Rumex* in summer feces; b) Poaceae in autumn feces; c) *E. rubrum* in winter feces and, d) *Nassauvia*, *Plantago* and Poaceae in spring feces.

3.3. Non-pollen palynomorphs

With respect to non-pollen palynomorphs, fungi spores identified as *Sporormiella*-type, *Sordaria*-type and Ascospores-type were also found in the samples (Table 3). Data from non-pollen palynomorphs give information for the feces identification, i.e. whether they belong to a carnivore or an herbivore animal (Ahmed and Cain, 1972).

4. Discussion

4.1. Modern feces pollen model

The present study allows knowing the seasonal pollen spectrum of the feces of guanaco. The different seasons were characterized by the following aspects:

4.1.1. Summer

The high pollen concentrations of *M. spinosum*, together with an entomophilous dispersal type suggest that this pollen type is possibly a food item. This taxon is part of the diet of the guanaco in the Santa Cruz province (Pelliza-Sbriller et al., 1997). It is a spiny shrub that forms cushions, a principal component of the shrub and grass steppes it grows both in low mountain slopes and in sandy soils (Correa, 1988; Ferreyra et al., 2006). The flowering and fruiting of *M. spinosum* occur from November to March (Damascos et al., 2008). Arroyo Kalin et al. (1981) performed a study about pollination ecology of communities from the Central Chile Andes, and they registered an *M. spinosum* flowering peak in January. Another important pollen type was Asteraceae subfam. Asteroideae-*Senecio* type; guanacos feed on this shrub which flowers in summer (Raedeke, 1980; Pelliza-Sbriller et al., 1997; Ferreyra et al., 2006). Its flowering peak has been recorded in February (Arroyo Kalin et al., 1981). *Rumex* appeared in the area only after the European contact. It flowers in summer.

4.1.2. Autumn

Raedeke (1980) and Bonino and Pelliza-Sbriller (1991) found that grasses are major components of the guanaco diet of Tierra del Fuego all year long. In this study, even though Poaceae was present in low pollen concentration in the autumn feces, the contribution of this pollen type to the assemblage is important. The low pollen concentration and the absence of certain dominant pollen types in the autumn feces could be due to the facts that the majority of plants were not within their pollinating period and that the pollen found in feces derived from pollen previously deposited in summer (Moe, 1983).

4.1.3. Winter

The high pollen concentration of *E. rubrum* could indicate intake of this taxon. The sample was collected in late winter, a time when *E. rubrum* begins flowering. *E. rubrum* is a dwarf shrub present in the humid-steppe; in some cases it originates "facies" attributed to anthropic action (Roig, 1998). Cushion heaths of *E. rubrum* form dense woody carpets that may cover many meters. It is a heliophilous plant that colonizes bare soils where no other species thrive, and invades over-grazed lands eliminating the original Poaceae (grass) cover. Their dark-red fruits are globose, fleshy and tasty (Correa, 1999; Ferreyra et al., 2006). *E. rubrum* is a very important component of the diet of guanacos of Tierra del Fuego (Raedeke, 1980).

4.1.4. Spring

Nassauvia is a food item for guanacos (Pelliza-Sbriller et al., 1997). The flowering peak was registered in February (Arroyo Kalin et al., 1981). The pollinium of *Plantago* was found in spring feces. *Plantago* comprises perennial herbs which grow in dry, sandy and saline soils from the Patagonian steppe (Correa, 1999). It flowers in summer (Ferreyra et al., 2006). The Poaceae pollen concentration was also significant in spring.

Mancini et al. (2002) carried out a pollen study based on surface sediment samples from the PMNP. The guanaco feces pollen spectra analyzed in this study showed similarities with surface sediment pollen spectra, exception made of the tree pollen that was less represented in feces than in sediments. King (1977) also found out that tree

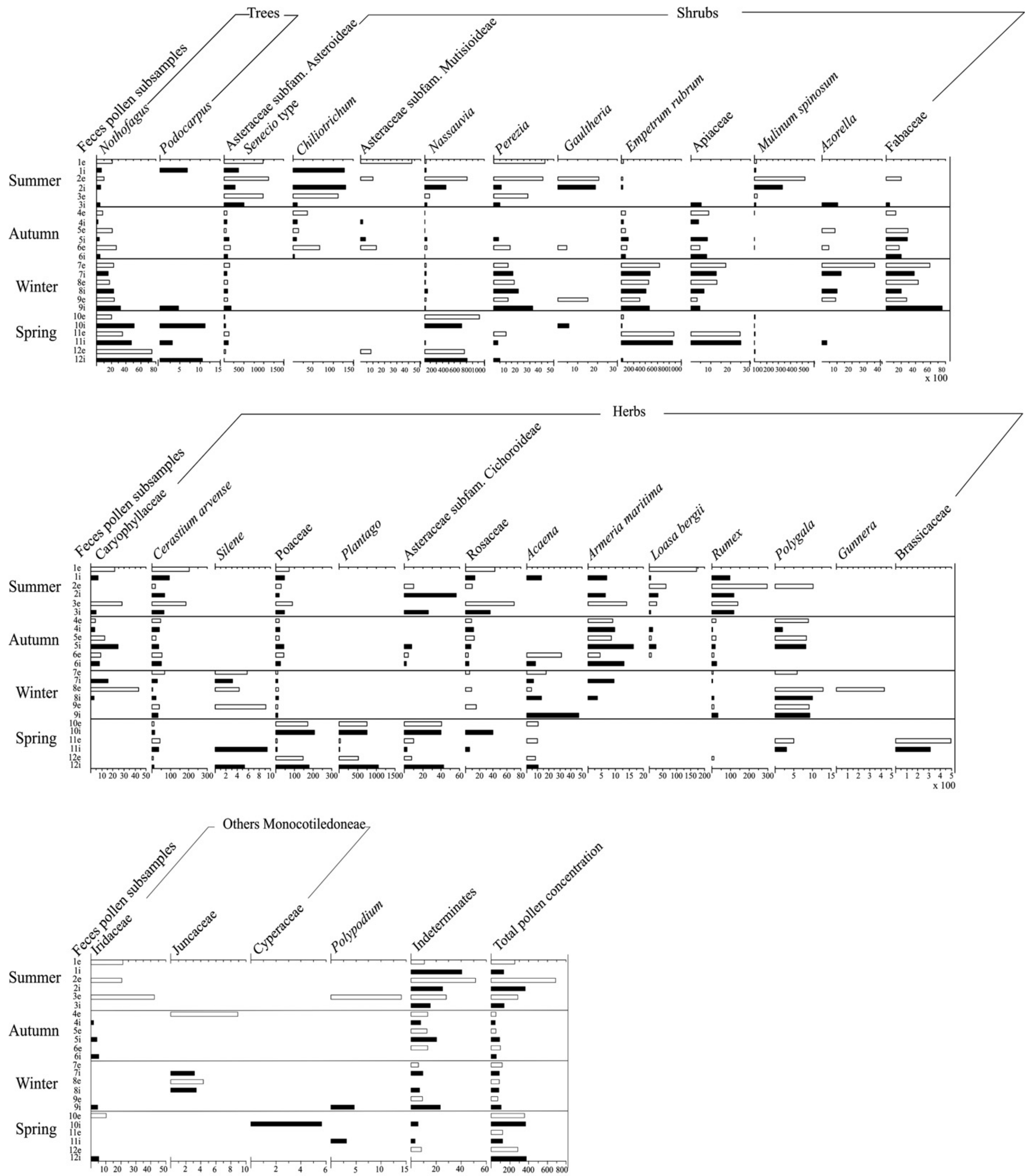

Fig. 5. Summary concentration pollen and spores diagram of guanaco feces for every season: ▭ surface subsamples, ■ inner subsamples; 1e–3i (summer), 4e–6i (autumn), 7e–9i (winter) and 10e–12i (spring).

pollen representation was less in feces than in surface sediments. Asteraceae subfam. Asteroideae, Poaceae and Caryophyllaceae were of great importance in the PMNP modern sediments (Mancini et al., 2002) as well as in the analysis of feces. Even though the abundance of *Perezia*, *Rumex*, and *Loasa bergii* was negligible in sediment samples, their presence in feces and their absence in sediments allow us to suggest the importance of analyzing pollen of feces together with pollen of sediments, in order to provide information about the composition of the vegetation of the guanaco's environment.

The greater abundance of certain pollen types from feces with respect to those in sediments could be due to the fact that pollen in feces is biased with an over-representation of food items; such are

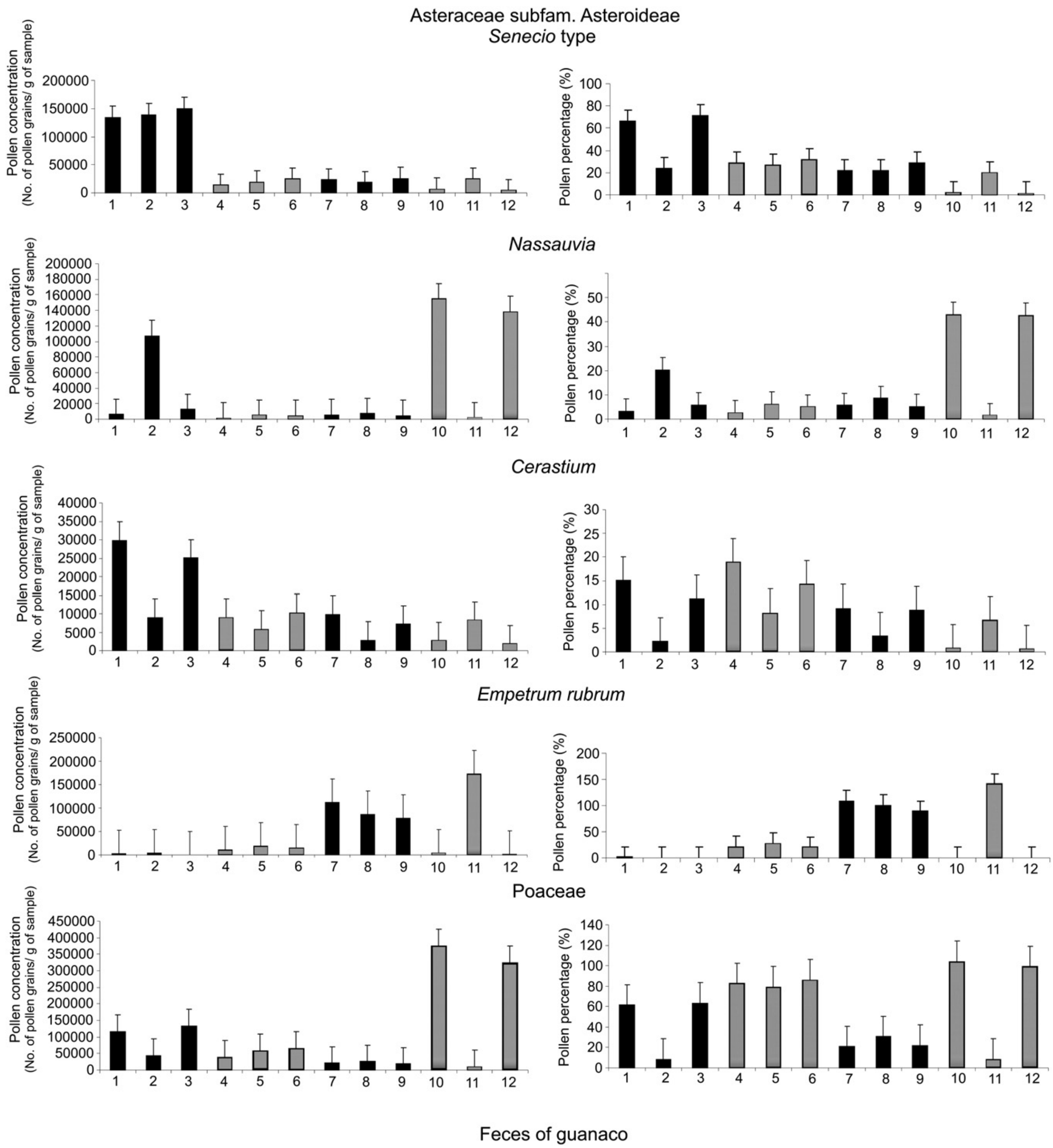

Fig. 6. Pollen percentage and concentration data of: Asteroideae-*Senecio* type, *Nassauvia*, *Cerastium*, *Empetrum rubrum* and Poaceae. Sample numbers: 1–3 summer; 4–6 autumn; 7–9 winter; 10–12 spring.

the cases of *E. rubrum*, *Nassauvia*, *M. spinosum* and *Plantago*. In this sense, *Nassauvia* and *M. spinosum* are entomophilous taxa, under-represented in sediments, although not in feces.

Pollen types recovered from the feces of guanaco agreed with those types characteristic of the vegetation of both the shrub steppe and the grass steppe. In spite of their low concentration, the anemophilous arboreal pollen types *Nothofagus* and *Podocarpus* found in feces belong to the Subantarctic Forest (Cabrera, 1976; Roig, 1998). *Podocarpus* is an extra regional pollen type developing in the most humid forests west of the Andes (Donoso Zegers, 2006).

The presence of coprophilous fungi in feces (like *Sporormiella*-type and *Sordaria*-type) offers information about the kind of consumer that produced the feces. Ahmed and Cain (1972) cited *Sporormiella* as an ascomycete fungus found only on the dung of herbivores. *Sporormiella* spores were found in feces of herbivores like elephants, giraffes, blue wildebeests, zebras and sheep (Ebersohn and Eicker, 1992; de Porras, 2010, among others).

4.2. Pollen contamination

Post-depositional pollen contamination of the superficial fecal subsamples was not confirmed in the observed samples. In other studies on pollen analysis of feces, the surface subsamples were discarded and the contaminant post-depositional pollen was not

Table 3
Number of fungi spores found in the samples.

Samples	*Sporormiella* type	*Sordaria* type	Ascospores type
1	2	–	1
2	–	–	–
3	3	–	1
4	–	–	1
5	2	–	3
6	4	1	1
7	4	–	12
8	12	3	7
9	28	2	3
10	10	2	3
11	57	3	2
12	12	–	–

considered (Moe, 1983; Bjune, 2000). Although the mucus covering the feces can act as a pollen trap (Alcover et al., 1999; Chaves, 2000), in our case the time spent between fecal depositions and sampling would probably not suffice to increase the pollen concentration in the surface of feces from modern samples.

Post depositional contamination was evidenced in camelid coprolites by Velázquez and Burry (2010) for significant differences in the concentration of *Nothofagus* pollen type between the coprolites surface and inner parts were found. Therefore, in order to corroborate diet seasonality it is suggested to analyze the inner feces part only, so the pollen types that could adhere to it after deposition are discarded.

4.3. Seasonality

Seasonal variations in the feces pollen concentration could be due to plant phenology (flowering period), to variations in diet and to supplies of palatable resources for guanacos. These are relatively firm hypotheses supported by the positive correlation between diet and food availability (Puig et al., 1996) and the particular flowering period of plants growing around the site.

Spaulding (1974) performed a pollen study of fresh feces from a single sheep; feces were collected twice-monthly, throughout 1 year, and he found annual variations in the pollen content of both entomophilous and anemophilous plants. Moreover, Bjune (2000) examined pollen and spores from fresh samples of feces of the Svalbard reindeer collected at all seasons, and showed variations among seasons, with distinct pollen types dominating each season.

The differences observed in this study could be due to factors such as plant phenology of individual species and to pollen production. Pollen production, dispersion and deposition varied throughout the year. Higher pollen concentrations for summer and spring feces could be due to the fact that most plants flower then. On the other hand, lower pollen concentration for autumn and winter feces could correspond to a low pollen production in these seasons (Bryant, 1974). Particularly, pollen concentration of *Cerastium* and Poaceae did not strictly correspond to pollen percentage data (Fig. 6). Low or high pollen concentrations were not always reflected when data are expressed in percentages (Fig. 6). As Reinhard et al. (2006) suggested the pollen concentration gives information about consumption, while the percentage is an unreal measurement of pollen intake (Chaves and Reinhard, 2006).

Alcover et al. (1999) suggested that the abundance of a particular pollen type, with both low production and pollen dispersal, in a coprolite of an herbivorous Artiodactyla, indicates an intentional pollen intake of such pollen type and, that it probably is a component of great importance in its diet. In order to make inferences about the intentional consumption of a particular taxon the pollen concentration as well as the ways of dispersion and pollen production must be known.

With regard to the type of pollen dispersal, in this study the dominant pollen types with entomophilous pollination were Asteraceae subfam. Asteroideae-*Senecio* type (Kasprzyk, 2005), *Nassauvia*, *M. spinosum* and *Cerastium* (Arroyo Kalin et al., 1982). Accordingly, because of the high pollen concentrations of *Nassauvia* and *M. spinosum*, the kind of dispersion and the fact that these taxa are the ones preferred by guanacos, probably the representatives of these taxa were consumed the most. Arroyo Kalin et al. (1982) pointed out that there are two subspecies of *Senecio* with anemophilous pollination. Thus, pollen type Asteraceae subfam. Asteroideae-*Senecio* type could have both kinds of pollen dispersal. Dominant pollen types with anemophilous pollination were *E. rubrum* (Kron and Chase, 1993), Poaceae and *Plantago*.

The micro-histological studies of feces may help to elucidate whether the high pollen concentrations of these pollen types are due to the intake of those taxa or to the contamination of plants consumed. To evaluate this last aspect, it is important to perform pollen extractions from parts of plants – stems, leaves and fruits – growing around the site.

4.4. Ecological importance

The guanaco is a pseudo-ruminant species that consumes diverse taxa depending on availability. It spends most of the time feeding in the shrub or grass steppes. Traditional studies on guanaco diets are carried out on the basis of feces plant fragments analysis (Raedeke, 1980; Puig et al., 1996; Pelliza-Sbriller et al., 1997). At the same time, pollen analysis can be used as a complement to these types of studies since they give information on the use of space seasonality of guanaco populations. The dominance of pollen types belonging to the shrub and grass steppes within the feces reflects the guanaco's home range. Implications of this research for modern ecologists is that the knowledge of the guanaco diet, being the guanaco a threatened species, represents a fundamental information for the species' regional sustainable management. Even though studies on plant fragments and pollen of feces reflect the dietary items, it should be taken into account that the information recovered by analysis of these inclusions corresponds to a very short period (less than a day) and it could be biased by individual preferences, feces seasonality – as shown by the results of this work – and illness, among other variables (Reinhard and Bryant, 1992).

4.5. Archeological implications

Pollen types from feces, with an important occurrence in every season, such as *M. spinosum* and Asteroideae-*Senecio* type in summer, *E. rubrum* in late winter and early spring, *Plantago* and *Nassauvia* in spring are representative of taxa with biological value as tags for seasonality. This information, together with variations in pollen concentration throughout the year, will be useful to compare with the results obtained from pollen analysis of coprolites recovered in caves from the PMNP.

The finding of camelid coprolites in Holocenic caves of CCP generated questions about the seasonal site use of camelids and man. Some authors have suggested winter camelid occupations of Patagonian caves as shelters to the inclemency of the weather (Borrero, 1990; Aschero et al., 2005; Fernández, 2010). Pollen analysis of camelid coprolites and its comparison with the seasonal modern feces model here obtained will allow clarifying the site use seasonality of guanacos during the Holocene. The archeological records of Patagonia show that human groups spent just a limited time of the annual cycle in caves, and that the occupation was alternating (Aschero et al., 2005). Related to this, results from pollen and plant fragment analyses of human coprolites from CCP7 have been obtained, that showed a probable spring–summer occupation (Martínez Tosto et al., 2012). The knowledge of seasonality in the shelter use by camelids that occupied the same environment hunter-gatherers did will provide a contribution to the dynamics of these native groups, since the guanaco was their main survival resource.

The characterization of the camelid modern feces pollen spectrum from different seasons opens the perspective of going deep into the past. Likewise, it permits the study of the information given by coprolites, inferred from the comparison of modern and fossil pollen spectra.

5. Conclusions

The guanaco modern feces analysis of PMNP showed variations in pollen content at different seasons. This information allowed constructing a modern feces model for different seasons in the area of study. The variations found could be attributed either to the plant's phenology, to the guanaco's diet or to the food availability. The dominant pollen types for every season, *M. spinosum* and Asteroideae-*Senecio* type in the summer feces, *E. rubrum* in the winter feces and *Plantago* and *Nassauvia* in the spring feces are seasonality indicators. In order to determine the probably consumed taxa, the pollen concentration was more representative than percentages. The post depositional pollen contamination was not confirmed, probably because of the short time passed between the feces deposition and the moment of collection. It is worth mentioning the importance of using a modern feces pollen model representing all the year seasons, just like the one presented here, in order to do studies on the use of space from the analysis of coprolites.

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