Available online at www.sciencedirect.com

ScienceDirect

Quaternary International 180 (2008) 22–29

Presence of *Hippidion* at two sites of western Argentina Diet composition and contribution to the study of the extinction of Pleistocene megafauna

Alejandro García[a,*], Eduardo Martínez Carretero[b], María A. Dacar[c]

[a]*CONICET, UNSJ (FFHA), UNCuyo (FFyL), 5400 San Juan, Argentina*
[b]*CONICET, Geobotany—CRICyT, UNSJ (FCEyN), Argentina*
[c]*CONICET, GIB Researching Group on Biodiversity, IADIZA, Argentina*

Abstract

The composition of *Hippidion* diet, and possible changes that could relate to its extinction, were evaluated in the Argentinean-Chilean Central Andes, a Neotropical environment characterized by arid to semiarid conditions (Andean hot and cold deserts). Microhistological analyses were made on feces of *Hippidion* found at Los Morrillos (31°43′S–68°42′W, 3000 m a.s.l.) and Gruta del Indio (34°35′S, 68°22′W, 660 m a.s.l.). At Gruta del Indio the diet of *Hippidion* was based mainly on woody species. At Los Morrillos, it was based on herbaceous species.

This flexibility in diet composition could be a relative adaptive advantage allowing a longer permanence of this species in comparison to others recorded in the region (such as *Megatherium* and *Mylodon*). Nevertheless, this advantage was not enough to guarantee its survival during the Holocene. Extinction could have been affected by diverse agents, such as growing aridification of the area, increasing competition with other species (mainly *Lama guanicoe*), and human presence, along with a relatively low population density (as expected from the limited presence of *Hippidion* at the archaeological and palaeontological sites of South America. At Gruta del Indio significant changes in the diet of *Hippidion* corresponding to different intervals of the period 31,000–9000 ^{14}C BP are not evident. Given this evidence for similar diets for *Hippidion* throughout the late Quaternary, other factors need to be considered to explain the extinction of this horse.

1. Introduction

The relation between the biogeographic history of the Neotropics and the general trends in the interactions between human populations and the neotropical fauna was one of the main concerns of the Symposium "Neotropical Zooarchaeology and Taphonomy" (ICAZ Conference, México, 2006). From this viewpoint, the disappearance of the Pleistocene mammal species was one of the most significant processes recorded at a continental range, although its understanding requires much further information regarding particular areas and cases.

The Argentinean-Chilean Central Andes, characterized by arid to semiarid environment conditions (Andean hot and cold deserts), with a critical role of water in vegetation and animal development, constitute an excellent area for analysing and evaluating the changes produced in the late Pleistocene and their possible relation to the early human peopling of the region. On the western slope, several Pleistocene archaeological sites have yielded an interesting archaeofaunal record associated with diverse cultural materials, mainly a rich lithic artefactual record (Varela et al., 1993; Núñez et al., 1994a; Jackson et al., 1997–98, 2004; Rojas et al., 2004). On the Argentine slope, archaeological and paleoecological Pleistocene sites are scarce (Lagiglia, 1956, 1979; Schobinger, 1971; Gambier, 1995; García and Lagiglia, 1999a; García et al., 1999; García, 2003). Nevertheless, some include in their stratigraphy feces of some species that became extinct in the late

---

*Corresponding author. Tel.: +54 264 4265979.
E-mail addresses: agarcia@logos.uncu.edu.ar (A. García), mcarrete@lab.cricyt.edu.ar (E. Martínez Carretero), mdacar@lab.cricyt.edu.ar (M.A. Dacar).

1040-6182/$ - see front matter © 2007 Elsevier Ltd and INQUA. All rights reserved.
doi:10.1016/j.quaint.2007.08.023

Pleistocene or early Holocene. This allows improvement of knowledge on the composition of their diets, and evaluation of possible changes that could relate to their disappearance. The analyses of feces of *Hippidion* found at the sites Los Morrillos (Gruta 1) (31°43′S–68°42′W, 3000 m a.s.l.) and Gruta del Indio (34°35′S, 68°22′W, 660 m a.s.l.) constitute the basis of present knowledge at a regional level, and an essential data source.

2. Materials and methods

The analysed feces were obtained from archaeological excavations made in the second half of the XXth Century. Gruta 1 of Los Morrillos was excavated in 1977 (Gambier, 1995) by removing artificial layers 10 cm thick. The feces were gathered from the western area of the back of the shelter, from a depth of 1.5 m; they were associated with bones and hooves of *Hippidion*. At Gruta 2 of the same locality, feces of *Hippidion* appeared along with bones and feces of *Megatherium*. These excrements were dated to 27,530 ± 800 ^{14}C BP (A 2930).

Samples from Gruta del Indio come from excavations done between 1997 and 2000. These feces coincide in size, form, and structure with those collected at Los Morrillos, which were assigned to *Hippidion*. The analysed feces have ovoid form and their size commonly ranged from 50 to 80 mm long and from 40 to 65 mm width. On the upper part of the layer containing the excrements, droppings were dry and their content showed good conservation, allowing observing the structure of the botanical elements. At the bottom of the layer, the excrements were more disaggregated and mixed with the sedimentary matrix. Lagiglia had previously recovered some bigger and more irregularly formed feces, which are assumed to correspond to *Mylodon* and/or *Megatherium*. Due to their morphology, smaller feces (Figs. 1 and 2) were assigned to *Hippidion*. In this sense, it is interesting to remember that Martin (1995), who was at Gruta del Indio in 1972, commented that the megafauna feces he saw at the site were smaller than any he and Austin Long had seen in the US and much smaller than the specimens they collected at the Mylodon Cave in Chile. For Martin (1995), the source of the feces remained a mystery.

At Gruta del Indio, sediment removal was carried out by *decapaging* with brush and metallic trowel two squares (R8 and R9) at the dripping line. The analysed feces come from the lower part of the stratigraphic sequence (Layer 3; Fig. 3). The feces were isolated, spatially associated with one another, and showed high levels of integrity (that decreases from the upper to the bottom part of the layer). Several specimens (obtained from different artificial levels inside this layer) were dated (Table 1) to ca. 31,000–9000 ^{14}C BP (LP 918, 925, 929, 1072, and 1075; García 2003).

Fig. 1. Relative location of early archaeological sites.

Fig. 2. Pleistocene mammal excrement assigned to *Hippidion* (from Gruta del Indio).

Each coprolite was regarded as a basic sampling unit. A 10-g sample was randomly obtained from each coprolite. For Gruta del Indio 37 samples were observed (L3: 2; L4: 4; L5: 10; L6: 10; and L9: 11), and 3 for Los Morrillos. This material was prepared for microscopic analysis using the methodology proposed by Dacar and Giannoni (2001). The relative frequency of appearance of different taxa was quantified for each of the 50 randomly chosen fields, at 400 × under an optical microscope. A comparison was made between microhistological plant samples and materials from Ruiz Leal (IADIZA) and Geobotany herbaria. Form and size of the stomas, occlusive cells, fibres and trichomes, and form of the testa (seed coat) of seeds were considered. Current plant communities were floristically studied in an area of 300 m around each site. The presence

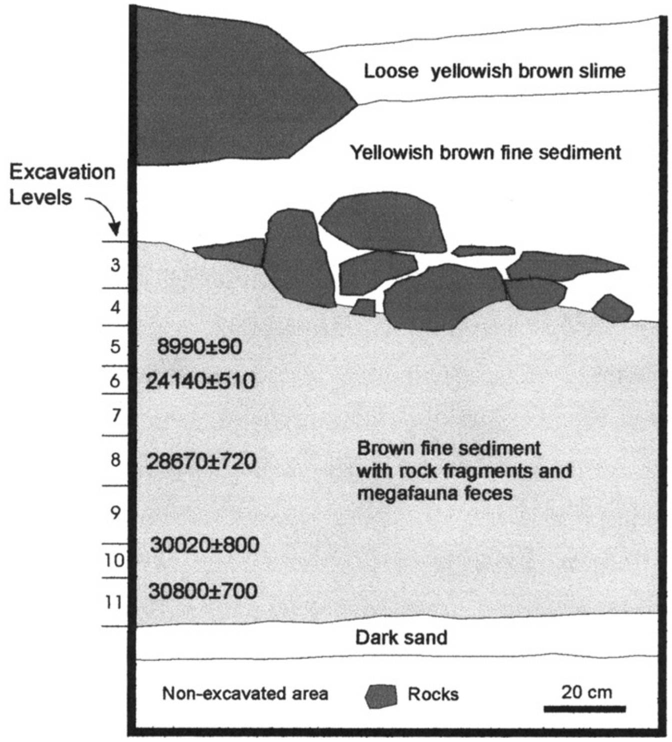

Fig. 3. Stratigraphy of the right area of Gruta del Indio, and location of the last dates obtained.

Table 1
Chronology of the artificial levels included in layer 3 of Gruta del Indio and at the bottom of Los Morrillos

Site	Level	Chronology	Laboratory and number
Gruta del Indio	3	ca. >8000<8990	
Gruta del Indio	4	ca. >8000<8990	
Gruta del Indio	5	8990±90	LP-925
Gruta del Indio	6	24,140±510	LP-1075
Los Morrillos	Bottom	27,530±800	A-2930
Gruta del Indio	8	28,670±700	LP-1072
Gruta del Indio	10	30,200±800	LP-929
Gruta del Indio	11	30,800±700	LP-918

of plant species determined for each archaeological level is indicated in Table 2. This data matrix was standardized by columns and analysed using cluster analysis, applying the Squared Euclidean distance for similarity and the Centroid method for amalgamation.

3. Results

Determinations obtained from microhistological analyses show the presence of numerous plant species, as observed in Table 2. Two groups were obtained from the similarity method: one including current and archaeological plant species from Los Morrillos (Puna level), and the other with samples from Gruta del Indio (Monte level) (Fig. 4).

According to these results, the diet of *Hippidion* at Gruta del Indio was based mainly on woody species (*Senna aphylla*, *Prosopis flexuosa* var., and *Acantholippia seriphioides*), which are common in the arid and hot lowland area. These plants were complemented by some herbaceous ones (such as *Aristida adscencionis* and *Digitaria californica*). Megathermic species such as *Pappophorum caespitosum*, *P. flexuosa* var. *depressa* and *Schinus fasciculata* indicate summer precipitation favouring the sprouting of shrubs and browsing. At Los Morrillos, instead, in an environment with *vegas* (wetlands) dominated by gramineous plants and scarce shrubs, the diet was based on herbaceous species (*Stipa frigida*, *Hordeum* sp.), which constitute 70% of the components in the analysed samples. A few woody plants typical of arid and cold environments (e.g. *Ephedra*) complement this diet. Usually, large mammals browse the foliage of shrubs and small trees. The capability of adapting to a diverse foraging offer would help explain the presence of *Hippidion* sp. in the cold and dry environment of Puna, as well as its longer permanence at Gruta del Indio. In the Monte environment (Gruta del Indio) browsing of shrubs, generally with protein contents higher than 6 g% g DM (Table 3), predominates; at Los Morrillos, the herbaceous forage available in the vegas, such as *Hordeum comosum*, common on the border of these humid environments, complements that of the scarce woody plants. Obtained data suggest that *Hippidion* would have made in each environmental situation a specialized use of the resources, related to the better protein quality of the forage offer (browsing of woody plants in dry and warm environments and foraging of herbaceous plants from vegas in the dry and cold ones). This versatility would explain its presence in two so dissimilar environments with an altitudinal difference of about 2000 m.

These data allow consideration of diverse aspects concerning the diet of *Hippidion* and the disappearance of this species. Firstly, differences between the diets at both analysed sites (only 350 km apart) are remarkable. This situation would indicate a high degree of variability in the feeding habits of this species at a regional level, directly related to the specific plant supply in each area. Thus, the contents of feces of Gruta del Indio and Los Morrillos would, respectively, reflect predominance of woody plants in the vegetation structure of Monte (steppe), corresponding to the first locality, and superiority of gramineous plants in the vega (wetland) environment characterizing the second site.

Secondly, as observed in Tables 1 and 2, no marked differences in the diet composition of specimens of ca. 31,000 and ca. 9000 ^{14}C BP are recorded, indicating that the extinction of *Hippidion* in the area would not be related to an eventual modification of the traditional food supply due to environmental changes occurred during the Last Glacial Maximum and to the subsequent warming during the Pleistocene–Holocene transition. The absence of *Accantholippia* and *Capparis* in the samples of levels 3

Table 2
Botanical determinations of contents of feces from Gruta del Indio and Los Morrillos, and comparison with current vegetation

Species/stratigraphic level	Gruta del Indio (Mendoza)					Current vegetatation (Gruta del Indio)	Los Morrillos (San Juan)	Current vegetation (Los Morrillos)
	L3	L4	L5	L6	L9		Bottom	
Senna aphylla[a]	*	*	*	*	*	*		
Prosopis flexuosa var. *depressa*[a]	*	*	*	*	*	*		
Pappophorum caespitosum[b]			*	*	*	*		
Acantholippia seriphioides[a]			*		*	*		
Schinus fasciculata[a]	*		*	*	*	*		
Capparis atamisquea[a]				*	*	*		
Aristida adscencionis[b]	*					*		
Digitaria californica[b]		*		*		*		
Larrea divaricata[a]			*			*		
Chenopodiaceae (Chenopodium af Papulosum ?)			*					
Chloridea (Chloris af Castilloniana)			*					
Poa sp.				*				
Lecanophora heterophylla[b]						*		
Tephrocactus aoracanthus[b]						*		
Bulnesia retama[a]						*		
Trichocereus candicans[b]						*		
Lycium tenuispinosum[a]						*		
Larrea cuneifolia[a]						*		
Cercidium praecox[a]						*		
Fabiana peckii[a]							*	*
Ephedra breana[a]							*	*
Descourainia sp.[b]							*	
Stipa frigida[b]							*	*
Hordeum sp.[b]							*	
Hordeum comosum[b]								*
Stipa chrysophylla[b]								*
Tarasa antofagastana[b]								*
Artemisia echegarayii[a]								*

[a] Woody plants.
[b] Herbaceous plants.

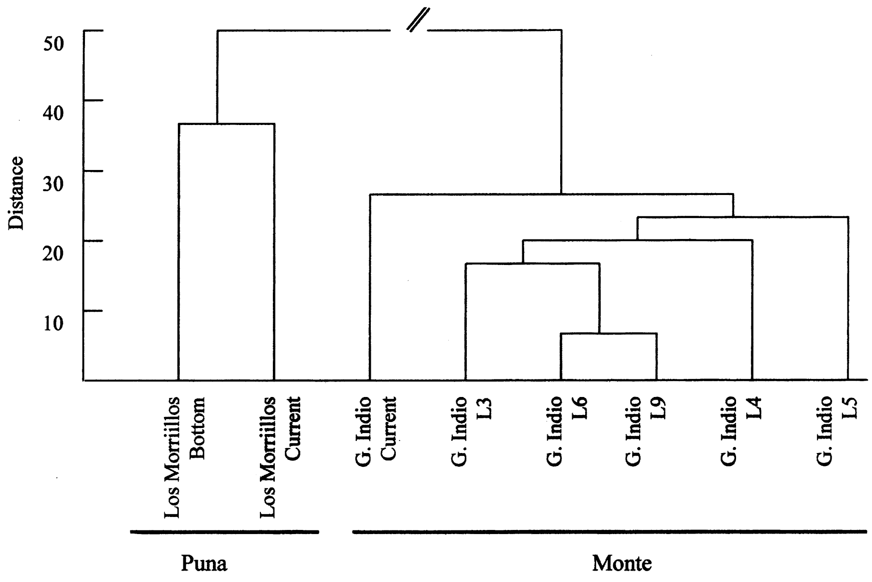

Fig. 4. Clustering considering presence of plant species at artificial levels and in current vegetation for both sites, Gruta del Indio and Los Morrillos.

Table 3
Protein contents (g%g DM—dry matter) of species included in the diet of *Hippidion*

	Total protein (g%g DM)	
	Gruta del Indio	Los Morrillos
Senna aphylla[a]	5.86	
Prosopis flexuosa var. *depressa*[a]	19	
Pappophorum caespitosum[b]	7.39	
Acantholippia seriphioides[a]	7.0	
Schinus fasciculate[a]	7.28	
Capparis atamisquea[a]		
Aristida adscencionis[b]	4.6	
Digitaria californica[b]	6.06	
Chenopodiaceae (Chenopodium af papulosum ?)	11.7	
Chloridea (Chloris af castilloniana)	9.14	
Fabiana peckii[a]		9.59
Ephedra breana[a]		15.26
Descourainia sp.[b]		
Stipa frigida[b]		–[c]
Hordeum sp. (af. comosum)[b]		8.5

[a] Woody plants.

[b] Herbaceous plants.

[c] In these environments values fluctuate between 4.4 and 5.9 g%g DM.

and 4 (between 8000 and 9000 ^{14}C BP) could be interpreted as indicative of a decline in the availability of those taxa. However, the *Hippidion* ability to adapt its diet to the resources available would have counteracted any negative incidence of a vegetation shift in the area.

This flexibility of the diet could have been an advantage that would have contributed to a longer permanence of this species compared to others that shared the same territory (such as *Megatherium* and *Mylodon*) that probably disappeared some 1000 years before. Excavations made in Gruta del Indio since the middle of the XXth Century (Lagiglia, 1956, 1974, 1977; Semper and Lagiglia, 1962–68; Lagiglia and García, 1999; García and Lagiglia, 1999b) have yielded remains of diverse extinct megafauna species mainly associated with samples of feces dated to the late Pleistocene (Lagiglia, 1979; García, 2003). Only one case had an early Holocene date: a bone of *Megatherium* dated to 9560 ± 90 ^{14}C BP (GrN 5772) (Lagiglia, 1979).

The diet adaptability of *Hippidion* would have enabled this species to inhabit territories with as marked environmental and altitudinal differences as the cold and dry Puna of San Juan (above 3000 m) and the warm Monte in the plain and piedmont in the centre of Mendoza, where Gruta del Indio is located at 660 m (Martínez Carretero et al., 2004).

This characterization of *Hippidion* as a consumer capable of diversifying its diet according to plant availability fits with the expectations of other researchers. For instance, Kaiser and Franz-Odendaal (2004), based on the opportunistic feeding strategies of modern *Equus* and on teeth marks of equine specimens from diverse African habitats, suggested that during the middle Pleistocene the South African species *Equus capensis* was able to behave as a forager in a habitat and as a mixed consumer in another habitat with less availability of grasses. The data imply that in this latter case *Hippidion* was not only capable of diversifying its diet but also of basing it mainly on woody plants (rich in proteins).

4. On the extinction of the regional megafauna

The search for the causes of extinction of the Pleistocene megafauna continues to be based on the classical positions related to anthropic actions (Martin, 1967, 1973; Mosimann and Martin, 1975), to environmental changes (Grayson, 1991; Yesner, 1996), and to diverse forms of interaction between both agents (Barnosky, 1989; Stuart, 1993; Barnosky et al., 2004). So, alternative ways of approaching the subject are necessary (MacPhee and Marx, 1997; Barnosky et al., 2004), one of these being the study of megafaunal feces.

Previous information indicates that in the Argentinean-Chilean Central Andes there is no agreement on the interpretations proposed for explaining the extinction. For Lagiglia (1974), early humans played a decisive role in the process of disappearance of Pleistocene megaherbivores. In a similar sense, although Núñez and collaborators (based on studies performed in Quereo and Taguatagua) considered at first that extinction was a response to the environment changes of the late Pleistocene (Núñez et al., 1987), in later papers they remarked on the incidence of human activity (Varela et al., 1993; Núñez et al., 1994a, b) and considered the early human groups as "hunters specialized on the overexploitation of microhabitats or eco-refuges" of extinct fauna.

On the other hand, García (1999) has pointed out the scarcity of remains of extinct megafauna effectively associated with human activities in the analysed area, and the previous presence and disappearance of some species in places only later inhabited by humans (including the shelters of Los Morrillos or the Gruta El Manzano).

The more recent archaeological information comes from the site Agua de la Cueva and from the last excavations at Gruta del Indio. At Agua de la Cueva, a shelter located in the transition of Monte–Puna conditions in the pre-Andean area of Mendoza, many lithic and archaeofaunistic remains were recovered from stratigraphic levels corresponding to the late Pleistocene and early Holocene. The numerous charcoal concentrations allowed obtaining a series of dates ranging from 10,900±190 (Beta 61409) to 7450±140 (Beta 90740) ^{14}C BP (García, 2004). The analysis of more than 800 lithic artefacts and 16,000 lithic remains indicates the development of behaviours related to the exploitation of basically local lithic and faunal resources. Almost all of the species recorded are extant at present. The only exception could be some specimens that have not yet been precisely determined, and could correspond to the extant vicuña (*Lama vicugna vicugna*) or to the extinct *Lama vicugna gracilis*. Nevertheless, these items are very few ($n = 16$). The record indicates a marked predominance of *Lama guanicoe*, complemented by minor species such as *Lagidium viscacia* and *Chaetophractus vellerosus*, although consumption of these species has not yet been proved (García, 2004). In the case of species like *Megatherium* or *Mylodon*, their absence at Agua de la Cueva can be explained by the relatively low carrying capacity of the area in relation to the feeding necessities of these animals.

The absence of equines at Agua de la Cueva is more difficult to understand. This probably could be related to competition with camelids (species showing an absolute predominance in the pre-Andean region in the last 11,000 years) and probably to environmental conditioning factors. Another alternative could be specialized hunting, mainly focused on guanacos, which would take the other species out of the archaeological record of the site, although this option is not considered viable because of the apparent opportunistic character of the hunting events recorded on diverse early sites from Chile and Argentina. During more recent excavations at Gruta del Indio, a few lithic remains were found into layers located above the one containing the remains of extinct megafauna. Those artifacts were only three little flakes, probably affected by postdepositional removal from upper layers (García and Lagiglia, 1999b). No other evidence (e.g. hearths) was recorded in direct association with megafauna feces or with the little fragments of bones of extinct fauna found in this layer. Some of the bones lately recovered at the site could be assigned to *Machrauquenia* sp. and *Hippidion* sp. (Miotti, personal communication; García, 2003).

Despite the numerous available ^{14}C dates from megafauna feces (tentatively assigned by Lagiglia to *Megatherium* or *Mylodon*), all are late Pleistocene, between 10,610±210 (A 1351) (Lagiglia, 1979; Long et al., 1998) and 12,375±115 (A 9571) ^{14}C BP (García, 2003). On the other hand, the cultural remains found by Lagiglia (1979) are so few ($n = 4$) that (even accepting the human–megaherbivores relation) it is too difficult to relate them to an important incidence on the extinction of local megafauna. Human activity is not involved in the disappearance of megafauna at Los Morrillos, since its record (*Hippidion* sp. and *Megatherium* sp.) has a chronology much earlier than the human arrival to the region.

Environmental hypotheses do not explain by themselves the megafauna extinction in the study area. Thus, according to the Habitat Loss hypothesis this process would have reduced or eliminated the areas with adequate conditions for megafauna survival (Barnosky, 1986; Koch and Barnosky, 2006). Nevertheless, in the Gruta del Indio area, the species included in the *Hippidion* diet had an increasingly growing presence in relation to the expansion of the arid Monte vegetation during the final Pleistocene and Holocene (D'Antoni, 1983). Also, this environmental situation does not support a regional co-evolutionary disequilibrium (Graham and Lundelius, 1984), which not only would have affected differentially the diverse megafauna species, but also could have been effectively responded to by the higher mobility and apparent diet diversification capacity of *Hippidion*.

5. Concluding remarks

In the current state of the debate, no firm proof exists of an important incidence of human activity on the disappearance of Pleistocene species at the regional level. On the other hand, available data do not permit causal linkage of this phenomenon to late Pleistocene environment changes. At Gruta del Indio significant changes in the composition of the feces of *Hippidion* corresponding to different intervals of the period ca. 31,000–9000 ^{14}C BP are not evident. So, a forced negative shift of diet (resulting from eventual marked environment changes related to the Last Glacial Maximum) should be discarded as cause of the regional extinction of *Hippidion*. At any rate, if these changes existed, the capacity of feeding diversification of this species, reflected by the record of Los Morrillos, would have constituted an efficient response to secure its survival (García et al., 2006). This flexibility in diet composition could be a relative adaptive advantage allowing for a longer permanence of this species in comparison to others recorded in the region (such as *Megatherium* and *Mylodon*), whose extinction in the Gruta del Indio area could have been some 100 or 1000 years earlier. Nevertheless, this advantage was not enough to guarantee its survival during the Holocene, which could have been affected by diverse agents, such as growing aridification of the area, increasing competition with other species (mainly *L. guanicoe*), and human presence, all of these related to a relatively low population density, as expected from the poor presence of *Hippidion* at the archaeological and palaeontological sites of Argentina (e.g. Alberdi et al., 2001). In short, although it could be a simple problem of sample scarcity, the chronological differences observed in the records of *Hippidion* from Los Morrillos and Gruta del Indio also suggest that the factors above mentioned could be part of a process explainable by a general mechanism (e.g. climate change) with specific regional situations involving other agents, as suggested by Borrero (1997) for Patagonia. In this case, this model of regional variability coincides with the marked climate change observed by authors such as D'Antoni (1980, 1983), Heusser (1983, 1990) and Núñez et al. (1994a, b) for the Pleistocene–Holocene transition in the Central Andes of Argentina and Chile.

Acknowledgements

Thanks to Hector D′Antoni (NASA) for reading the text, and to N. Horak (IADIZA) for the revision of the English version. We especially thank Mariana Mondini and Sebastián Muñoz for their kind invitation. We deeply thank the suggestions and comments from Bruce MacFadden, Donald Jackson and María Teresa Alberdi on the manuscript. This research was funded by Fundación Antorchas, CONICET, UNCuyo, UNSJ and PIP 02912 (CONICET).

References

Alberdi, M.T., Miotti, L., Prado, J.L., 2001. Hippidion saldiasi Toth, 1899 (Equidae, Perissodactyla, at the Piedra Museo Site (Santa Cruz, Argentina): its implication for the regional economy and environmental reconstruction. Journal of Archaeological Science 28, 411–419.

Barnosky, A., 1986. "Big Game" extinction caused by late Pleistocene climatic change: Irish Elk (*Megaloceros giganteus*) in Ireland. Quaternary Research 25, 128–135.

Barnosky, A., 1989. The Late Pleistocene event as a paradigm for widespread mammal extinction. In: Donovan, S. (Ed.), Mass Extinctions: Processes and Evidence. Belhaven Press, London, pp. 235–254.

Barnosky, A., Koch, Feranec, P.R., Wing, S., Shabel, A., 2004. Assessing the causes of Late Pleistocene extinctions on the continents. Science 306, 70–75.

Borrero, L., 1997. La extinción de la megafauna en la Patagonia. Anales del Instituto de la Patagonia 25, 89–102.

D'Antoni, H., 1980. Los últimos 30 mil años en el sur de Mendoza, Argentina. Memorias III Coloquio sobre Paleobotánica y Palinología. Col. Cient. Prehistoria, SEP INAR, México, pp. 83–108.

D'Antoni, H., 1983. Pollen analysis of Gruta del Indio. Quaternary of South America and Antartic Peninsula 1, 83–104.

Dacar, M., Giannoni, S., 2001. A simple method for preparing reference slides of seed. Journal of Range Management 54 (2), 191–193.

Gambier, M., 1995. Hallazgo de fauna extinta en Los Morrillos. Revista Ansilta 10, 16–20.

García, A., 1999. La extinción de la megafauna pleistocénica en los Andes Centrales Argentino-Chilenos. Revista Española de Antropología Americana 29, 9–30.

García, A., 2003. On the coexistence of man and extinct Pleistocene megafauna at Gruta del Indio (Argentina). Radiocarbon 45 (1), 33–39.

García, A., 2004. Los primeros pobladores de los Andes Centrales Argentinos. Una mirada a los estudios sobre los grupos cazadores-recolectores tempranos de San Juan y Mendoza. Zeta, Mendoza.

García, A., Lagiglia, H., 1999a. A 30,000-year-old megafauna dung layer from Gruta del Indio (Mendoza, Argentina). Current Research in the Pleistocene 16, 116–118.

García, A., Lagiglia, H., 1999b. Avances en el estudio del registro pleistocénico tardío de la Gruta del Indio (Mendoza). Cuadernos del Instituto Nacional de Antropología y Pensamiento Latinoamericano 18, 167–174.

García, A., Martínez Carretero, E., Dacar, M., 2006. Dietary diversity of Hippidion in western Argentina. Current Research in the Pleistocene 23, 163–164.

García, A., Zárate, M., Páez, M., 1999. The Pleistocene–Holocene transition and human occupation in the Central Andes of Argentina: Agua de la Cueva locality. Quaternary International 53/54, 43–52.

Graham, R., Lundelius, E., 1984. Coevolutionary disequilibrium and Pleistocene extinction. In: Martin, P., Klein, R. (Eds.), Quaternary Extinctions: A Prehistoric Revolution. University of Arizona Press, Tucson, pp. 223–249.

Grayson, D., 1991. Late Pleistocene mammalian extinctions in North America: taxonomy, chronology, and explanations. Journal of World Prehistory 5 (34), 193–231.

Heusser, C., 1983. Quaternary pollen record from Laguna de Taguatagua, Chile. Science 220, 1432–1469.

Heusser, C., 1990. Ice age vegetation and climate of subtropical Chile. Palaeogeography, Palaeoclimatology, Palaeoecology 80, 107–127.

Jackson, D., Báez, P., Seguel, R., 1997–98. Nuevas evidencias estratigráficas para el complejo Huentelauquén en la Provincia del Choapa, IV Región. Revista Chilena de Antropología 14, 145–156.

Jackson, D., Méndez, C., de Souza, P., 2004. Poblamiento paleoindio en el norte-centro de Chile: evidencias, problemas y perspectivas. Complutum 15, 165–176.

Kaiser, Th., Franz-Odendaal, T., 2004. A mixed-feeding Equus species from the middle Pleistocene of South Africa. Quaternary Research 62, 316–323.

Koch, P., Barnosky, A., 2006. Late Quaternary extinctions: state of the debate. Annual Review of Ecology, Evolution, and Systematics 37, 215–250.

Lagiglia, H., 1956. Estudios Arqueológicos en el Rincón del Atuel (Dpto. San Rafael, Mendoza). Anales de Arqueología y Etnología XII, 227–287.

Lagiglia, H., 1974. Atuel IV frente a la prehistoria americana. Ms. presented at the III Congreso Nacional de Arqueología Argentina, Salta.

Lagiglia, H., 1977. Arqueología y ambiente natural de los valles del Atuel y Diamante. Ph.D. Dissertation, Facultad de Ciencias Naturales y Museo, Universidad Nacional de la Plata.

Lagiglia, H., 1979. Dinámica cultural en el centro oeste y sus relaciones con áreas aledañas argentinas y chilenas. In: Actas del VII Congreso de Arqueología de Chile, Altos de Vilches, vol. II, pp. 531–560.

Lagiglia, H., García, A., 1999. Las ocupaciones tempranas del Atuel (nuevos estudios en la Gruta del Indio). In: Actas del XII Congreso Nacional de Arqueología Argentina, La Plata, vol. III, pp. 251–255.

Long, A., Martin, P., Lagiglia, H., 1998. Ground Sloths and humans at Gruta del Indio–Argentina. Radiocarbon 40, 693–700.

MacPhee, R., Marx, P., 1997. The 40,000-year plague: humans, hyperdisease and first-contact extinctions. In: Goodman, S., Patterson, B. (Eds.), Natural Change and Human Impact in Madagascar. Smithsonian Institution Press, Washington, pp. 169–217.

Martin, P., 1967. Prehistoric overkill. In: Martin, P., Wright, S. (Eds.), Pleistocene Extinctions: The Search for a Cause. Yale University Press, New Haven, pp. 75–120.

Martin, P., 1973. The discovery of America. Science 179, 969–974.

Martin, P., 1995. Rediscovering the desert laboratory. In: Steadman, D., Mead, J. (Eds.), Late Quaternary Environments and Deep History: A Tribute to Paul s. Martin, The Mammoth Site of Hot Springs, South Dakota, Inc. Scientific Papers, vol. 3. Hot Springs, South Dakota, pp. 1–24.

Martínez Carretero, E., García, A., Dacar, M., 2004. First data on differential use of the environment by Pleistocene megafauna species (San Juan, Argentina). Current Research in the Pleistocene 21, 91–92.

Mosimann, J., Martin, P., 1975. Simulating overkill by paleoindians. American Scientist 63, 304–313.

Núñez, L., Varela, J., Casamiquela, R., 1987. Ocupación Paleoindio en el Centro-Norte de Chile: Adaptación circunlacustre en las tierras bajas. In: Investigaciones paleoindias al sur de la línea ecuatorial, Taraxacum, San Pedro de Atacama, Chile, pp. 142–185.

Núñez, L., Varela, J., Casamiquela, R., Schiappacasse, V., Niemeyer, H., Villagrán, C., 1994a. Cuenca de Taguatagua en Chile: el ambiente del Pleistoceno y ocupaciones humanas. Revista Chilena de Historia Natural 67 (4), 503–519.

Núñez, L., Varela, J., Casamiquela, R., Villagrán, C., 1994b. Reconstrucción multidisciplinaria de la ocupación prehistórica de Quereo, centro de Chile. Latin American Antiquity 5 (2), 99–118.

Rojas, G., Stehberg, R., Aspillaga, E., Prieto, A., 2004. Diagrama de Correlación de Hallazgos Bióticos, Abióticos y Cronológicos de Caverna Piuquenes. Chungará 36, 547–550.

Schobinger, J., 1971. Una punta de tipo "cola de pescado" de la Crucesita (Mendoza). Anales de Arqueología y Etnología XXVI, 89–97.

Semper, J., Lagiglia, H., 1962–68. Excavaciones arqueológicas en el Rincón del Atuel (Gruta del Indio). Revista Científica de Investigaciones I (4), 89–158.

Stuart, A.J., 1993. The failure of evolution: late Quaternary mammalian extinctions in the Holartic. Quaternary International 1, 101–107.

Varela, J., Núñez, L., Casamiquela, R., 1993. Geología del Cuaternario de la Depresión Central de Chile entre Santiago y Laguna de Taguatagua. Taller Internacional "El Cuaternario de Chile," Santiago.

Yesner, D., 1996. Environments and peoples at the Pleistocene–Holocene boundary in the Americas. In: Straus, L.G., Eriksen, B.V., Erlandson, J.M., Yesner, D.R. (Eds.), Humans at the End of the Ice Age; the Archaeology of the Pleistocene–Holocene Transition. Plenum, New York, pp. 243–253.