Climate and changes in mammal diversity during the late Pleistocene–Holocene in the Pampean Region (Argentina)

JOSÉ LUIS PRADO, MARÍA TERESA ALBERDI, BEATRIZ AZANZA, and BEGOÑA SÁNCHEZ

Prado, J.L., Alberdi, M.T., Azanza, B., & Sánchez, B. 2001. Climate and changes in mammal diversity during the late Pleistocene–Holocene in the Pampean Region (Argentina). — *Acta Palaeontologica Polonica* **46**, 2, 261–276.

The association of changes in mammal diversity with periods of global climatic change is suggestive of a causal relationship. Two important features in the testing of this climatic model are as follows: the timing and the pattern of the diversity changes, and the particular climatic variables examined, since different patterns of evolutionary interactions would be expected depending on different climatic variables. In order to analyse the relationship between climate change and faunal events, we need to establish a set of comparable data. To provide a finely resolved picture of both climatic and faunal events, the last 32,500-years were divided into 13 chronological units of 2,500-years each. The limit of 32,500-years was imposed by the availability of good localities with radioisotopic calibration. Climatic stability was measured in these analyses in terms of cycles per unit of time, the amount of variation in temperature per unit of time, and the magnitude of change between modal temperature of one interval less modal temperature from preceding interval. The data presented here suggest that the primary effect of climatic change is on: (1) levels of extinction (or migration) of large mammals; and (2) diversity and origination (or immigration) of small mammals.

Key words: Pleistocene, Holocene, climatic change, mammals, diversity, extinction.

José Luis Prado, INCUAPA – Departamento de Arqueología, Universidad Nacional del Centro. Del Valle 5737. B7400JWI Olavarría, Argentina;
María Teresa Alberdi [malberdi@mncn.csic.es] and Begoña Sánchez, Departamento de Paleobiología. Museo Nacional de Ciencias Naturales, CSIC. José Gutiérrez Abascal, 2, 28006 Madrid, Spain;
Beatriz Azanza, Departamento de Ciencias de la Tierra, Universidad de Zaragoza. 50009 Zaragoza, Spain.

Introduction

Megafaunal extinctions in South America occurred at the same time as the major climatic deterioration associated with the last glacial cycle; this fact has prompted con-

siderable speculation about the extent to which these events are causally related (Borrero 1984; Politis & Prado 1990; Prado *et al.* in press). Several authors suggest that climatic change, or other natural factors that directly affected the Pleistocene fauna, drove the larger mammals into extinction (Axelrod 1967; Graham & Lundelius 1984; Grayson 1984; Guthrie 1984; Graham & Grimm 1990). In addition, during the last two decades a number of authors (e.g., Vrba 1985, 1988; Foley 1993; Vrba *et al.* 1995; Webb & Opdyke 1995; Behrensmeyer *et al.* 1997) have linked major changes in the composition of mammalian communities with global climatic oscillations. This has led to some specific theories about climate change as the driving force in faunal turnover and diversity in mammals (Vrba 1993). In order to test this climatic forcing model we need to take into account two important factors: (1) the timing and the way in which the changes in diversity patterns occurred, and (2) the particular climatic variables considered. Because climatic change is not a simple phenomenon, different patterns of faunal diversity change would be expected depending on which particular climatic variables are involved.

Data derived from oxygen isotopes of ice cores from Antarctica have shown that there may be as many as 10 main climatic oscillations during the last 40,000 years. Any development of the climatic forcing model should therefore take into account this complexity, and also attempt to detail the causal links between climate and diversity change.

Biological processes can be analysed at different time scales, such as ecological or evolutionary time. Different scales may reveal different aspects of the processes. Ecological time is concerned with immediate responses to environmental change, whereas evolutionary time refers to long term effects of environmental change upon biota. The late Quaternary mammal record of the Pampean Region, especially that of the last 40,000 years, links ecological and evolutionary time and offers a unique opportunity to examine in detail the processes of changes in diversity as a result of environmental fluctuations.

In this paper we attempt to explore the quantitative relationship between climatic change and the pattern of mammal turnover and diversity in the Pampean Region. We also seek to provide an empirical basis for the causes of change in the course of late Pleistocene mammal extinction.

Previous studies

Geological context. — Most of the selected sites were developed in the eolian and fluvial-lacustrine deposits widespread in the Pampean Region. Fidalgo *et al.* (1973, 1975, 1991), and Dillon & Rabassa (1985) revised the stratigraphic nomenclature of this area. Based on geomorphological evidence, as well as textural and compositional analyses of the late Pleistocene and Holocene deposits, they proposed two stratigraphic units; the Luján Formation with three Members – La Chumbiada, Guerrero and Río Salado; and the La Postrera Formation (Fig. 1). The former is of fluvial-lacustrine origin, and the latter is eolian. These eolian deposits, extensively covering southern Buenos Aires Province, comprise sandy loess, very fine sand sheets and dunefields (Zárate & Blasi 1993).
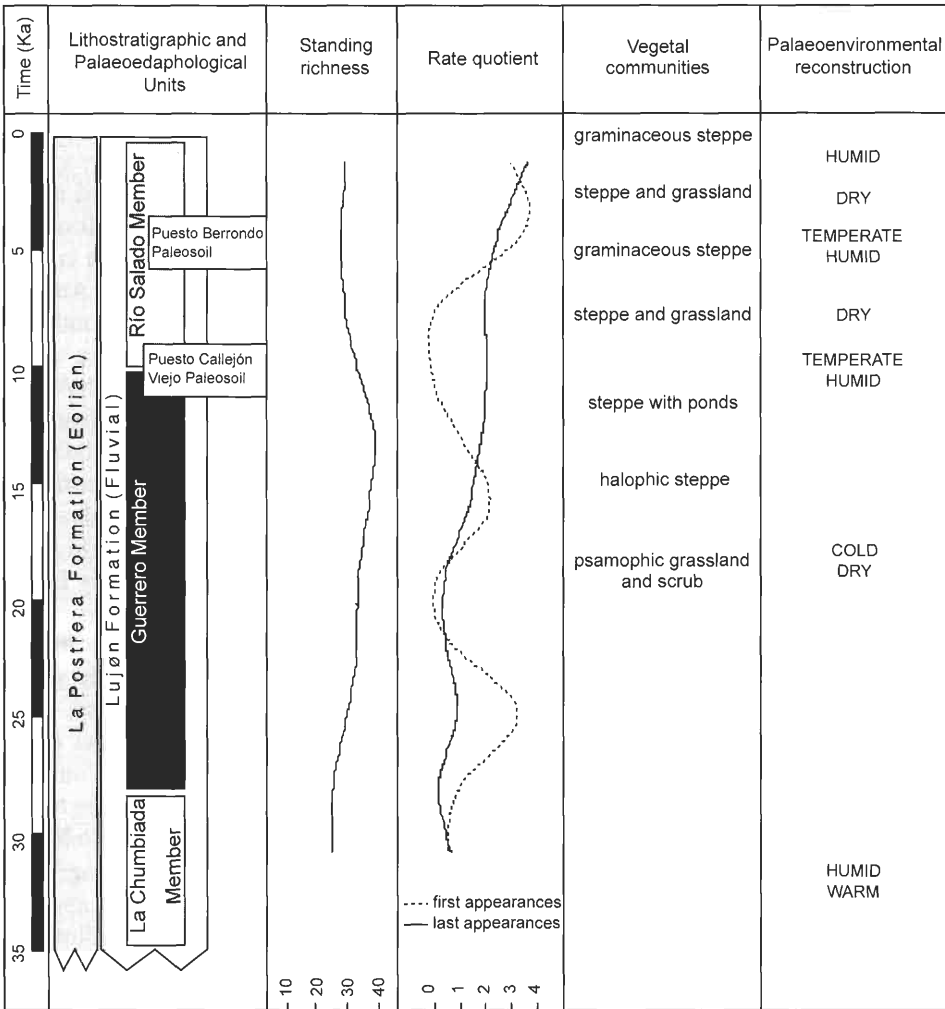
Fig. 1. Diversity and turnover change through the late Pleistocene to the Holocene in the Pampean Region. Data from Table 1. Lithostratigraphic and palaeoedaphological units *sensu* Fidalgo *et al.* (1973) and Dillon & Rabassa (1985). Palaeoenvironmental reconstruction after Prado *et al.* (in press).

The Luján Formation is represented by a floodplain that extensively covers the main river in the Buenos Aires Province (Fidalgo *et al.* 1973). The lower part of this Formation is mainly a fluvial deposit (La Chumbiada and Guerrero Members) and the upper part is essentially marsh lacustrine (Río Salado Member). The age of the La Chumbiada Member is greater than 28,900 ± 400 years BP (Carbonari *et al.* 1992), while the Guerrero Member ranges from 28,600 ± 2,400 to 13,070 ± 120 years BP. The Río Salado Member extends from 10,840 ± 380 to 3,395 ± 307 years BP (Bonadonna *et al.* 1995). Two edaphostratigraphic units were recognised in the sequence (Fig. 1). The first one, called the Puesto Callejón Viejo paleosoil (dated by ^{14}C around 10,070 ± 140 years BP on pedogenetic carbonate; 9,710 ± 100 years BP on land snails; and 8,940 ± 130 years BP on organic components) is placed in the upper part of the

Guerrero Member. The second one, called the Puesto Berrondo paleosoil, is located in the upper part of the Río Salado Member (Fidalgo *et al.* 1991; Bonadonna *et al.* 1995). The latter paleosoil shows a humid regime that may have existed at the time of the Holocene marine transgression, with a maximum sea level at 5,000 to 6,000 years BP (Schnack 1987; Zárate & Flegenheimer 1991).

Environmental scenario. — The mammal-bearing sediments were deposited under arid to semi-arid climatic conditions, alternating with more humid ones (Tonni & Fidalgo 1978). Palaeoclimatic evidence indicated that this fluctuation was a consequence of the interaction between the South Pacific and the South Atlantic Anticyclone air masses (Iriondo & García 1993). The present day winds from the South Pacific Anticyclone lose their humidity on the west side of the Andes and arrive to the Pampean plain cold and dry from the SW and the South. The winds of the South Atlantic Anticyclone are warmer and more humid, and arrive to the Pampean plain from the NE. The improvement of the environmental conditions between 11,000 and 10,000 is coincident with the arrival of early hunter-gatherer human groups in the Argentinean pampas, and with the megafaunal extinction (Politis *et al.* 1995). Careful analyses of the changes produced during this interval allow the evaluation of the possibility that environmental changes were the main cause for the late Pleistocene and early Holocene extinction. Several studies show important environmental modifications in the Pampean Region at the end of the Pleistocene and the beginning of the Holocene (Tonni & Fidalgo 1978). The $^{18}O/\,^{16}O$ and $^{13}C/^{12}C$ composition of carbonatic shells were measured for four fluvial series (Las Brusquitas, Empalme Querandíes, Paso Otero and Quequén Salado) belonging to the Luján Formation (Bonadonna *et al.* 1995). This analysis referred La Chumbiada Member to a warm and dry environment around 30,000 years BP (Fig. 1), followed by a cold and dry one that ended at the top of Guerrero Member, older than 10,000 years BP. At the bottom of the Río Salado Member an abrupt drop (more than 2 δ‰) in the oxygen value is recorded. This change may correspond to the inception of Holocene atmospheric conditions. Temperate and humid conditions prevailed during the deposition of Río Salado Member sediments, which appear to record a marked damp event localised around 6,000 to 8,000 years BP (Fig. 1). Pollen analyses from the Pampean region (Quattrocchio *et al.* 1994) show that the community of the Pleistocene–Holocene transition in the area was characterised by steppe and aquatic pollen of alluvial fans. The Guerrero Member shows a characteristic assemblage of halophic steppes and psammophic grassland with scrub, typical from open habitats and dry and cold conditions (Fig. 1). The Pleistocene–Holocene transition was also characterised by the migration of climatic isolines, found 750 km Northeast of their present positions. There is general agreement that glaciers in the Andes started to recede from their Last Glacial Maximum limits by ca. 18,000 years ago (Clapperton 1993). Evidence of a distinct glacial re-advance in the Andes at ca. 15,000–14,000 and 12,500–10,000 years BP suggests that a climatic reversal halted the change to interglacial conditions (Porter *et al.* 1992). In general, climates prior to 14,000 years BP were colder than today and atmospheric circulation patterns were probably different from those currently prevalent. The early Holocene was marked by a widespread recession of glaciers in most parts of the Andes (Heusser 1974), but there was a return to cooler and more humid conditions after ca. 5,000 years BP (Mercer 1982).

Methodological approaches

In order to analyse the relationship between climate and mammal evolution we need to establish a set of comparable data. To this end it is necessary to compile several measurements for both climatic and faunal events by chronological intervals.

The following data were used for each equal time unit:

Climatic data. — The best available record of climatic change is derived from the oxygen isotopic record from ice cores. The isotopic curves presented by Merlivat *et al.* (1979) were used to compile the following variables defined by Foley (1994; Table 1):

Number of climatic cycles

Maximum $\delta^{18}O$ ($\cong$ maximum temperature)

Minimum $\delta^{18}O$ ($\cong$ minimum temperature)

Modal temperature

Magnitude of climatic variation (maximum temperature – minimum temperature)

Magnitude of climatic changes (modal temperature of one interval less modal temperature from preceding interval).

Data were obtained from the National Climatic Data Center, database of National Oceanic and Atmospheric Administration NOAA Paleoclimatology Program (http://www.julius.ngdc.noaa.gov/paleo/icecore/antarctica/domec/domec_data.htlm).

Table 1. Climatic data for last 40,000 years.

Interval ka		Number of cycles	$\delta^{18}O$ (max)	$\delta^{18}O$ (min)	Climatic variation (max.-min.)	Mode $\delta^{18}O$	Magnitude of climatic change
0	2.5	29.5	−47.65	−51.6	3.49	−49.9	
2.5	5	9.5	−49.24	−50.69	1.45	−49.8	0.1
5	7.5	10	−49.12	−51.33	2.21	−49.7	0.1
7.5	10	11	−48.01	−51.23	3.22	−50.1	0.4
10	12.5	7.5	−48.03	−51.66	3.63	−49.6	0.5
12.5	15	3.5	−50.53	−52.88	2.35	−51.7	2.1
15	17.5	3	−52.83	−55.94	3.11	−54.9	3.2
17.5	20	3	−54.82	−55.72	0.9	−55.1	0.2
20	22.5	2.5	−54.97	−55.88	0.91	−55.1	0
22.5	25	4	−55.05	−56	0.95	−55.4	0.3
25	27.5	3	−54.53	−55.81	1.28	−55.2	0.2
27.5	30	3	−54.49	−55.75	1.26	−55.3	0.1
30	32.5	2.5	−53.58	−55.12	1.54	−54.9	0.4
32.5	35	2.5	−53.39	−55.57	2.18	−54.8	0.1
35	37.5	3.5	−53.43	−55.09	1.66	−55.1	0.3
37.5	40	2	−52.14	−54.53	2.39	−53.3	1.8

Palaeontological data. — The Pleistocene–Holocene mammal record comes from Prado *et al.* (in press). The use of equal time interval units requires precise ordering of first and last appearance datum of taxa. Such data are not directly available from the late Pleistocene mammal record of the Pampean Region, because most data come from isolated localities and age calibrations are not sufficiently precise.

'Large' mammals can be defined in various ways. We used the criteria following by Martin (1984). Since most mammal species which became extinct in the late Pleisto-

cene approximated or exceeded 45 kg (100 lbs.) in adult body mass, animals of this size or larger will be assigned to the 'megafauna'; those under 45 kg will be considered 'small'.

We used the program CONJUNCT Version 1.5 of Alroy (1992, 1994) following the analysis of 'disjunction distribution ordination' (DDO; Alroy 1992), which operates without the use of stratigraphic information. Chronological information can be inferred detecting which taxa have overlapping (conjuncts) or non-overlapping (disjunction) distributions over a set of faunal lists. The procedure, involving correspondence analysis, generates theoretical spaces composed of two distributional boundaries or edges for each taxon in each dimension. The 'best' solution in this procedure is to search for a parsimonious arrangement of edges that minimise the number of implied conjunctions among taxa that appear to be disjunct. The localities are also ordered within the edge sequence. The position is determined by the mean of the number of the rightmost left edge and the number of the leftmost right edge. The edge sequence was calibrated by regression at the midpoint of the locality range against estimated radioisotopic ages. Linear regression was statistically significant ($r^2 = 0.86$). The last 32,500-years were divided into 13 intervals of 2,500 years each. This order of magnitude was selected for not eclipsing both climatic and faunal events. The limit of 32,500 years was imposed by the availability of good localities with radioisotopic calibration.

For each time interval faunal diversity and turnover were measured as follows (see Table 2): standing richness, first occurrence rate quotient (FRQ), and last occurrence rate quotient (LRQ).

Diversity changes through time were measured as the standing richness (Harper 1975) which standardises the number of taxa that actually or potentially occur at each time interval. Standing richness (N_{sr}) was calculated following Maas *et al.* (1995):

$$N_{sr} = N_{bda} + N_{rt} + 1/2 \ (N_f + N_l - N_o)$$

where N_f is the number of first appearances in the time interval, N_l is the number of last appearances in the time interval, N_o is the number of species known only for that time interval. N_{bda} is the number of species recorded before, during, and after the time interval, and N_{rt} is the number of species ranging through the time interval.

A change in diversity does not necessarily imply the restructuring of the mammal community. According to equilibrium theory (MacArthur & Wilson 1967), extinction and origination (immigration and speciation) events could occur independently of each other, and yet yield equilibrium species diversity. Disruptions of equilibrium could be caused by rapid turnover, in which multiple extinctions are followed by a wave of originations. Because *in situ* speciation and immigration may not be distinguishable we treat both as 'first occurrences'. Similarly, local extinctions are treated as 'last occurrences'.

Rate quotients normalise the number of first and last occurrences in the intervals by taking into account differences in species richness (Gingerich 1987). They are calculated as the ratio of observed to expected turnover:

$$RQ = R_o / R_e$$

where R_o is the observed number of first or last occurrences and R_e is expected number of first or last appearances. Expected rate is calculated using linear regression of the

Table 2. Mammalian specific turnover and richness for the 13 equal time intervals recognised in the last 32.500 years in the Pampean Region. N: number of species. Nsr: standing richness, calculated following Maas *et al.* (1995). Obs.: observed, Exp.: expected. RQ: Rate Quotient. Overall significance of the observed turnover pattern are given following Barry *et al.* (1995) by chi-square goodness-of-fit, and χ^2 values are also given for each interval. Significant high observed turnover is indicated by '+' and significant low values are indicated by '-' based on comparison with a bootstrapped distribution generated for 10,000 simulations (Maas *et al.* 1995). (+ +) or (- -) at p < 0.1, and (+) or (-) at p < 0.5, respectively.

Interval	N	Nsr	first Obs.	first Exp.	χ^2	first RQ		last Obs.	last Exp.	χ^2	last RQ	
32.5–30	25							2				
30–27.5	24	23	1	1.67	0.27	0.6	(- -)	1	1.915	0.44	0.522	(-)
27.5–25	25	24	2	1.82	0.02	1.097	(- -)	0	2.056	2.06	0	(-)
25–22.5	34	29.5	9	2.81	13.61	3.200		2	2.902	0.28	0.689	
22.5–20	35	33	3	3.56	0.09	0.843	(-)	1	3.500	1.78	0.286	(-)
20–17.5	35	34	1	3.79	2.05	0.264	(-)	1	3.679	1.95	0.272	(-)
17.5–15	44	37.5	10	4.66	6.12	2.147		5	4.333	0.10	1.154	
15–12.5	45	40	6	5.34	0.08	1.125		8	4.826	2.09	1.658	
12.5–10	37	33.5	0	3.67	3.67	0	(-)	7	3.589	3.24	1.951	
10–7.5	31	28	1	2.52	0.92	0.397	(-)	5	2.660	2.06	1.880	
7.5–5	34	27	8	2.33	13.75	3.427	(+)	6	2.503	4.89	2.400	(-)
5–2.5	37	29	8	2.71	10.30	2.948		10	2.820	18.28	3.546	(-)
2.5–0	55		28									

natural logarithm of the observed number of first or last occurrences on the natural logarithm of species richness (Gingerich 1987). To assess the overall significance of the observed turnover pattern, we used chi-square goodness-of-fit to test the departure of the observed pattern from an expected distribution of first and last occurrences (Barry *et al.* 1995). Our null hypotheses considered first or last occurrences to be equally distributed in all intervals. An alternative approach is the bootstrapping method formulated by Gilinsky (1991) and modified by Maas *et al.* (1995). This method permits a test of the null hypothesis that first or last occurrences are randomly distributed among faunal intervals. The test distribution of each interval consists of expected numbers of first or last occurrences generated for each of 10,000 simulations. For each simulation, species ranges are shuffled randomly among intervals taking into account that each species has only one first occurrence datum and one last occurrence datum, and ranges are not allowed to be truncated.

To determine the strength of association between climatic and faunal events we used the bivariate correlation program included in SPSS (version 9). We used scatter diagrams on faunal versus climatic variables to evaluate if the relationships were linear. To test the results of bivariate analysis we used multiple regression analysis (using the same statistical package). Multiple regression is appropriate to estimate which climatic variable correlate best with patterns in species richness, origination and extinction. We used the stepwise variable selection method in which variables can be entered or removed from the model depending on either the significance of the F value, or the F value itself. In our analysis, variables were entered when the significance of the F value was ≤ 0.05 and removed from the model when the significance of the F value was ≥ 0.1.

Results

Patterns of turnover and diversity. — The species diversity pattern shows a single peak, with relative high diversity at ca. 14,000 years BP (Fig. 1). For the late Pleistocene–Holocene of the Pampean Region area, expected first occurrences were calculated from the following adjustment:

$$R_e = \exp [2.103 \ln(Nsr) - 6.082]$$

and expected last occurrences were calculated as:

$$R_e = \exp [1.67 \ln(Nsr) - 4.586]$$

The first and last occurrences rate quotients (FRQ and LRQ, respectively) track one another closely between 32,000 to 15,000 years, thus suggesting that a broad range of rates are possible within the equilibrium. Both rates show high value at 25,000 years BP. From 15,000 years BP onwards, the equilibrium is disrupted. The first-occurrence rate quotient shows high values around 15,000 and 5,000 years BP and low values ca. 20,000 and 10,000 years BP (Fig. 1). Last occurrences rate quotient increases greatly from 20,000 to 10,000 BP, after which it was maintained at a high value, up to 5000 years BP, when it increased to the historical level. The coincidence after 5000 years BP of high values of first and last rate quotients seems indicative of a turnover pulse during Holocene times. For each interval the observed numbers of first or last occurrences were compared to the expected numbers generated for each of the 10,000 simulations. Bootstrapping test suggests that these values differ significantly from the expected ones (Table 2). First and last occurrences were significantly heterogeneous among intervals ($\chi^2 = 50.88$ for first occurrence and $\chi^2 = 37.16$ for last occurrence, respectively; $p < 0.01$ and degrees of freedom = 10), thus leading us to reject the null hypothesis.

Climatic patterns. — Table 3 shows a matrix of correlation coefficients between the climatic variables. The climate of the last 32,500 years BP showed a gradual transition between a cooling phase during the late Pleistocene to more temperate conditions during Holocene times. Significant relationships were found between time and maximum of $\delta^{18}O$ values, minimum of $\delta^{18}O$ values, and number of cycles for each period. A significant association was also found between maximum of $\delta^{18}O$ values, minimum of $\delta^{18}O$ values, and climatic variation as measured through $\delta^{18}O$ values. Furthermore, although temperature variables are closely related to each other, the magnitude of change and the variability in climate and climatic stability are not significantly correlated. Foley (1994) found similar results in the analyses of two climatic records, using intervals of 0–2.6 Ma and 0–5 Ma associated with hominid evolution. Thus, our analysis confirms Foley's view that climatic change is not a simple phenomenon, and that different patterns of climatic-faunal evolutionary interactions would be expected depending on which climatic variables are examined. Also, note that a significant correlation does not imply causality. Likewise, a lack of correlation does not necessarily mean that there is no inter-linking of variables.

Relationship between climatic and faunal events. — The climatic hypothesis predicted that a significant statistical relationship should occur between climatic and fau-

Table 3. Correlation coefficients between climatic variables for the 40,000 years dataset. $* = p < 0.05$ and $** = p < 0.01$.

	M. clim. variation	M. clim. changes	Max. $\delta^{18}O$	Min. $\delta^{18}O$	Mode $\delta^{18}O$	No cycles
Magnitude climatic changes	1					
Magnitude climatic variation	0.374	1				
Max. $\delta^{18}O$	−0.004	0.809**	1			
Min. $\delta^{18}O$	−0.168	0.609*	0.958**	1		
Mode $\delta^{18}O$	−0.215	−0.287	−0.35	−0.336	1	
Number cycles	−0.27	−0.576*	0.705**	0.637*	−0.206	1

Table 4. Significant correlation coefficients between faunal events and 40,000 years climatic variables (all species). $* = p < 0.05$ and $** = p < 0.01$.

	Richness	FRQ	LRQ
Number cycles		0.820**	
Max. $\delta^{18}O$			0.589*
Min. $\delta^{18}O$			0.654*
Mode $\delta^{18}O$	−0.686*		
Magnitude of changes	0.705*		

Table 5. Significant correlation coefficients between faunal events and 40,000 years climatic variables, with standing richness and rate quotients considered separately in small and large mammals (> 45 kg and < 45 kg). $* = p < 0.05$ and $'' = p < 0.01$.

	Richness > 45 kg	Richness < 45 kg	LRQ > 45 kg	FRQ < 45 kg
Number cycles	-0.872**	0.758**		0.869**
Max. $\delta^{18}O$	-0.644*	0.832**	0.729**	
Min. $\delta^{18}O$	-0.777**	0.881**		
Mode $\delta^{18}O$		-0.612*		
Climatic variation			0.908**	

nal events. A number of interesting patterns emerged in this analysis. Table 4 shows a significant positive correlation between first occurrences and number of cycles in each interval, as well as between LRQ (last occurrence rate quotient) and both maximum and minimum $\delta^{18}O$ values. Standing richness also is positively correlated with the magnitude of climatic variation, but negatively correlated with modal temperature. Fig. 2 shows the number of cycles and the FRQ. The positive relationship observed between both variables is statistically significant, according to a least squares regression adjustment: $R = 0.87$; $R^2 = 0.67$; $F = 22.6$ $(p < 0.01)$.

When we considered large and small mammals separately, there was a highly significant negative relationship between the richness of large mammals and the number of cycles (Table 5), but maximum and minimum $\delta^{18}O$ values were also significant. In contrast with the results of bivariate analysis, multiple regression (Table 6A) indicated that only number of cycles was statistically significant (Fig. 3A).

Table 6. Results of a multiple regression analyses using the significant variables from Table 5 as factors.

Data set	Factor	Model	p
A.	Intercept	included	0.0001
Dependent variable:	Number of cycles	included	0.0005
Standing richness > 45 kg	Max. $\delta^{18}O$	excluded	0.1850
	Min. $\delta^{18}O$	excluded	0.8280
B.	Intercept	included	0.0001
Dependent variable:	Min. $\delta^{18}O$	included	0.0001
Standing richness < 45 kg	Number of cycles	excluded	0.5350
	Mode $\delta^{18}O$	excluded	0.0310
	Max. $\delta^{18}O$	excluded	0.8000
C.	Intercept	included	0.0160
Dependent variable:	Climatic variation	included	0.0001
Last Rate Quotient > 45 kg	Max. $\delta^{18}O$	excluded	0.4090

The bivariate correlation suggested that, taken one at a time, four variables (minimum and maximum $\delta^{18}O$, number of cycles and modal temperature) had a significant positive relationship with richness of small mammal species (Table 5). Once these variables are included in a multiple regression, the significance of maximum $\delta^{18}O$, modal temperature and number of cycles disappears (see Table 6B and Fig. 3B).

Again, the data present in Table 5 show significant positive relationship of LRQ of large mammals with maximum $\delta^{18}O$ and magnitude of climatic variation. But when we considered both climatic variables as independent in the multiple regression, only the magnitude of climatic variation was statistically significant (Table 6C and Fig. 3C).

Fig. 3D shows the number of cycles and the FRQ of small mammal species. The positive relationship observed between both variables is statistically significant: $R = 0.86$; $R^2 = 0.75$; $F = 30.9$ ($p < 0.001$).

Discussion

Turnover and diversity. — Several lines of evidence indicate that in the Pleistocene–Holocene transition there were significant changes in the physical environment (Zárate 1999). Nevertheless, the pattern of first and last occurrence rate quotients at this time does not differ significantly from the expected values, and similar results are obtained in the bootstrapping analysis. In spite of this, the maximum in species diversity is reached around 14,000 years BP after which it declines. Only the biotic event, which took place during the middle Holocene, shows significant turnover with respect to the sampling.

Temperature effects. — The result confirms the view that climatic change is not a simple phenomenon and that different patterns of faunal change would be expected depending upon which climatic variables were considered. The most significant result is that there appears to be no statistically significant relationship between first or last appearances and changes in temperature. In contrast, some relationship was found between species richness and temperature. The richness of small mammals showed a significant positive relationship with the variation in low temperature.
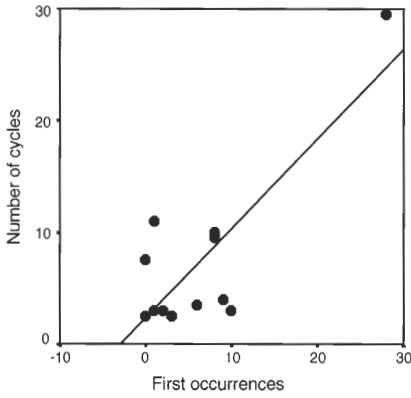
Fig. 2. Regression analysis of first occurrences and number of climatic cycles.
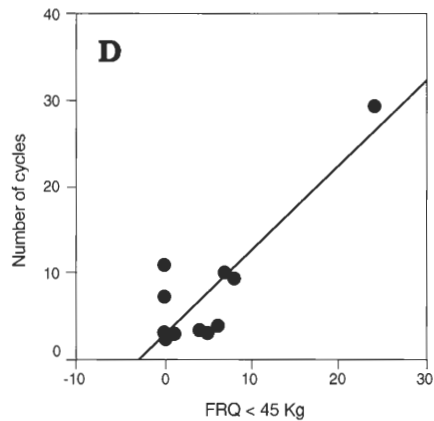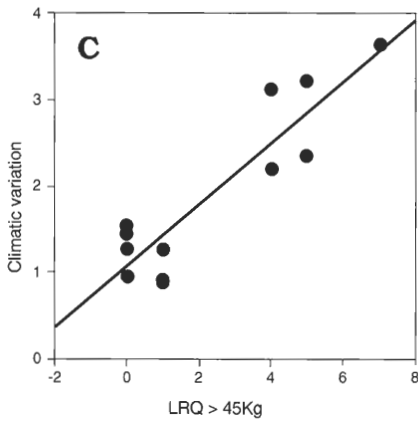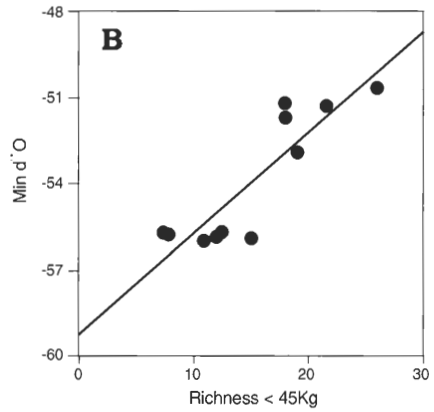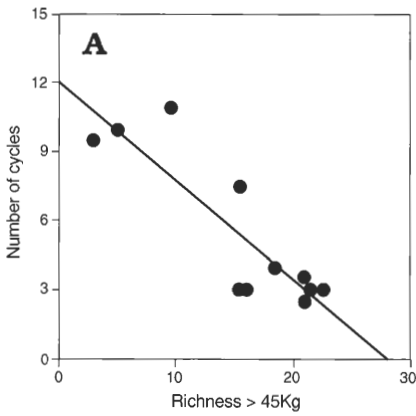

Fig. 3. **A**. Regression analysis of standing richness of large mammal and number of climatic cycles, $R^2 = 0.76$, $F = 28.4$ ($P < 0.001$). **B**. Regression analysis of standing richness of small mammal and minimum $\delta^{18}O$, $R^2 = 0.77$, $F = 31.2$ ($P < 0.001$). **C**. Regression analysis of last occurrence rate quotient of large mammal and magnitude of climatic variation, $R^2 = 0.82$, $F = 46.9$ ($P < 0.001$). **D**. Regression analysis of first occurrence rate quotient of small mammal and number of climatic cycles, $R^2 = 0.75$, $F = 30.9$ ($P < 0.001$).

Climatic stability. — The discussion above has focused on the actual change in climate as measured through temperature. However, it may be the case that the temperature itself is not the critical variable, but rather it is the degree of stability. It is possible that regardless of the direction of change, a decrease in climatic stability could have an effect on diversity. Climatic stability was measured in this analysis in terms of the number of major oscillations or cycles per unit of time, the amount of variation in temperature per unit of time (estimated from the difference between maximum and minimum δ^{18} O values), and the magnitude of change. The first occurrence rate quotients of small mammals did seem to be greater when marked climatic changes took place, as shown by their association with the number of cycles. When species richness is examined in relation to climatic stability an association is found with the magnitude of climatic change. Also, last occurrences of large mammals occurred following marked climatic change.

The potential impact of humans. — Research on the earliest hunter-gatherers of South America has focused mainly on the timing of human arrival, their dispersal, and their impact on the late Pleistocene mammal extinction. An association between human artefacts and extinct mammals has been shown since the last century (Roth 1899) and several specific studies have provided a chronological scheme that has united local sequences over part of South America. Nevertheless, most of these problems continue to be a key issue for American archaeology. Some broad syntheses of this dispersal and of the timing of human entry have been presented recently (Ardila & Politis 1989; Bryan 1986).

In the Pampean Region there are several archaeological sites where extinct mammals were recorded: Arroyo Seco 2, La Moderna, Cerro La China 1, Zanjón Seco 2, Laguna Tres Reyes (Politis *et al.* 1995) and Paso Otero 5. Each of these sites has special characteristics and different kinds of mammal associations.

In addition, the influence of the early hunter-gatherers is difficult to quantify. Not enough information is available to evaluate the extent to which the pressure caused by hunting affected the faunal equilibrium. Nevertheless, *prima facie,* this analysis suggests that the large mammal extinction process was a phenomenon that was initiated prior to the arrival of humans in the Pampean Region. There is evidence that indicates humans were present in the Pampean Region around 11,000 BP, and that they coexisted with the now extinct large mammals for three thousand years or more. In summary, this analysis supports the idea that the extinction event began a few thousand years before the arrival of humans and that it was primarily climatic change, followed by several millennia of coexistence with the hunter-gatherer group, that selected large mammals for extinction. Politis *et al.* (1995) suggest that humans played a secondary role in the extinction of the native South American fauna, but were more important for the extinction of the immigrant fauna such as horses and mastodons.

Final remarks

The effect of climate on mammal evolution can be said to be complex. Climate does have an effect on migration, origination, and extinction, but our results suggest that the effect is different for large and small mammals. In the entire set of our analyses,

only the diversity of small mammals shows a statistically significant association with respect to variations in low temperature. In contrast, the influence of climate stability (magnitude of climatic variation) is more marked on the extinction of large mammals.

There is a lot of evidence and theory to support a relationship between body mass and climate in the ecology and the evolution of mammals. Body size is the single most useful predictor of a species biology, because it is one of the most important determinants of body architecture and physiology (Schmidt-Nielsen 1975; Alexander *et al.* 1981; McNab 1990) and ecology (Hutchinson & MacArthur 1959; McNab 1971; Damuth 1981; Janis 1988). Recent studies (Lessa & Fariña 1996; Lessa *et al.* 1997), based on late Pleistocene mammals from America, suggested that larger mammals were more prone to extinction than smaller ones. They showed that body mass was the primary factor statistically associated with the probability of extinction. Our analysis supports this hypothesis.

Nevertheless, the data presented here suggest that, even allowing for this interpretation of relationships between climate and faunal events, climatic change alone is not sufficient to explain the patterns of species richness and first and last occurrences. Other important factors that played a significant role were local competitive conditions. Climatic events will alter the environments and resources within those environments. This will lead to change in competitive relationships between and within species, and it is these modified competitive relationships that are likely to lead to evolutionary repercussions.

On the other hand, the impact of humans on large mammal extinction in the Pampean Region was probably not as great as in North America, but was still important. In sum, we hypothesised that climatic change, primarily, followed by several millennia of coexistence with the hunter-gatherer group, could have selected large mammals for extinction.

Acknowledgements

References

Alexander, R.M.N., Jayes, A.S., Maloiy, G.M.O., & Wathuta, E.M. 1981. Allometry of the leg muscles of mammals. — *Journal of Zoology* **194**, 539–552.
Alroy, J. 1992. Conjunction among taxonomic distributions and the Miocene mammalian biochronology of the Great Plains. — *Paleobiology* **18**, 326–343.
Alroy, J. 1994. Appearance event ordination: a new biochronologic method. — *Paleobiology* **20**, 191–207.
Ardila, G.C. & Politis, G. 1989. Nuevos datos para un Viejo Problema: Investigaciones y discusiones en torno del poblamiento de América del Sur. — *Boletín del Museo del Oro (Bogotá)* **23**, 3–45.

Axelrod, D.I. 1967. Quaternary extinction of large Mammals. — *University of California Publications in Geological Sciences* **74**, 1–42.

Barry, J.C., Morgan, M.E., Flynn, L.J., Pilbeam, D., Jacobs, L.L., Lindsay, E.H., Raza, S.M., & Solounias, N. 1995. Patterns of faunal turnover and diversity in the Neogene Siwaliks of Northern Pakistan. — *Palaeogeography, Palaeoclimatology, Palaeoecology* **115**, 209–226.

Behrensmeyer, A.K., Todd, N.E., Potts, R., & McBrinn, G.E. 1997. Late Pliocene faunal turnover in the Turkana Basin, Kenya and Ethiopia. — *Science* **278**, 1589–1594.

Bonadonna, F.P., Leone, G., & Zanchette, G. 1995. Composición isotópica de los fósiles de gasterópodos continentales de la provincia de Buenos Aires. Indicaciones Paleoclimáticas. *In*: M.T. Alberdi, G. Leone, & E.P. Tonni (eds.), *Evolución biológica y climática de la Región Pampeana durante los últimos 5 millones de años. Un ensayo de correlación con el Mediterráneo occidental*, 75–104. Monografías, Museo Nacional de Ciencias Naturales, CSIC, Madrid.

Borrero, L. 1984. Pleistocene extinctions in South America. — *Quaternary of South America and Antarctic Peninsula* **2**, 115–126.

Bryan, A. 1986. *New Evidence for the Pleistocene Peopling of the America*. 368 pp. Center for the Study of the Early Man, University of Maine, Orono.

Carbonari, J.E., Huarte, R.A., & Figini, A.J. 1992. Miembro Guerrero, formación Luján (Pleistoceno, pcia Buenos Aires) edades [14]C. *Actas III Jornadas Geológicas Bonaerense*, 245–247.

Clapperton, C. 1993. *Quaternary Geology and Geomorphology of South America*. 796 pp. Elsevier, Amsterdam.

Damuth, J.D. 1981. Population density and body size in mammals. — *Nature* **290**, 699–700.

Dillon, A. & Rabassa, J. 1985. Miembro La Chumbiada, Formación Luján (Pleistoceno, provincia de Buenos Aires); una nueva unidad estratigráfica del valle del río Salado. *Resúmenes I Jornadas Geológicas Bonaerenses*, p. 27.

Fidalgo, F., De Francesco, F.O., & Colado, U. 1973. Geología superficial en las hojas Castelli, J.M. Cobo y Monasterio (Pcia de Buenos Aires). — *Actas V Congreso Geológico Argentina* **4**, 27–39.

Fidalgo, F., De Francesco, F.O., & Pascual, R. 1975. Geología superficial de la Llanura Bonaerense. *Relatorio VI Congreso Geológico Argentino*, 103–138.

Fidalgo, F., Riggi, J.C., Correa, H., & Porro, N. 1991. Los 'Sedimentos Postpampeanos' continentales en el ámbito sur bonaerense. — *Revista Asociación Geológica Argentina* **46**, 239–256.

Foley, R.A. 1993. African terrestrial primates: the comparative evolutionary biology of *Theropithecus* and the Hominidae. *In*: N. Jablonski (ed.), Theropithecus *as a Case Study in Evolutionary Biology*, 245–270. Cambridge University Press, Cambridge.

Foley, R.A. 1994. Speciation, extinction and climatic change in hominid evolution. — *Journal of Human Evolution* **26**, 275–289.

Gilinsky, N.L. 1991. Bootstrapping and the fossil record. *In*: N.L. Gilinsky & P.W. Signor (eds.), *Analytical Paleobiology*, 185–206. Paleontological Society of the University of Tennessee, Knoxville.

Gingerich, P.D. 1987. Extinction of Phanerozoic marine families. — *Geological Society of America, Abstracts with Programs* **19**, 677.

Graham, R.W. & Grimm, E.C. 1990. Effects of Global Climate Change on the Patterns of Terrestrial Biological Communities. — *Trends in Ecology & Evolution* **5**, 289–292.

Graham, R.W. & Lundelius, E.L. 1984. Coevolutionary disequilibrium and Pleistocene extinction. *In*: P.S. Martin & R.G. Klein (eds.), *Quaternary Extinctions: A Prehistoric Revolution*, 223–249. University of Arizona Press, Tucson.

Grayson, D.K. 1984. Explaining Pleistocene Extinctions. Thoughts on the structure of a debate. *In*: P.S. Martin & R.G. Klein (eds.), *Quaternary Extinctions: A Prehistoric Revolution*, 807–823. University of Arizona Press, Tucson.

Guthrie, R.D. 1984. Mosaics, allelochemics and nutrients. An ecological theory of late Pleistocene megafaunal extinction. *In*: P.S. Martin & R.G. Klein (eds.), *Quaternary Extinctions: A Prehistoric Revolution*, 259–298. University of Arizona Press, Tucson.

Harper, C.W. Jr. 1975. Standing diversity of fossil groups in successive intervals of geologic time: A new measure. — *Journal of Paleontology* **49**, 752–757.

Heusser, C.J. 1974. Vegetation and climate of the southern chilean lake district during and since the last interglaciation. — *Quaternary Research* **4**, 290–315.

Hutchinson, G.E. & MacArthur, R.H. 1959. A theoretical ecological model of size distribution among species of animals. — *The American Naturalist* **93**, 117–125.

Iriondo, M., & Garcia, N.O. 1993. Climatic variations in the Argentina plains during the last 18,000 years. — *Palaeogeography, Palaeoclimatology, Palaeoecology* **101**, 209–220.

Janis, C. M. 1988. An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preferences. *In*: D.E. Russell, J.P. Santoro & D. Sigogneau-Russell (eds.), Proceedings of the VIIth International Symposium on Dental Morphology. — *Mémoires Museum national Histoire natural, Paris* **53**, 367–387.

Lessa, E.P. & Fariña, R.A. 1996. Reassessment of extinction patterns among the Late Pleistocene mammals of South America. — *Palaeontology* **39**, 651–662.

Lessa, E.P., Van Valkenburgh, B., & Fariña, R.A. 1997. Testing hypotheses of differential mammalian extinctions subsequent to the Great American Biotic Interchange. — *Palaeogeography, Palaeoclimatology, Palaeoecology* **135**, 157–162.

Maas, M.C., Anthony, M.R.L., Gingerich, P.D., Gunnell, G.F., & Krause, D.W. 1995. Mammalian generic diversity and turnover in the Late Paleocene and Early Eocene of the Bighorn and Crazy Mountains Basins, Wyoming and Montana (USA). — *Palaeogeography, Palaeoclimatology, Palaeoecology* **115**, 181–207.

MacArthur, R.H. & Wilson, E.O. 1967. *The Theory of Island Biogeography*. 207 pp. Princeton University Press, Princeton.

Martin, P.S. 1984. Prehistoric overkill: the global model. *In*: P.S. Martin & R.G. Klein (eds.), *Quaternary Extinctions: A Prehistoric Revolution*, 354–403. University of Arizona Press, Tucson.

McNab, B.K. 1971. On the ecological significance of Bergmann's rule. — *Ecology* **52**, 845–854.

McNab, B.K. 1990. The physiological significance of body size. *In*: J. Damuth & B.J. MacFadden (eds.), *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*, 11–23. Cambridge University Press, Cambridge.

Mercer, J.H. 1982. Holocene glacier variations in southern Patagonia. — *Striae* **18**, 35–40.

Merlivat, L., Jouzel, J., & Pourchet, M. 1979. A 30,000 year isotope climatic record from Antarctic ice. — *Nature* **280**, 644–648.

Politis, G.G. & Prado, J.L. 1990. La influencia del hombre en las extinciones faunísticas del Pleistoceno/Holoceno en América: el caso Pampeano. *Memorias del Simposio de Arqueología y Antropología física del V Congreso Nacional de Antropología, Memoria eventos científicos ICFES*, Colombia, 31–63.

Politis, G.G., Prado, J.L., & Beukens, R.P. 1995. The human impact in Pleistocene–Holocene extinctions. *In*: E. Johnson (ed.), *South America – The Pampean Case. Ancient Peoples and Landscapes*, 187–205. Museum of Texas Tech University, Lubbock, Texas.

Porter, S.C., Clapperton, C.M., & Sugden, D.E. 1992. Chronology and dynamics of deglaciation along and near the Strait of Magellan, southernmost South America. — *Sveriges Geologiska Undersökning*, Ser. Ca. **81**, 233–239.

Prado, J.L., Azanza, B., Alberdi, M.T., & Gómez, G. (in press). Mammal community and global change during late Pleistocene–Holocene in the Pampean Region, Argentina. *Festschrifrt in Memory of Professor Wilhelm Schüle*.

Quattrocchio, M.E., Borromei, A.M., & Grill, S. 1994. Cambios vegetacionales y fluctuaciones paleoclimáticas en el Pleistoceno tardío, Holoceno del Sudoeste de la provincia de Buenos Aires (Argentina). — *Resúmenes VI Congreso Argentino de Paleontología y Biostratigrafía*, Trelew-Chubut, p. 10.

Roth, S. 1899. El mamífero misterioso de la Patagonia *Grypotherium domesticum*. II. Descripción de los restos encontrados en la Caverna de Última Esperanza. — *Revista del Museo de La Plata* **9**, 421–453.

Schnack, E.J. 1987. The emerged Quaternary shorelines in Argentina. Eustatic signature and correlations: Atlantic South Ocean. *Resúmenes 'Cuaternario de América del Sur', Reunión Final. Proyecto 201 (IGCP-UNESCO)*.

Schmidt-Nielsen, K. 1975. Scaling in biology: the consequences of size. — *Journal Experimental of Zoology* **194**, 287–307.

Tonni, E.P. & Fidalgo, F. 1978. Consideraciones sobre los cambios climáticos durante el Pleistoceno tardío – Reciente en la provincia de Buenos Aires. Aspectos ecológicos y zoogeográficos relacionados. — *Ameghiniana* **15**, 235–253.

Vrba, E.S. 1985. Environment and evolution: alternative causes of the temporal distribution of evolutionary events. — *South African Journal of Science* **81**, 229–236.

Vrba, E.S. 1988. Late Pliocene climatic events and human evolution. *In*: F. Grine (ed.), *Evolutionary History of the 'Robust' Australopithecines*, 405–426. Aldine de Gruyter, New York.

Vrba, E.S. 1993. Turnover-pulses, the Red Queen, and related topics. — *American Journal of Science* **293a**, 418–452.

Vrba, E.S., Denton, G.H., Partridge, T.C., & Burckle, L.H. (eds.) 1995. *Paleoclimate and Evolution with Emphasis on Human Origins*. 547 pp. Yale University Press, New Haven and London.

Webb, S.D. & Opdyke, N.D. 1995. Global climatic influence on Cenozoic Land Mammal Faunas. *In*: Broad on Earth Sciences and Resources (ed.) *Effects of Past Global Change on Life*, 184–208. Studies in Geophysics National Academy Press, Washington.

Zárate, M.A. 1999. The Pleistocene/Holocene transition and Human Occupation in South America. — *Quaternary International* **53–54**, 1–99.

Zárate, M. & Blasi, A. 1993. Late Pleistocene–Holocene Eolian deposits of the Southern Buenos Aires province, Argentina: A preliminary model. — *Quaternary International* **17**, 15–20.

Zárate, M. & Flegenheimer, N. 1991. Geoarchaeology of the Cerro La China Locality (Buenos Aires, Argentina): Site 2 and Site 3. — *Geoarchaeology* **6**, 273–294.