

THE EXTINCTION OF SOME SOUTH AMERICAN CAMELIDS: THE CASE OF *Lama (Vicugna) gracilis*

Jorge Cajal¹, Eduardo P. Tonni², and Viviana Tartarini²

¹Fundación para la Conservación de las Especies y el Medio Ambiente (FUCEMA), Av. de Mayo 1190, 2° piso, 1085 Ciudad Autónoma de Buenos Aires, Argentina [Corresponding author: Jorge Cajal <j_cajal@hotmail.com>]. ²División Paleontología Vertebrados, Museo de La Plata, Paseo del Bosque s/n°, B1900FWA La Plata, Argentina.

ABSTRACT. *Lama (Vicugna) gracilis* (Gervais and Ameghino, 1881) is a Camelidae that inhabited the low plains of Argentina and Uruguay during the Pleistocene and early Holocene. Considering that *Lama gracilis* was a vicariant of *L. vicugna* in the low plains, sympatry cases between *Lama guanicoe* and *Lama vicugna* are analyzed to test the hypothesis that considers the competence for the same resource as the cause of extinction of *Lama gracilis*. It is concluded that the reduced populations of *L. gracilis* were forced to extinction especially by hunting pressure of paleoindian groups.

RESUMEN. La extinción de algunos camélidos sudamericanos: el caso de *Lama (Vicugna) gracilis*. *Lama (Vicugna) gracilis* (Gervais y Ameghino, 1881) es un camélido que habitó las planicies bajas de la Argentina y Uruguay durante el Pleistoceno y el Holoceno temprano. Considerando que *Lama gracilis* fue un vicariante de *L. vicugna* en las planicies bajas, se analizan los casos de simpatria entre *Lama guanicoe* y *Lama vicugna* para poner a prueba la hipótesis que considera la competencia por el mismo recurso, como la causa de la extinción de *Lama gracilis*. Se concluye que las poblaciones reducidas de *L. gracilis* fueron forzadas a la extinción por la presión de caza de grupos paleoindios.

Key words. Camelidae. Extinction. Pleistocene. South America.

Palabras clave. América del Sur. Camelidae. Extinción. Pleistoceno.

Although there is no consensus among authors regarding the taxonomic status of living South American camelids, there is agreement in recognizing two wild species: the guanaco, *Lama guanicoe* Müller, 1776, and the vicuña *Vicugna vicugna* (Molina) Miller, 1924 (or *Lama vicugna* Molina, 1782; for a recent discussion from a molecular and chromosomal point of view, see Marín et al., 2007).

Menegaz et al. (1989) reframed the taxonomy of the genus *Lama* through a multivariate morphological and morphometric study, including the modern South American Camelidae and those of the Pleistocene of the

Patagonian and Pampean regions. These authors consider the guanaco as a single species included in the subgenus *Lama*: *Lama (Lama) guanicoe*, and the vicuña as a subgenus of *Lama* including two species, the living one *Lama (Vicugna) vicugna* (Molina, 1782) and the extinct *Lama (Vicugna) gracilis* (Gervais and Ameghino, 1881). They conclude that *Lama (V.) gracilis* and *Lama (V.) vicugna* are more closely related to each other than with *Lama (Lama) guanicoe*.

Recently, Weinstock et al. (2009) sustained that "In light of the combined genetic and morphological arguments discussed above, we

argue that the fossil remains assigned to *L. gracilis* probably belong to *V. vicugna*...” In any case, it should be noted that molecular analysis, based on few genetic markers (e.g. from mt DNA) not always match fossil records (see Cajal, 2006; Marin et al., 2006).

During the late Pleistocene and early Holocene, *Lama gracilis* inhabited the Patagonian region and east of the Pampean region. Outside Argentina, there are records in Uruguay for the late Pleistocene before 40 000 radiocarbon years BP (Ubilla, 2004) and for the early Holocene (10 480 to 11 090 radiocarbon years BP; cited as *Lama* sp. by Ubilla et al., 2007; M. Ubilla personal communication, 2008).

In Argentina, *L. gracilis* is stratigraphically associated to *L. guanicoe* at least in four sites locations of the Santa Cruz Province: La María (10 967 ± 55 radiocarbon years BP, Paunero, 2002), Los Toldos (12 600 ± 650 radiocarbon years BP; Cardich et al., 1973; Cardich, 1987), El Ceibo (ca. 11 000 radiocarbon years BP; Cardich, 1987) and Piedra Museo (units 6 to 4, dated between 12 890 ± 90 and 9230 ± 105 radiocarbon years BP; Miotti and Salemme, 2003). In the Chilean sector of the island of Tierra del Fuego, in the site Tres Arroyos 1, one mandibular symphysis referred to *Vicugna* sp. by Prieto and Canto (1997) probably pertains to *L. gracilis*; it is stratigraphically associated to *L. guanicoe* in a level dated 10 630 ± 90 radiocarbon years BP (Massone and Prieto, 2004). This radiocarbon date is a taxon-date obtained on bone collagen, and it is similar to other three taxon-dates obtained on *L. guanicoe* bones from the site Cueva del Medio (10 450 ± 100, 10 710 ± 190, and 10 850 ± 130 radiocarbon years BP; see Nami and Nakamura, 1995). In the great majority of cases, in which not taxon-dates proved the coexistence of both species, the stratigraphical association averaged a short period of time. Consequently, it is considered as coeval in a broad sense. In all these sites, the remains of *L. guanicoe* are always dominant over those of *L. gracilis*.

According to the information given by Menegaz et al. (1989) and new findings, at the east of the Pampean region (Buenos Aires

province) there is a stratigraphic association between *L. guanicoe* and *L. gracilis* in the middle Pleistocene (< 0.78 Ma and > 0.126 Ma) of the Reconquista River. In the late Pleistocene, this association is verified in Paso Otero (Necochea County), in the La Chumbiada and Guerrero members of the Luján Formation. The Guerrero Member was dated between ca. 24 000 and ca. 10 000 radiocarbon years BP (Tonni et al., 2003), whereas the La Chumbiada Member seems to be older than 35 000 radiocarbon years BP (L. Pomi, personal communication 2008), being its temporal extension unknown.

The vicuña has a poor palaeontological record, restricted to the areas of its modern distribution; the oldest records are that of the Atacama dessert, Chile, with a radiocarbon dating of 11 700 radiocarbon years BP (Kuch et al., 2002) and between 12 600 and 10 200 cal. year BP (Grosjean et al., 2005).

In this paper, the cases of sympatry between *L. guanicoe* and *L. vicugna* are taken as modern analogues to test the hypothesis which considers the competition for the same resource as the cause for the extinction of *L. gracilis*.

Today, the vicuña inhabits the high plains or Andean altipampas from northern Peru, Western Bolivia, North-Eastern and Central Chile, and North-Western Argentina down to the north region of San Juan Province (Cajal, 1991). In Argentina, it inhabits the Puna and high-Andean areas contiguous with the Puna. The vicuña has three levels of occupation in the territory with respect to the guanaco: a) altitudinal segregation, where there is no overlap between both species (in Peru, northeast of Bolivia, north of Chile –from 8° to 20° S; b) they share the altitudinal level but with incipient spatial segregation, in Tarija (Bolivia), Sierras de Zenta, Santa Victoria, Chañi and Lipán, in Jujuy, Abra de Acay in Salta and high-Andean areas (excluded de Puna stricto sensu) in Catamarca; c) high superposition degree (sympatry), in the altipampas of a fringe of the Cordillera Frontal between 27° 56' S and 29° 35' S.

Studies performed during four consecutive years (1978-1984) in the Cordillera Frontal,

San Juan Province, demonstrated that both the vicuña and the guanaco showed a constant pattern relative to the mean size of their respective family groups, social structure, territorial behaviour (intra and interspecific), and population increase (census number per years). These species also display a high degree of diet overlap, and to some extent of spatial use, regardless of the differences in the pattern of habitat use and preference of sectors according to the social group and time of the year (Cajal, 1989, Cajal and Bonaventura, 1998).

In the sympatry area, both guanacos and vicuñas are clearly grazers (although they also browse on bushes and cactaceae). According to Cajal (1989), in the case of the vicuña the grass represents 88% and shrub / cacti 12% of diet, while in guanaco the grass represents 87% and shrub / cacti 13% of diet. Coexisting wild camelids respond in the same way when facing the available food at a given place and time (e.g. *Stipa* grass). Certainly, the genus *Stipa* is the main component of the diet of both species. A test of multiple comparisons among plant species ordered according to the amount of their mean frequency in the diet showed that *Stipa* is in both camelid species, the most important group, clearly distinguished from other plants (Cajal, 1989). This larger presence of *Stipa* in the respective diets is related to supply. Within perennial plants, this genus is outstanding by its larger percentile presence (> 40 %) when analyzing the plant cover of the high plain (altipampas) or steppes of the region.

The physiography where the vicuñas and guanacos are sympatric is like a high plains archipelago originated by ravines, creeks, rivers, and mountains. This configuration defines limited areas or sectors. A comparative analysis of the use of these sectors by both species (test of equality of means with heterogeneous variances using the Games and Howell method, MCHETV, see Sokal and Rohlf, 1981), revealed that for both, the guanaco and the vicuña, some sectors were significantly different to others, while others did not show such differences. Considering both species as a block, some sectors were used in a signifi-

cantly different way, while in others, differences were not observed. According to Q values of this method, the vicuña turned out more sensitive than the guanaco with respect to the different sectors (Cajal, 1989). It should be noted that two species by definition have always differences, regardless how close related they are.

The body mass of *L. gracilis* estimated with regression equations for artiodactyls (Scott, 1990), based on the transverse width of the head of the humerus and maximum width of the distal epiphysis, is between 50.36 and 64.32 kg. Hence, its mass is similar to that of the vicuña (45-55 kg) and quite different from that of the guanaco (80-120 kg).

Both *L. gracilis* and the vicuña show dental specializations for abrasive grasses (i.e., *Stipa*). Functionally, the dental specialization of incisors in both species (see Menegaz et al., 1989) tends to optimize the intake of abrasive grasses (pastures) with high silica content. In this regard, a positive correlation has been mentioned between silica and palatability (Adler et al., 2004).

L. gracilis inhabited, during the late Pleistocene and early Holocene, the low plains from the Pampean region to Patagonia. Considering that the oldest records belong probably to the middle Pleistocene of the Pampean region, Menegaz et al (1989:170-171) postulated a southward retraction of *L. gracilis* during the late Pleistocene. There are no evidences to confirm this hypothesis, since in Patagonia there is no paleontological record of the late Pleistocene prior to ca. 12 000 years BP. *L. gracilis* seems to have followed the expansion of the Pampean fauna toward the end of the Pleistocene –around 12 000 years BP, as verified with several species present in both regions during that period (Borrero, 1999, 2005; Tonni and Carlini, 2008).

Menegaz et al (1989) pointed out that post-glacial climatic changes affected the distribution of different groups of Grammineae and influenced deeply in the retraction and extinction of *L. gracilis*. In this sense, they suggest that the present distribution of *L. vicugna* is related to that of microthermal grammineae

groups, especially to those best adapted to arid environments, rather than to those specialized to life in mountains. On the contrary, the guanaco is a generalist herbivore, adapted to a wide range of vegetation and habitats, which places it, according to some authors, out of the competence with other herbivores of this size (Raedeke and Simonetti, 1988).

According to Menegaz et al. (1989) the extinction of *L. gracilis* was caused by an unfavourable competence with the guanaco in the exploitation on similar niches (Menegaz et al., 1989:171), being the competence a causal source of extinction. However, using a modern analogue, in sympatry, both guanacos and vicuñas feed on the same food resources. If resources are scarce, competition may be the outcome of shared limiting resources. It does not matter who ate the food if it is gone. The shortage can affect the individuals of both species as a whole. There is no evidence for competition at that time and place in the Cordillera Frontal. However, it does not indicate that competition between individuals of the same species and between those of both species occurs when food resources are scarce. Neither does it mean that the competition caused by food scarcity necessarily implies the displacement (or extinction) of one species by the other; nor that it is a factor involved in future evolutionary changes.

Other causes that led to extinction must be considered, beyond the interspecific competence. One of them is the hunting burden exerted by paleoindians, a hypothesis taken to an extreme by Martin (1984) in his model of blitzkrieg, as the cause of massive extinction of the end of the Pleistocene in North America, and by extension, in South America.

The zooarchaeological records demonstrate the effects of hunting pressure on camelids, both in guanaco and *L. gracilis*. However, the relative frequency of the remains indicates a bias towards the first species with respect to the second. This may result from the reduced populations of *L. gracilis* by the end of the Pleistocene. In this regard, Cione et al. (2009) considered that the temperature and humidity increase of the interglacials, during the Qua-

ternary, caused a decrease of the biomass of the mammals adapted to open areas. These authors indicate that the studies based on geochemical and dust proxies in Greenland, Antarctica, and South America glaciers attest that the present interglacial period is not substantially different from the preceding ones. The arrival of humans in South America was the sole new biological or geological event that occurred in the present interglacial period. In consequence, the entrance of men and their pressure on a numerically reduced population would have been the factor that led to local extinction (extirpation) or total (global) extinction. The different extinction of related species (e.g., between Cervidae and Camelidae, cited by Cione et al., 2009), may correspond to subtle differences in ecological plasticity.

If *L. gracilis*—unlike the guanaco—, had environmental sensitivity and strict trophic and habitat requirements, similar to those of the vicuña in modern high plains, the climatic change in low plains (Tonni et al., 1999) could have reduced their populations up to levels in which hunting pressure of paleoindian groups led them to extinction.

Alternatively, if it is proved that *L. gracilis* and *L. vicugna* (or *Vicugna vicugna*) are the same species (see Weinstock et al., 2009), the local extinction in the low areas and their retraction to regions of the high plains or Andean altipampas, can be attributed also to the anthropic action that not only includes the hunt burden but also other factors (i.e., environmental change and etological changes caused by the human presence).

Acknowledgements. The authors are grateful to Agencia Nacional de Promoción Científica y Tecnológica, Comisión de Investigaciones Científicas de la provincia de Buenos Aires, and Universidad Nacional de La Plata for financial support.

LITERATURE CITED

ADLER PB, DG MILCHUNAS, WK LAUENROTH, OE SALA, and IC BURKE. 2004. Functional traits of graminoids in semi-arid steppes: a test of grazing histories. *Journal of Applied Ecology* 41:653-663.

- BORRERO LA. 1999. The faunas of the Pleistocene/Holocene boundary in the Seno de la Ultima Esperanza, Chile. Pp. 59-62, *in*: Zooarchaeology of the Pleistocene/Holocene Boundary (JC Driver, ed.). BAR Internacional Series 800.
- BORRERO LA. 2005. Taphonomy of late Pleistocene faunas at Tierra del Fuego-Patagonia. *Journal of South America Earth Sciences* 20:115-120.
- CARDICH A. 1987. Arqueología de Los Toldos y El Ceibo (Provincia de Santa Cruz, Argentina). Investigaciones paleoindias al sur de la línea ecuatorial. *Estudios Atacameños* 8:98-117.
- CARDICH A, L CARDICH, and A HAJDUK. 1973. Secuencia arqueológica y cronológica radiocarbónica de la cueva 3 de Los Toldos (Santa Cruz, Argentina). *Relaciones Sociedad Argentina de Antropología* 7:85-123.
- CAJAL JL. 1989. Uso de hábitat por vicuñas y guanacos en la Reserva San Guillermo, Argentina. *Vida Silvestre Neotropical* 2:21-31.
- CAJAL JL. 1991. An integrated approach toward the management of wild camelids in Argentina. Pp. 305-321, *in*: Latin American Mammalogy: History Biodiversity and Conservation (M Mares and D Schimidly, eds). University of Oklahoma Press.
- CAJAL JL. 2006. Revisión de Libros: Investigación, Conservación y Manejo de Vicuñas. B Vila (ed). 2006. Proyecto MACS-Argentina-INCO-Unión Europea. *Mastozoología Neotropical* 13:283-287.
- CAJAL JL and S BONAVENTURA. 1998. Densidad poblacional y dinámica de los grupos familiares de guanacos y vicuñas en la Reserva de Biosfera de San Guillermo. Pp. 161-167, *in*: Bases para la conservación y manejo de la puna y cordillera frontal de Argentina: El rol de las reservas de biosfera (JL Cajal, JJ García Fernández, and R Tecchi, eds.). UNESCO (Uruguay) – FUCEMA, Montevideo.
- CIONE AL, EP TONNI, and LH SOIBELZON. 2009. Did humans cause the late Pleistocene-early Holocene mammalian extinctions in South America in a context of shrinking open areas? Pp. 125-144, *in*: American Megafaunal extinctions at the end of the Pleistocene (G Haynes, ed.) . Springer Publ.
- GROSJEAN M, L NUÑEZ, and I CARTAJENA. 2005. Palaeoindian occupation of the Atacama Desert, northern Chile. *Journal of Quaternary Science* 20:643-653.
- KUCH M, N ROHLAND, JL BETANCOURT, C LATORRE, S STEPPAN, and HN POINAR. 2002. Molecular analysis of an 11,700-year-old rodent midden from the Atacama Desert, Chile. *Molecular Ecology* 11:913-924.
- MARÍN JC, AE SPOTORNO, and JC WHEELER. 2006. Sistemática molecular y filogeografía de camélidos sudamericanos: Implicancias para su conservación y manejo. Pp. 85-100, *in*: Investigación, Conservación y Manejo de Vicuñas (B Vilá, ed.). Proyecto MACS-Argentina-INCO-Unión Europea, Buenos Aires.
- MARÍN JC, C ZAPATA, BA GONZÁLEZ, C BONACIC, JC WHEELER, C CASEY, M BRUFORD, RE PALMA, E POLIN, MA ALLIENDE, and AE SPOTORNO. 2007. Sistemática, taxonomía y domesticación de alpacas y llamas: nueva evidencia cromosómica y molecular. *Revista Chilena de Historia Natural* 80:121-140.
- MARTIN P. 1984. Prehistoric overkill: the global model. Pp 354-403, *in*: Quaternary Extinctions: A Prehistoric Revolution (PS Martin and RG Klein, eds). University of Arizona Press.
- MASSONE M and A PRIETO. 2004. Evaluación de la modalidad cultural Fell 1 en Magallanes. *Chungara*, vol. especial, pp. 303-315, Arica, Chile.
- MENEGAZ AN, FJ GOIN, and E ORTIZ JAUREGUIZAR. 1989. Análisis morfológico y morfométrico multivariado de los representantes fósiles y vivientes del género *Lama* (Artiodactyla, Camelidae). Sus implicancias sistemáticas, biogeográficas, ecológicas y biocronológicas. *Ameghiniana* 26:153-172.
- MIOTTI LL and MC SALEMME. 2003. When Patagonia was colonized: people mobility at high latitudes during Pleistocene/Holocene transition. *Quaternary International* 109-110:95-111.
- MIOTTI L, M VÁZQUEZ, and D HERMO. 1999. Piedra Museo: Un yamagoo pleistocénico de los colonizadores de la Meseta de Santa Cruz: El estudio de la arqueofauna. *Actas de las III Jornadas de Arqueología de la Patagonia*, pp. 113-136. Bariloche.
- NAMI HG. and T NAKAMURA. 1995. Cronología radiocarbónica con AMS sobre muestras de hueso procedentes del sitio Cueva del Medio (Ultima Esperanza, Chile). *Anales del Instituto de la Patagonia* 23:125-134.
- PAUNERO RS. 2002. The presence of a Pleistocenic colonizing culture in La Maria archaeological locality: Casa del Minero 1. Pp. 127-132, *in*: Ancient Evidences for Paleo South Americans: From Where The South Winds Blow (L Miotti, M Salemme, and N Flegenheimer, ed.). Texas A&M University Press.
- PRIETO A and J CANTO. 1997. Presencia de un lamoide atípico en la cueva Lago Sofa 4 (Última Esperanza) y Tres Arroyos (Tierra del Fuego) Región de Magallanes, Chile. *Anales del Instituto de la Patagonia (Serie Ciencias Humanas)* 25:147-150.
- RAEDEKE KJ and JA SIMONETTI. 1988. Food habits of *Lama guanicoe* in the Atacama desert of northern Chile. *Journal of Mammalogy* 69:198-201.
- SCOTT KM. 1990. Postcranial dimensions of ungulates as predictors of body mass. Pp. 301-336, *in*: Body Size in Mammalian Paleobiology: Estimation and Biological Implications (J Damuth and BJ MacFadden, eds.). Cambridge University Press.
- SOKAL R. and F ROHLF 1981. *Biometry: The principles and practice of statistics in biology research*. Second edition, 859 pp. W. H. Freeman & Co.
- TONNI EP, AL CIONE, and AJ FIGINI. 1999. Predominance of arid climates indicated by mammals in the pampas of Argentina during the late Pleistocene and Holocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 147:257-281.
- TONNI EP, R HUARTE, JE CARBONARI, and A FIGINI. 2003. New radiocarbon chronology for the Guerrero Member of the Luján Formation (Buenos

- Aires, Argentina): palaeoclimatic significance. *Quaternary International* 109-110:45-48.
- TONNI EP and AA CARLINI. 2008. Neogene vertebrates from Patagonia (Argentina): their relationship with the most significant climatic changes. Pp. 269-284, *in*: *The Late Cenozoic of Patagonia and Tierra del Fuego* (J Rabassa, ed.). *Development in Quaternary Science* 11
- UBILLA M. 2004. Mammalian biostratigraphy of Pleistocene fluvial deposits in northern Uruguay, South America. *Proceedings of the Geologists' Association* 115:347-357.
- UBILLA M, D PEREA, A RINDERKNECHT, and A. CORONA. 2007. Mamíferos del cuaternario de Uruguay. *Bioestratigrafía y paleoambientes*. Workshop "Cuaternario RS: integrando conocimientos", pp. 45-47, Canoas, Rio Grande do Sul, Brasil.
- WEINSTOCK J, B SHAPIRO, A PRIETO, JC MARÍN, BA GONZÁLEZ, PGM THOMAS, and E WILLERSLEV. 2009. The Late Pleistocene distribution of vicuñas (*Vicugna vicugna*) and the "extinction" of the gracile llama (*Lama gracilis*): New molecular data. *Quaternary Science Reviews* 28:1369-1373.