

Darwin's Legacy:

The Status of Evolutionary Archaeology in Argentina

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HUMAN HOLOCENE COLONIZATION, DIET BREADTH AND NICHE CONSTRUCTION IN SIERRAS OF CORDOBA (ARGENTINA)

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Abstract

This chapter focuses on how human colonization of Sierras of Cordoba (Argentina) impact on the high-ranked prey resource density –i.e. *Lama guanicoe*-. Three hypothetical scenarios were modelled altering the encounter rate of *L. guanicoe* and predicting how its variation should broaden or narrow the optimal diet of human societies. Diachronic trends in the *Lama* sp. encounter rate were analyzed with two quantitative indices that compare its relative abundance in the assemblages: the “camelid index” and the “artiodactyls index”. The archaeofaunal record reflects the temporal decrease in *Lama* sp. frequency through the Holocene. This taxonomical trend is associated to a decrease in their encounter rate as a result of human over-exploitation under specific ecological conditions. The results draw to the conclusion that a broad-spectrum diet which may not be an exclusively Late Holocene phenomenon and its origins may be found in earlier processes beginning during the Middle Holocene. Thus, the incorporation of small-scale agriculture around ca. 1200-1000 BP cannot be satisfactorily explained only by external factors such as climate changes, the diffusion and/or arrival of new biological populations. Research should consider that past human cultural activities played a dynamic role in this process through niche construction, co-directing subsequent cultural changes that are seen in the archaeological record.

KEYWORDS: ARCHAEOLOGY, NICHE CONSTRUCTION, SIERRAS DE CÓRDOBA

Resumen

Este capítulo se focaliza en como la colonización humana de las Sierras de Córdoba (Argentina) impactó sobre la densidad del recurso del mayor ranking –i.e. *Lama guanicoe*-. Se plantean 3 escenarios hipotéticos alterando la frecuencia de encuentro con *L. guanicoe* y prediciendo como su variación va a ampliar o estrechar la dieta óptima de las sociedades humanas. Las tendencias diacrónicas en las frecuencias de encuentro con *L. guanicoe* se analizaron con 2 índices cuantitativos que comparan su abundancia relativa en los conjuntos: el “índice de camélidos” y el “índice de artiodáctilos”. El registro arqueofaunístico refleja una caída en la frecuencia de *Lama* sp. a través del Holoceno. Este patrón es asociado a una reducción en la tasa de encuentro como resultado de la sobreexplotación humana bajo condiciones ecológicas específicas. Los resultados indican que una dieta de amplio espectro no es un fenómeno exclusivamente del Holoceno Tardío y sus orígenes deben buscarse tempranamente en el Holoceno Medio. En consecuencia, la incorporación de prácticas agrícolas a pequeña escala ca. 1200-1000 AP no puede ser explicada satisfactoriamente por factores externos, como cambios climáticos, difusión y/o el arribo de nuevas poblaciones biológicas. Las investigaciones deben considerar que las actividades culturales prehispánicas jugaron un rol dinámico en este proceso a través de la construcción de nicho, codirigiendo los subsecuentes cambios culturales que se observan en el registro arqueológico.

PALABRAS CLAVE: ARQUEOLOGÍA, CONSTRUCCIÓN DE NICHOS, SIERRAS DE CÓRDOBA

Introduction

Humans, as many organisms, modify local environments through resource selection, emitting detritus, constructing shelters and pathways, etc. with spectacular ecological and evolutionary consequences. This process is known in Evolutionary Biology as “niche engineering” or more recently “niche construction” and consider that no species has more greatly amplified this ability than humans (Laland et al 2001; Odling-Smee 2007; Odling-Smee et al 2003; B. Smith 2007). Thus, *Homo sapiens* not only adapts to different environmental conditions but also interacts with them, modifying natural selective pressures which will be inherited to his descendants (Laland et al 2001).

Human Holocene colonization of Sierras of Córdoba (Argentina) and its impact on the high-ranked prey resource density –e.g. *Lama guanicoe*– are analyzed under this perspective. Prey density simulations and Diet Breadth Model predictions (Stephen & Krebs 1986) were used to assess human predation pressure on local *L. guanicoe* demography. Niche Construction Theory (Odling-Smee et al 2003) is used as a behavioral and evolutionary framework to understand main changes in Sierras of Córdoba Holocene archaeological record, including the increased importance of low-return resources and the incorporation of small-scale agriculture at the end of the Holocene.

This chapter is focused on faunal analysis from six archaeological sites located in Sierras of Córdoba upper mountain grassland range dated on from Early Holocene to Late Holocene. This environment was the habitat for ungulate herds such as the guanaco (*Lama guanicoe*) and pampas deer (*Ozotoceros bezoarticus*), main profitable prey for Holocene hunter-gatherers and horticulturalists. Thus, temporal variations in taxonomic resource abundance provide an excellent opportunity to examine the resource intensification process previously proposed for the region (e.g. Berberían et al 2008; Medina 2008; Medina & Rivero 2007; Pastor 2007a; Recalde 2009; Rivero 2009;).

Environment and Human Colonization of the Sierras of Córdoba

The Sierras of Córdoba are a low-altitude mountain range (500-2790 m) with a complex of peaks, valleys, steep slopes and high-plains that are especially interesting from a human evolutionary ecology point of view. In a simplified scheme, most of the regional plant communities were included in the Sierra Chaco which is a semi-arid xerofic forest dominated by small trees and shrubs with edible wild fruits such as algarrobo (*Prosopis* spp.), chañar (*Geoffroea decorticans*), mistol (*Zizyphus mistol*), molle de beber (*Lithraea molleoides*), etc. (Luti et al. 1979; Demaio et al. 2002) (Figure 1). The fauna of Sierra Chaco is dominated by low-diversity neotropical small-sized mammals adapted to closed-vegetation environments such as the brown-brocket deer (*Mazama guazoupira*), collared peccary (*Pecari tajacu*), vizcachas (*Lagostomus maximus*), armadillos (*Dasypodidae* spp.), small caviomorph rodents (*Caviinae* spp. and *Ctenomyiinae* spp.), etc. (Bucher and Abalos 1979).

Above 1500 m changes in floristic composition though altitudinal gradient results in high-plain known as upper mountain grassland range (Luti et al. 1979). From South to North the main high-plains are Pampa de Achala (2,000 m), Pampa de San Luís (1,900 m) and Pampa de Olaen (1,100 m). Zoogeographically they are included in the Sub-Andean District of the Andean-Patagonian Sub-region (Ringuelet 1961) which included now-extincted prey species of great economic

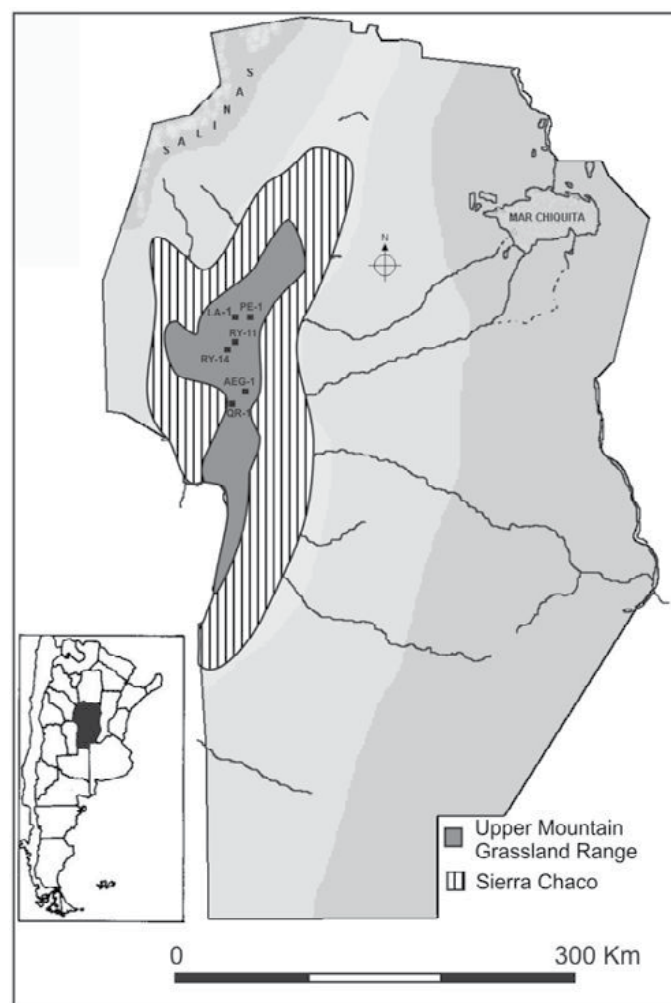


FIGURE 1. MAP OF CÓRDOBA PROVINCE (ARGENTINA) INDICATING SITE LOCATIONS DISCUSSED IN THE TEXT.

importance due to their body size, such as guanaco, pampas deer, taruca (*Hippocamelus* sp.) and the south-american ostrich (*Rhea* sp.). Thus, the upper mountain grassland range constitutes a “faunistic island” of 6,000 km² surrounded by chaquenian environments, providing geographical isolation and refuge to an interesting Andean-Patagonian biota (Figure 1) (Bucher & Abalos 1979; Cabido *et al.* 1998; Cei 1972; Polop 1989; Ringuet 1961).

Palaeoclimatic information indicates that the mountain vegetation during the Pleistocene-Holocene Transition was different from the present. The grassland has a greater extension due to cold and dry climate conditions, connecting the high-plain to lowland grasslands, precordilleran and cordilleran zones of central and northwestern Argentina (Adams & Faure 1997; Carignano 1999; Piovano *et al.* 2010; Sanabria & Argüello 2003). This allowed the flow of several Andean-Patagonian faunal species, including *L. guanicoe*. The establishment of subtropical conditions at 6000 BP redefined the landscape with the formation of the Sierra Chaco vegetational belt and the biogeographical isolation of Andean-Patagonian biota above 1,500 m (Sanabria & Argüello 2003; Teta *et al.* 2005).

There is a combination of factors that enhance the chance that the “faunistic island” of the upper mountain grassland range will be highly-vulnerable to human predation (Nagaoka 2002:422). First, population size is generally smaller and the loss of individuals within this population is often more severe. Second, geographic isolation means that there is no replacement population, reducing the genetical flow and decreasing its long-term reproductive viability. Finally, preys will be severely impacted by the arrival of new predators in the local ecosystem, mainly if the predators were efficient hunters such as humans.

The earliest evidence of humans in the Sierras of Cordoba is dated at ca. 11,000 BP and it was obtained at the El Alto 3 site, on the Pampa de Achala (Rivero & Roldán 2005). However, the human occupation during the Pleistocene-Holocene Transition was not intense, with a low-visibility archaeological record. After 8,000 BP the regional archaeological record increases progressively its visibility, reaching its highest level towards the end of the Late Holocene (Berberían *et al.* 2008; Rivero 2009; Rivero & Berberían 2008). During this time the Sierras of Cordoba evidenced a process of colonization and stabilization of human occupation (*sensu* Borrero 1994-1995), involving population growth, the seasonal use of low-ranked mountain microenvironments and the incorporation of small-scale agriculture ca. 1200-1000 BP (Berberían *et al.* 2008; Pastor 2006; Medina 2008).

The high-plains were exploited as the main large-game hunting territory through the Holocene sequence, so the isolated artiodactyl herds were subjected to a continuous human predation pressure during this time. This situation may cause anthropogenic-induced reduction in ungulate prey abundance so that human foragers should respond by increasing diet breadth (Medina & Rivero 2007). Thus, the archaeofaunal record available for the Sierras of Cordoba upper mountain grassland range ca. 7200-360 BP must be evaluated to assess the human impact on the prehistoric environment and how foragers adapt to the changing environmental situations that they create. This procedure would also offer valuable information about past ecosystems and how they changed during the Holocene, as well as measure human contribution to that process (Grayson 2001; Lyman & Cannon 2004).

Evolutionary Ecology, Niche Construction and Diet Breadth Model

Evolutionary Ecology (sometimes referred to as Human Behavioral Ecology) is the study of adaptative design and its ecological setting through the application of natural selection theory (Winterhalder & Smith 1992; Bird & O’Connell 2006; Broughton *et al.* 2010). Human capacity for rapid adaptative adjustments to changing socio-ecological conditions is considered the product of natural selection, whereas specific behavioral response are not (Boone & Smith 1998; O’Connell 1995; Winterhalder & Smith 1992). The Evolutionary Ecology approach uses formal optimization models to explore the fitness-related cost and benefits of behavioral alternatives in specific socio-ecological context.

Thus, the environment is considered a key variable to explain variability in human behaviors (Bird & O'Connell 2006; Winterhalder & Smith 1992). As human behaviors leaves intentional or unintentional material traces –i.e. the archaeological record– Evolutionary Ecology can generate expectations about prehistoric behaviors and their empirical consequences (Bird & O'Connell 2006; O'Connell 1995).

Because Evolutionary Ecology often focuses on how behavior adjusts to environmental changes extrinsic to the organism as well as those resulting from its own activities, this framework is inextricably tied to Niche Construction Theory (Broughton et al 2010). The central premise of the niche construction perspective is that human cultural activities play an active role in the evolutionary process modifying the selective pressures of the environment that drive further behavioral, cultural and genetical changes in human population (Odling-Smee et al 2003). Ecological inheritance is a key concept in this theoretical framework, referring to the selective environments that the new generations inherit from their genetic or ecological ancestors, who have modified it on evolutionary time-scales through niche construction (Laland et al 2001; Odling-Smee 2007; Odling-Smee et al 2003).

A basic model of Evolutionary Ecology easy to integrate with the niche construction approaches is the Diet Breadth Model, because it draws on the same evolutionary logic (Broughton et al 2010). The Diet Breadth Model is specifically designed to predict which resources will be pursued or ignored when encountered by forager searching in a homogeneous environment (Bettinger 1991; Hill & Hawkes 1983; Kaplan & Hill 1992). It considers that the main objective of foraging activities is to maximize the capture of energy or post-encounter return rate –i.e. the amount of energy gathered per unit of time after encountering a resource (*sensu* Kelly 1995)–. Thus, foragers concentrate this effort pursuing a set of high-return prey types rather than taking low-return smaller animals when encountered.

The Diet Breadth Model predicts that prey types were included in the diet according to their profitability. Those with a high post-encounter return rate should always remained in the diet and were pursued upon encounter. Thus, its archaeological frequency reflects their abundance in the local environment (Broughton & Grayson 1993; Grayson et al 2001). Only if the encounter rate of the high-return prey types decreases due to climate changes and/or human-induced prey depression (Broughton 1999) the diet should be broadened to include more abundant low-return resources (Bettinger 1991; Bird & O'Connell 2006; Broughton 1994; Kaplan & Hill 1992; Kelly 1995; E. Smith 1983; Winterhalder 1981a, 1981b; Winterhalder & Smith 2000). However, prey types with lower profitability than the overall net caloric return rate should always be ignored regardless of their abundance in the landscape. This hypothetical point is defined as the “Optimal Diet Breadth” or “Local Optimum” (Kaplan & Hill 1992; E. Smith 1983; Winterhalder 1981a). This is:

$$E_j/h_j > \sum \lambda_i * E_j / \sum \lambda_i * h_i + I, \quad (1)$$

where λ_i is the encounter rate of each resource, E_j the net energy obtained and h_j the handling time (Muscio 2004).

The application of the Diet Breadth Model in archaeology requires that the potential preys were ordinal-ranked according to their profitability. Thus, a ranking was built based on the post-encounter return rate of the main taxa available in the Sierras of Cordoba upper mountain grassland range (Table 1). Caloric yields and handling times were obtained from similar taxa from the taxonomic, anatomical and metrical points of view (Hill & Hawkes 1983; Medina 2008; Muscio 1999, 2004; Yacobaccio *et al.* 1998). Only 60% of artiodactyls' eviscerated carcass was considered edible, while 70% of bird and 85% of small mammal carcasses were suitable for food (Byers & Ugan 2005) (Table 1).

Common name	Body size (kg)	Calories/kg	Caloric yield	Handling time (hr)*	Density (ind./km ²)	References
Guanaco	140	1090	91560	3,3	10	Parera (2002)
Greater Rhea	30	1900	39900	1,46	6,7	Medina (2008)
Taruca	70	1200	50400	2,5	1	Parera (2002)
Pampas Deer	45	1200	32400	1,67	5	Parera (2002)
Lesser Rhea	20	1900	26600	1,46	5	Medina (2008)
Armadillo	3,6	3000	4832	0,929	60	Parera (2002)
Duck	1	1230	861	0,369	115	Byers y Ugan (2005)
Pampas Vizcacha	8	1141	4792	1,457	700	Parera (2002)
Tinamou	0,34	1900	452,2	0,37	7,5	Medina(2008)
Tuco-tuco	0,7	1200	714	0,35	1271	Parera (2002)
Cuy	0,25	1200	252	0,35	2400	Parera (2002)

*: Handling times refers to the post-encounter activities incumbent on the depredator to transfer a living prey item from the environment into its digestive tract, including pursuing, butchering, processing and consuming resources. These data was obtained from Medina (2008).

TABLE 1. PARAMETERS CONSIDERED IN THE OPTIMAL DIET BREADTH.

L. guanicoe is the high-ranked prey type followed by the south-american ostrich, cervids and, finally, small rodents.

According to Diet Breadth Model, *Lama* sp. will be taken whenever possible and its archaeological frequency should reflect its abundance during the Holocene. This reasoning allows three hypothetical scenarios to be modelled altering the encounter rate of *L. guanicoe* and predicting how its variation should broaden or narrow the optimal diet of human societies.

Scenario 1:

Considering densities of 10 ind./km² for *L. guanicoe*, the optimal diet includes artiodactyls that inhabited the Sierras of Cordoba whose body size varies from ca. 30 kg (*O. bezoarticus*) to ca. 140 kg (*L. guanicoe*). Flightless-birds *Rhea* sp. with a body size of 20-30 kg are also be exploited. Instead, small and medium-sized mammals and other vertebrates weighting less than 15 kg will be dropped from the diet (Table 2).

Common name	λ_i Encounter rate (ind./hr)	h_i Handling times (hr)	E_i Kilocaloric yield	E_i/h_i Post-encounter return rate (Kcal/hr)	$\lambda_i \cdot E_i$ Encounter rate / Kcal	$\lambda_i \cdot h_i$ Handling time (hr/Kg)	$? \lambda_i \cdot h_i + I$ Pursuing + handling times (hr)	$? \lambda_i \cdot E_i$ (Kcal/hr)	$? \lambda_i \cdot E_i / ? \lambda_i \cdot h_i + I$ Overall Return rate (Kcal/hr)
Guaraco	0,07	3,3	91560	27745	6409,2	0,231	1,231	6409,2	5206
Greater Rhea	0,046	1,46	39900	27328	1835,4	0,06716	1,29816	8244,6	6350
Taruca	0,007	2,5	50400	20160	352,8	0,0175	1,31566	8597,4	6534
Pampas deer	0,035	1,67	32400	19401	1134	0,05845	1,37411	9731,4	7081
Lesser Rhea	0,035	1,46	26600	18219	931	0,0511	1,42521	10662,4	7481
Armadillo	0,42	0,929	4832	5201	2029,44	0,39018	1,81539	12691,84	6991
Pampas vizcacha	4,9	1,457	4792	3288	23480,8	7,1393	8,95469	36172,64	4039
Duck	0,81	0,369	861	2333	697,41	0,29889	9,25358	36870,05	3984
Tinamou	0,05	0,37	452,2	1222	22,61	0,0185	9,27208	36892,66	3978
Tuco-tuco	8,9	0,35	408	1165	3631,2	3,115	12,38708	40523,86	3271
Cuy	16,8	0,35	252	720	4233,6	5,88	18,26708	44757,46	2450

Note: The shaded area shows the taxa included in the optimal diet breadth.

TABLE 2. OPTIMAL DIET BREADTH ACCORDING TO SCENARIO 1.

Scenario 2:

With a density of 5 ind./km² for *L. guanicoe*, the optimal diet shows no significant difference from Scenario 1. Artiodactyls and *Rhea* sp. will be pursued during subsistence activities. Medium and small-vertebrates continue being ignored (Table 3).

Scenario 3:

Finally, *L. guanicoe* densities of 1 ind./km² reduce the encounter rate with the high-ranked resource and the model predicts the addition of medium-sized mammals (ca. 5 kg) such as dasypodids (Table 4). Artiodactyls and *Rhea* sp. continue being the main pursued prey due to their profitability, but *L. guanicoe* will be found less frequently in deposits. Smaller-sized taxa are still not included in the diet.

Common name	λ_i Encounter rate (ind./hr)	h_j Handling times (hr)	E_j Kilocaloric yield	E_j/h_j Post-encounter return rate (Kcal/hr)	$\lambda_i \cdot E_j$ Encounter rate / Kcal	$\lambda_i \cdot h_j$ Handling time (hr/Kg)	$? \lambda_i \cdot h_j + I$ Pursuing + handling times (hr)	$? \lambda_i \cdot E_j$ (Kcal/hr)	$? \lambda_i \cdot E_j /$ $? \lambda_i \cdot h_j + I$ Overall Return rate (Kcal/hr)
Guanaco	0,035	3,3	91560	27745	3204,6	0,1155	1,1155	3204,6	2872
Greater Rhea	0,046	1,46	39900	27328	1835,4	0,06716	1,18266	5040	4261
Taruca	0,007	2,5	50400	20160	352,8	0,0175	1,20016	5392,8	4493
Pampas deer	0,035	1,67	32400	19401	1134	0,05845	1,25861	6526,8	5185
Lesser Rhea	0,035	1,46	26600	18219	931	0,0511	1,30971	7457,8	5694
Armadillo	0,42	0,929	4832	5201	2029,44	0,39018	1,69989	9487,24	5581
Pampas vizcacha	4,9	1,457	4792	3288	23480,8	7,1393	8,83919	32968,04	3729
Duck	0,81	0,369	861	2333	697,41	0,29889	9,13808	33665,45	3684
Tinamou	0,05	0,37	452,2	1222	22,61	0,0185	9,15658	33688,06	3679
Tuco-tuco	8,9	0,35	408	1165	3631,2	3,115	12,27158	37319,26	3041
Cuy	16,8	0,35	252	720	4233,6	5,88	18,15158	41552,86	2289

Note: The shaded area shows the taxa included in the optimal diet breadth.

TABLE 3. OPTIMAL DIET BREADTH ACCORDING TO SCENARIO 2.

Common name	λ_i Encounter rate (ind./hr)	h_j Handling times (hr)	E_j Kilocaloric yield	E_j/h_j Post-encounter return rate (Kcal/hr)	$\lambda_i \cdot E_j$ Encounter rate / Kcal	$\lambda_i \cdot h_j$ Handling time (hr/Kg)	$? \lambda_i \cdot h_j + I$ Pursuing + handling times (hr)	$? \lambda_i \cdot E_j$ (Kcal/hr)	$? \lambda_i \cdot E_j /$ $? \lambda_i \cdot h_j + I$ Overall Return rate (Kcal/hr)
Guanaco	0,007	3,3	91560	27745	640,92	0,0231	1,0231	640,92	626
Greater Rhea	0,046	1,46	39900	27328	1835,4	0,06716	1,09026	2476,32	2271
Taruca	0,007	2,5	50400	20160	352,8	0,0175	1,10776	2829,12	2553
Pampas deer	0,035	1,67	32400	19401	1134	0,05845	1,16621	3963,12	3398
Lesser Rhea	0,035	1,46	26600	18219	931	0,0511	1,21731	4894,12	4020
Armadillo	0,42	0,929	4832	5201	2029,44	0,39018	1,60749	6923,56	4307
Pampas vizcacha	4,9	1,457	4792	3288	23480,8	7,1393	8,74679	30404,36	3476
Ducks	0,81	0,369	861	2333	697,41	0,29889	9,04568	31101,77	3438
Tinamou	0,05	0,37	452,2	1222	22,61	0,0185	9,06418	31124,38	3433
Tuco-tuco	8,9	0,35	408	1165	3631,2	3,115	12,17918	34755,58	2853
Cuy	16,8	0,35	252	720	4233,6	5,88	18,05918	38989,18	2158

Note: The shaded area shows the taxa included in the optimal diet breadth.

TABLE 4. OPTIMAL DIET BREADTH ACCORDING TO SCENARIO 3.

Sites, faunal record and methodology

The study focused on 15528 bone specimens collected in the archaeological sites Arroyo El Gaucho 1, Quebrada del Real 1, Rio Yuspe 11, Rio Yuspe 14, Los Algarrobos 1 and Puesto La Esquina 1 (Figure 1, Table 5). During its excavations, sediments were sieved with a fine-screen 2 mm mesh to allow recovery of small vertebrate and macro-botanical remains. The archaeofaunal data was ordered by radiocarbon dating (Medina 2008; Rivero 2009; Rivero *et al.* 2010).

Arroyo El Gaucho 1 (AEG-1; 1843 m) is a rock-shelter situated in Quebrada del Condorito National Park in the Pampa de Achala (Rivero 2009). Two overlapped cultural Components were detected in stratigraphy during its excavation. Lower component (C1) is associated with lanceolate projectile points and bifaces that were radiocarbon dated at 7160±90 years BP (LP-1722, charcoal). The upper component (C2) is characterized by triangular projectile points with slightly to markedly concave bases radiocarbon dated at 3590±60 years BP (LP-1599; charcoal) and 3700±70 years BP (LP-1612; charcoal).

Taxón	AEG1 (C1)	QR1 (C1)	AEG1 (C2)	QR1 (C2)	RY11	LAI1	RY14	PEI
<i>Lama</i> cf. <i>L. guanicoe</i>	649	100	355	277	141	4	7	57
<i>Ozotoceros bezoarticus</i>	11	0	27	0	2	1	0	238
cf. <i>Hippocamelus</i>	0	1	0	1	0	0	0	0
Odocoileinae	0	0	0	6	22	0	4	0
Artiodactyla	288	25	61	24	71	20	5	82
<i>Lagostomus maximus</i>	0	0	0	0	0	0	1	1
<i>Micocavia australis</i>	0	9	0	59	0	0	0	0
<i>Galea leucoblephara</i>	0	103	0	393	0	0	0	0
Caviinae	316	243	88	859	33	0	2	47
<i>Ctenomys</i> sp.	2	264	7	587	0	5	0	8
Caviomorpha	0	0	0	1	0	0	0	4
<i>Oxymycterus</i>	0	0	0	0	0	0	0	1
<i>Reithrodon</i> sp.	0	0	0	2	0	0	0	0
<i>Holochilus</i> sp.	3	8	3	44	0	0	0	8
Criceidae	0	0	0	6	6	0	0	5
Rodentia	5	6	317	25	6	3	1	11
Dasipodidae	3	0	3	0	22	4	3	36
<i>Pseudalopex</i> sp.	0	1	0	10	0	0	0	0
Felinae	0	0	0	1	0	0	0	0
Carnivora	0	0	0	11	0	0	0	0
Mammalia (med.-large size)	1628	139	1065	236	598	67	78	199
Mammalia (small size)	35	5	16	4	17	1	3	7
Anura cf. Leptodaelylidae	0	0	0	0	0	0	0	4
<i>Tupinambis</i> sp.	0	0	0	0	0	0	0	20
Sauria sp.	0	0	0	0	0	0	0	1
Rheidae (eggshell)	0	0	0	0	9	0	5	33
<i>Tupinambis</i> sp.	0	0	0	0	0	0	0	20
Sauria sp.	0	0	0	0	0	0	0	1
Rheidae (eggshell)	0	0	0	0	9	0	5	33
<i>Fulica</i> sp.	0	0	0	3	0	0	0	0
<i>Eudromia</i> sp.	0	2	0	0	0	0	0	3
<i>Nothura</i> sp.	0	0	0	0	0	0	0	28
Tinamidae	0	0	0	1	2	0	0	2
Anatidae	1	0	0	1	0	0	0	0
Passeriformes	0	0	0	1	0	0	0	0
Falconiformes	0	2	0	1	0	0	0	0
Aves (small size)	4	0	2	7	0	1	1	7
NUSP	589	1	298	237	1853	302	64	1910
NSP	3534	909	2242	2797	2752	408	174	2712

From Medina (2008, 2009), Pastor (2005, 2007b) y Rivero et al (2010)

TABLE 5. NUMBER OF IDENTIFIED SPECIMENS PER TAXON (NISP) FOR THE UPPER MOUNTAIN GRASSLAND RANGE ASSEMBLAGES (CÓRDOBA PROVINCE, ARGENTINA).

Quebrada del Real 1 (QR1; 1914 m) is a rock-cave located in the Pampa de Achala Provincial Hydrical Reserve (Rivero *et al.* 2010). Three cultural Components were detected during its excavation. The lowest component (C1) was associated to lanceolate projectile points and charcoal dated at 5980±50 years BP (LP-2133). The middle component (C2) is characterized by the presence of triangular projectile points with slightly to markedly concave bases dated at 2950±90 years BP (LP-2042; charcoal). Finally, the top component (C3) contains small-stemmed triangular arrowpoints as well as pottery fragments. This assemblage was temporal-assigned to the Late Holocene but not included in this paper due to absence of radiocarbon dates.

Río Yuspe 11 (RY11; 1810 m) is a rock-shelter located in Pampa de Achala (Pastor 2007a, 2007b). Due to the high-frequency of surface unmovable grinding artifacts and the stratigraphical data, the occupation was associated to animal and vegetal large-group food processing and consumption tasks. The site was dated at 1540±50 BP (LP-1658; charcoal) and 1170±50 BP (LP-1449; charcoal). This chronology positions RY11 in a contemporary context to the spread of some technological innovation such as pottery and small-scale agriculture.

Río Yuspe 14 (RY14; 1860 m) is a small rock-shelter with archaeological occupations dated at 640±70 BP (LP-1514; charcoal). The archaeological remains indicate domestic activities, possibly by small-family units related to Late Holocene seasonal large-game hunting dispersal of co-residential groups from Sierra Chaco environment (Pastor 2005, 2007a).

Los Algarrobos 1 (LA11, 1100 m a.s.l) is an open-air archaeological site located in the Pampa de Olaen (Medina 2008). The analysis of superficial and stratigraphical archaeological remains confirmed its use as an agricultural and residential site dated at 949±40 BP. (AA64818, charcoal).

Finally, Puesto La Esquina 1 (PE1, 1140 m) is an open-air site located in the associated-rich soil of a well-protected gorge of the Pampa de Olaen (Medina 2008). The pottery, bone, lithic and palaeobotanical evidence, as well as an archaeological floor and a hearth, indicate the development of multiple-activities such as the production, storage, processing, cooking, and consumption of foodstuffs, the manufacture, maintenance, and discarding of artifacts, etc.. Thus, PE1 was interpreted as a semi-sedentary residential base or village. Two charcoal samples from overlapping layers were dated at 365±38 BP. (AA64816) and 362±43 BP. (AA64815), placing its occupations near to the Spaniard arrival and indicating the high-resolution of the deposit.

The high-frequency of burning damage, cutmarks and percussion marks on bones, not treated in depth in this paper, indicate that humans were the main agents that formed these faunal assemblages (Medina 2008; 2009; Medina & Rivero 2007; Medina *et al.* 2009; Rivero 2009; Rivero *et al.* 2010; Rivero *et al.* 2010; Pastor 2005, 2007a; 2007b). Thus, the samples offer an excellent opportunity to assess without taxonomic ambiguity changes in human diet breadth through the Holocene.

Taxonomic abundance was quantified as the Number of Identified Specimens per Taxon (NISP). Teeth were quantified as separate entities, regardless of whether they are found articulated or isolated. This methodology facilitates the interassemblage comparability despite post-depositional processes that might have affected them (Lyman 2008; Stiner 1994). Number of Specimens (NSP) and Number of Unidentified Specimens (NUSP) were also considered (Lyman 2008).

Diachronic trends in the *Lama* sp. encounter rate were analysed with two quantitative indices that compare its relative abundance in the assemblages at a different taxonomical resolution. The “camelid index” shows the relation between Camelidae and Cervidae bone specimens calculated as:

$$I_c = \frac{\sum NISP \text{ Lama sp.}}{\sum (NISP \text{ Lama sp.} + NISP \text{ Cervidae})} \quad (2)$$

Instead, the “artiodactyl index” reflects the relation between the artiodactyls and small-vertebrates bones frequency with the same logic that underlies the previous index:

$$I_a = \frac{\sum NISP (\text{Lama sp.} + \text{Cervidae} + \text{Artiodactyls})}{\sum NISP (\text{Lama sp.} + \text{Cervidae} + \text{Artiodactyls} + \text{small-vertebrate})} \quad (3)$$

Results and Discussion

The model predicts that artiodactyls and *Rhea* sp. should always be in the optimal diet breadth. Only when the density of guanaco decreases to 1 ind./km², armadillos would be an economical option in the evolutionary ecology optimization point of view. Other small-vertebrates such as caviomorph-rodents remained theoretically excluded from the diet, even when *L. guanicoe* has a low-density values.

The upper mountain grassland range zooarchaeological record is in agreement with these expectations (Table 5). Indeed, the artiodactyls were exploited across the Holocene (Figure 2). Camelids were the main prey-type exploited by human foragers since the Early Holocene (Rivero 2009). However, *Lama* sp. decreases its archaeological abundance, particularly towards the Late Holocene (Table 6 & 7, Figures 2, 3, & 4).

Conversely, cervids such as *Ozotoceros* sp. increase their frequency since the Middle Holocene and they are the most abundant prey in Late Holocene assemblage of Puesto La Esquina 1 (Medina 2009; Medina & Rivero 2007). However, the prehispanic *Ozotoceros* sp. bone remains look like larger than present-day population parameters, stressing the possibility of a extinct local subspecies, species or even a new genus (see González 1960; Menghin & González 1954). Future studies of metrical and non-metrical comparative variation as well as DNA molecular analysis should solve this taxonomical question.

Few bone specimens of Odocoileinae cf. *Hippocamelus* sp. were identified in Early and Middle Holocene assemblages of Quebrada del Real 1. *Hippocamelus* sp. was also found in Middle Holocene deposits of the classic archaeological sites Ongamira and Intihuasi caves (González 1960; Menghin & González 1954). If the geographical distribution of *Hippocamelus* sp. in the Sierras of Cordoba was confirmed, this would be associated with low-density values and its absence in Late Holocene deposits would be explained by its local extinction.

The medium-sized mammal Euphractinae spp. were also identified in the assemblages. Their archaeological frequency is low in the Early Holocene deposits, but bony dermal scutes of these armadillos increase towards the Late Holocene (see Medina 2009). According to model predictions, this taxonomical pattern indicates a decrease in the *L. guanicoe* encounter rate. Thus, foragers would have to concentrate their subsistence effort pursuing lower-ranked prey than artiodactyls.

The predation of the south-american ostrich is only suggested by low-quantities of eggshell specimens, which are temporally-restricted to Late Holocene deposits. *Rhea* bones were not found. A possible explanation of its absence may be related to the fact that carcasses were not discarded in the sites, were fragmented into small-unidentified pieces and/or were destroyed by bone mineral density-mediated attritional processes. However, the low-NISP of eggshells might suggest that this flight-less bird did not inhabit the upper mountain grassland range and their eggs were transported from lowlands.

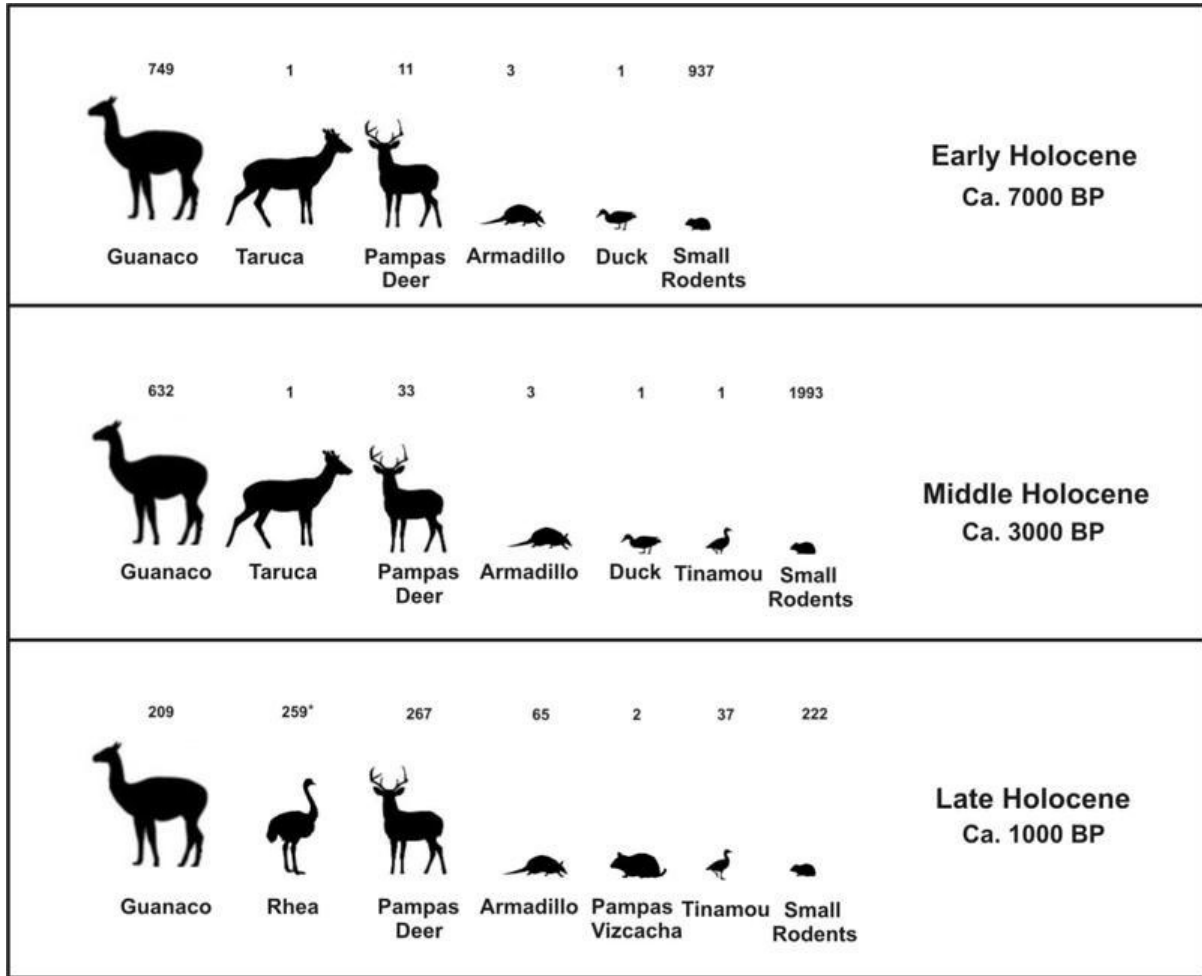


FIGURE 2. NUMBER OF IDENTIFIED SPECIMENS PER TAXON (NISP) FOR THE UPPER MOUNTAIN GRASSLAND RANGE ASSEMBLAGES (CÓRDOBA PROVINCE, ARGENTINA).

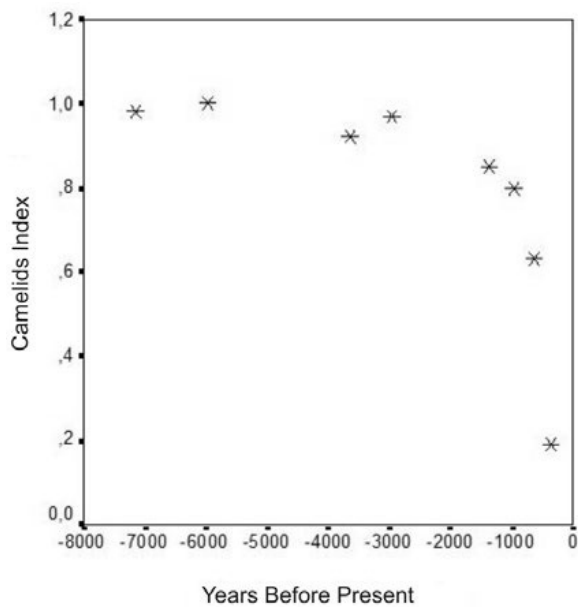


FIGURE 3. TEMPORAL TRENDS IN CAMELIDS ABUNDANCE FOR THE UPPER MOUNTAIN GRASSLAND RANGE ASSEMBLAGES (CÓRDOBA PROVINCE, ARGENTINA).

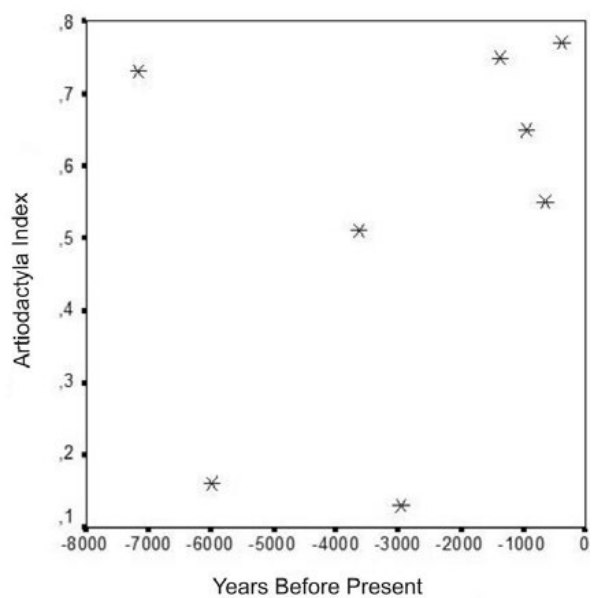


FIGURE 4. TEMPORAL TRENDS IN ARTIODACTYLA ABUNDANCE FOR THE UPPER MOUNTAIN GRASSLAND RANGE ASSEMBLAGES (CÓRDOBA PROVINCE, ARGENTINA).

Site	Date (BP)	Camelids Index	Artiodactyla Index
AEG1-C1	7160	0,98	0,73
QR1-C1	5980	1	0,16
AEG1-C2	3637	0,92	0,51
QR1-C2	2950	0,97	0,13
RY-11	1361	0,85	0,75
LA-1	949	0,8	0,65
RY-14	640	0,63	0,55
PE-1	364	0,19	0,77

TABLE 6. RESULTS OF THE “CAMELIDS INDEX” AND THE “ARTIODACTYLA INDEX” FOR THE UPPER MOUNTAIN GRASSLAND RANGE ASSEMBLAGES (CÓRDOBA PROVINCE, ARGENTINA).

Index	Chi-Cuadrado	Valor <i>p</i>
Camelids : Deers	1454,44	0,000
Artiodactyla : Rodents	2130,52	0,000

TABLE 7. CHI-SQUARE TEST LINEAR TRENDS FOR THE UPPER MOUNTAIN GRASSLAND RANGE ASSEMBLAGES (CÓRDOBA PROVINCE, ARGENTINA).

The optimal diet breadth never predicts the anthropic predation of small-vertebrates. Nevertheless, caviomorph-rodents (*Lagostomus maximus*, *Ctenomys* sp., Caviinae, etc.), cricetid-rodents (*Holochilus* sp.) and birds (Tinamidae, *Anas* sp., etc.) are found in the assemblages with unequivocal traces of human interaction such as cut-marks and burning damage. Two hypothesis would explain their archaeological presence:

Hypothesis 1: Participation of women and children in the economy

Ethnoarchaeological and ethnographic studies in small-scale societies pointed out that subsistence activities are divided according to sex and age differences. Women and children do not participate directly in adult men large-game hunting, although they usually collaborate with the processing and transportation of the prey body parts to the base camp. Their economical participation focuses on the daily provision of food foraging low-return and easy to capture resources, such as small-animals, fruits and tubers (Zeanah 2004; Byers & Ugan 2005 Prates 2008; Bird & Bliege Bird 2000; Wadley 2009). Thus, the identification of small-vertebrates in the sites, specially in Middle Holocene deposit, might be related to the archaeological consequence of these sexual and age-linked foraging practices.

Hypothesis 2: Problems in the population-resource relationship

An alternative explanation argues that the small animals were exploited as a result of anthropogenic reduction in high-ranked prey density. Thus, a prey simulation model was used to examine the long-term stability of a human subsistence system based on *L. guanicoe*, the high-ranked but susceptible to over-exploitation prey type in Sierras of Cordoba (Medina and Rivero 2007). The simulation employed biological and ecological variables of *L. guanicoe* (e.g. weight, density, population dynamics) and humans populations (e.g. calory requirements, demographic growth) to predicts how these model parameters behave when one of them was altered (e.g. population density). Medina and Rivero's (2007) model predicts that one-prey subsistence system focused on *L. guanicoe* should not be

maintainable as far from the Middle Holocene ca. 6000 BP. At this threshold, habitat fragmentation and human predation produces a dramatic decrease in their local abundance. Human forager should respond by reducing prey selectivity and adding small-vertebrates that normally were marginally outside of the optimal diet (Rivero 2009; Medina & Rivero 2007).

According to this hypothesis, the declining trend in *L. guanicoe* prey density and the increase of the diet breadth constitute an obvious case of niche construction because humans alter the selective pressure through their own cultural activity and drive further adaptive adjustments. Thus, the predictions of Medina and Rivero (2007) prey simulation models resemble the “Route 1” path of Odling-Smee et al (2003: 338), in which the socioecological environment modified by cultural niche construction directs the evolutionary dynamics of the human societies.

CONCLUSIONS

The archaeofaunal record from the Sierras of Cordoba upper mountain grassland range reflect the temporal decrease in *Lama* sp. frequency through the Holocene. This taxonomical trend is associated here to a decrease in their encounter rate as result of human over-exploitation under specific ecological conditions. Conversely, Odocoleinae increase their abundance during this period and their importance in the subsistence is greater than *Lama* sp. towards the Late Holocene. Small-rodents were present at low-NISP values since Early Holocene, but their frequency increases significantly from Middle to Late Holocene faunal assemblages. This pattern cannot be explained only with the Hypothesis 1 and is interpreted as a human behavioral adjustment to the *L. guanicoe* prey depression in agreement with Hypothesis 2.

However, only a preliminary evaluation of the model predictions was carried out in this chapter. The assessment of the model performance requires to eliminate the potentially sampling bias and the chronological gaps –including the absence of pleistocene faunal assemblages- through regional-scale archaeological studies. Furthermore, the analysis of the predator-prey dynamics and the evolutionary history of the human societies should be integrated with non-faunal evidence to expand its explanatory power. Thus, the changes in projectile point design, the development of new technologies –e.g. grinding tools, pottery, etc.–, the frequency of archaeobotanical remains and the variability in home range size mobility should also be considered, with special attention to their effects on foraging efficiency, demography, mobility, territorial defence, social differentiation, palaeopathology, etc.

The chapter also points out how the neo-darwinian evolutionary logic allows the operationalization of highly-predictive models about human colonization process and its effect on the ungulate prey resource they exploit. This is the opposite to the non-evolutionary approaches which claim for an unwarranted equilibrium between humans and the environment (Redman 1999; Smith & Wishnie 2000; Winterhalder & Lu 1997). The *Homo sapiens* spread through the evolutionary scenarios of Argentina should promote co-evolutionary dynamics similar to the ones proposed here (Kelly 1999; Winterhalder 1981b). Nevertheless, different results from local extinction –e.g. domestication, dispersion of species, high-efficiency subsistence systems based on Camelidae, etc. (López 2009; Stahl 2009; Yacobaccio 2001)- should be considered due to the variability in the specific socio-ecological settings.

The archaeology of the Sierras of Cordoba should advance in the obtention of new faunal assemblages to test the model predictions with a high empirical robustness. However, the available archaeological data supports a broad-spectrum diet which may not be an exclusively Late Holocene phenomenon and its origins may be found in earlier processes beginning during the Middle Holocene. Thus, the incorporation of small-scale agriculture around ca. 1200-1000 BP cannot be satisfactorily explained only by external factors –e.g. climate changes, the diffusion and/or arrival of new biological populations, etc.-. A niche construction conception of evolution as a long-term behavioral cumulative process should also be taken into account. Indeed, research should consider that past human cultural activities played a dynamic role in this process through niche construction, co-directing subsequent cultural changes that are seen in the archaeological record.

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