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Rheidae Egg Human Exploitation and Stable Isotopes: Trends from West Central Argentina

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ABSTRACT Rheidae eggshells are abundant in the archaeological record of west central Argentina. Eggs were more important in human diet than the bird meat itself, as with many other Ratite species around the world. Currently, two species inhabit the south and central areas of Argentina and Chile (*Rhea pennata* and *Rhea americana*), with different geographical distributions and diet but with similar behaviour. In this paper, we use $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopes from Rheidae eggshells to explore the ratite diet, its spatial differences in the archaeological record, and their importance in human diet, and as a way to approach human mobility in hunter-gatherer societies from west central Argentina. There was a significant correlation between both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotope data and the Rheidae species' distribution in the landscape, showing differences in their past diet and territoriality. Additionally, the unexpected $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotope values in the Altoandina Desert area suggest human transport of the Rheidae eggs to these locations. The isotopic data from the eggshells need to be incorporated into the ecological history of the region in order to understand past human diet and mobility. Copyright © 2013 John Wiley & Sons, Ltd.

Key words: eggshells; human mobility; Ratite diet; Rheidae; South America; stable isotopes

Introduction

Archaeologists have emphasised human subsistence on large mammalian prey in west central Argentina (Neme and Gil, 2008; Otaola *et al.*, 2012). Guanacos (*Lama guanicoe*) had been assumed to be a more significant prey to understand human strategies, subsistence, and mobility (Neme, 2007; Neme and Gil, 2008; Otaola *et al.*, 2012). However, during the last 5 years, research has shown a decrease in the importance of guanacos in human diet in relationship to other prey (Gil and Neme, 2002; Neme and Gil, 2008; Corbat *et al.*, 2009; Giardina, 2012). In this framework, different papers have called to attention the use of other taxa that provides a more realistic perspective about the variation in the zooarchaeological record in west central Argentina and surrounding areas (Giardina, 2010; Medina *et al.*, 2011; Fernández, 2012).

Rheidae (*Rhea americana* and *Rhea pennata*) eggshell fragments are ubiquitous in archaeological sites in southern Mendoza during the entire Holocene. These remains suggest that eggs were very important to human diet. Giardina (2010) proposed that this Rheidae resource had been significant to the human diet at least during part of their dietary year. In neighbouring areas, similar perspectives have been recently proposed (Quintana and Mazzanti, 2001; Quintana, 2008; Prates, 2009; Prates and Acosta Hospitaleche, 2010; Medina *et al.*, 2011).

Stable isotope analysis provides a strong line of evidence for the discussion of topics in ecology, diet, and environment (Robbins *et al.*, 2005; Fry, 2006; Michener and Lajtha, 2007; Clementz *et al.*, 2009; Richards and Trinkaus, 2009; Panarello *et al.*, 2010; Barberena, 2012). In west central Argentina, stable isotope analysis has focused on the study of dietary patterns in human populations, particularly in the emergence of domestic plants and human mobility (Gil, 2003; Gil *et al.*, 2006; Gil *et al.*, 2011; Ugan *et al.*, 2012). During the last decade, carbon stable isotope studies in Ratites' eggshell fragments around the world permitted the discussion of

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different paleoecological topics such as the Pleistocene megafaunal extinction and changes in vegetation (von Schirnding *et al.*, 1982; Miller *et al.*, 1997, 1999, 2005; Johnson *et al.*, 1999; Clarke *et al.*, 2006; Lee-Thorp and Sponheimer, 2007; Janz *et al.*, 2009; Praderio *et al.*, 2012). Changes in the $\delta^{13}\text{C}$ values of flightless birds from Oceania during the late Pleistocene have demonstrated their versatility in the use of changing vegetal resources (Johnson *et al.*, 1999; Miller *et al.*, 1999; Clarke *et al.*, 2006).

Our research focuses on eggshell geochemical information ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) as a means to discuss their use by humans in the region. The significant ecological and altitudinal variation (between 500 and 4000 masl) in southern Mendoza makes it an adequate study area to observe these isotopic patterns. Stable isotopes from eggshells allow researchers to discuss environmental variability, climate, and Ratite diet with implications for human diet and mobility (von Schirnding *et al.*, 1982; Ambrose *et al.*, 2011).

In this paper, we explore two problems. First, we analyze the spatial distribution of eggshell fragments recorded from Rheidae ecological distribution to understand the interconnection of Rheidae biogeography, human use, and human mobility. Second, we test if the eggshell stable isotope can introduce a more enriched $\delta^{13}\text{C}$ signal in human diet. We then examine the potential contribution of the eggshells' isotopic signal with isotopic variability in human bone from the same area. The use of eggshell stable isotopes enhances our understanding of regional isotopic ecology when evaluating its significance in human diet. Therefore, the paper presents a characterisation of the Rheidae diet in the region. Next, we analyze the movement of eggshells as artifacts in a broad, spatial scale in order to discuss human exchange and/or human mobility (Ambrose *et al.*, 2011). Finally, we summarise the importance of incorporating isotope data to understand past human diet and mobility. The ecology of the region and the previous research on stable isotopes of animal and human bones have demonstrated a strong line of evidence to explore different aspects of the archaeological record, mostly focusing on human diet and mobility (Gil *et al.*, 2010, 2011, 2012; Ugan *et al.*, 2012).

Human subsistence–mobility in southern Mendoza

The first human occupations in the study area are dated to ca. 11 000 years BP (Lagiglia, 1968, 1975; García, 1995). Most of the southern Mendoza region was

occupied by hunter-gatherers until the arrival of the first Europeans. There is evidence of domestic plant remains in some areas adjacent to the Atuel and Diamante Rivers, which suggests the introduction of these kinds of resources sometime between 2000 and 1000 years BP (Lagiglia, 1968, 1980, 1999; Gil *et al.*, 2011). However, the importance of domestic plants in human populations is still uncertain (Gil, 2006; Gil *et al.*, 2009, 2011). The archaeofaunal record from several archaeological sites shows changes in the use of animals by the human population during the late Holocene (Neme, 2007; Neme and Gil, 2008; Otaola *et al.*, 2012). Such changes indicate an increase in smaller prey (lower ranked) consumption and, as a consequence, the decline in the relative proportion of Artiodactyla (big prey) in the archaeological assemblages. These changes in human diet have strong implications in residential mobility (Szuter and Bayham, 1989; James, 1990; Winterhalder and Goland, 1997; Neme and Gil, 2008, 2012). When human populations start to concentrate their efforts in harvesting the low rank resources (plants, fish, birds, etc.), they spend more time in the same location processing them (Neme, 2009). The increase of staying in the camps implies the over exploitation of the high return rate of prey around their camps, which begin to be less abundant over time (Neme and Gil, 2008).

In southern Mendoza, exploitation of the guanaco led to the incorporation of different, small prey including species of bird like the *Rhea* sp., which were previously ignored by hunters probably because of their high pursuit cost during the hunt (Giardina, 2010). Within the zooarchaeological assemblages of some early sites from the late Pleistocene and early Holocene can be found Rheidae eggshells that have been burnt, suggesting that they were a component of human diet (Neme *et al.*, 2011; Gil *et al.*, 2012). Furthermore, there is evidence of an increase in Rheidae egg consumption with time in most of the archaeological sites from the region (Giardina, 2010), suggesting the growth in their importance within the human diet.

The Rheidae in southern Mendoza ecosystems

As a part of west central Argentina, southern Mendoza has significant environmental variability (Abraham and Rodríguez Martínez, 2000; González Loyarte *et al.*, 2010) that can be explored at different scales (Neme and Gil, 2012). From an ecological perspective, southern Mendoza includes three main deserts: the

Altoandina Desert, Patagonia Desert, and Monte Desert. The Altoandina Desert is located between 2200 and 4500 masl and is characterised by the presence of Asteraceae and Poaceae that are well adapted to snow, cold stress, and strong winds (Roig, 1960; Cabrera, 1976). The Patagonia Desert, located between 2200 and 1500 masl, is characterised as a xeric bushy steppe of *Mulinum* spp., *Chuquiraga* spp., and *Festuca* spp., among others (Cabrera, 1971; Roig *et al.*, 2000). The Monte Desert (Roig *et al.*, 2000) is characterised by xerophytic vegetation and an arboreal stratum dominated by *Prosopis flexuosa* (Roig *et al.*, 2000).

The animal biogeography in this area can be divided into two main units: 'Fauna de Montaña' (Mountain Fauna) located in the previously mentioned Altoandina and Patagonia deserts and 'Fauna de Llanura' (Plains Fauna) in the Monte Desert (Roig, 1972). The first is characterised by the presence of camelids (*L. guanicoe*), carnivores such as the grey fox (*Lycalopex griseus*) and puma (*Felis concolor*), small rodents, and several species of birds. The 'Fauna de Llanura' is a more diverse group, including the previously mentioned species in addition to other small mammals, such as viscacha (*Lagostomus maximus*), armadillo (*Chaetophractus vellerosus* and *Zaedyus pichiy*), and nutria (*Myocastor coypus*) among others, and large, flightless birds, such as *R. pennata* and *R. americana*.

The study area is located in a temperate zone—a Mediterranean and continental region with an arid to semi-arid climate with an average annual precipitation of 250 mm. This area is exposed to anticyclones from the Atlantic (centred mostly on the Monte Desert) and the Pacific Ocean (centred mostly on Patagonia and Altoandina deserts). From the morpho-climatic aspect, this region is highly contrasting because of its geographical relief, dominant masses of maritime air, and rainy season. Because of the great distance travelled, the humid winds of the Atlantic precipitate scarce humidity, while the winds from the Pacific precipitate at the mountain range of the Andes, arriving at this region as dry and warm winds (Abraham and Rodríguez Martínez, 2000). Influenced by Pacific anticyclones, the Andes belong to the Altoandina and Patagonia deserts, while the oriental plains, influenced by the Atlantic anticyclones, belong to Monte Desert (Roig, 1972).

Currently, two Rheidae species occupy the study area (*R. americana* and *R. pennata*). There is almost no overlap between them, suggesting that each has adapted to different environmental conditions, predominately influenced by the distribution of vegetal species. *R. americana* biogeography is distributed from northern Brazil to northern Patagonia, living in open

fields and landscapes with sparse trees (del Hoyo *et al.*, 1992; Drenowatz, 1995; Rebores and Fernández, 1997, 2005). *R. pennata*'s distribution is mostly in Patagonia Desert, includes southern Mendoza and all of Patagonia with the exception of the Tierra del Fuego province.

In southern Mendoza, *R. americana* occupies the Monte Desert and *R. pennata* the Patagonia Desert (Blake, 1977; del Hoyo *et al.*, 1992; Sarasqueta, 1995; Pelliza Sbriller and Sarasqueta, 2004), but Rheidae species do not occupy the Altoandina Desert (Tambussi and Acosta Hospitaleche, 2002, Figure 1). The ecotone between the Monte and Patagonia deserts, in addition to seasonal fluctuations in annual precipitation patterns, generates spatial variation in the boundary that separates these species. The difference in vegetation is significant in the isotopic ecology. Research in the region has shown a correlation between altitude and C₃ and C₄ plant frequencies (Cavagnaro, 1988; Llano, 2009). The patterns show a complete dominance of C₃ plants over ~2200 masl (Altoandina Desert), a dominance of C₃ over C₄ plants between 2200 and 1500 masl (Patagonia Desert), and a dominance of C₄ plants below 1500 masl, mostly in the Monte Desert (Cavagnaro, 1988; Llano, 2009).

Both species of Rheidae are omnivorous and generalists but mostly herbivorous (Bruning, 1974; Bonino *et al.*, 1986; del Hoyo *et al.*, 1992). Although *R. americana* is a generalist species, it tends to prefer dicotyledonous plants (Martella *et al.*, 1996; Pereira *et al.*, 2003). *R. americana* faeces found in the foothills of the Mendoza Province (Paoletti and Puig, 2007) contained predominantly shrubs (such as *Lycium* spp.) and grasses (such as *Stipa* spp.) and, in lower proportions, other shrubs such as *Adesmia horrida* and herbs such as *Nassauvia axillaris*, *Astragalus* spp., *Conyza lorenrzi*, *Erodium cicutarium*, and *Gomphera pumila*. They also found cactus seeds (*Maihueniopsis glomerata*), insects, and rocks. The material ingested by *R. americana* is classified as perennial grasses, annual grasses, and woody graminoides plants (Pelliza Sbriller and Sarasqueta, 2004). On the other hand, *R. pennata* has a generalist diet consisting mainly of shrub species (Bonino *et al.*, 1986; Camezzana, 1987). They consume leaves, seeds, and a small percentage of insects (Paoletti and Puig, 2007). The diet of *R. pennata* represents an adaptation to the shrub-steppe, shrub-grass, and predominantly the herb and shrub categories presented earlier (Pelliza Sbriller and Sarasqueta, 2004). *R. pennata* does not always feed on the same shrubs or herbs, varying the proportions of vegetation consumed according to the location and season (Pelliza Sbriller and Sarasqueta, 2004).

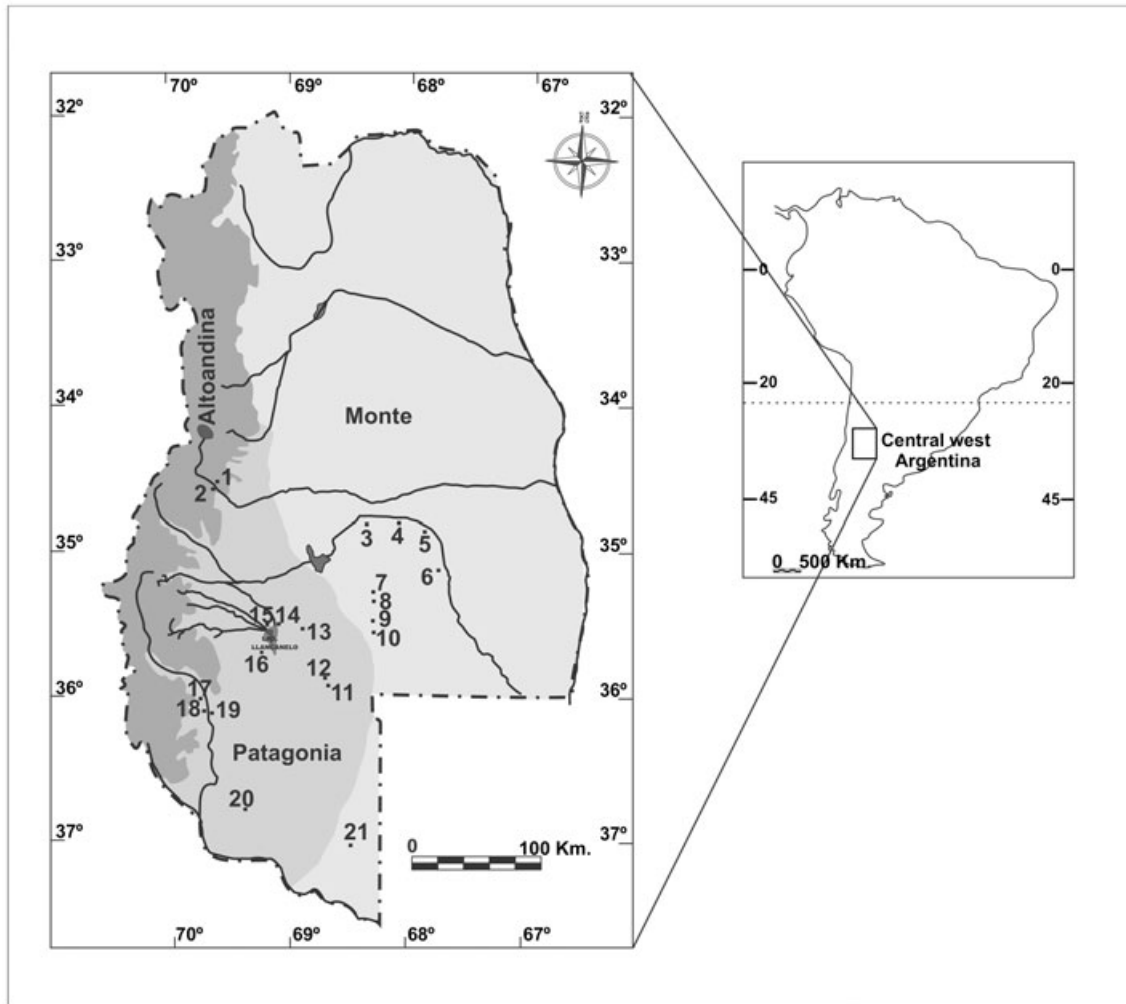


Figure 1. Mendoza Province showing the ecological regions and the archaeological sites mentioned in the text. 1—El Mallín, 2—Alero Montiel, 3—RA-1, 4—MDA II LG-1, 5—MDA-IV EB 3, 6—La Olla, 7—Lole 6, 8—Lole 7, 9—Puesto Ortubia, 10—Agua de los Caballos, 11—Cu, 12—LP-2, 13—La Corredera, 14—Llan 22, 15—Llan 29, 16—Llan, 17—Cueva de Luna, 18—El Manzano, 19—Alero Puesto Carrasco, 20—APE-1, 21—Chacha 4.

With variations in food throughout the year, both species can be linked to nutritional requirements and, in part, reproductive activity (Pereira *et al.*, 2003). In this sense, during the 90-day egg laying season, the females prefer to consume plants richer in calcium and phosphorus such as *Astragalus* spp. (Camezzana, 1987). Based on Paoletti and Puig (2007) studies, Llano (2009) discovered that the southern Puna (*R. pennata*) diet included 60% C_3 , and less than 10% C_4 and Crassulacean acid metabolism (CAM) plants; other remains were not identified taxonomically.

Both Rheidae species have similar patterns in terms of their nesting behaviour (Pereira *et al.*, 2003), especially in their choices of nesting, which have strong implications for human use. Every year, each female lays approximately 20 eggs (Camezzana, 1987),

sharing the nest with between two and eight other female Rheidae. Finally, the male remains in the nest until the chicks hatch. As a result, each nest contains between 25 and 40 eggs that can be easily harvested by humans at very low energetic costs. The amount of eggs in each nest is no less than 21 000 kcal, approximately 630 kcal per egg; this amount is almost equal in value to the entire, adult bird, which is around 24 000 kcal (Giardina, 2006). When we take into account the processing cost of the bird meat, energy cost is even greater, while the eggs have little or no processing cost. This difference in processing gives us an idea about the importance of Rheidae eggs in the human diet in relation to other resources and can explain why they were highly exploited during the entire Holocene.

Rheidae eggshells in the archaeological record

Researchers have focused on the importance of Rheidae eggs to humans in the past by focusing on taxonomic quantification of subsistence and social problems (Bonomo *et al.*, 2008; Quintana, 2008; Apolinaire and Turnes, 2010; Fiore and Borella, 2010; Giardina, 2010; Medina *et al.*, 2011). Although the Rheidae are the largest birds in South America and, in most areas, is the second largest animal in size after the guanaco, the evidence of bone remains of this flightless bird in the southern Mendoza archaeological record is scarce (Table 1). Bone specimens of the Rheidae appear in the archaeofaunal record in southern Mendoza only during the last 3000 years BP. However, eggshell specimens are recorded in large numbers for the last *ca.* 8000 years BP. Table 1 presents details with reference to the avian zooarchaeological record in southern Mendoza. As shown here, the avian bone NISP never reaches 20% of the zooarchaeological assemblages in the region (Giardina, 2012; Otaola *et al.*, 2012).

This increasing record of Rheidae eggshell in the south of the Mendoza Province indicates that this resource has had a growing importance in the human diet (Table 1; Giardina, 2010) in all of the environments where these birds were available. The greater and earlier consumption of Rheidae eggs rather than the bird meat itself was remarked by several archaeologists around the world (Janz *et al.*, 2009; Giardina, 2010; Medina *et al.*, 2011). All of them attributed this particular situation to the fact that these flightless birds are harder to hunt than most of the other prey, especially because of their speed. On the other hand, the eggs are easy to find and harvest for every member of the hunter-gatherer band. This situation is particularly evident in Africa with the Ostrich (*Struthio camelus*), in South America with the Greater Rhea (*R. americana*) and the Lesser Rhea (*R. pennata*), in Australia and New Guinea with the three species of *Casuaris* (*Casuaris casuaris*, *Casuaris bennetti*, and *Casuaris unappendiculatus*), and in eastern Asia with the extinct Ostrich (*Struthio anderssoni*). Only the Emu (*Dromaius novaehollandiae*) and the extinct Moas have a different behaviour associated with hunting them as a food source; their range mobility included few if any variations, and they did not run as fast as other Ostrich. It permitted the hunting of this kind of prey in a relatively easy way (O'Connell, 2000; Nagaoka, 2005; Janz *et al.*, 2009).

In the archaeological record of southern Mendoza, most of the eggshell fragments are burnt, not engraved or perforated, suggesting their use by human populations as a food source. In other regions, there is evidence of its use as recipients or symbolic objects

(Giardina, 2010). In this last case, one can expect more spatial movement of the eggshell than in the first one. The eggshells' durability permits that even the smallest fragments can be recovered and analyzed, becoming an important source of archaeological information (Miller *et al.*, 2005; Janz *et al.*, 2009; Giardina, 2010; Medina *et al.*, 2011).

As previously mentioned, present Rheidae occupy the Monte and Patagonia deserts, but not environments higher than 2000 masl, such as the Altoandina Desert (Figure 1). Nevertheless, at least two of the archaeological sites in this study with an eggshell record (El Mallín and Alero Montiel, Figure 1) are unexpectedly located in the Altoandina Desert (Figure 1) at ~2500 masl. The question is if this eggshell is of local provenance, demonstrating a different Rheidae past distribution, or if the eggshell is non-local.

Stable isotopes and Rheidae eggshells: methodology and techniques

Plants that utilise the C₃ (Calvin) and C₄ (Hatch–Slack) photosynthetic pathways fractionate atmospheric carbon differently during the synthesis of plant carbohydrates (Ehleringer and Cerling, 2002; Marshall *et al.*, 2007). The mean $\delta^{13}\text{C}$ of C₃ plant foliage is approximately -26.5‰ and of C₄ grasses is approximately -12.5‰ (O'Leary, 1988; Farquhar *et al.*, 1989; Fogel and Cifuentes, 1993; Diefendorf *et al.*, 2010). Plants that use CAM employ a combination of the C₃ and C₄ photosynthetic pathways and have a carbon isotope composition intermediate between those of C₃ and C₄ plants (Osmond, 1978). During tissue synthesis of consumers, the isotopic composition of the diet is passed on and modified from its original value (Ambrose and De Niro, 1986; Ambrose, 1993, 2000). The amount of isotopic fractionation that occurs varies with tissue type and between classes of organic compounds. Bone collagen is generally 5‰ enriched relative to the diet (Vogel, 1978; Bocherens and Drucker, 2003; Hedges and Reynard, 2007), ostrich eggshell proteins are approximately 2‰ enriched relative to the diet (von Schirnding *et al.*, 1982), and ostrich calcite is approximately 16‰ enriched relative to the diet (von Schirnding *et al.*, 1982; Johnson *et al.*, 1998). The $\delta^{13}\text{C}$ composition of ostrich eggshells can be used to calculate the percentage of C₃ and C₄ plants consumed using a two-end member mixing model (von Schirnding *et al.*, 1982; Johnson *et al.*, 1998).

Being an herbivore, the isotope ratio of the ostrich's food is a function of the mixture between a diet

Table 1. Avian zooarchaeological record in southern Mendoza, abundance in NISP

Taxa	Agua de los Caballos		Puesto Ortubia-1		La Coderrera		Los Peuquenes-2		La Olla		Rincon del Atuel-1		La Peligrosa Diamante		Arroyo Cueva Malo 3		Cueva Palulo de Luna		Alero Puesto Carrasco		Grua del Manzano ABC		Grua del Manzano D		O Jo de Agua
	1	2	1	1357	1	24	1	3573	1	1	1	1	1	1	3	18	136	36	25	170	199	199	199	199	
Greater Birds indet.	2																								
Rheidae indet.	1	[940]		[1357]		1	[3573]																		
<i>Rhea pennata</i>				1																					
<i>Rhea americana</i>	2																								
Median Birds indet.	1			[9]																					
Tinamidae indet.	5	[118]																							
<i>Eudromia elegans</i>	4																								
Anseriformes indet.																									
Anatidae indet.																									
<i>Anas</i> sp.																									
<i>Anas platylea</i>																									
<i>Anas georgica</i>																									
<i>Anas</i>																									
<i>specularioides</i>																									
<i>Chloetaga</i>																									
<i>melanoptera</i>																									
Rallidae indet.																									
Charadriiformes indet.																									
<i>Attagis gayi</i>																									
Scolopacidae indet.																									
Columbidae indet.																									
<i>Zenaidura auriculata</i>	1			1																					

Values between brackets are number of plates of dermal bone (see details in Giardina, 2012; Otaola et al., 2012).

composed of 100% of C₃ plants and of 100% of C₄ plants (Johnson *et al.*, 1997; Segalen *et al.*, 2002). The ostrich eggshells exhibit enrichment in ¹³C relative to their diet (Johnson *et al.*, 1997; Segalen *et al.*, 2002):

$$\delta^{13}\text{C}_{\text{eggshell}} = \delta^{13}\text{C}_{\text{diet}} + 16.2 \quad (1)$$

$$\delta^{13}\text{C}_{\text{diet}} = X(-26.5) + (1 - X)(-12.5) \quad (2)$$

$$[\% \text{C}_3 \text{ plants}] = \{(-\delta^{13}\text{C}_{\text{eggshell}} + 3.7)/14\} \times 100 \quad (3)$$

$$[\% \text{C}_4 \text{ plants}] = \{1 - (-\delta^{13}\text{C}_{\text{eggshell}} + 3.7)/14\} \times 100 \quad (3')$$

Where X and $(1 - X)$ are the percentages of C₃ and C₄ resources consumed. From Equations 1 and 2, we can deduce the percentage of C₃ or C₄ plants in the diet as in Equations 3 and 3' (Segalen *et al.*, 2002).

Isotopic record reliability has been verified for domestic ostriches by experiments with controlled amounts of C₃ and C₄ plant diets (von Schirnding *et al.*, 1982). We surmise that the isotopic turnover rate of Rheidae is similar to that of quail eggshells and is on the order of 3 to 5 days. In natural environments, ostriches are opportunistic breeders and typically lay between 8 and 12 eggs during a 2-week time period (Bertram, 1992). Egg-laying depends on the buildup of sufficient nutrient stores in the ostriches (Sauer and Sauer, 1966) and usually occurs a few months after the rainy season (Sinclair, 1978).

The eggshells have two components—calcium carbonate and organic matrix. When all the components of eggshells are taken together, they consist of around 3.5% organic matter, 1.5% water, and 95% inorganic matter (von Schirnding *et al.*, 1982). These components make ratite eggshells durable and, therefore, abundant in archaeological sites (Lee-Thorp and Sponheimer, 2007). During the shell synthesis, the amount of Ca₂ + in the blood increases. Specialised cells secrete the organic components that permit the precipitation of calcium ions associated with carbonate ions (derived from metabolic CO₂) to form the eggshell.

Eggshells can yield $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{18}\text{O}$ proxy information reflecting conditions during the short egg-laying season. The $\delta^{13}\text{C}$ in eggshells is related to the diet of the birds (von Schirnding *et al.*, 1982). Ostriches are mixed feeders whose diet can include succulents as well as annual grasses and forbs; therefore, $\delta^{13}\text{C}$ data can indicate the presence of C₃ and C₄ grasses in addition to CAM plants (Stern *et al.*,

1994). The turnover rate of eggshells is rapid, where the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of eggshell proteins are in complete isotopic equilibrium with the diet within 4 days of the diet switch (Johnson, 1995; Johnson *et al.*, 1998). The isotopic composition of carbon in eggshells from ratites reflects the isotopic composition of the diets from these birds between 3 and 5 days, and the carbonate values in $\delta^{13}\text{C}$ are enriched in 16‰ in relation to the diet (Johnson *et al.*, 1999).

The oxygen isotope composition of a biomineral depends upon (i) temperature of formation, (ii) kinetic and equilibrium fractionations that occur during formation of the mineral, and (iii) the isotopic composition of the animal's body water (Koch *et al.*, 1989; Johnson *et al.*, 1998; Schwarcz *et al.*, 2010). The temperature of formations constant for warm-blooded animals and kinetic and equilibrium effects can often be estimated under controlled experiments. The composition of the body water of an animal is dependent on isotopes of ingested waters (drinking water, plant water, and metabolised water), respiratory gases, and the relative contributions of each to the biomineral.

The $\delta^{18}\text{O}$ data reflect aridity as well as the provenance of the specimens. Because ostriches are drought-tolerant, $\delta^{18}\text{O}$ primarily reflects leaf water enrichment due to evapotranspiration under hot, dry conditions (Lee-Thorp and Sponheimer, 2007). The $\delta^{18}\text{O}$ of the plant-leaf water increases with decreasing relative humidity and with increasing temperature (Flanagan *et al.*, 1991; Johnson *et al.*, 1998). The $\delta^{18}\text{O}$ of rainwater across southern Mendoza ranges from more depleted in the mountain ranges to the west (Altoandina–Patagonia deserts), to more enriched in the lowland, or Monte Desert (Vogel *et al.*, 1975; Osterra and Dapeña, 2003; IAEA/WMO, 2006; Hoke *et al.*, 2009). As was presented earlier, two different precipitation sources influence the region, Pacific and Atlantic anticyclones, giving significant seasonal–spatial variation and isotopic differences in the meteoric water (Hoke *et al.*, 2013). Because of the high variability in $\delta^{18}\text{O}$ data, large numbers of analyses are required (Lee-Thorp and Sponheimer, 2007).

In order to characterise spatiotemporal variation in the Rheidae diet, 245 archaeological Rheidae fragmented eggshells were processed in the Carnegie Institution of Washington (Washington, DC). Those samples were excavated from 21 archaeological sites in southern Mendoza (Figure 1; Table 2), whose chronology has been estimated by radiocarbon association and/or diagnostic artifacts. The samples range between *ca.* 9000 years BP and 200 years BP. The sample provenance includes a wide range of ecological units with altitudes ranging

Table 2. Descriptive stable isotope data from southern Mendoza archaeological eggshell samples

AAL/ISO	Nº	Archaeological site	Age	Region	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	masl
12796	1	ALERO MONTIEL	LH	Altoandina	-8.9	37.5	2500
12797	2	ALERO MONTIEL	LH	Altoandina	-7.9	42.0	2500
12798	3	ALERO MONTIEL	LH	Altoandina	-10.0	33.2	2500
12799	4	ALERO MONTIEL	LH	Altoandina	-10.4	31.9	2500
12800	5	ALERO MONTIEL	LH	Altoandina	-10.6	36.4	2500
12801	6	ALERO MONTIEL	LH	Altoandina	-6.8	41.7	2500
12802	7	ALERO MONTIEL	LH	Altoandina	-10.4	33.8	2500
12803	8	ALERO MONTIEL	LH	Altoandina	-9.7	31.5	2500
12804	9	ALERO MONTIEL	LH	Altoandina	-8.6	38.7	2500
12805	10	ALERO MONTIEL	LH	Altoandina	-7.8	41.8	2500
12806	11	ALERO MONTIEL	LH	Altoandina	-8.6	33.0	2500
12807	12	ALERO MONTIEL	LH	Altoandina	-8.2	40.0	2500
12808	13	ALERO MONTIEL	LH	Altoandina	-8.8	31.8	2500
12809	14	ALERO MONTIEL	LH	Altoandina	-8.3	40.0	2500
12810	15	ALERO MONTIEL	LH	Altoandina	-8.3	36.2	2500
12811	16	ALERO MONTIEL	LH	Altoandina	-9.3	39.3	2500
12812	17	ALERO MONTIEL	LH	Altoandina	-9.8	31.0	2500
12813	18	ALERO MONTIEL	LH	Altoandina	-10.7	34.4	2500
12814	19	ALERO MONTIEL	LH	Altoandina	-8.7	38.7	2500
12815	20	ALERO MONTIEL	LH	Altoandina	-11.5	32.3	2500
12260A	236	ALERO MONTIEL	LH	Altoandina	-7.1	32.2	2500
12263A	239	ALERO MONTIEL	LH	Altoandina	-8.5	39.8	2500
12263B	240	ALERO MONTIEL	LH	Altoandina	-8.4	32.9	2500
12832	37	EL MALLÍN	LH	Altoandina	-9.5	33.3	1900
12833	38	EL MALLÍN	LH	Altoandina	-9.8	28.6	1900
12834	39	EL MALLÍN	LH	Altoandina	-11.2	33.6	1900
12835	40	EL MALLÍN	LH	Altoandina	-11.5	33.3	1900
12836	41	EL MALLÍN	EH	Altoandina	-10.3	34.2	2000
12837	42	EL MALLÍN	EH	Altoandina	-9.9	38.6	2000
12838	43	EL MALLÍN	EH	Altoandina	-9.7	34.6	2000
12839	44	EL MALLÍN	EH	Altoandina	-10.0	38.6	2000
12840	45	EL MALLÍN	EH	Altoandina	-10.1	38.6	2000
12841	46	EL MALLÍN	EH	Altoandina	-7.5	42.6	2000
12842	47	EL MALLÍN	LH	Altoandina	-9.9	31.2	2500
12843	48	EL MALLÍN	LH	Altoandina	-8.4	39.6	2500
12844	49	EL MALLÍN	LH	Altoandina	-8.6	35.9	2500
12845	50	EL MALLÍN	LH	Altoandina	-8.2	35.1	2500
12846	51	EL MALLÍN	LH	Altoandina	-8.6	39.9	2500
12847	52	EL MALLÍN	EH	Altoandina	-10.2	32.7	2500
12848	53	EL MALLÍN	EH	Altoandina	-9.7	35.3	2500
12849	54	EL MALLÍN	EH	Altoandina	-8.5	39.4	2500
12850	55	EL MALLÍN	EH	Altoandina	-10.1	33.0	2500
12851	56	EL MALLÍN	EH	Altoandina	-9.8	39.0	2500
12852	57	EL MALLÍN	EH	Altoandina	-6.9	50.4	2500
12853	58	EL MALLÍN	EH	Altoandina	-10.1	36.4	2500
12854	59	EL MALLÍN	EH	Altoandina	-10.2	33.1	2500
12816	21	EL MALLÍN	LH	Altoandina	-10.0	36.2	2500
12817	22	ACA-1	LH	Monte	-9.0	38.6	1200
12818	23	ACA-1	LH	Monte	-10.7	37.0	1200
12819	24	ACA-1	LH	Monte	-5.9	40.2	1200
12820	25	ACA-1	LH	Monte	-10.5	41.4	1200
12821	26	ACA-1	LH	Monte	-9.0	40.3	1200
12822	27	ACA-1	LH	Monte	-10.2	36.4	1200
12823	28	ACA-1	LH	Monte	-8.8	38.8	1200
12824	29	ACA-1	LH	Monte	-10.5	36.7	1200
12960	165	ACA-1	LH	Monte	-7.6	41.5	1200
12961	166	ACA-1	LH	Monte	-10.5	36.2	1200
12962	167	ACA-1	LH	Monte	-7.5	40.2	1200
12963	168	ACA-1	LH	Monte	-7.6	45.5	1200
12964	169	ACA-1	LH	Monte	-7.3	48.1	1200
12965	170	ACA-1	LH	Monte	-10.6	36.9	1200
12966	171	ACA-1	LH	Monte	-6.9	43.2	1200
12976	181	ACA-1	LH	Monte	-7.5	37.2	1200
12977	182	ACA-1	LH	Monte	-9.0	37.0	1200

(Continues)

Rheidae Egg Human Exploitation And Stable Isotopes

Table 2. (Continued)

AAL/ISO	N ^o	Archaeological site	Age	Region	δ ¹³ C	δ ¹⁸ O	masl
12978	183	ACA-1	LH	Monte	-10.5	36.4	1200
12256A	233	ACA-1	LH	Monte	-9.3	37.3	1200
12872	77	ACA-1	LH	Monte	-9.2	37.2	1200
12873	78	ACA-1	LH	Monte	-5.8	39.5	1200
12874	79	ACA-1	LH	Monte	-6.3	40.9	1200
12875	80	ACA-1	LH	Monte	-11.2	35.9	1200
12876	81	LO	LH	Monte	-8.5	43.5	530
12877	82	LO	LH	Monte	-9.2	34.0	530
12878	83	LO	LH	Monte	-6.9	39.6	530
12879	84	LO	LH	Monte	-7.0	40.5	530
12880	85	LO	LH	Monte	-6.7	35.8	530
12881	86	LOLE-5	LH	Monte	-9.2	38.8	1000
12882	87	LOLE-5	LH	Monte	-11.1	38.3	1000
12883	88	LOLE-5	LH	Monte	-8.9	40.9	1000
12884	89	LOLE-5	LH	Monte	-11.4	38.6	1000
12885	90	LOLE-5	LH	Monte	-9.2	38.0	1000
12886	91	LOLE-6	LH	Monte	-10.8	28.6	1000
12887	92	LOLE-6	LH	Monte	-10.7	28.7	1000
12888	93	LOLE-6	LH	Monte	-11.0	28.5	1000
12889	94	LOLE-6	LH	Monte	-10.3	36.3	1000
12890	95	LOLE-6	LH	Monte	-7.5	39.0	1000
12891	96	LOLE-6	LH	Monte	-10.2	34.9	1000
12257A	234	LOLE-6	LH	Monte	-8.9	39.4	1000
12261A	237	LOLE-6	LH	Monte	-8.1	38.7	1000
12262A	238	MDA II LG-1	LH	Monte	-9.2	36.5	530
12264A	241	MDA II LG-1	LH	Monte	-8.6	37.6	530
12264B	242	MDA II LG-1	LH	Monte	-9.7	38.0	530
12265A	243	MDA II LG-1	LH	Monte	-6.8	41.3	530
12265B	244	MDA II LG-1	LH	Monte	-7.1	42.7	530
12270A	251	MDA-IV EB 3	LH	Monte	-11.3	35.2	530
12270B	252	MDA-IV EB 3	LH	Monte	-8.5	41.1	530
12271A	253	MDA-IV EB 3	LH	Monte	-9.8	36.8	530
12272A	254	MDA-IV EB 3	LH	Monte	-11.1	34.8	530
12273A	255	MDA-IV EB 3	LH	Monte	-10.1	40.3	530
12273B	256	MDA-IV EB 3	LH	Monte	-10.5	37.3	530
12855	60	MDA-IV EB 3	LH	Monte	-10.2	37.2	530
12856	61	PO-1	LH	Monte	-10.5	29.4	1300
12857	62	PO-1	LH	Monte	-11.1	30.6	1300
12858	63	PO-1	LH	Monte	-10.0	37.0	1300
12859	64	PO-1	LH	Monte	-7.5	42.2	1300
12860	65	PO-1	LH	Monte	-9.0	34.3	1300
12861	66	PO-1	LH	Monte	-6.1	42.8	1300
12862	67	PO-1	LH	Monte	-9.0	34.6	1300
12863	68	PO-1	LH	Monte	-9.0	31.3	1300
12864	69	PO-1	LH	Monte	-8.5	40.7	1300
12865	70	PO-1	LH	Monte	-9.8	34.9	1300
12866	71	PO-1	LH	Monte	-10.8	31.6	1300
12867	72	PO-1	LH	Monte	-8.6	41.6	1300
12868	73	PO-1	LH	Monte	-10.4	29.7	1300
12268A	249	PO-1	LH	Monte	-9.5	37.4	1300
12269A	250	PO-1	LH	Monte	-8.0	42.0	1300
12936	141	PO-1	LH	Monte	-6.4	42.1	1300
12937	142	PO-1	LH	Monte	-7.9	39.3	1300
12938	143	PO-1	LH	Monte	-10.5	29.7	1300
12939	144	PO-1	LH	Monte	-10.6	29.3	1300
12274A	257	PO-1	LH	Monte	-10.5	29.3	1300
12274B	258	PO-1	LH	Monte	-5.2	47.6	1300
12274C	259	RA-1	LH	Monte	-10.2	35.7	700
12912	117	RA-1	LH	Monte	-5.0	47.5	700
12913	118	RA-1	LH	Monte	-10.1	36.4	700
12914	119	RA-1	LH	Monte	-6.9	35.3	700
12915	120	RA-1	LH	Monte	-5.6	44.5	700
12916	121	RA-1	LH	Monte	-9.8	45.1	700
12917	122	RA-1	LH	Monte	-10.3	36.5	700

(Continues)

Table 2. (Continued)

AAL/ISO	Nº	Archaeological site	Age	Region	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	masl
12918	123	RA-1	LH	Monte	-9.0	38.6	700
12919	124	RA-1	LH	Monte	-6.7	42.7	700
12920	125	RA-1	LH	Monte	-9.0	41.0	700
12922	127	RA-1	LH	Monte	-7.6	44.8	700
12923	128	RA-1	LH	Monte	-10.8	37.0	700
12924	129	RA-1	LH	Monte	-7.8	38.9	700
12925	130	RA-1	LH	Monte	-9.9	45.5	700
12926	131	RA-1	LH	Monte	-6.1	38.0	700
12927	132	RA-1	LH	Monte	-11.1	33.3	700
12928	133	RA-1	LH	Monte	-8.9	39.9	700
12929	134	RA-1	LH	Monte	-9.6	33.7	700
12930	135	RA-1	LH	Monte	-7.9	45.0	700
12994	199	CHACHA 4	LH	Monte	-9.3	41.0	1500
12995	200	CHACHA 4	LH	Monte	-9.2	38.6	1230
12996	201	CHACHA 4	LH	Monte	-8.1	32.3	1230
12997	202	CHACHA 4	LH	Monte	-9.1	38.4	1230
12998	203	CHACHA 4	LH	Monte	-9.4	41.2	1230
12999	204	CHACHA 4	LH	Monte	-7.8	32.5	1230
13000	205	CHACHA 4	LH	Monte	-9.3	41.3	1230
13001	206	CHACHA 4	LH	Monte	-9.2	41.4	1230
13002	207	CHACHA 4	LH	Monte	-10.0	38.2	1230
12931	136	APE-1	LH	Patagonia	-9.1	33.4	1600
12981	186	APE-1	LH	Patagonia	-10.7	31.3	1600
12982	187	APE-1	LH	Patagonia	-9.8	33.2	1600
12983	188	APE-1	LH	Patagonia	-10.4	31.8	1600
12984	189	APE-1	LH	Patagonia	-11.8	29.8	1600
12985	190	APE-1	LH	Patagonia	-9.8	29.9	1600
12948	153	APE-1	LH	Patagonia	-10.3	37.7	1600
12949	154	LA CODERRERA	LH	Patagonia	-11.6	32.5	1320
12950	155	LA CODERRERA	LH	Patagonia	-10.4	33.5	1320
12951	156	LA CODERRERA	LH	Patagonia	-13.1	36.7	1320
12952	157	LA CODERRERA	LH	Patagonia	-10.5	35.8	1320
12940	145	LP-2	LH	Patagonia	-10.9	33.9	1100
12941	146	LP-2	LH	Patagonia	-10.7	38.0	1100
12942	147	LP-2	LH	Patagonia	-10.6	41.6	1100
12943	148	LP-2	LH	Patagonia	-11.9	29.2	1100
12944	149	LP-2	LH	Patagonia	-8.5	39.5	1320
12945	150	LP-2	LH	Patagonia	-10.5	38.2	1320
12946	151	LP-2	LH	Patagonia	-10.9	37.3	1320
12947	152	LP-2	LH	Patagonia	-9.8	37.6	1320
12266A	245	LP-2	LH	Patagonia	-10.6	34.8	1320
12266B	246	LP-2	LH	Patagonia	-9.9	41.0	1320
12267A	247	LP-2	LH	Patagonia	-10.3	34.0	1320
12267B	248	LP-2	LH	Patagonia	-11.5	34.4	1320
12825	30	LP-2	LH	Patagonia	-11.4	35.2	1320
12826	31	LP-2	LH	Patagonia	-10.2	38.1	1320
12827	32	LP-2	LH	Patagonia	-9.4	37.5	1320
12828	33	LP-2	LH	Patagonia	-8.9	38.7	1320
12829	34	LP-2	LH	Patagonia	-11.4	31.0	1320
12986	191	LP-2	LH	Patagonia	-9.8	40.4	1320
12987	192	LP-2	LH	Patagonia	-10.7	34.1	1320
12988	193	LP-2	LH	Patagonia	-12.0	35.2	1320
12989	194	LP-2	LH	Patagonia	-11.0	36.2	1320
12990	195	LP-2	LH	Patagonia	-10.6	36.2	1320
12991	196	LP-2	LH	Patagonia	-9.6	38.0	1320
12992	197	LP-2	LH	Patagonia	-12.0	31.8	1320
12993	198	LP-2	LH	Patagonia	-9.3	38.6	1320
13003	208	APC	LH	Patagonia	-10.4	36.0	1500
13004	209	APC	LH	Patagonia	-10.5	35.4	1500
13006	211	APC	LH	Patagonia	-10.3	35.2	1500
13007	212	APC	LH	Patagonia	-10.6	35.5	1500
12953	158	APC	LH	Patagonia	-9.4	28.3	1500
12954	159	APC	LH	Patagonia	-10.3	34.9	1500
12955	160	APC	LH	Patagonia	-10.4	35.1	1500

(Continues)

Table 2. (Continued)

AAL/ISO	Nº	Archaeological site	Age	Region	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	masl
12956	161	APC	LH	Patagonia	-10.5	35.2	1500
12957	162	APC	LH	Patagonia	-10.1	35.5	1500
12958	163	CU	LH	Patagonia	-8.7	39.0	2000
12959	164	CU	LH	Patagonia	-7.1	35.1	2000
12892	97	CU	LH	Patagonia	-9.2	32.9	2000
12893	98	CU	LH	Patagonia	-6.4	40.2	2000
12894	99	CUEVA DE LUNA	LH	Patagonia	-9.0	37.9	1500
12895	100	CUEVA DE LUNA	LH	Patagonia	-10.8	23.5	1500
12896	101	CUEVA DE LUNA	LH	Patagonia	-9.2	32.9	1500
12897	102	CUEVA DE LUNA	LH	Patagonia	-11.1	38.4	1500
12898	103	CUEVA DE LUNA	LH	Patagonia	-11.6	34.8	1500
12899	104	CUEVA DE LUNA	LH	Patagonia	-10.9	25.8	1500
12900	105	CUEVA DE LUNA	LH	Patagonia	-9.0	37.8	1500
12901	106	CUEVA DE LUNA	LH	Patagonia	-11.6	34.0	1500
12902	107	CUEVA DE LUNA	LH	Patagonia	-9.3	36.7	1500
12903	108	CUEVA DE LUNA	LH	Patagonia	-11.6	33.6	1500
12904	109	CUEVA DE LUNA	LH	Patagonia	-10.9	38.2	1500
12905	110	CUEVA DE LUNA	LH	Patagonia	-11.9	32.8	1500
12906	111	CUEVA DE LUNA	LH	Patagonia	-11.2	36.5	1500
12907	112	CUEVA DE LUNA	LH	Patagonia	-8.6	37.7	1500
12908	113	CUEVA DE LUNA	LH	Patagonia	-10.8	36.4	1500
12909	114	CUEVA DE LUNA	LH	Patagonia	-11.4	33.9	1500
12910	115	CUEVA DE LUNA	LH	Patagonia	-11.5	34.0	1500
12911	116	CUEVA DE LUNA	LH	Patagonia	-10.1	33.0	1500
12259A	235	CUEVA DE LUNA	LH	Patagonia	-11.8	33.9	1500
13009	214	CUEVA DE LUNA	LH	Patagonia	-10.4	38.4	1500
13010	215	CUEVA DE LUNA	LH	Patagonia	-9.9	27.5	1500
13011	216	CUEVA DE LUNA	LH	Patagonia	-11.7	32.7	1300
13012	217	CUEVA DE LUNA	LH	Patagonia	-11.3	33.8	1300
13013	218	Gruta del Manzano	MH	Patagonia	-10.0	31.8	1300
13014	219	Gruta del Manzano	LH	Patagonia	-11.5	35.7	1300
13015	220	LLAN	LH	Patagonia	-6.8	36.3	1300
13016	221	LLAN	LH	Patagonia	-9.6	34.4	1300
13017	222	LLAN	LH	Patagonia	-9.8	39.0	1300
13018	223	LLAN 22	LH	Patagonia	-8.5	26.0	1400
13019	224	LLAN 22	LH	Patagonia	-11.6	24.9	1400
13020	225	LLAN 22	LH	Patagonia	-9.4	38.5	1400
13021	226	LLAN 2	LH	Patagonia	-10.6	33.2	1400
13022	227	LLAN 2	LH	Patagonia	-9.8	33.3	1400
13023	228	LLAN 2	LH	Patagonia	-7.9	38.5	1400
13024	229	LLAN 2	LH	Patagonia	-11.4	31.5	1400
13025	230	LLAN 2	LH	Patagonia	-9.2	32.8	1400
13026	231	LLAN 2	LH	Patagonia	-10.6	39.4	1400
13027	232	LLAN 29	LH	Patagonia	-9.2	29.9	1400
12967	172	LLAN 29	LH	Patagonia	-9.1	31.8	1400
12968	173	LLAN 29	LH	Patagonia	-10.5	36.4	1400
12969	174	LLAN 29	LH	Patagonia	-8.8	36.4	1400
12970	175	LLAN 29	LH	Patagonia	-8.1	33.3	1400
12971	176	LLAN 29	LH	Patagonia	-7.5	40.4	1400
12972	177	LLAN 29	LH	Patagonia	-8.7	38.2	1400
12973	178	LLAN 29	LH	Patagonia	-8.5	37.6	1400
12974	179	LLAN 29	LH	Patagonia	-9.4	40.7	1400
12975	180	LLAN 29	LH	Patagonia	-9.3	32.9	1400

Temporal units (from Neme and Gil, 2008): LH, Late Holocene (4000 BP–present); MH, Middle Holocene (8000–4000 BP); EH, Early Holocene (10 000–8000 BP).

between 500 and 2500 masl. The eggshell fragments come from different archaeological contexts including caves, rock shelters, open-site deposits, and surface sites (Figure 1). These sites include all types of contexts such as multiple activity sites and special purpose sites, which represent different tasks, number of

individuals, and duration of stay. In those few cases where more than one egg fragment from the same level was taken, we took fragments from different sectors of the excavation units and with different colours or states of preservation to avoid the problem of over representing the same egg.

For the carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotope analysis of eggshell calcite, a small (~10 mg) fragment of each eggshell was rinsed with deionised water to remove surface contaminants and then acid-etched in a centrifuge under a vacuum using 2 M hydrochloric acid to dissolve ~30% of the fragment (by weight). Acid-etched samples were then rinsed three times with deionised water and air dried in a fume hood. The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values were determined using a Finnegan Gas Bench interfaced with a Finnegan MAT 252 mass spectrometer (Carnegie Institution of Washington, Washington, DC). Isotopic results are expressed as δ values, $\delta^{13}\text{C}$ and $\delta^{18}\text{O} = 1000 * [(R_{\text{sample}} / R_{\text{standard}}) - 1]$, where R sample and R standard are the $^{13}\text{C}/^{12}\text{C}$ or $^{18}\text{O}/^{16}\text{O}$ ratios of the sample and standard, respectively. The standards are Vienna-Pee Dee Belemnite limestone for carbon and Vienna Standard Mean Ocean Water for oxygen. The units are expressed as parts per thousand, or per mil (‰). The within-run standard deviation of several calcite standards was $\leq 0.2\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values.

Results and discussion

Table 2 displays in detail the results of the stable isotope data from southern Mendoza archaeological eggshell samples. Isotopic information was correlated with the desert and altitudinal units (Figure 1; Table 2). Using the deserts as units, we compared eggshell data from archaeological sites located in Altoandina ($n = 47$), Patagonia ($n = 96$), and Monte ($n = 102$) deserts. The altitudinal analysis explores the data, considering the

altitude of the archaeological site in metres above sea level (Figure 1; Table 1). First, we derive the Rhea diet from the $\delta^{13}\text{C}$ eggshell results and infer spatial patterns in terms of the ecological area. Second, in order to complement the spatial trends, we present the $\delta^{18}\text{O}$ from the same samples. Both isotope trends demonstrate a spatial pattern that is explained in terms of material culture/human mobility. Third, we explore the potential role of eggs in human diet.

Rheidae diet, drinking water, and the provenance of eggshells

The $\delta^{13}\text{C}$ values range from -13.1‰ to -5‰ , with a mean of -9.4 ± 1.48 and median of -9.8‰ (Figure 2). This implies a wide range of variation in the Rheidae diet, which could respond to significant differences between individual diets (Figure 2). Using Formula (3), we estimate a diet composition between 100% and 60% of C_3 plants. This proportion is in agreement with Paoletti and Puig (2007) macrobotanical analysis as was traduced in isotopic diet by Llano (2009). This means that Rheidae diet is mostly based on C_3 but with a variable component of C_4 plants. In order to explore this information in terms of environmental trends, the isotopic data are analyzed using previously defined ecological areas.

Table 3 details $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ statistics by desert. The mean value of the Altoandina samples ($n = 47$) is -9.2‰ and ranges between -11.5‰ and -6.8‰ (Table 3). Using Formula (3), these results imply a diet composed of 90% C_3 plants with a range of

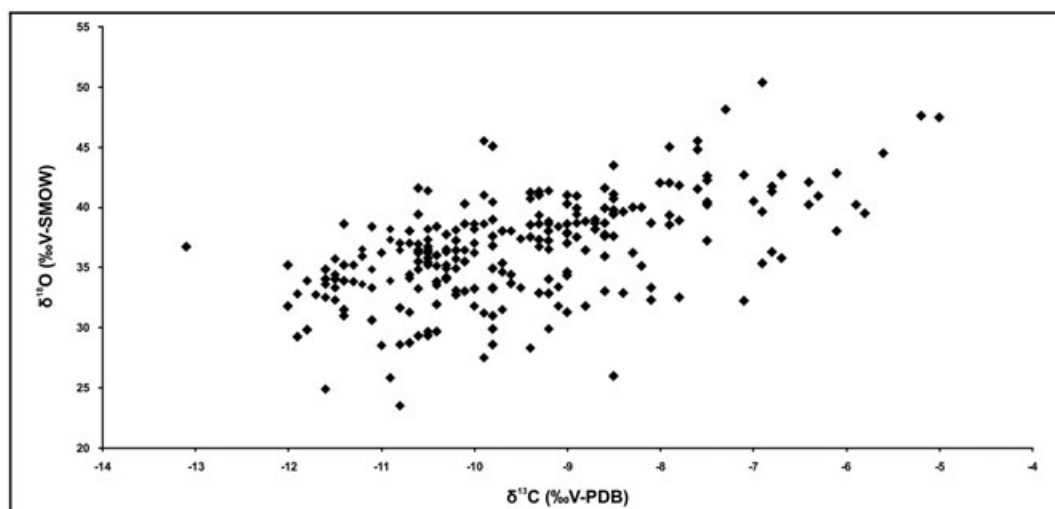


Figure 2. Relationship and variability in eggshells $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$. V-PDB, Vienna-Pee Dee Belemnite limestone; V-SMOW, Vienna Standard Mean Ocean Water.

Table 3. Basic statistics in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ from the three ecological areas

	Altoandina		Patagonia		Monte	
	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
Maximum	-6.8	50.4	-6.4	41.6	-5	48.1
Minimum	-11.5	28.6	-13.1	23.5	-11.4	28.5
Mean	-9.2	36.2	-10.5	34.9	-8.9	38.1
Standard deviation	1.16	4.1	1.23	3.6	1.57	4.3
Median	-9.7	35.9	-10.4	35.2	-9.2	38.2

approximately of 70% to 100% of C_3 plants in the diet. Patagonia samples show a $\delta^{13}\text{C}$ mean value of -10.5‰ that implies a diet composed of 100% C_3 plants. The area presents a range between -13.1‰ and -6.4‰ corresponding to an estimated diet range between 75% and 100% C_3 plants. Monte eggshell samples, with a $\delta^{13}\text{C}$ mean value of -8.9‰ , correspond to a Rheidae diet composed of 90% C_3 plants, but its range between -11.4‰ and -5‰ shows a variation estimated between 100% and 62% of C_3 plants in the diet. These results show a significant difference among Patagonia and Altoandina samples (one-way ANOVA $F = 16.7$, $p = 7.316\text{E}-05$) and between Patagonia and Monte eggshell samples (one-way ANOVA $F = 35.87$, $p = 9.936\text{E}-09$). There is no significant difference between Altoandina and Monte samples (one-way ANOVA $F = 1.64$, $p = 0.21$).

Figure 3 illustrates the comparative trends in $\delta^{13}\text{C}$ from the eggshells between different deserts. These results show a difference in Rheidae diet between Monte and Patagonia, where the Rheidae currently inhabit. In both cases, C_3 plants are comparatively the most significant to Rheidae diet, but in Monte, there are more C_4 plants than in Patagonia. Figure 4

correlates the $\delta^{13}\text{C}$ values (average by site) with the altitude of the site locations where the samples were taken. The results show a weak correlation ($r = -0.11$) that increases ($r = -0.30$) when we exclude those sites outside of the natural Rheidae distribution (Altoandina Desert; >2200 masl). There is an unexpected inconsistency with the values in the Altoandina eggshell samples (>2200 masl), which is clearly shown in Figure 4.

On the other hand, the $\delta^{18}\text{O}$ values in eggshells range between 23.5‰ and 50‰ , with a mean $36.48 \pm 4.2\text{‰}$ and median 36.5‰ . Like the analysis of Rheidae diet, as shown with $\delta^{13}\text{C}$, this range implies a broad range of water source precedence (Figure 2). As was noted by Johnson *et al.* (1998), the isotopic variability measured in the Rheidae eggshell samples implies that the bulk of the ostrich body water is derived from an alternative water source (e.g., plant-leaf water). Rheidae feeding habits are variable throughout the course of a few days, whereby consumption of plants with differing $\delta^{18}\text{O}$ values likely contributes to the variable $\delta^{18}\text{O}$ values of eggshells laid by free-range birds (Johnson *et al.*, 1998). Table 3 presents this information according to deserts in order to differentiate $\delta^{18}\text{O}$ water sources. These results (Figure 5) show a significant

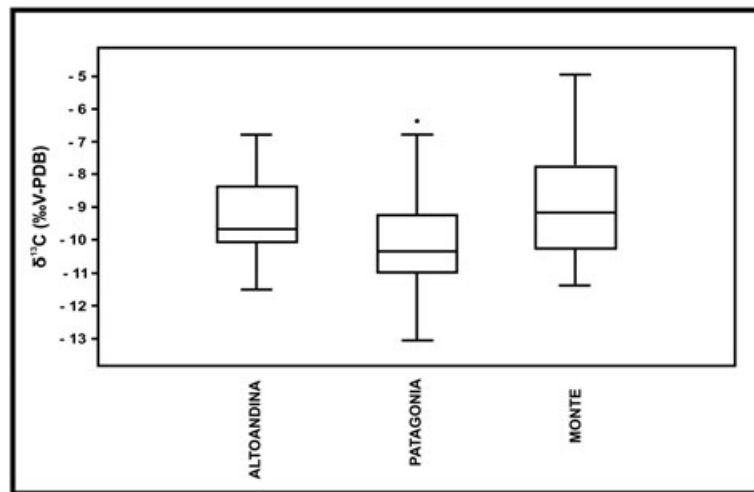


Figure 3. Comparative trends in eggshells $\delta^{13}\text{C}$ from ecological areas. V-PDB, Vienna-Pee Dee Belemnite limestone.

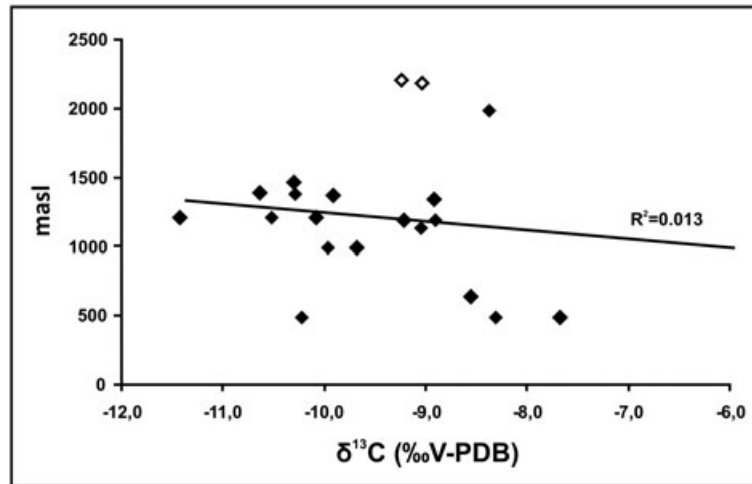


Figure 4. Altitudinal variation in eggshells $\delta^{13}\text{C}$. The 'white symbols' are Altoandina Desert samples. V-PDB, Vienna-Pee Dee Belemnite limestone.

difference between Patagonia and Altoandina samples (one-way ANOVA $F = 3.908$, $p = 0.05$), and Patagonia and Monte samples (one-way ANOVA $F = 30.77$, $p = 9.343\text{E}-08$), but not a significant difference between Altoandina and Monte samples (one-way ANOVA $F = 2.639$, $p = 0.106$).

The variability in evapotranspiration can explain the variation in $\delta^{18}\text{O}$ (Koch et al., 1989; Johnson et al., 1998). Low relative humidity and high temperatures increase evaporative enrichment in source waters and increase transpiration in plants, which should consequently be reflected as isotopically enriched Rheidae eggshells (Johnson et al., 1998). According to Roig et al. (1991), evapotranspiration is significantly different among Monte (arid/semi-arid), Patagonia (sub-humid), and Altoandina (humid) deserts. Following this criterion, it can be expected that the Monte–Patagonia–

Altoandina sequence is in direct relation with depleted $\delta^{18}\text{O}$ values. Our results confirm these expected trends in Monte and Patagonia. Monte has a more enriched $\delta^{18}\text{O}$ average value than Patagonia. However, the results of the Altoandina samples show an unexpected enriched $\delta^{18}\text{O}$ average value. The Altoandina eggshells have an intermediate $\delta^{18}\text{O}$ median value between Monte and Patagonia and not the more depleted values, as was expected in terms of ecologic and climatic variables. The Patagonia samples have more depleted $\delta^{18}\text{O}$ values than the Monte ones, but those from Altoandina have greater enriched values with respect to Patagonia. This trend is contrary to what was expected but closer to Monte samples (Figure 5). The correlation between the altitude and the isotopic signal from the eggshell samples is weak ($r = -0.45$), but it became stronger ($r = -0.62$) when we excluded

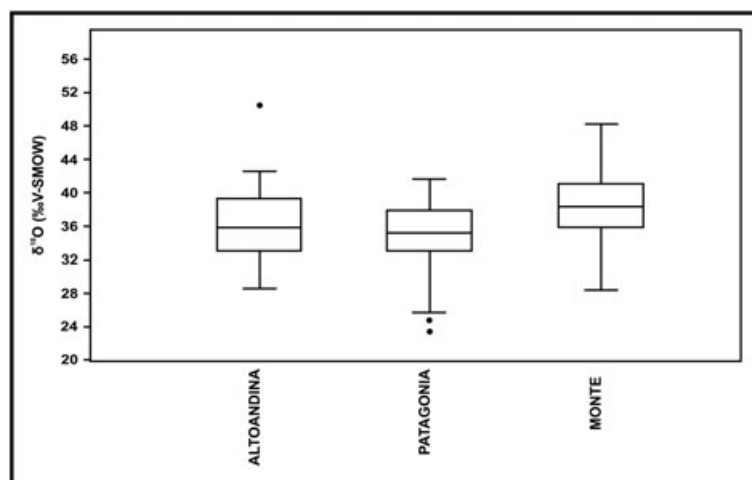


Figure 5. Comparative trends in eggshells $\delta^{18}\text{O}$ from ecological areas. V-SMOW, Vienna Standard Mean Ocean Water.

samples from the non-Rheidae distribution area (Altoandina, Figure 6).

The differences in the $\delta^{13}\text{C}$ values of eggshell fragments between archaeological sites located in the Monte Desert from those located in the Patagonia Desert could be explained by the natural distribution of C_4 plants (more abundant in Monte than in Patagonia). In this way, each area has expected isotopic patterns in accordance with the ecology of each desert (Monte and Patagonia). However, in the Altoandina Desert, which is presently no longer occupied by *Rhea* sp., the isotopic signal in the eggshells does not reflect the expected values according to the isotopic ecology of the area. The differences between the Patagonia and Altoandina eggshells' $\delta^{13}\text{C}$ signal and the similarities between the Altoandina and the Monte eggshell samples are more difficult to explain using the same criteria (the natural distribution of C_3 – C_4 plants). First, in the Altoandina Desert, there is no presence of C_4 plants, contrary to the obtained results with the more enriched values in the eggshell recorded here. Second, biogeographically, there is no distribution of Rheidae in this environment. In Patagonia and Monte, Rheidae never reach 1700 masl, and the archaeological sites in the Altoandina ecosystem are located at more than 2000 masl. Third, Altoandina and Monte are not contiguous deserts (Figure 1). The weak correlation between $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ with altitude reflects the non-expected $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values (Figures 4 and 6) recorded in Altoandina samples. Figure 2 shows a significant correlation between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ with ecological implications ($r = 0.55$), which implies a direct relationship and confirms the differentiation in both isotopes between Monte and Patagonia.

The eggshells recorded in Altoandina are deposited in an ecological area that was not inhabited by Rheidae. Two possibilities could explain this record. First, human exchange and/or mobility in the past could have been responsible for depositing the eggshells in the Altoandina Desert. Second, Rheidae could have occupied the Altoandina Desert in the past but not today. This last idea is rejected by the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values from eggshell samples. The stable isotopes from Altoandina eggshell samples have unexpected values with the location and ecology that demonstrates a stronger affinity with Monte rather than Patagonia. These samples were not a consequence of a different distribution of *Rhea* in the Patagonia Desert or a *Rhea* occupation of Altoandina in the past. In this sense, the $\delta^{13}\text{C}$ values in the Altoandina eggshell samples are similar to Monte but different from those in Patagonia (Figure 7). The $\delta^{18}\text{O}$ shows a mixed pattern between Patagonia and Monte, but in no way are the values expected to be found among samples from highland areas such as the Altoandina (Figure 7). The isotopic values in Altoandina Desert eggshell are contra-intuitive because of the Patagonia Desert boundary with Altoandina, but there is not a close, spatial relationship contact between the Monte and Altoandina deserts (Figure 1). The implication is that these eggshell samples are non-local and have been transported from a Monte–Patagonian ecotone to their present location—a distance of at least 60 km.

The eggs, as a subsistence resource, are available in the Monte/Patagonia deserts in late spring/early summer, when the Altoandina Desert begins to be seasonally occupied by humans. If the eggs were transported, a high calorie source

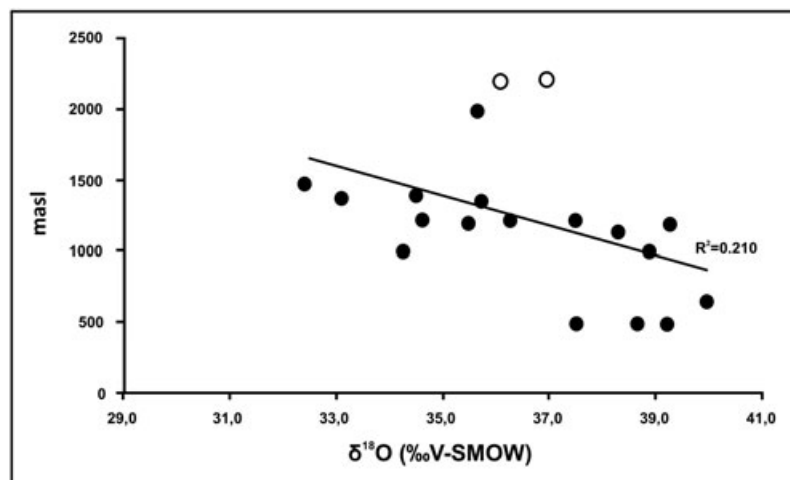


Figure 6. Altitudinal variation in eggshells $\delta^{18}\text{O}$. The 'white symbols' are Altoandina Desert samples. V-SMOW, Vienna Standard Mean Ocean Water.

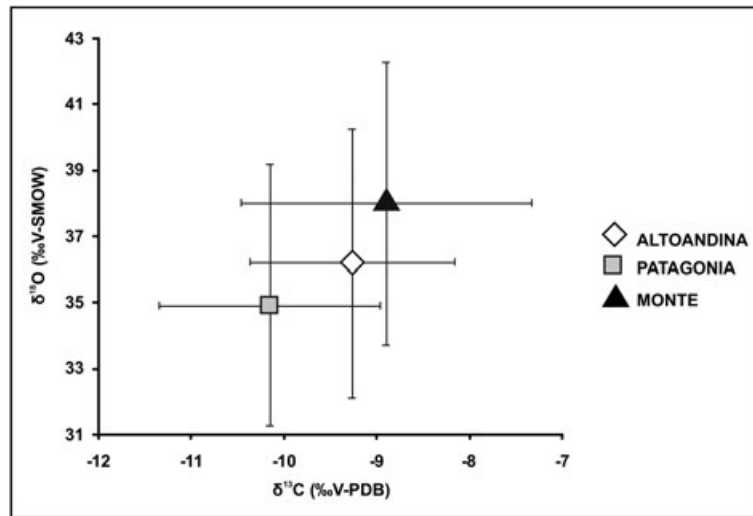


Figure 7. Trends in eggshells $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ by ecological areas. V-PDB, Vienna-Pee Dee Belemnite limestone; V-SMOW, Vienna Standard Mean Ocean Water.

was carried in the first moment of annual highland occupation. There is no evidence of eggshell ornaments in the area, and it can be considered that eggshells were generated as a consequence of subsistence activity. However, other uses such as containers need to be considered.

These preliminary trends show that eggshells can be used to explore the distribution of past human occupation ranges and/or their exchange systems. Recently, researchers have demonstrated the meaning of non-local items in human strategies in northern Patagonia (Neme & Gil, 2006; Salgán *et al.*, 2012), but the role of eggshells has not been previously considered.

Isotope ecology, egg consumption, and human diet

Rheidae egg consumption was a part of the human diet in the past, at least during the late Holocene in southern Mendoza (Giardina, 2010). In order to improve our knowledge regarding human isotopic diet in the region, it is necessary to address whether or not these Rheidae eggs have distinctive isotopic signals and incorporate that information into isotopic diet models (Gil *et al.*, 2011, 2012). In the study area, an enrichment in human bone collagen over bone apatite was recently noted (Gil *et al.*, 2010). This implies a protein source more enriched than the energy source (Ambrose & Norr, 1993), contrary to a scenario with incorporation of C_4 plants such as maize (Gil *et al.*, 2010). There were also humans with high $\delta^{13}\text{C}$ values before maize incorporation (approx. -15‰), when the $\delta^{13}\text{C}$ collagen average was around -18‰ (Gil *et al.*, 2010). Both situations generate the necessity to explore resources other than maize to explain this

high $\delta^{13}\text{C}$ and a way to improve our understanding of the isotopic ecology of southern Mendoza and northern Patagonia (Otaola and Ugan, 2011).

Previous $\delta^{13}\text{C}$ on Rheidae bone collagen from southern Mendoza specimens (mostly *R. pennata* recorded in Patagonia ecosystems) show average values of $-20.5 \pm 0.5\text{‰}$ (Gil *et al.*, 2010). In the bone apatite, the average is $-11.8 \pm 0.3\text{‰}$, while the difference in the collagen–apatite is 8.7‰ ($n = 4$). Eggshell calcite values presented here have an average value of $-9.4\text{‰} \pm 1.48$. The difference between eggshell calcite and bone apatite in the study area is 2.5‰ . Von Schirnding *et al.* (1982) found a similar value (3‰) between bone collagen and the organic fractions of eggshells.

The difference between Patagonia and Monte eggshells' $\delta^{13}\text{C}$ likely implies stronger C_4 signals in the Monte diet rather than in the Patagonia Rheidae diet. Eggshell $\delta^{13}\text{C}$ values indicate that *Rhea* sp. reliance on C_3 plants was high in all studied regions. *Rhea* foraging in the Patagonia desert consumed virtually no C_4 plant foods, and those foraging in the Monte Desert consumed an average of merely 10% C_4 plant foods. Thus, consumption of *Rhea* sp. eggs would have a negligible, if any, contribution to enriched $\delta^{13}\text{C}$ in human foraging populations. Therefore, this resource cannot explain the enriched $\delta^{13}\text{C}$ in collagen found in archaeological human bones in the study area.

Conclusion

The increase of eggshells fragments in the archaeological record from southern Mendoza demonstrates the

important role that this resource played in the hunter-gatherer diet during the entire Holocene, in agreement with the similar use of Ratite species around the world (Grobelaar and Goodwin, 1952; Rudner, 1953; Plug, 1982; Churcher, 1983; Churcher *et al.*, 1997; Morris, 2005; Janz *et al.*, 2009; Texier *et al.*, 2010). The ratite egg high economic return, mediated by the large amount of calories and their easy harvest, explains why they may have been more important than many of the other animal and plant resources and even the Rhea meat itself (Giardina, 2010).

This isotopic approach has shown that the eggshell fragments could help understand different aspects of human diet, mobility, territoriality, and the paleobiogeography of ratite species in different ecosystems. The $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ signals coincide with the vegetal resources eaten by the Rhea and the water distribution in the region, and reflecting possibly the differential biogeography of both Rhea species (*R. pennata* in Patagonia Desert and *R. americana* in Monte Desert) on the landscape. A high correlation between the isotopic values with the regional biogeographic areas defined in this work and the altitude suggests that the human population was mostly taking eggs from surrounding areas of the sites. The significant isotopic difference between eggs from Monte and Patagonia can be used as a good indicator for spatial provenience provenance of this resource. On the other hand, a clear inconsistency between the isotope data and the geographical distribution of the samples comes from those sites located in the cordilleran region (Altoandina Desert). Its samples show high $\delta^{18}\text{O}$ values and less depleted $\delta^{13}\text{C}$ values than those expected using the isotope biogeography model. The absence of Rheidae species in this environment (up to 2000 masl) indicates that the eggs must have been transported to sites by humans in the past. These transported eggs reflect the isotopic values ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$) from their origin in Monte. Thus, the isotopes were a good indicator to reconstruct the probable provenance of the eggs.

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