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journal homepage: <http://www.elsevier.com/locate/jas>Isotopic values of diet of *Blastocerus dichotomus* (marsh deer) in Paraná Basin, South AmericaDaniel M. Loponte^{a,*}, María J. Corriale^b^a Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Instituto Nacional de Antropología y Pensamiento Latinoamericano, 3 de Febrero 1378, C1426BJN Buenos Aires, Argentina^b IEGEBA, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Grupo de Estudios sobre Biodiversidad en Agroecosistemas, Departamento de Biodiversidad y Biología experimental, FCEN, Universidad de Buenos Aires, Pabellón II, 4° piso, Lab. 14, Buenos Aires, Argentina

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ABSTRACT

The marsh deer (*Blastocerus dichotomus*, Illiger, 1815) is the largest contemporary South American deer, and its habitat includes the floodplains and wetlands of eastern South America. Throughout the Holocene these deer were widely used by indigenous societies, from the southern banks of the Amazon River to the Río de la Plata River, and from the Andean foothills to the Atlantic Ocean. However, despite the enormous ecological and archaeological importance of this ungulate in the region, our knowledge of the isotopic values of their diet is almost nonexistent. This paper is the first systematic approach to the study of the isotopic values of this mammal's diet, using archaeological and present-day samples from interconnected watersheds of the Paraná and Uruguay rivers in east-central Argentina. The results obtained from 24 measurements indicate an average value of $-21.09 \pm 1.46\text{‰}$ in $\delta^{13}\text{C}$ collagen, with a low coefficient of variation (6.92%). The data indicate a marked preference for consumption of plants with a C_3 photosynthetic pathway. Most of the observed variability in the isotopic values corresponds to the period 900–1430 ^{14}C years BP, a time range during which the values show higher consumption of C_4 plants. This it could be related with a period where temperature and associated humidity increased, synchronous in the area with the Medieval Climate Anomaly.

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1. Introduction

The marsh deer (*Blastocerus dichotomus*, Illiger, 1815) is the largest contemporary South American deer (Cabrera and Yepes, 1940). Males weigh around 150 kg, with females weighing about 30% less (Miranda et al., 2009; Weber and Gonzalez, 2003). This sexual dimorphism is consistent with osteometric variability found in this species (Loponte, 2004). The height of adult males including the head is approximately 2 m, with body length reaching about 2 m also.

The marsh deer has a broad spatial distribution in South America, from the southern banks of the Amazon River to the Río de la Plata River, covering an area of approximately 7,000,000 km² that includes central and southern Brazil, eastern Peru and Bolivia, central Paraguay, northeastern Argentina, and riverbanks and the Atlantic coast in Uruguay (Azara, 1902; Jungius, 1976; Schaller and Vasconcelos, 1978; Weber and Gonzalez, 2003; Whitehead, 1972)

(Fig. 1). Although these deer were also present in northeastern Brazil during the Pleistocene (Magalhaes et al., 1992; Pinder and Grosse, 1991), there is no paleontological or archaeological evidence for the Holocene north of latitude 10° S. Today, significant relic populations exist in Pantanal, Brazil, and Iberá and the Paraná Delta in Argentina (Beccaceci, 1994; Mauro et al., 1998; Pinder and Grosse, 1991; Varela et al., 2000).

Historical references mainly, and biogeographical patterns modeled by computer as secondary information source (cf. Politis et al., 2011), suggest that the meridional boundary of marsh deer in South America is the middle estuary of the Río de la Plata River (34° 50' SL; 57° 56' WL'), considering the current climate parameters. Based on ecological information, Loponte (2004) suggested that this ungulate would have extended not only to the estuary of Salado River, but till the end of San Borombón bay within the present climate (36° 20' SL; 56° 47' WL'), where the Río de la Plata River meets the Atlantic Ocean. New archaeological findings in Late Holocene deposits of this area support this hypothesis (Silveira et al., 2010) (Fig. 1).

The habitat of *B. dichotomus* is focused on extensive South American wetlands (marshes, swamps and floodplains) associated

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Fig. 1. Approximate distribution of marsh deer during the late Holocene, after European colonization. The dot indicates the origin of the modern samples and the triangle the provenience of the archaeological samples.

mainly with the Paraná River basin and the Atlantic slope of southeastern Brazil, dominated by the Atlantic forest. Previous studies on habitat use in Pantanal (Schaller and Vasconcelos, 1978; Tomas et al., 1997; Tomas and Salis, 2000), Iberá (Tomas et al., 1997), and from the floodplains of the Paraná River (Pinder, 1996), indicate that aquatic habitats covered in up to 70 cm of water are used by marsh deer (Schaller and Vasconcelos, 1978; Silva and Mauro, 2002). It has a specially adapted webbed hooves, which make it possible to move in the soft soils typical of these habitats and fragmented landscapes by deep bodies of water, and which make it easy for these deer to colonize insular environments.

The marsh deer's diet consists mainly of aquatic macrophytes or other plants that can tolerate seasonal flooding (Tomas et al., 1997; Tomas and Salis, 2000). Its dentition consists of low-crowned teeth typical of browser, and it has been classified as such by some authors (Coimbra Filho, 1972; Hofmann et al., 1976; Weber and González, 2003). In contrast, other researchers have classified this species as a grazer (Bunnell, 1982; Nogueira Neto, 1973). The existence of a multiple types of information has led to *B. dichotomus* being regarded as a deer with a mixed dietary strategy (Tomas and Salis, 2000).

The South American archaeological record indicates that *B. dichotomus* was heavily hunted during the Holocene across central and southern Brazil and northeastern Argentina (Acosta, 2005; Caggiano, 1984; Loponte and Acosta, 2004; Pérez Jimeno, 2007; Santini and De Santis, 2011; Sartori and Colasurdo, 2011). However, despite this species' archaeological and ecological importance, there have still been no systematic studies on the isotopic values of its diet. The objective of this study is therefore to determine the isotopic values of the marsh deer diet through measurements obtained on bone collagen from both modern and

sub-fossil individuals recovered in the Paraná Basin, and to analyze any spatial and temporal trends existing in these values (Fig. 1).

2. Materials and methods

2.1. Environmental and temporal contexts of the samples analyzed

For this study, we obtained 24 isotopic readings for different individuals of *B. dichotomus*, with 20 of these samples coming from 16 different archaeological sites, all located within the wetlands of the lower Paraná River (between 33 and 34° S and 59–60° W). Another sample was obtained from an archaeological site located on the alluvial plain of the middle Paraná River (Fig. 2). The chronological range of these samples is bounded within the late Holocene, with dates ranging from 680 ± 60 to 2296 ± 34 ^{14}C years BP. Archaeological samples were recovered in a subtropical wetland, where fauna are adapted to the seasonal flooding patterns of the Paraná River. This regime has a pulse of flooding at the end of the summer, with a peak between February and March, and a contraction during the colder period, especially from May to July. In summer, average and maximum temperatures are 18 °C and 40.7 °C respectively, and in winter, average and minimum temperatures are 11 °C and –5.7 °C (Révora, 2011). The annual average rainfall of 1000 mm is concentrated during the summer and early autumn. Most of the vegetation consists of C_3 plants (87%), with 12% C_4 plants and 1% CAM plants or plants with mixed photosynthetic patterns (Madanes et al., in press).

This wetland is composed of different landscape units that have been subjected to various types of analysis in recent years (Bonfils, 1962; Madanes et al., in press; Malvárez, 1999). Samples from the continental sector of this wetland (sector I, Fig. 2) can be considered as a group distinct from those recovered in insular areas in the center and the flooded plains in the northeastern area of the wetland, which have more fluvial fragmentation (sectors II, III, and IV, Fig. 2). In contrast, the continental area of the wetland is in contact with the Pampas, which was not colonized by marsh deer. This steppe is composed of well-drained high ground that influence the ecology of the sector I. Some analyses also suggest a differential distribution of vegetation between these two landscape macro-units (Madanes et al., in press).

From a chronological point of view, the samples are grouped in two different sets. The older set covers the period from 2300 to 1500 ^{14}C years BP, while the second set dates to the range of 1060–680 ^{14}C years BP. Multiple lines of evidence have identified the existence of a biocenosis similar to that of the present since the beginning of the third millennium BP (Loponte, 2008; Loponte et al., 2012; Tonello and Prieto, 2010), without excluding the possible existence of some minor-scale climatic fluctuations during the late Holocene.

The other three samples analyzed here are modern, and come from deer that died from natural causes few years ago. These were collected in the Rincon del Socorro Park (28° 38' S, 57° 25' W) in the subtropical Iberá wetlands, which run from the East bank of the Paraná River to the center of the province of Corrientes (Fig. 3). This area contains relics of Pleistocene channels of the Paraná River (Neiff and Poi de Neiff, 2005), and extends nearly 200 km from north to south with a width of approximately 50 km. It includes a total of almost 10,000 km² of wetland environments (marshes and swamps), shallow lakes, and extensive areas of grassland (Carnevali, 2003). Climate is subtropical-humid, with hydric and thermal seasonality. Rainfall occurs in all seasons but it is heavier in spring and summer. Annual average rainfall of 1700 mm (Neiff and Poi de Neiff, 2005). In summer average and maximum temperatures are 27 °C and 44 °C, respectively, and in winter average and minimum temperatures are 16 °C and –2 °C, respectively (EEA

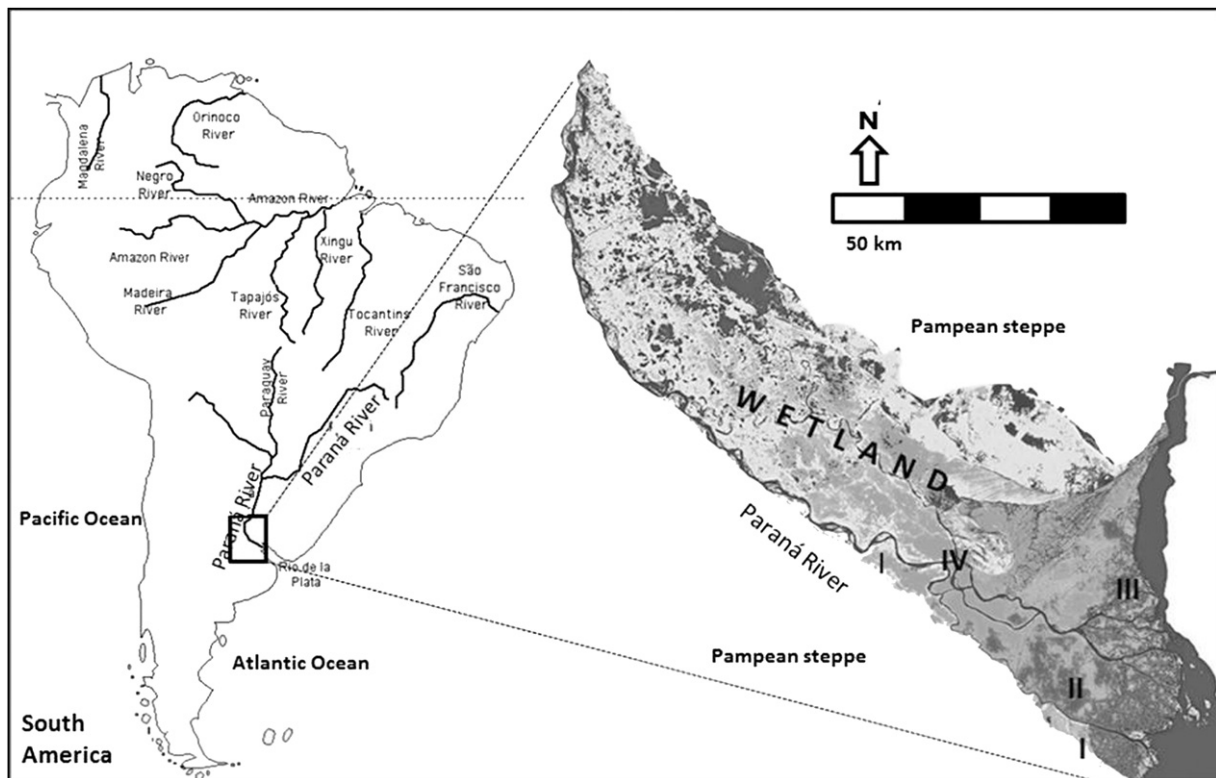


Fig. 2. Wetland of the Lower Paraná River.

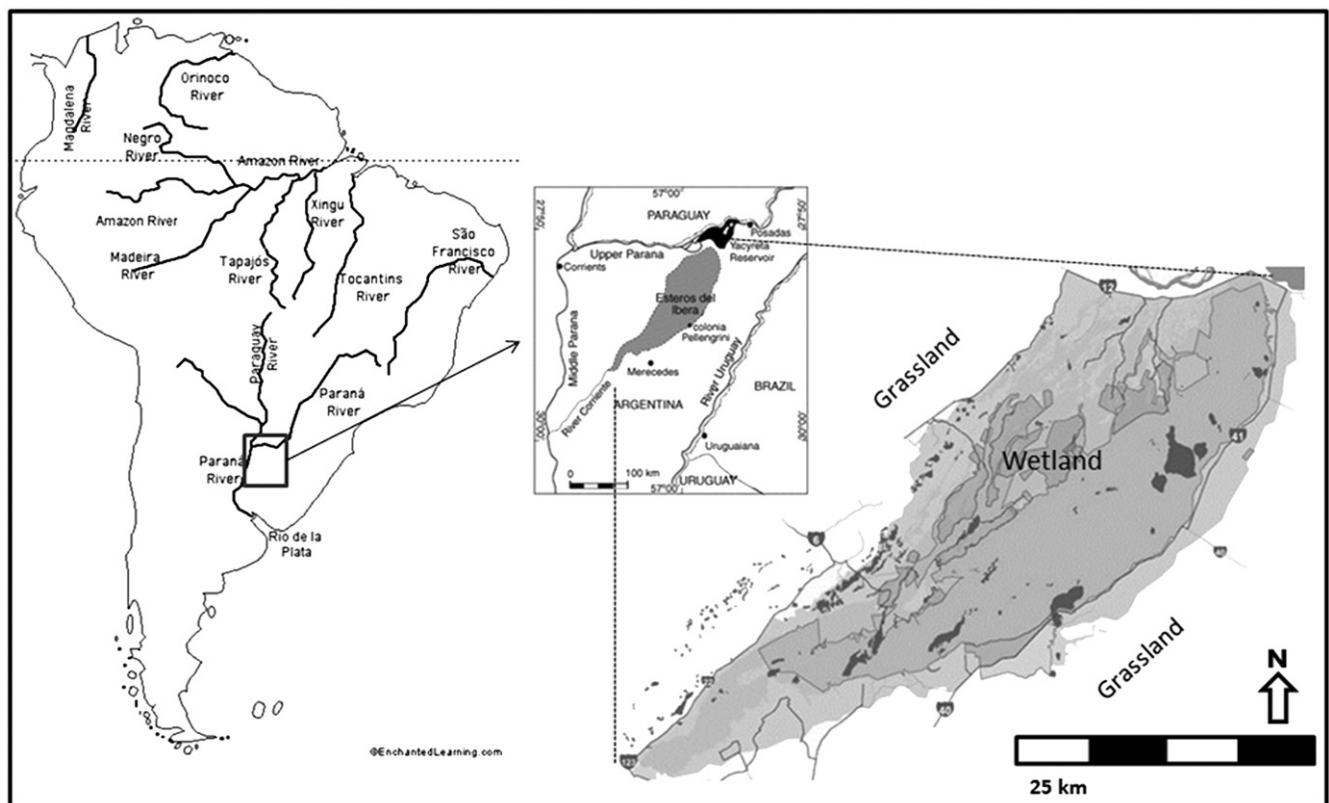


Fig. 3. Iberá wetland.

Mercedes, INTA, 2010). In areas of high topographic gradient that divide the wetlands, grasslands predominate, which have a higher proportion of C_4 plants, while the great marshes are dominated by C_3 plants (Corriale et al., in press; Corriale and Loponte, in preparation).

2.2. Isotopic analysis

All measurements, including those for modern samples, were obtained from bone collagen (there are no available values of apatite). Fourteen of the samples were processed at the Instituto de Geocronología y Geología Isotópica at the University of Buenos Aires (AIE sample codes), one at the Center for Applied Isotopic Studies, University of Georgia (UGA sample code), seven at the Mass Spectrometry Laboratory at the University of Arizona (AA sample codes), and two at Beta Analytic (Beta sample codes). The isotopic values from the last two laboratories were obtained as part of the radiocarbon dating process. All samples exhibited a C/N ratio between 2.9 and 3.6.

The measurements are expressed in isotopic values compared with those obtained in Cretaceous fossil belemnites (Vienna Pee Dee Belemnite), with values being negative in relation to this pattern. Plants that employ the Calvin carbon fixation cycle (C_3 photosynthetic pathway) have average values of -27.5‰ ($\delta^{13}\text{C}$) while those using the Hatch-Slack mode (C_4 photosynthetic pathway) have average $\delta^{13}\text{C}$ values of -12.5‰ . The latter pathway is characteristic of most tropical grasses. A third photosynthetic pathway is called CAM (crassulacean acid metabolism), which is an adaptation in plants in arid environment, which reduces stress related to lack of water. The $\delta^{13}\text{C}$ values for plants using this photosynthetic pathway varies between -27‰ and -12‰ (Ambrose, 1993; Lee-Thorp et al., 1989; Pate, 1994). In both of the wetland areas involved in this work, this functional group has a very restricted distribution.

Multiple studies have shown that $\delta^{13}\text{C}$ values measured in the collagen ($\delta^{13}\text{C}_{\text{Cco}}$ hereinafter) of large herbivores is enriched by approximately 5‰ compared to the tissue consumed (Lee-Thorp et al., 1989). Therefore, pure C_3 diets yield values of around -21‰

while pure C_4 plant diets have measurements around -7.5‰ . In the inorganic bone fraction (apatite), these values are around -13.5‰ and -1‰ respectively (Lee-Thorp and Van Der Merwe, 1987; Sullivan and Krueger, 1981). Also, the enrichment of carbon in the apatite is usually around 9‰ higher than in the collagen. This happens because the carbon in the apatite is in isotopic equilibrium with CO_2 from the blood, which is derived from the oxidation of glucose and other substances. These values are thus more representative of the values of carbohydrates and fats, whereas the organic carbon comes mainly from the protein fraction of the diet. As a result, the $\delta^{13}\text{C}$ of the inorganic fraction reports on the diet as a whole, whereas organic collagen reports mostly on the protein fraction (Krueger and Sullivan, 1984; Pate, 1994).

2.3. Statistical analysis

Correlation analyses were conducted in order to evaluate the relationships between $\delta^{13}\text{C}_{\text{Cco}}$ (collagen) and latitude and between $\delta^{13}\text{C}_{\text{Cco}}$ and radiocarbon dates obtained by Accelerator Mass Spectrometry (AMS). In order to evaluate the influence of chronology and the landscape units in $\delta^{13}\text{C}_{\text{Cco}}$ values obtained of samples from archaeological sites, a general linear mixed model (GLMM) was applied, with the $\delta^{13}\text{C}_{\text{Cco}}$ value as the dependent variable, and the time period (between either 2300 and 1500 ^{14}C years BP or 1060 and 680 ^{14}C years BP) and the landscape units (I and II–III–IV) as the independent ones. To validate the simple model corresponding to these restrictions, we calculated the proportion of variability among the $\delta^{13}\text{C}_{\text{Cco}}$ values accounted for by the various factors. When significant differences were found, comparisons were carried out using a Fisher LSD test ($\alpha = 0.05$). We used Infostat software for all of the statistical analyses (Di Rienzo et al., 2011).

3. Results

The isotopic values from the deer bone collagen show a higher proportion of C_3 plant consumption, since the average measurement is -21.09‰ , with a low coefficient of variation (Table 1, Fig. 4). Although there is a slight decrease in the values as a time function,

Table 1
Values for $\delta^{13}\text{C}$, collagen obtained from *B. dichotomus* bone tissue.

	Location/Site	Sector	Sample code	$\delta^{13}\text{C}_{\text{Cco}}$ (‰)	^{14}C years BP	Latitude (G. g.)
Iberá	Iberá 1	Iberá	AIE 26919	-23.3	Modern	28.54
	Iberá 2	Iberá	AIE 26921	-23.2	Modern	28.54
	Iberá 3	Iberá	AIE 26917	-22.7	Modern	28.54
Lower Paraná Wetland	La Bellaca site 2	I	AIE 26941	-17.1	680 ± 80	34.38
	Arroyo Fredes	II	AIE 26927	-22.0	690 ± 70	34.18
	Cerro Lutz	III	AIE 26923	-21.6	790 ± 42	34.63
	Punta canal	I	AIE 26931	-17.7	900 ± 80	34.38
	El Cazador site 3	I	AIE 26939	-22.0	920 ± 43	34.32
	Guazunambí	I	AIE 26929	-21.8	940 ± 60	34.30
	Guazunambí	I	Beta 147109	-19.0	940 ± 60	34.30
	Anahí	I	AIE 26937	-20.1	1020 ± 70	34.28
	Anahí	I	UGA 9907	-20.3	1020 ± 70	34.28
	Garín	I	AIE 26935	-20.7	1060 ± 60	34.37
	Cerro Mayor 1	III	AA97457	-21.2	1574 ± 45	33.37
	Cerro Mayor 2	III	AA97469	-21.7	1561 ± 45	33.37
	Túmulos de Campana 2	I	Beta-172059	-21.06	1640 ± 70	34.19
	Túmulos de Campana 2	I	AIE 26933	-21.5	1640 ± 70	34.19
	La Argentina	III	AA97463	-21.5	1645 ± 34	33.53
	Río Lujan site 2	I	AA97458	-21.3	1692 ± 46	34.26
	Médanos de Escobar	I	AA97465	-21.9	1752 ± 33	34.35
	Lechiguanas 1 (IV)	IV	AA97461	-21.2	2267 ± 34	33.73
	Lechiguanas 1 (IV)	IV	AA97467	-21.4	2290 ± 34	33.73
	Arroyo Sarandí	I	AIE 26925	-20.9	n/d	34.30
	Campo Binaghi	MP	AIE 26947	-21.0	n/d	31.63
Mean				-21.09		
Standard deviation				1.46		
Coefficient of variation				6.92		

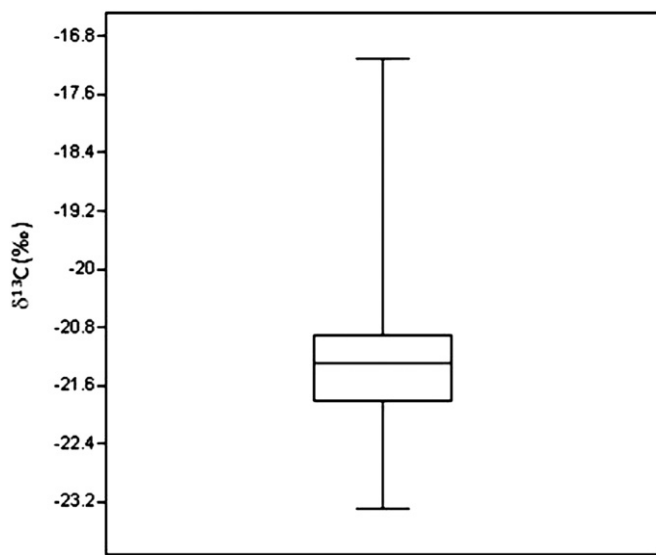


Fig. 4. Boxplot of $\delta^{13}\text{C}_{\text{co}}$ values from *B. dichotomus* bone tissue.

Table 2

Central tendency and dispersion values for collagen for two different periods of the Late Holocene. P1: period between 1574 ± 45 and 2290 ± 34 ^{14}C years BP. P2: period between 680 ± 80 and 1060 ± 60 ^{14}C years BP.

Period	N	Mean	S.D.	CV	Min	Max
P2	10	-20.23	1.78	8.80	-22	-17.1
P1	9	-21.41	0.24	1.23	-21.9	-21.2

4. Discussion

The isotopic values from marsh deer bone collagen indicate the consumption of plants from both the C_3 and C_4 functional groups, although the average isotopic diet shows a marked predominance of the first ones. These results are consistent with field observations in slightly modified environments such as Pantanal (Silva and Mauro, 2002) and the Paraná Delta (Beccaceci, 1996; Tomas et al., 1997; Varela, 2003). In the latter region, consumption of 33 plant species has been reported for *B. dichotomus*, with less than 18% of these being C_4 plants (Beccaceci, 1996; Tomas et al., 1997; Varela, 2003). This predominant consumption of C_3 plants could be due to a variety of factors. The selection of certain food items is based upon availability, the cost of foraging, and food chemistry (Caughley and Sinclair, 1994; Corriale et al., 2011; Illius and Gordon, 1993), which along with the risk of predation and intra- and inter-specific competition, combine to define the diet (Lima and Dill, 1990; Sutherland, 1983; Wiens, 1989). It is likely that increased consumption of C_3 plants could not only be due to greater availability of that type of resource in the Paraná Delta, where 87% of vegetation is made up of C_3 plants (Madanes et al., in press). However, this increase could also be associated with the higher nutritional quality of plants with this photosynthetic pattern. In fact, C_3 plants have higher levels of sugars and proteins, and lower levels of fiber, silica and hardness than C_4 plants (Barbehenn, 1993; Barbehenn and Bernays, 1992; Barbehenn et al., 2004; Bernays and Hamai, 1987; Caswell et al., 1973; Van Soest, 1994; Wilson et al., 1983). This makes them more digestible as food and allows more efficient metabolism to take place. Since we have not yet apatite values, we ignore other differences between individuals who have a differential consumption of plants with low protein content (cf. Ambrose, 1993). This is an aspect that has yet to be explored both individually and regionally, and should be considered when analyzing the diets of hunter–gatherers in the basin.

There is a significant difference between the average of $\delta^{13}\text{C}_{\text{co}}$ values in deer from the Paraná Delta (-20.79‰) and the deer from the Iberá wetlands (-23.06‰). Since there is no isotopic data available in relation to the marsh deer's diet in the more northern areas of its distribution, such as southern and central Brazil, we cannot yet assess whether this trend in increased consumption of C_3 plants inversely proportional to sample's latitude represents a real pattern. Another explanation would be related to the Paraná Delta's higher level of environmental heterogeneity compared to the Iberá wetlands, since the Paraná Delta possesses a large number of different micro-patches within small areas of the landscape (Malvárez, 1999). In contrast, the Iberá wetland has less environmental variability with extensive floodplains dominated by C_3 plants in the depressed zones, as well as grassland areas composed mainly by C_4 plants in the higher zones (Corriale et al., in press; Corriale and Loponte, in preparation). There are some data that suggest that the preferences of C_3 plants in Iberá wetland by marsh deer, reflects a specific selection of its foraging behavior rather than the regional availability of plant types. In fact, isotopic values of diet of *Hydrochaeris hydrochaeris* (capybara) obtained in the same area are heavier than marsh deer's values (Corriale and Loponte, in preparation). This probably shows a different selectivity between

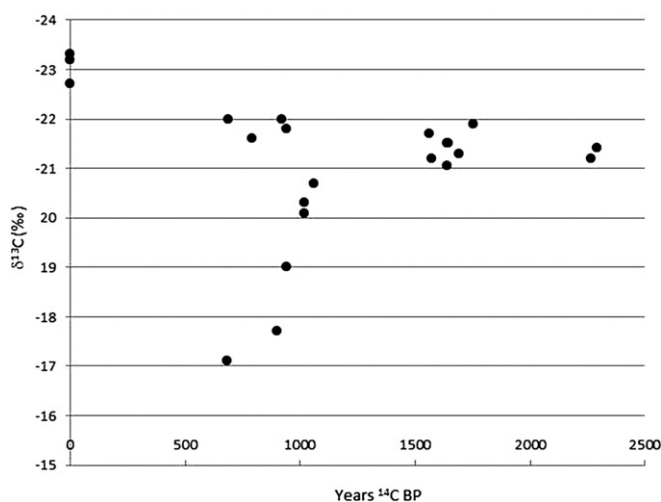


Fig. 5. Collagen $\delta^{13}\text{C}$ values and chronology of the samples.

the correlation is not significant ($R_s = -0.28$, $p = 0.213$). This lack of significant association could be related to the dispersion of isotopic values in the 1100–700 ^{14}C years BP time range, while for the period of 2300–1500 ^{14}C years BP, little variability exists (Fig. 5 and Table 2).

On the other hand, we found a significant correlation between $\delta^{13}\text{C}$ collagen values and latitude ($R_s = 0.50$; $p = 0.017$), with increased consumption of C_3 plants at lower latitudes. This is essentially due to the samples from the Iberá wetlands (mean -23.06‰) having lower values than those from the lower Paraná (mean -20.79‰).

The fitted GLMM shows that $\delta^{13}\text{C}_{\text{co}}$ did not vary significantly between landscape units ($F_{1, 19} = 0.78$, $p = 0.3896$), nor between landscape units and periods (period \times LU: $F_{1, 19} = 2.63$, $p = 0.1255$), but there were significant differences in $\delta^{13}\text{C}_{\text{co}}$ by time period ($F_{1, 19} = 6.67$, $p = 0.0208$). In fact, $\delta^{13}\text{C}_{\text{co}}$ values for samples dated to the period between 1100 and 700 ^{14}C years BP were higher than those for period between 2300 and 1500 ^{14}C years BP (see Table 2).

both species (a ruminant vs. a monogastric rodent) not tied to the environmental availability of plants, but to different feeding behaviors. Also, these results suggest that marsh deer feed preferentially in flooded areas which concurrently provides greater coverage against predators (cf. Pinder and Grosse, 1991) rather than in grasslands bordering the lakes.

In the archaeological samples, there is substantial variability in the values for samples from the period 680 ± 80 to 1060 ± 60 ^{14}C years BP (see Fig. 5 and Table 2), which correspond to the range of 895–1433 calendar years (using the ShCal04 calibration curve for the Southern Hemisphere). This span of time coincides with the existence of a warm event in South America that took place between 900 and 1350 years BP, synchronous with the Medieval Climate Anomaly (Neukom et al., 2011 and references therein). During this same time period, considerable variability is seen in geomagnetic activity measured in archaeological pottery recovered in the area (Gogichaishvili et al., 2012). This supports the idea of the existence of changes in some sensitive environmental parameters (see Courtillot et al., 2007; Gallet et al., 2006). The existence of a warm pulse during this time range could have generated a greater abundance of C_4 plants, which could explain the increased incidence of this functional group in the marsh deer's diet (cf. Ehleringer et al., 1997; Ehleringer and Cerling, 2002; Lattanzi, 2010).

Variations in the diet of *B. dichotomus*, as reflected in carbon isotope values, are also consistent with this deer's classification as a browser by some authors and as a grazer by others. In this sense, the data presented here suggest that this mammal can develop a relatively broad foraging range, supporting its classification as a mixed-strategy herbivore (Tomas and Salis, 2000). Also, the data also support the interpretations of the many researchers who have pointed out that this mammal's distribution is mainly regulated by the existence of flood habitats that provide shelter and rest, rather than by the existence of specific types of food (cf. Tomas et al., 2001).

5. Conclusions

This first approach to using isotopic values to analyze the diet of *B. dichotomus* shows that this ungulate eats plants representing both functional groups, although with a strong intake of C_3 plants. In Iberá wetland, this preference seems to be more pronounced, suggesting this ungulate preferably used flooded areas to feed. Variations in $\delta^{13}\text{C}_{\text{CO}}$ values seem to relate to variability in climate parameters and changes linked with these, and also hypothetically with latitude, although no data from the northern areas of the marsh deer's range in South America are available, and therefore more samples are needed to further test this hypothesis.

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