



Original Investigation

Use of stable carbon isotope ratio for foraging behavior analysis of capybara (*Hydrochoerus hydrochaeris*) from Esteros del Iberá, Argentina

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ABSTRACT

We analyzed different aspects of the foraging behavior and habitat use for feeding of the capybara (*Hydrochoerus hydrochaeris*) using carbon stable isotopes ($^{13}\text{C}/^{12}\text{C}$) measured in bone collagen and by direct observation. Stable carbon isotope ratio analysis is used to determine the proportion of plant functional types consumed (C_3 and C_4 photosynthetic patterns). These data were further compared with the distribution of the plant functional types available in the different environments of the study area. There was a high variability in bone isotope values, and although some specimens showed a C_4 -based diet, data suggested a tendency toward a predominant consumption of C_3 plants. The proportion of functional types in the diet of capybaras differed from their availability in the study area indicating a differential use of environments. We obtained similar conclusions by direct observation of capybaras. The high variability in isotope values and foraging behavior of the species may explain its high ecological plasticity in terms of both diet composition and selection of foraging sites.

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Introduction

Animals face the challenge of obtaining an adequate quality and sufficient quantity of food to meet nutritional requirements (Stephens and Krebs, 1986; Grier and Burk, 1992). In particular, herbivores make several choices during foraging that are determined by their innate preferences and by experiences learned from the environment (Provenza et al., 1992; Shettleworth, 1998). These choices define the foraging strategy adopted by herbivores, together with different factors such as food availability, nutritional value and intra and interspecific competition, among others (Gutiérrez, 1998). Thus, for example, the different cover types used by a species may represent relatively variable nutritional scenarios according to the abundance and composition of plant species present in each of them (Gutiérrez, 1998). In this way, the plasticity of foraging behavior to temporal changes in forage availability

and quality may translate into increased fitness by better utilization of resources (Bergman et al., 2001).

The capybara (*Hydrochoerus hydrochaeris*) is a large semi-aquatic rodent native to wetlands in South America (Emmons, 1997). It is a gregarious and territorial species (Herrera and Macdonald, 1987, 1989), which uses different habitats close to water bodies (Ojasti, 1973; Quintana and Rabinovich, 1993; Corriale et al., 2013a). Its diet has been studied by several authors in different habitats and most of them agree that the capybara is a selective herbivore (González-Jiménez and Escobar, 1977; Quintana et al., 1994; Barreto and Herrera, 1998; Forero-Montaña et al., 2003), which consumes protein-rich plants near water bodies (González Jiménez, 1978), particularly grasses and short, tender sedges (Escobar and González-Jiménez, 1976; Quintana et al., 1994, 1998a,b). However, the capybara also shows a more generalist behavior under certain conditions, for example when quality or/and offer of forage decrease (Barreto and Herrera, 1998; Borges and Colares, 2007).

There have been numerous studies on the feeding behavior of capybaras in the Colombian savanna and Amazonian region (Jorgenson, 1986; Aldana Dominguez et al., 2002; Forero-Montaña et al., 2003; Arteaga and Jorgenson, 2007), Venezuelan savanna

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(Escobar and González-Jiménez, 1976; Herrera and Macdonald, 1989; Barreto and Herrera, 1998), Brazilian Pantanal (Alho et al., 1989; Rodiney and Pott, 1996) and Lower Delta of the Paraná River in Argentina (Quintana et al., 1994, 1998a). In contrast, there is little information on foraging behavior in the ecoregion Esteros del Iberá, which shows a high diversity of aquatic environments and sustains the largest capybara population in Argentina (Bolkovic et al., 2006). The wetlands and climate-hydrological conditions in this ecoregion differ markedly from those in the rest of the distribution area of the species. The studies mentioned above investigated the feeding behavior of capybaras using microhistological fecal analysis, direct observation or signs of activity but none applied stable carbon isotope ratio ($^{13}\text{C}/^{12}\text{C}$; $\delta^{13}\text{C}$) of bone collagen. This analysis allows us to infer different aspects of feeding behavior and habitat use by animals (Vogel, 1978; Van Der Merwe et al., 1988; Cerling et al., 2003; Sponheimer et al., 2003). Just a single value of the $^{13}\text{C}/^{12}\text{C}$ ratio of bone collagen has been reported for capybaras in the Lower Delta of the Parana River (-12%), but the result was most probably influenced by the presence of maize plots (cf. Madanes et al., 2010). The stable carbon isotope approach is based on anatomical and physiological differences in the pattern of carbon fixation among plants, which allows determination of the functional types of the vegetation (C_3 and C_4 plants) consumed by animals (Smith and Epstein, 1971; Vogel, 1978). Plants using the Calvin cycle of carbon dioxide fixation (C_3 photosynthetic pathway) have average $\delta^{13}\text{C}$ values of -26.5% , while those using the Hatch-Slack cycle (C_4 photosynthetic pathway) have average $\delta^{13}\text{C}$ values of -12.5% (Krueger and Sullivan, 1984; Comstock and Ehleringer, 1992; Ambrose, 1993a,b; Ambrose and Norr, 1993; Ehleringer and Cerling, 2001). Because of the close relationship between the photosynthetic groups and abiotic factors, the isotopic composition of the diet may provide information on environmental characteristics or habitat use (Van Der Merwe et al., 1988; Tieszen, 1991). The C_4 plants are related to warm, dry environments; this pathway is typical of most tropical grasses (Smith and Brown, 1973; Theerl and Stowe, 1976; Boutton et al., 1980; Cavagnaro, 1988). In the study area most of C_4 plants are represented by grasses and forbs, however, it is likely to find C_3 grasses and forbs in wetter areas such as transition zones (Corriale et al., 2013b). C_3 plants are mainly represented by shrubs and aquatic species.

The advantage of using stable carbon isotope over others methods (direct observation or fecal analysis) is that the isotopic value of bone brings information of diet of the last 5–10 years of the specimen (Ambrose, 1993a,b). Because the capybara's life expectancy is approximately 10 years (Ojasti, 1973; Aldana Dominguez et al., 2002), the technique may be used to estimate diet over the lifetime of the animal.

The objective of this work is to analyze the use of stable carbon isotope ratio in bone collagen to explore foraging behavior of capybara (*Hydrochoerus hydrochaeris*) from Esteros del Iberá, Argentina. We aim to compare results obtained using this method to those obtained from direct observation of the individuals.

Material and methods

Study area

The study was conducted in the Park Guayaibí ($28^{\circ}00\text{S}$ $57^{\circ}18\text{W}$), a former livestock farm located to the north of central Iberá Macrosystem, in Los Campos District (Carnevali, 2003), Corrientes province, Argentina. According Olson et al. (2001) this Macrosystem corresponds to Flooded grasslands and savannas ecoregion. The study site covers an area of about 750 ha corresponding to a sandy ridge bordered by marshes. The sandy ridge includes five rounded shallow lakes of wind-pseudokarstic origin (Carnevali,

2003; Conservation Land Trust, 2006; Fig. 1). The landscape presents different cover types, is dominated by "paja colorada" grassland (upland areas), and mainly represented by *Andropogon lateralis*, *Axonopus fissifolius* and *Rhynchospora barrosiana* (Corriale et al., 2013b). The rounded shallow lakes have a well-defined surface area, and contain water almost permanently. In the ecotone between the terrestrial and aquatic palustrine environments, there are two transition zones at different heights; during the rainy season (spring-summer), the upper one is occasionally waterlogged whereas the lower one is permanently waterlogged. In the low-lying area there are floating patches of soils ("embalsados") and limnetic areas with aquatic palustrine vegetation. Some temporary ponds filled with water only during periods of prolonged and heavy rainfalls are also present on the sandy ridge. The area corresponds to a private ecological reserve under low grazing pressure, where grassland areas are subject to low-intensity burns during autumn and winter (Corriale et al., 2013b). The study area has not large predators and hunting practices of native wildlife is forbidden. Accordingly, the population density of capybara is high relative to other areas. Thereafter, this populations present group sizes of about 17–35 individuals (Corriale, 2010; Herrera et al., 2011; Corriale and Herrera, 2014) with a seasonal mortality of adult individuals during the winter (Gorósábel, 2013).

Climate is subtropical-humid, with hydric and thermal seasonality. Rainfall occurs in all seasons but it is heavier in spring and summer; annual rainfall ranges between 1700 and 1800 mm. In summer average and maximum temperatures are 27°C and 44°C , respectively, and in winter average temperature is 16°C , with the historical record of minimum temperature over the past 50 years being -2°C (Neiff and Poi de Neiff, 2005).

Measurements of isotopic values in bone collagen

Around 1000 mg of the temporal bone (skull) of 17 capybaras found dead in the field were used to estimate collagen $\delta^{13}\text{C}$ values. All selected specimens were adults according to the criteria of Ojasti (1973; skulls with suture between presphenoid and basisphenoid ossified). We determined collagen $\delta^{13}\text{C}$ values at the Institute of Geochronology and Isotope Geology (INGEIS, CONICET) and in the Stable Isotope Ratio Facility for Environmental Research of Utah University. The C:N ratios are useful as an indicator of contamination and/or degradation of "collagen" (DeNiro, 1985; Schoeninger et al., 1989; Ambrose, 1990). In modern animals and humans, the contamination is likely when the atomic C:N ratio falls outside the range 2.9–3.6 (DeNiro, 1985). All samples had a C:N ratio ranging between 2.9 and 3.6 thus they are appropriate to obtain reliable isotopic data (DeNiro, 1985; Ambrose, 1990).

Isotopic results are reported in terms of $\delta^{13}\text{C}$ to the Vienna Pee Dee Belemnite standard (fossil belemnites from the Cretaceous). According to this standard, plants exhibit negative $\delta^{13}\text{C}$ values; plants using the Calvin cycle of carbon dioxide fixation (C_3 photosynthetic pathway) have average $\delta^{13}\text{C}$ values of -26.5% (from -22 to -34), while those using the Hatch-Slack cycle (C_4 photosynthetic pathway) have average $\delta^{13}\text{C}$ values of -12.5% (from -8 to -16). The latter pathway is typical of most tropical grasses. The third pathway, called CAM (Crassulacean acid metabolism), is an adaptive mechanism of plants in arid environments, which reduces stress caused by water deficiency (Krueger and Sullivan, 1984; Comstock and Ehleringer, 1992; Ambrose, 1993a,b; Ambrose and Norr, 1993; Ehleringer and Cerling, 2001; Malainey, 2010). The CAM pathway yields $\delta^{13}\text{C}$ values ranging between -27% and -12% (Ambrose, 1993a,b; Lee-Thorp et al., 1989; Pate, 1994); CAM functional plants have been included in the diet analysis, but had a low cover in the study area (0.26%).

Different studies have shown that bone collagen $\delta^{13}\text{C}$ values of large herbivores is enriched by 5% relative to the collagen ingested

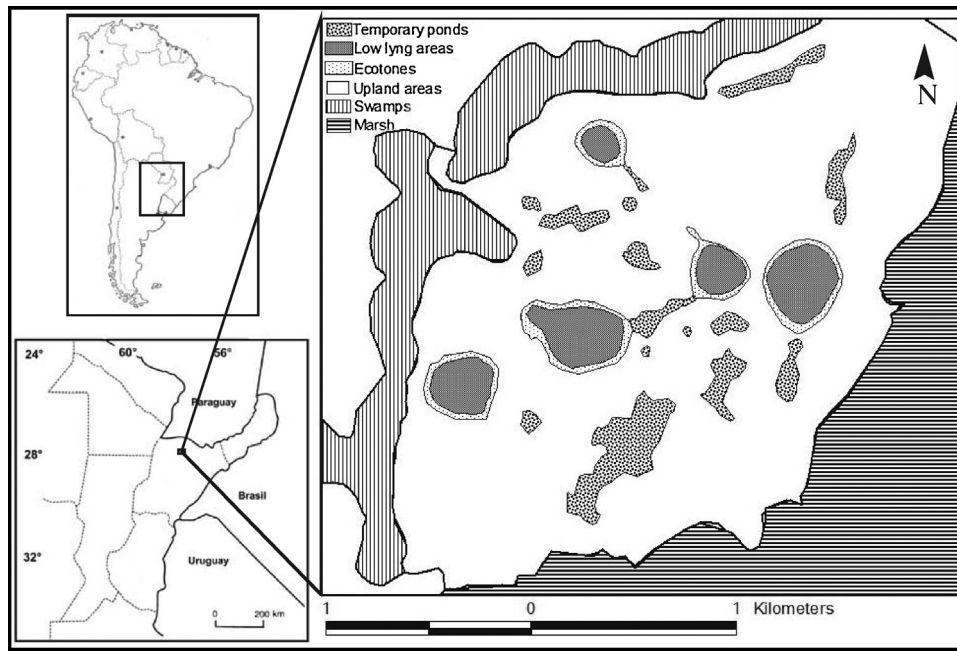


Fig. 1. Location of the study area (28° 00' S 57° 18' W) and thematic map of the environments in the study area from aerial photograph interpretation (scale 1:20,000). Ecotones include upper and lower transition zones (Corriale et al., 2013b).

(Schoeninger and DeNiro, 1983; Lee-Thorp et al., 1989; Ambrose and Norr, 1993). Therefore, animals with a pure C_3 diet show bone collagen $\delta^{13}C$ values and apatite (inorganic fraction) $\delta^{13}C$ values of -22% and -13% , respectively, while values for animals with a pure C_4 diet are -7.5% and -1% , respectively (Sullivan and Krueger, 1981; Lee-Thorp and Van Der Merwe, 1989; Van der Merwe, 1989). The content of carbon in apatite is usually 9% higher than in collagen because apatite carbon is in isotopic equilibrium with CO_2 in blood (Krueger and Sullivan, 1984; Pate, 1994). Thus, the apatite value derives from the oxidation of glucose, other carbohydrates and lipids, while organic carbon derives exclusively from the protein fraction of the diet. On this basis, the $\delta^{13}C$ value of the inorganic fraction provides information on the total diet and that of collagen mainly provides information on the dietary protein fraction (Krueger and Sullivan, 1984; Pate, 1994).

Use and selection of photosynthetic types

The percentage of C_3 plants ($\%C_3$) incorporated into bone collagen was calculated using the equation ($\%C_3$) = $-100 (\delta^{13}C - 5 + 12.5) / (26.5 - 12.5)$ (cf. Hu et al., 2007), where the $\delta^{13}C$ value is obtained from the sample, and 12.5 and 26.5 are the average $\delta^{13}C$ values for C_4 and C_3 plants, respectively (Smith and Epstein, 1971; Vogel, 1978). The complement to 100% corresponds to the percentage of C_4 plants incorporated into bone collagen. Results of percentage of C_3 and C_4 plants were rounded to five percent taking into account the variations in animal-food discrimination effects, the variations in plant isotope composition and the stochastic effects (Codron and Codron, 2009; Codron et al., 2007a, 2012).

To estimate selection for different photosynthetic types (C_4 and C_3 plants) we used a study of use vs. availability of resources (Thomas and Taylor, 1990, 2006). The selection for C_4 and C_3 plants was estimated by Jacobs' selection index (J ; Jacobs, 1974) and Manly's resource selection index (b ; Manly et al., 1993). Jacobs' selection index was calculated as $J = (r - p) / [(r + p) - 2rp]$, where r is the proportion of the functional type in the diet and p is the proportion of the functional type available in the study area. J varies from -1 (not consumed) to $+1$ (highly consumed); $J = 0$ indicates that the

functional type is consumed in proportion to availability. We used the Student's t -test with $n - 1$ degrees of freedom to compare the average value of J with the null hypothesis $J = 0$ (the environment is used in proportion to availability). For the Manly's resource selection index, the proportion of functional type i selected (w_i) was estimated as $w_i = p_u / p_d$, where p_u is the proportion of functional type i in the diet and p_d is the proportional availability of functional type i ; w_i was then standardized using equation $b_i = w_i / \sum_{i=1}^H w_i$, where H is the number of photosynthetic types. The b_i value can be interpreted as the probability that, for any selection event, an animal would choose the photosynthetic type i over all others assuming all photosynthetic types were available to the animal in equal proportion (Mcloughlin et al., 2004). Student's t -test for paired samples was used to compare the b_i value for the different photosynthetic types.

Estimation of the photosynthetic pathway proportion and the isotopic values of the available vegetation in the different cover types of the study area

A total of 1200 censuses were conducted seasonally (150 censuses per season during 2 years) in proportion to the surface area of the different cover types (Corriale et al., 2013b). We estimated the abundance-cover of the vegetation using the Braun-Blanquet's scale with modifications (Mueller-Dombois and Ellenberg-Ellenberg, 1974) and percentage of dry matter, bare ground and water surface free of vegetation where appropriate. We used $1\text{ m} \times 1\text{ m}$ plots if the cover types were dominated by a single herbaceous stratum and $5\text{ m} \times 5\text{ m}$ plots if otherwise. All plant species found in each cover type were characterized according to their photosynthetic pathway (C_3 , C_4 , intermediate C_3-C_4 and CAM plants), based on information gathered from the literature (see inter alia Black et al., 1969; Black, 1971; Smith and Brown, 1973; Waller and Lewis, 1979; Jones, 1988). Then, taking into account the abundance-cover of each photosynthetic type for each cover type used by the capybaras (upland, upper and lower transition, low-lying and temporary ponds; Fig. 1) $\delta^{13}C$ values we estimated for each cover type. The $\delta^{13}C$ values we estimated for each cover

type result then of product from the average $\delta^{13}\text{C}$ value of each photosynthetic pathway (-26.5‰ and -12.5‰ for C_3 and C_4 photosynthetic pathway, respectively; Ehleringer and Cerling, 2001) and percentage of each photosynthetic pathway in each cover type.

We also estimated the $\delta^{13}\text{C}$ value of the vegetation present in all the study area considering the representativeness of each cover type in landscape. Moreover, taking into account that several authors indicate that the diet of capybaras is based on grasses and forbs (Escobar and González-Jiménez, 1976; González-Jiménez and Escobar, 1977; Quintana et al., 1994, 1998a, 1998b; Barreto and Herrera, 1998; Forero-Montaña et al., 2003), we estimated the percentage of grasses and forbs with C_3 and C_4 photosynthetic pathways in the studied environments and their expected $\delta^{13}\text{C}$ values based on the average values of the C_3 and C_4 photosynthetic types. One-sample *t* tests were used to compare the bone collagen $\delta^{13}\text{C}$ values and the expected $\delta^{13}\text{C}$ values based on the values of the C_3 and C_4 photosynthetic types present in the different cover types and the study area. In this case, a Bonferroni correction *p*-value has been applied for multiple testing (Bonferroni-corrected significance level: $0.05/7 = 0.007$; Rice, 1989; Sokal and Rolf, 1995).

Use and selection of foraging habitats by direct behavioral observations

We carried out seasonal surveys during 2 years. Since capybaras are territorial and naturally aggregated in social units (Herrera and Macdonald, 1987), we considered each capybara group as the observational unit. The feeding behavior of 10 capybara groups resident in the rounded shallow lakes was observed by scan sampling (Martin and Bateson, 1991). Capybara groups were watched at a distance between 10 and 300 m on a platform at 2 m above ground, using a Bushnell Spacemaster 60 mm prismatic telescope with a 15–45 \times zoom lens when capybaras were at distances greater than 100 m, or with Tasco 8–20 \times 50 binoculars when they were at distances of up to 100 m. The daily proportion of individuals of each social group grazing in each environment or cover type was recorded every 15 min during daytime, from 07:00 am to a 06:15 pm in spring, summer and winter and from 07:45 am to 05:30 pm in autumn; the number of records varied according to seasonal changes in day length.

To estimate habitat use for different cover types, we calculated the average proportion of capybaras that foraged daily in each studied cover type during 2 years for each group. From the proportions of use of different cover types the isotopic values of the vegetation in each environment were estimated. Thus, the expected composition of $\delta^{13}\text{C}$ was obtained of the sum of the products of the proportions of use of each cover type and $\delta^{13}\text{C}$ estimated for each cover type.

In particular, to examine what cover types may be more represented in the diet according to the composition of functional groups, we analyzed which values $\delta^{13}\text{C}$ of each environment were within the 95% confidence interval of the mean isotopic values $\delta^{13}\text{C}$ in bone collagen measured. From the proportions of use of different cover types the isotopic values of the vegetation in each cover type were estimated.

To estimate habitat selection for different cover types, we used a study of use vs. availability of resources (Thomas and Taylor, 1990, 2006), in which the proportion of grazing capybaras in each group in each cover type (number of grazing individuals in each cover type/total number of grazing individuals) is compared to the proportion of each cover type in the study area. We used a design type II which takes into account the proportion of grazing capybaras in each group, but the availability is estimated at the population

level (for all groups). Foraging habitat selection was analyzed by the indices mentioned above, i.e. Jacobs' selection index and Manly's resource selection index.

Results

Isotopic values of capybara's bone collagen and use and selection of photosynthetic types

The values of $\delta^{13}\text{C}$ obtained from the bone collagen allow us to infer a high variation in the dietary composition among individuals. However, there was a tendency toward a C_3 -based diet although 29% of individuals had a diet based primarily on C_4 plants (Table 1). Jacobs's index indicated that C_3 and C_4 plants were consumed in different proportion than available; C_3 plants were selected (mean value = 0.56; *t*-statistics for one sample = 9.21; *p* = 0.0001) while C_4 plants were consumed less than available (mean value = -0.56 ; *t*-statistics for one sample, *t* = -9.21 ; *p* = 0.0001). According to the Manly's index, the probability of being consumed was higher for C_3 (mean value = 0.78) than for C_4 plants (mean value = 0.22; Student's *t*-test for paired samples, *t* = 9.29; *p* = 0.0001).

Photosynthetic type proportion and the isotopic values of the available vegetation in the different cover types of the study area

Taking into account the percentages of C_3 and C_4 grasses and forbs in the study area, the expected $\delta^{13}\text{C}$ value was -13.42 (Table 2). The $\delta^{13}\text{C}$ values obtained from bone collagen were less than this value (Student's *t*-test for one sample = -3.47 ; *p* = 0.003; Table 2). This result means that capybaras would not feed grasses and forbs in the available proportion in the study area.

In regard to habitat use, the $\delta^{13}\text{C}$ values obtained from bone collagen differed from that expected on the basis of the percentages of C_3 and C_4 in the study area, suggesting that capybaras did not use the different foraging habitats in proportion to availability (Student's *t*-test for one sample, *t* = -6.34 , *p* = 0.001; Bonferroni-corrected *p* = 0.007). Only $\delta^{13}\text{C}$ values of ecotones (upper transition: *t* = 0.52, *p* = 0.608; and lower transition: *t* = 2.03, *p* = 0.060; Bonferroni-corrected *p* = 0.007) and temporary ponds (*t* = 2.24, *p* = 0.039; Bonferroni-corrected *p* = 0.007) did not show differences (Table 3). Remaining habitats showed differences between their estimated $\delta^{13}\text{C}$ values and the $\delta^{13}\text{C}$ values obtained from bone collagen (low-lying: *t* = 7.96, *p* = 0.0001; embalsado: *t* = 6.48, *p* = 0.0001; and upland: *t* = -8.36 ; *p* = 0.0001).

Use and selection of foraging habitats by direct behavioral observations

Jacobs' selection index indicated that the ecotones were the most used cover types, the low-lying areas were the least used cover types and the other cover types (temporary ponds and upland areas) were used in proportion to availability (Table 4). The Manly's index indicated that the ecotones had the highest probability of use for foraging (Fig. 2).

No significant differences were found between the $\delta^{13}\text{C}$ values of bone collagen across habitat types (mean value: -15.7 ± 0.3 ; Table 1) and that expected on the basis of the percentages of habitat use obtained by direct observation (estimated $\delta^{13}\text{C}$: -17.54 ; Fig. 3) (Student's *t*-test for one sample, *t* = 1.59; *p* = 0.131).

Discussion

The $\delta^{13}\text{C}$ values of bone collagen obtained from capybaras in the studied area allow us to infer information regarding feeding resources at different scales of analysis, including the relative

Table 1

Bone collagen $\delta^{13}\text{C}$ values, percentages (%) of C_3 and C_4 plants in the diet of capybaras and preference indices. J: Jacobs' index; b: Manly's index; CV: coefficient of variation; CI: confidence interval.

Sample	Bone $\delta^{13}\text{C}$ (‰)	C_4 plants	C_3 plants	J C_4	J C_3	b C_4	b C_3
Hh1	-14.2 ± 0.3	50	50	-0.45	0.45	0.27	0.73
Hh2	-19 ± 0.3	20	80	-0.86	0.86	0.07	0.93
Hh3	-16.1 ± 0.3	40	60	-0.93	0.93	0.18	0.82
Hh4	-20.2 ± 0.3	10	90	-0.53	0.53	0.03	0.97
Hh5	-18.8 ± 0.3	20	80	-0.85	0.85	0.08	0.92
Hh6	-15.3 ± 0.3	45	55	-0.54	0.54	0.23	0.77
Hh7	-14.2 ± 0.3	50	50	-0.45	0.45	0.27	0.73
Hh8	-11.7 ± 0.3	70	30	-0.11	0.11	0.45	0.55
Hh9	-20.0 ± 0.3	10	90	-0.92	0.92	0.04	0.96
Hh10	-15.9 ± 0.3	40	60	-0.63	0.63	0.19	0.81
Hh11	-13.4 ± 0.3	60	40	-0.35	0.35	0.32	0.68
Hh12	-13.5 ± 0.3	55	45	-0.37	0.37	0.31	0.69
Hh13	-14.7 ± 0.3	50	50	-0.51	0.51	0.24	0.76
Hh14	-11.9 ± 0.3	70	30	-0.15	0.15	0.43	0.57
Hh15	-16.7 ± 0.3	35	65	-0.70	0.70	0.15	0.85
Hh16	-13.7 ± 0.3	55	45	-0.39	0.39	0.30	0.70
Hh17	-17.3 ± 0.3	30	70	-0.74	0.74	0.13	0.87
Average	-15.7 ± 0.3	40	60	-0.56	0.56	0.22	0.78
SD	2.7	19	19	0.25	0.25	0.13	0.13
CV	17.0	45	30	44.91	44.75	57.71	16.03
CI	-17.05; -14.31						

Table 2

Percentage of grasses and forbs (GF) with C_3 , C_4 and intermediate C_3 – C_4 photosynthetic pathways in the studied cover types and their expected $\delta^{13}\text{C}$ values based on the average values of the C_3 and C_4 photosynthetic types.

Cover types	GF C_3	GF C_4	GF C_3 – C_4	% GF in ENV	Expected $\delta^{13}\text{C}$ (‰)
Low-lying	50.1	10.9	39.0	16.3	-22.6
Embalsados	35.6	23.0	41.5	29.0	-20.7
Upper transition	13.3	51.8	34.9	42.5	-17.0
Lower transition	36.8	35.7	27.6	24.0	-19.8
Temporary ponds	28.7	45.2	26.1	26.9	-18.6
Upland	2.0	96.0	2.0	61.3	-12.9
Study area	4.2	91.5	4.3	55.7	-13.4

Table 3

Percentage of abundance-cover of different photosynthetic types in the studied cover types and $\delta^{13}\text{C}$ values expected based on the average values of the different photosynthetic types. Un: species undetermined or of unknown photosynthetic pathway.

Cover types	C_3 plants	C_4 plants	C_3 – C_4 plants	CAM	Un	Expected $\delta^{13}\text{C}$ (‰)
Low-lying	64.4	3.7	6.6	2.0	8.2	-21
Embalsados	52.0	8.9	12.8	1.2	11.3	-20
Upper transition	38.0	23.3	14.9	2.3	3.2	-16
Lower transition	49.0	10.0	6.8	0.8	1.6	-17
Temporary ponds	50.6	14.0	7.3	0.4	2.4	-17
Upland	9.4	58.9	1.2	0.02	1.0	-10
Study area	16.2	51.3	2.4	0.2	1.9	-12

dietary contribution of the photosynthetic types and the use of the foraging environment. Our results indicate that capybaras consume both C_3 and C_4 plants but in different proportion than availability. The selection of C_3 over C_4 plants would be explained by a better nutritional composition of C_3 (higher carbohydrate and protein content and lower content of fiber and silica, leaf tenderness) (Caswell et al., 1973; Bernays and Hamai, 1987; Barbehenn and Bernays, 1992; Barbehenn, 1993; Van Soest, 1994; Barbehenn et al., 2004). The selection by capybaras of species having high protein

and energy content is in agreement with the results of other studies (Ojasti, 1973; González-Jiménez and Escobar, 1977; González Jiménez, 1978; Barreto and Herrera, 1998; Álvarez, 2002; Corriale et al., 2011). However, several studies indicate that C_3 plants properties do not make it more easily digestible than C_4 plants (high lignin, and secondary compound) (Hummel et al., 2006; Codron et al., 2007b). In some cases C_3 grasses may be more easily digested than C_4 grasses, but even then, the pattern is not completely clear (Robinson et al., 2006).

Table 4

Average values of Jacobs' selection index (Jm) and results of Student's *t*-test for one parameter under the null hypothesis of no selection ($H_0: J = 0$). Significance level at $p < 0.05$. SD: standard deviation.

Cover types	Jm	SD	t	Two-tailed <i>p</i> -value
Ecotone	0.73	0.09	16.19	<0.001
Temporary ponds	0.25	0.32	-1.64	0.136
Upland	-0.46	0.15	-1.16	0.278
Low-lying	-0.2	0.31	-3.72	0.005

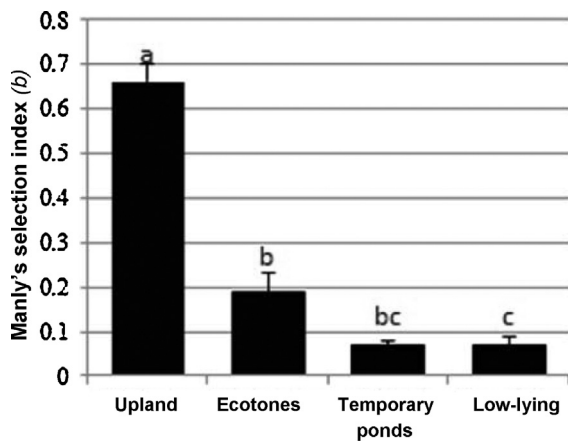


Fig. 2. Values of Manly's selection index (b) for 10 groups of capybaras obtained during 2 years of seasonal sampling. Different letters indicate significant differences at $p < 0.05$.

In addition, C_3 plants were more available in habitats that are waterlogged during the warmer months (temporary ponds, upper and lower transition). Capybaras may consume C_3 plants in the transition zones while foraging close to the water bodies in order to reduce thermoregulation costs and predation risk (Corriale et al., 2013a). In Argentina, the coypu (*Myocastor coypus*) also restricts its diet to vegetation near water bodies and this behavior has been interpreted as an antipredator strategy (Borgnia et al., 2000; Guichón et al., 2003). However, the *Myocastor coypus* lives in smaller groups than capybara, a fact that can make detection of predators less effective. Moreover, the $\delta^{13}C$ values of bone collagen from subfossil coypus indicated a tendency to a C_3 -based diet (-19.97% , $n = 5$; Loponte et al., 2013). The consumption of both photosynthetic types was also observed in other capybara populations in Argentina (Delta del Paraná and south of Entre Ríos province; Madanes et al., 2010). The proportion of C_3 and C_4 plants in the diet and their selection were highly variable among these populations.

The capybaras in the study area may feed on a variety of species and their diet includes other species besides grasses and forbs, because the bone collagen $\delta^{13}C$ values are lower than expected $\delta^{13}C$ values according to the availability grasses and forbs in the study area. The results of the isotopic diet do not show a selection for grasses and forbs as observed for other populations (Escobar and González-Jiménez, 1976; Nogueira Filho, 1996; Quintana et al., 1998a,b). However, our results support the nutritional benefit hypothesis (Gosling, 1981; Hobbs and Swift, 1988; Guichón et al., 2003; Corriale et al., 2011). This would indicate that the foraging

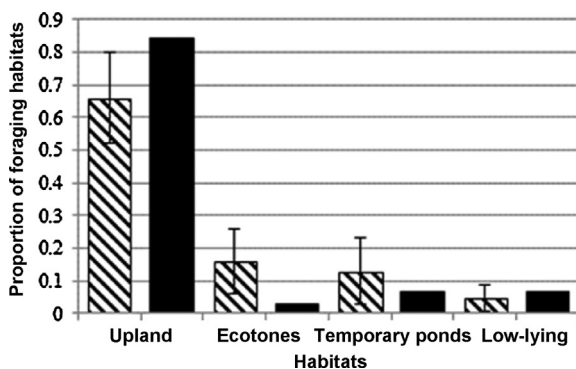


Fig. 3. Proportion of foraging habitats used (bars with diagonal weft) by 10 groups of capybaras during 2 years of seasonal sampling and proportion of available habitats (black bars) in the study area.

quality of the selected species is higher than that of species not consumed or consumed in lower proportion than available.

In considering habitat use, collagen $\delta^{13}C$ values were more similar to the $\delta^{13}C$ values of plants in the ecotones (upper and lower transition; Table 2), which is in line with the result obtained from the habitat use analysis. Temporary ponds did not show differences using Bonferroni correction factor, this could be due to the marked fluctuation in the water level determines the floristic composition of this environment from terrestrial to aquatic-palustrine species similar to ecotones (Corriale et al., 2013b). This could show the limitations of this methodology in the estimation of habitat use in cases where different environments have a similar composition of C_3 and C_4 photosynthetic types. In addition, the $\delta^{13}C$ values of bone collagen also show a selection of C_3 plants in these cover types. This may support the hypothesis that capybaras select C_3 plants despite their low availability in the transition zones. The use of upland areas for grazing has also been recorded for other capybara populations (Ojasti, 1973; Escobar and González-Jiménez, 1976; Jorgenson, 1986; Emmons, 1997; Herrera and Macdonald, 1989; Aldana-Domínguez et al., 2007). The $\delta^{13}C$ value of bone collagen reflects the diet of the last 5–10 years of the specimen, and the annual climate variations affect isotopic readings. For example, long-lasting droughts may affect forage availability mainly in the upland areas, forcing species to move to more humid sites (Corriale, 2010). Consequently, the variations between collagen $\delta^{13}C$ values and the $\delta^{13}C$ values estimated from direct observations of habitat use could be due not only to interannual and interseasonal variations in food availability but also to extrinsic causes including biotic factors (e.g. predation risk), abiotic factors (e.g. air temperature) and animal intrinsic factors (energetic requirements). In addition, $\delta^{13}C$ values of different plants present variations within the same species (even within single plants) (Leavitt and Long, 1982; Farquhar et al., 1989). In natural environments, variation in temperature, precipitation, relative humidity and vapor pressure deficit lead to differences in $\delta^{13}C$ in plant tissues up to 5‰ (Panek and Waring, 1995; Garcia et al., 2004). Therefore, the behavior of capybaras observed in the field and the $\delta^{13}C$ values measured in bone collagen would be the result of the interaction among these factors.

This work reports $\delta^{13}C$ values in the bone collagen of capybaras for the first time and shows that the combined use of stable carbon isotope ecology and traditional methodologies provides a useful tool to assess and analyze different aspects of the feeding ecology of herbivores (Cerling et al., 2003; Sponheimer et al., 2003; Codron et al., 2007b).

Conclusions

Although the $\delta^{13}C$ values measured in bone collagen of capybaras from the Guayabí Park indicated a tendency toward a C_3 -based diet, there was a high variability with one individual even showing a C_4 -based diet. The stable carbon isotope ratio analysis and direct observation showed similar habitat use estimations; both revealed a differential habitat use in the study area. The combined use of both methodologies is useful to investigate aspects of feeding behavior at the macrohabitat scale (habitat use and selection) and microhabitat scale (use and selection of items or functional types for foraging).

The high variability in foraging behavior among individuals (observed in $\delta^{13}C$ values of bone collagen and direct observation) would allow the species to adapt to habitats with different composition of photosynthetic types and would allow adapt to changes in the composition of photosynthetic types in a particular habitat. Therefore, this could explain the high ecological plasticity of capybaras to withstand environmental changes of different magnitude

and ecological constraints, such as competition and/or predation. Such plasticity is consistent with the known ability of capybaras to colonize different environments.

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References

- Aldana Dominguez, J., Forero, J., Betancur, J., 2002. Dinámica y estructura de la población de chigüiros (*Hydrochaeris hydrochaeris*: Rodentia, Hydrochaeridae) de Caño Limón, Arauca, Colombia. *Caldasia* 24, 445–458.
- Aldana-Domínguez, J., Vieira-Muñoz, M.I., Ángel-Escobar, D.C. (Eds.), 2007. Estudios sobre la ecología del chigüiro (*Hydrochoerus hydrochaeris*), enfocados a su manejo y uso sostenible en Colombia. Instituto Alexander von Humboldt, Bogotá D.C.
- Alho, C.J.R., Campos, Z.M.S., Gonçalves, H.C., 1989. Ecology, social behavior and management of the capybara (*Hydrochoerus hydrochaeris*) in the Pantanal of Brasil. In: Redford, K.H., Eisenberg, J.F. (Eds.), *Advances in Neotropical Mammalogy*. Sandhill Crane Press, Florida, pp. 163–194.
- Álvarez, M.R., 2002. Manejo sustentable del carpincho (*Hydrochoerus hydrochaeris*, Linnaeus 1766) en Argentina: un aporte al conocimiento de la biología de la especie desde la cría en cautiverio Tesis de doctorado. Universidad de Buenos Aires, Buenos Aires.
- Ambrose, S.H., 1993a. Isotopic analysis of paleodiets: methodological and interpretive considerations. In: Sandford, M.K. (Ed.), *Investigations of Ancient Human Tissue: Chemical Analysis in Anthropology*. Gordon and Breach Science Publishers, Langhorne, pp. 59–129.
- Ambrose, S.H., Norr, L., 1993. Experimental evidence for the relationship of the carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate. In: Lambert, J.B., Grupe, G. (Eds.), *Prehistoric Human Bone: Archaeology at the Molecular Level*. Springer-Verlag, New York, pp. 1–37.
- Ambrose, S.H., 1990. Preparation and characterization of bone and tooth collagen for isotopic analysis. *J. Archaeol. Sci.* 17, 431–451.
- Ambrose, S.H., 1993b. Isotopic analysis of paleodiets: methodological and interpretive considerations. In: Sandford, M.K. (Ed.), *Investigations of Ancient Human Tissue, Chemical Analysis in Anthropology*. Gordon & Breach Science Publishers, Pennsylvania, pp. 59–130.
- Arteaga, M.C., Jorgenson, J.P., 2007. Hábitos de desplazamiento y dieta del capibara (*Hydrochoerus hydrochaeris*) en la Amazonia colombiana. *Mastozool. Neotrop.* 14 (1), 11–17.
- Barbehenn, R.V., 1993. Silicon: an indigestible marker for measuring food consumption and utilization by insects. *Entomol. Exp. Appl.* 67, 247–251.
- Barbehenn, R.V., Bernays, E.A., 1992. Relative nutritional quality of C₃ and C₄ grasses for a graminivorous lepidopteran, *Paratrytone melane* (Hesperiidae). *Oecologia* 92, 97–103.
- Barbehenn, R.V., Chen, Z., Karowe, D.N., Spickard, A., 2004. C₃ grasses have higher nutritional quality than C₄ grasses under ambient and elevated atmospheric CO₂. *Global Change Biol.* 10, 1565–1575.
- Barreto, G.R., Herrera, E.A., 1998. Foraging patterns of capybaras in a seasonally flooded savanna of Venezuela. *J. Trop. Ecol.* 14, 87–98.
- Bergman, C.M., Fryxell, J.M., Gates, C.C., Fortin, D., 2001. Ungulate foraging strategies: energy maximizing or time minimizing? *J. Anim. Ecol.* 70, 289–300.
- Bernays, E.A., Hamai, J., 1987. Head size and shape in relation to grass feeding in Acridoidea (Orthoptera). *Int. J. Insect Morph. Embryol.* 16, 323–336.
- Black, C.C., 1971. Ecological implications of dividing plants into groups with distinct photosynthesis production capacities. In: Cragg, J.B. (Ed.), *Advances in Ecological Research*. Academic Press, New York, pp. 87–114.
- Black, C.C., Chen, T.M., Brown, R.H., 1969. Biochemical basis for plant competition. *Weed Sci.* 17, 334–338.
- Bolkovic, M.L., Quintana, R.D., Ramadori, D., Elisethc, M., Rabinovich, J., 2006. Proyecto carpincho. In: Godet, M., Dalmás, G. (Eds.), *Manejo de fauna silvestre en la Argentina. Programas de uso sustentable*. Dirección de Fauna Silvestre, Secretaría de Ambiente y Desarrollo Sustentable, Buenos Aires, pp. 105–119.
- Borges, L.V., Colares, I.G., 2007. Feeding habits of Capybaras (*Hydrochoerus hydrochaeris*, Linnaeus 1766), in the Ecological Reserve of Taim (ESEC-Taim) – South of Brazil. *Braz. Arch. Biol. Technol.* 50, 409–416.
- Borgnia, M., Galante, M.L., Cassini, M.H., 2000. Diet of *Myocastor coypus* in agrosystems of the Argentinian Pampas. *J. Wildl. Manage.* 64, 354–361.
- Boutton, T.W., Bruce, N., Smith, B.N., Tyrone-Harrison, A., 1980. Carbon isotope ratio and crop analyses of *Arphia* (Orthoptera Acrididae) species in southeaster Wyoming Grassland. *Oecologia* 45, 299–306.
- Carnevali, R., 2003. El Iberá y su entorno fitogeográfico. EUDENE, Argentina.
- Caswell, H., Reed, F., Stephenson, S.N., 1973. Photosynthetic pathways and selective herbivory: a hypothesis. *Am. Nat.* 107, 465–480.
- Cavagnaro, R., 1988. Distribution of C₃ and C₄ grasses at different altitudes in a temperate arid region of Argentina. *Oecologia* 76, 273–277.
- Cerling, T.E., Harris, J.M., Passey, H., 2003. Diets of East African Bovidae based on stable isotope analysis. *J. Mamm.* 84, 456–470.
- Codron, D., Sponheimer, M., Codron, J., Newton, I., Lanham, J.L., Clauss, M., 2012. The confounding effects of source isotopic heterogeneity on consumer-diet and tissue-tissue stable isotope relationships. *Oecologia* 169, 939–953.
- Codron, D., Codron, J., 2009. Reliability of δ¹³C and δ¹⁵N in faeces for reconstructing savanna herbivore diet. *Mamm. Biol.* 74, 36–48.
- Codron, D., Codron, J., Lee-Thorp, J.A., Sponheimer, M., de Ruiter, D.J., Sealy, J., Grant, R., Fourie, N., 2007b. Diets of savanna ungulates from stable carbon isotope composition of faeces. *J. Zool.* 273, 21–29.
- Codron, D., Lee-Thorp, J.A., Sponheimer, M., Codron, J., 2007a. Nutritional content of savanna plant foods: implications for browser/grazer models of ungulate diversification. *Eur. J. Wildl. Res.* 53, 100–111.
- Comstock, J.P., Ehleringer, J.R., 1992. Plant adaptation in the Great Basin and Colorado Plateau. *Great Basin Nat.* 3 (52), 195–215.
- Conservation Land Trust, 2006. Los Esteros del Iberá: Importancia de su Conservación. Corrientes, Argentina.
- Corriale, M.J., Herrera, E., 2014. Patterns of habitat use and selection by the capybara (*Hydrochoerus hydrochaeris*): a landscape-scale analysis. *Ecol. Res.* 29, 191–201.
- Corriale, M.J., (Tesis Doctoral) 2010. Uso y selección de hábitat del carpincho (*Hydrochoerus hydrochaeris*) a distintas escalas espacio-temporales en los esteros del Iberá, Corrientes, Argentina. Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires.
- Corriale, M.J., Arias, S.M., Quintana, R.D., 2011. Forage quality of plant species consumed by capybaras (*Hydrochoerus hydrochaeris*) in the Paraná River Delta, Argentina. *Rangeland Ecol. Manage.* 64 (3), 257–263.
- Corriale, M.J., Muschetto, E., Herrera, E.A., 2013a. Influence of group sizes and food resources in home-range sizes of capybaras from Argentina. *J. Mamm.* 94 (1), 19–28.
- Corriale, M.J., Picca, P.I., di Francescantonio, D., 2013b. Seasonal variation of plant communities and their environments along a topographic gradient in the Iberá wetland, ancient Paraná floodplain, Argentina. *Phytocoenologia* 43, 53–66.
- DeNiro, M.J., 1985. Postmortem preservation and alteration of in vivo bone collagen isotope ratios in relation to paleodietary reconstruction. *Nature* 317, 806–809.
- Ehleringer, J.E., Cerling, T.E., 2001. Photosynthetic pathways and climate. In: Schulze, E.D., Heimann, M., Harrison, S., Holland, E., Lloyd, J., Prentice, I.C., Schimel, D.S. (Eds.), *Global Biogeochemical Cycles in the Climate System*. Academic Press, New York, pp. 267–277.
- Emmons, L.H., 1997. Neotropical Rainforest Mammals: A Field Guide, 2nd ed. The University of Chicago, Chicago.
- Escobar, A., González-Jiménez, E., 1976. Estudio de la competencia alimenticia de los herbívoros mayores del Llano inundable con referencia especial al chigüiro (*Hydrochaeris hydrochaeris*). *Agron. Trop.* 26, 215–227.
- Forero-Montaña, J., Betancur, J., Cavelier, J., 2003. Dieta del capibara *Hydrochaeris hydrochaeris* (Rodentia: Hydrochaeridae) en Caño Limón, Arauca, Colombia. *Rev. Biol. Trop.* 51, 579–590.
- García, A.M., Vieira, J.P., Winemiller, K.O., Grimm, A.M., 2004. Comparison of the 1982 e 1983 and 1997 e 1998 El Niño effects on the shallow-water fish assemblage of the Patos Lagoon estuary (Brazil). *Estuaries* 27, 905–914.
- González Jiménez, E., 1978. Digestive physiology and feeding of capybara (*Hydrochoerus hydrochaeris*). In: Rechcigl, M. (Ed.), *Handbook Series in Nutrition and Food*. CRC Press, Cleveland, pp. 163–177.
- González-Jiménez, E., Escobar, A., 1977. Flood adaptation and productivity of savanna grasses. In: *Proceedings XIII International Grassland Congress*. Leipzig Akademik Verlag, Berlin, pp. 510–514.
- Gorosábel, A., (Tesis de Licenciatura) 2013. Mortalidad de carpinchos (*Hydrochoerus hydrochaeris*) en una zona libre de presión de caza en los Esteros del Iberá, Argentina. Universidad de Buenos Aires, Buenos Aires.
- Gosling, L.M., 1981. Climatic determinants of spring littering by feral coypus, *Myocastor coypus*. *J. Zool.* 195, 281–288.
- Grier, J.W., Burk, T., 1992. *Biology of Animal Behaviour*, 2nd ed. Mosby Year Book, St. Louis, Missouri.
- Guichón, M.L., Benitez, V.B., Abba, A., Borgnia, M., Cassini, M.H., 2003. Foraging behaviour of coypu *Myocastor coypus*: why do coypus consume aquatic plants? *Acta Oecol.* 24, 241–246.
- Gutiérrez, G., 1998. Estrategias de forrajeo. In: Ardila, R., López, W., Pérez, A.M., Quiñones, R., Reyes, F. (Eds.), *Manual de Análisis Experimental del Comportamiento*. Librería Nueva, Madrid, pp. 359–381.
- Herrera, E.A., Macdonald, D.W., 1987. Group stability and the structure of a capybara population. *Symp. Zool. Soc. Lond.* 58, 115–130.
- Herrera, E.A., Macdonald, D.W., 1989. Resource utilization and territoriality in group-living capybaras (*Hydrochoerus hydrochaeris*). *J. Anim. Ecol.* 58, 667–679.
- Herrera, E.A., Salas, V., Congdon, E.R., Corriale, M.J., Tang-Martínez, Z., 2011. Capybara social structure and dispersal patterns: variations on a theme. *J. Mamm.* 92, 12–20.
- Hobbs, N.T., Swift, D.W., 1988. Grazing in herds: when are nutritional benefits realized? *Am. Nat.* 131, 760–764.
- Hu, Y., Wang, G., Cui, Y., Dong, Y., Guan, L., Wang, C., 2007. Palaeodietary study of Sanxingcun Site, Jintan, Jiangsu. *Chin. Sci. Bull.* 52, 660–664.
- Hummel, J., Südekum, K.H., Streich, W.J., Clauss, M., 2006. Forage fermentation patterns and their implications for herbivore ingesta retention times. *Funct. Ecol.* 20, 989–1002.
- Jacobs, J., 1974. Quantitative measurement of food selection. *Oecologia* 14, 413–417.

- Jones, M.B., 1988. Photosynthetic responses of C₃ and C₄ wetlands species in a tropical swamp. *J. Ecol.* 76, 253–262.
- Jorgenson, J.P., 1986. Notes on the ecology and behavior of capybaras in northeastern Colombia. *Vida Silvestre Neotrop.* 1, 31–40.
- Krueger, H.W., Sullivan, C.H., 1984. Models for carbon isotope fractionation between diet and bone. In: Turlund, J.E., Johnson, P.E. (Eds.), *Stable Isotopes in Nutrition*, vol. 258. American Chemical Society, Symposium Series, pp. 205–222.
- Leavitt, S.W., Long, A., 1982. Evidence for “C/C” fractionation between tree leaves and wood. *Nature* 298, 742–744.
- Farquhar, G.D., Ehleringer, J.R., Hubick, K.T., 1989. Carbon isotope discrimination and photosynthesis. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 40, 503–537.
- Lee-Thorp, J., Van Der Merwe, N.J., 1989. Carbon Isotope analysis of fossil bone apatite. *S. Afr. J. Sci.* 83, 712–715.
- Lee-Thorp, J.A., Sealy, J.C., Van Der Merwe, N.J., 1989. Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. *J. Archaeol. Sci.* 16, 585–599.
- Loponte, D., Feuillet Terzaghi, R., Corriale, M.J., Sartori, J., Acosta, A., 2013. Horticulturalists, hunter-gatherers and their preys in the isotopic landscape of the lower Paraná. *M.S.*
- Madanes, N., Quintana, R.D., Biondini, M., Loponte, D., 2010. Relationships between photosynthetic plant types in the diet of herbivore mammals and in the environment in the lower Paraná river basin, Argentina. *Rev. Chil. Hist. Nat.* 83, 309–319.
- Malainey, M.E., 2010. In: Orser Jr., C.E., Schiffer, M.B. (Eds.), *A Consumer's Guide to Archaeological Science: Analytical Techniques*. Springer, New York/Dordrecht/Heidelberg/London.
- Manly, B., McDonald, L., Thomas, D., 1993. *Resource Selection by Animals. Statistical Design and Analysis for Field Studies*. Chapman & Hall, London.
- Martin, P., Bateson, P., 1991. *La medición del comportamiento*. Alianza Universidad. Versión española de Fernando Colmenares, 1st ed. Alianza, Madrid.
- Mcloughlin, P.D., Walton, L.R., Cluff, H.D., Paquet, P.C., Ramsay, M.A., 2004. Hierarchical habitat selection by tundra wolves. *J. Mamm.* 85, 576–580.
- Mueller-Dombois, D., Ellenberg-Elleberg, E., 1974. *Aims and Methods of Vegetation Ecology*. John Wiley & Sons, New York.
- Neiff, J.J., Poi de Neiff, A.S.G., 2005. Situación ambiental en la ecorregión Iberá. In: Brown, A., Martínez Ortiz, U., Acerbi, M., Corchera, J. (Eds.), *La situación ambiental argentina 2005*. Fundación Vida Silvestre Argentina, Buenos Aires, pp. 177–183.
- Nogueira Filho, S.L.G., 1996. *Manual de Criação da Capivara*. Centro de Produções Técnicas, CPT, Viçosa MG.
- Ojasti, J., 1973. *Estudio biológico del chigüire o capibara*. Fondo Nacional de Investigaciones Agropecuarias (FONAIAP), Caracas.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R., 2001. Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience* 51 (11), 933–938.
- Panek, J.A., Waring, R.H., 1995. Carbon isotope variation in Douglas-fir foliage: improving the 13C-climate relationship. *Tree Physiol.* 15, 657–663.
- Pate, D., 1994. Bone chemistry and paleodiet. *J. Archaeol. Method Theory* 1 (2), 161–209.
- Provenza, F.D., Pfister, J.A., Cheney, C.D., 1992. Mechanisms of learning in diet selection with reference to phytotoxicosis in herbivores. *J. Range Manage.* 45, 36–45.
- Quintana, R.D., Monge, S., Malvárez, A.I., 1994. Feeding habits of capybara (*Hydrochaeris hydrochaeris*) in afforestation areas of the Lower Delta of the Parana River, Argentina. *Mammalia* 58, 569–580.
- Quintana, R.D., Monge, S., Malvárez, A.I., 1998a. Feeding patterns of capybara (*Hydrochaeris hydrochaeris*) (Rodentia, Hydrochaeridae) and cattle in the non-insular area of the Lower Delta of the Paraná River, Argentina. *Mammalia* 62, 37–52.
- Quintana, R.D., Monge, S., Malvárez, A.I., 1998b. Composición y diversidad de las dietas del capibara (*Hydrochaeris hydrochaeris*) y del ganado doméstico en un agroecosistema del centro de Entre Ríos, Argentina. *Ecotrópicos* 11, 34–44.
- Quintana, R.D., Rabinovich, J., 1993. Assessment of capybara (*Hydrochaeris hydrochaeris*) populations in the wetlands of Corrientes, Argentina. *Wetlands Ecol. Manage.* 2, 223–230.
- Rice, W.R., 1989. Analyzing tables of statistical tests. *Evolution* 43, 223–225.
- Robinson, T.F., Sponheimer, M., Roeder, B.L., Passey, B., Cerling, T.E., Dearing, M.D., Ehleringer, J.R., 2006. Digestibility and nitrogen retention in llamas and goats fed alfalfa, C₃ grass, and C₄ grass hays. *Small Rum. Res.* 64, 162–168.
- Rodiney, M., Pott, A., 1996. Dieta del capybara (*Hydrochaeris hydrochaeris*) basada en análisis microhistológico de las heces. *Vida Silv. Neotrop.* 5, 151–153.
- Schoeninger, M.J., Moore, K.M., Murray, M.L., Kingston, J.D., 1989. Detection of bone preservation in archaeological fossil samples. *Appl. Geochem.* 4, 281–292.
- Schoeninger, M.J., DeNiro, M.J., 1983. Stable nitrogen isotope ratios of bone collagen reflect marine and terrestrial components of prehistoric human diet. *Science* 220, 1381–1383.
- Shettleworth, S.J., 1998. *Cognition, Evolution, and Behavior*. Oxford University Press, New York.
- Smith, B.N., Brown, W.V., 1973. The Kranz syndrome in the Gramineae as indicated by carbon isotopic ratios. *Am. J. Bot.* 60, 505–513.
- Smith, B.N., Epstein, S., 1971. Two categories of 13C/12C ratios for higher plants. *Plant Physiol.* 47, 380–384.
- Sokal, R.R., Rolf, F.J., 1995. *Biometry: The Principles and Practice of Statistics in Biological Research*, 3rd ed. W.H. Freeman, New York.
- Sponheimer, M., Lee-Thorp, J.A., De Ruiter, D.J., Smith, J.M., Van Der Merwe, N.J., Reed, K., Grant, C.C., Ayliffe, L.K., Robinson, T.F., Heidelberg, C., Marcus, W., 2003. Diets of southern African Bovidae: stable isotope evidence. *J. Mamm.* 84, 471–479.
- Stephens, D.W., Krebs, J.R., 1986. *Foraging Theory*. Princeton University Press, Princeton.
- Sullivan, C.H., Krueger, H.W., 1981. Carbon isotope analysis in separate chemical phases in modern and fossil bone. *Nature* 292, 333–335.
- Theerl, J.A., Stowe, L.G., 1976. Climatic patterns and the distribution of C₄ grasses in North America. *Oecologia* 23, 1–12.
- Thomas, D.L., Taylor, E.J., 1990. Study designs and tests for comparing resource use and availability. *J. Wildl. Manage.* 54 (2), 322–330.
- Thomas, D.L., Taylor, E.J., 2006. Study designs and tests for comparing resource use and availability II. *J. Wildl. Manage.* 70, 324–336.
- Tieszen, L.L., 1991. Natural variations in the carbon isotope values of plants: implications for archaeology, ecology, and paleoecology. *J. Archaeol. Sci.* 18, 227–248.
- Van der Merwe, N.J., 1989. Natural variation in C13 concentration and its effect on environmental reconstruction using C12/C13 ratios in animal bones. In: Price, T.D. (Ed.), *The Chemistry of Prehistoric Human Bone*. Cambridge University Press, pp. 105–125.
- Van Der Merwe, N.J., Lee-Thorp, J.A., Bell, R.H.V., 1988. Carbon isotopes as indicators of elephant diets and African environments. *Afr. J. Ecol.* 26, 163–172.
- Van Soest, J.P., 1994. *Nitrogen Metabolism*. Nutritional Ecology of the Ruminant. Cornell University Press, Ithaca, New York.
- Vogel, J.C., 1978. Isotopic assessment of the dietary habits of ungulates. *S. Afr. J. Sci.* 74, 298–301.
- Waller, S.S., Lewis, J.K., 1979. Occurrence of C₃ and C₄ photosynthetic pathways in North American grasses. *J. Range Manage.* 32, 12–28.