

## Exploring the use of stable carbon isotope ratios in short-lived leporids for local paleoecological reconstruction

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### Abstract

Most ecological proxies used in archaeological research operate at scales that are too coarse-grained for consideration of hunter-gatherer adaptive decisions. Hunter-gatherers adapt to local ecological conditions and short (e.g. seasonal, yearly) time frames. Our goal is to develop proxies to identify ecological shifts at fine-grained temporal and spatial scales for archaeological research. We use stable carbon isotope ratios ( $\delta^{13}\text{C}$ ) in bone collagen from 58 modern leporids from two distinct ecological areas in the American Southwest as a proxy to reconstruct vegetation and climate patterns at fine-grained scales. Higher  $\delta^{13}\text{C}$  values in collagen of cottontail (*Sylvilagus* sp.) and jackrabbit (*Lepus* sp.) collected in the northern Chihuahuan Desert of New Mexico and West Texas suggest a more  $\text{C}_4$ /crassulacean acid metabolism (CAM) dominated local vegetation when contrasted to samples from Kerr County in Central Texas. Comparisons of temperature and precipitation patterns between the two areas, along with vegetation data, suggest that key ecological differences, reflected in the collagen isotopic compositions, are likely related to rainfall amounts and the type of green forage available to leporids, especially during winter months. Leporids in dry areas may be relying on CAM plants, including prickly pear, which has a  $\text{C}_4$  isotopic signature. Alternative resources are likely to be available in wetter areas such as Central Texas.

### Introduction

Reconstructions of past ecological conditions in archaeological research often rely on proxy data, such as shifts in pollen frequencies, which operate at variable spatial and temporal scales. While appropriate for many concerns, most ecological proxies operate at scales that are too coarse-grained for consideration of human adaptive decisions. Hunter-gatherers and agriculturalists adapt to local rather than regional ecological conditions, and to changes that occur on a seasonal or yearly time frame, not shifts that happen over centuries (Winterhalder and Leslie, 2002). Archaeologists need to develop high-resolution ecological proxies that operate at scales that are coterminous with those used by humans in making adaptive decisions.

In this paper, we explore the use of stable carbon isotope ratios ( $\delta^{13}\text{C}$ ) of bone collagen in cottontails (*Sylvilagus* sp.) and jackrabbits (*Lepus* sp.) as potential high-resolution proxies to reconstruct vegetation and climate patterns at short-term temporal and spatial scales. We have used samples from an archaeological assemblage from Texas, USA to monitor ecological shifts (Munoz *et al.*, 2011; Kemp, 2008) and are currently investigating other archaeological assemblages in the American Southwest. We focus on refining the application through a comparison of  $\delta^{13}\text{C}$  values in bone collagen ( $\delta^{13}\text{C}_{\text{collagen}}$ ) of leporids from two distinct ecological settings.  $\delta^{13}\text{C}$  values of modern leporids collected in southern New Mexico and West Texas ( $n=26$ ) suggest that these areas have a stronger  $\text{C}_4$ /CAM signature relative to those collected in Kerr County in Central Texas ( $n=32$ ). Comparisons of temperature and precipitation patterns between the two areas, along with vegetation transects data, suggest that key ecological differences reflected in the collagen are likely related to rainfall amounts and the type of green forage available to leporids, especially during the winter months.

As a paleoecological proxy, leporids have several advantages. Jackrabbit and cottontail diets incorporate a variety of plants, with grasses, forbs, shrubs, and succulents consumed in response to availability, growing conditions (*i.e.* temperature, rainfall, and plant dormancy), and moisture content. Analyses of the stomach contents of *Lepus* collected in southern Arizona (Vorhies and Taylor, 1933) suggest a seasonal preference for grasses in the spring and midsummer, following rains. As grass production declines in early fall and winter, rabbits concentrate on browse consisting primarily of mesquite (*Prosopis glandulosa*). Cactus, such as prickly pear (*Opuntia* sp.) and cholla (*Echinocereus fendleir*), are more heavily consumed during drier months. Similar

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seasonal trends, with grasses preferred in the late spring, summer, and early fall, forbs and shrubs in the fall and winter, and shrubs and succulents in winter and early spring are reported for jackrabbits in a variety of regions (Best, 1996; Currie and Goodwin, 1966; Fatehi *et al.*, 1988; Hayden, 1966; Hoffman *et al.*, 1993;

Table 1. Carbon and nitrogen isotope results from modern leporid bone collagen samples.

Laboratory	CAR-ref	Genus	Area	Collection date	$\delta^{13}\text{C}^*$	Carbon (%)	$\delta^{15}\text{N}$	Nitrogen (%)	Replicates**
NAU	709.1	<i>Lepus</i>	1	Spring 2009	-17.3	45.3	6.1	15.9	1
NAU	710.1	<i>Lepus</i>	1	Spring 2009	-15.8	43.4	11.1	15.7	1
NAU	711.1	<i>Lepus</i>	1	Spring 2009	-17.2	44.8	5.6	16.3	1
NAU	712.2	<i>Lepus</i>	1	Spring 2009	-18.8	44.4	6.3	15.8	1
NAU	713.1	<i>Lepus</i>	1	Spring 2009	-19.7	43.2	7.0	15.4	1
NAU	714.1	<i>Lepus</i>	1	Spring 2009	-20.0	43.5	8.9	15.4	1
NAU	715.1	<i>Lepus</i>	1	Spring 2009	-19.9	44.6	8.7	15.8	1
NAU	744.1	<i>Lepus</i>	1	Spring 2009	-17.1	39.7	6.7	14.1	2
Geochron	na	<i>Lepus</i>	1	07-06-1991	-15.3	na	na	na	2
Geochron	na	<i>Lepus</i>	1	19-10-1991	-16.9	na	na	na	3
Geochron	na	<i>Lepus</i>	1	16-09-1991	-17.3	na	na	na	1
Geochron	na	<i>Lepus</i>	1	18-10-1991	-16.7	na	na	na	1
Geochron	na	<i>Lepus</i>	1	12-11-1991	-21.3	na	na	na	1
Geochron	na	<i>Lepus</i>	1	28-06-1991	-13.3	na	na	na	1
Geochron	na	<i>Lepus</i>	1	16-09-1991	-16.9	na	na	na	1
Geochron	na	<i>Lepus</i>	1	04-06-1992	-19.2	na	na	na	1
NAU	359.1	<i>Sylvilagus</i>	1	Spring 2009	-19.5	39.5	6.1	13.6	2
NAU	361.1	<i>Sylvilagus</i>	1	Spring 2009	-18.9	35.5	6.5	12.2	1
NAU	362.1	<i>Sylvilagus</i>	1	Spring 2009	-19.9	39.5	7.0	13.9	1
NAU	363.1	<i>Sylvilagus</i>	1	Spring 2009	-21.1	40.3	5.8	14.2	1
NAU	364.1	<i>Sylvilagus</i>	1	Spring 2009	-16.4	40.8	5.7	14.5	1
NAU	365.1	<i>Sylvilagus</i>	1	Spring 2009	-19.9	42.1	5.5	14.8	1
NAU	366.1	<i>Sylvilagus</i>	1	Spring 2009	-19.8	42.7	6.6	15.1	1
NAU	367.1	<i>Sylvilagus</i>	1	Spring 2009	-19.9	41.9	5.7	14.8	1
NAU	368.1	<i>Sylvilagus</i>	1	Spring 2009	-18.5	42.2	6.0	15.1	1
NAU	369.1	<i>Sylvilagus</i>	1	Spring 2009	-16.2	41.3	5.8	14.4	1
NAU	356.1	<i>Lepus</i>	2	24-02-2008	-15.2	40.5	7.5	13.6	1
NAU	743.1	<i>Lepus</i>	2	29-08-2009	-15.7	40.7	6.5	13.9	3
NAU	799.1	<i>Lepus</i>	2	14-05-1997	-23.4	41.0	3.7	14.6	1
NAU	810.1	<i>Lepus</i>	2	20-05-1999	-17.6	40.6	2.8	14.5	1
NAU	815.1	<i>Lepus</i>	2	14-05-1998	-23.3	43.2	1.8	15.1	1
NAU	816.1	<i>Lepus</i>	2	14-05-1996	-19.3	41.4	5.3	14.5	1
NAU	817.1	<i>Lepus</i>	2	14-05-1997	-23.2	41.4	3.0	14.6	1
NAU	819.1	<i>Lepus</i>	2	14-05-1998	-22.2	40.8	2.3	14.1	1
NAU	820.1	<i>Lepus</i>	2	14-05-1996	-20.6	41.4	2.5	14.5	2
NAU	826.1	<i>Lepus</i>	2	20-05-1996	-17.9	42.3	5.2	14.8	1
NAU	828.1	<i>Lepus</i>	2	14-05-1997	-18.7	42.2	3.6	14.8	1
NAU	830.1	<i>Lepus</i>	2	17-05-1998	-20.6	41.3	3.6	14.6	2
NAU	831.1	<i>Lepus</i>	2	16-05-1996	-16.2	41.1	3.2	14.6	1
NAU	833.1	<i>Lepus</i>	2	14-05-1998	-21.7	37.5	4.3	12.8	1
NAU	835.1	<i>Lepus</i>	2	13-05-1998	-20.4	43.2	3.8	15.1	1
NAU	857.1	<i>Lepus</i>	2	20-05-1999	-22.3	41.4	2.8	14.9	1
NAU	360.1	<i>Sylvilagus</i>	2	03-06-2009	-17.5	39.7	4.0	14.1	1
NAU	519.1	<i>Sylvilagus</i>	2	16-05-1996	-20.7	40.1	2.3	14.5	2
NAU	797.1	<i>Sylvilagus</i>	2	16-05-1996	-17.6	41.4	8.3	14.2	1
NAU	801.1	<i>Sylvilagus</i>	2	21-05-1996	-18.4	40.5	2.7	14.5	1
NAU	803.1	<i>Sylvilagus</i>	2	15-05-1997	-24.3	41.2	2.0	14.6	1
NAU	805.1	<i>Sylvilagus</i>	2	20-05-1996	-21.2	39.8	2.6	14.2	1
NAU	811.1	<i>Sylvilagus</i>	2	14-05-1998	-23.4	39.8	2.5	13.8	1
NAU	814.1	<i>Sylvilagus</i>	2	16-05-1996	-20.4	39.7	5.7	13.6	1
NAU	818.1	<i>Sylvilagus</i>	2	13-05-1996	-18.0	42.6	4.9	15.0	1
NAU	821.1	<i>Sylvilagus</i>	2	14-05-1996	-21.5	41.5	3.1	14.4	1
NAU	822.1	<i>Sylvilagus</i>	2	20-05-1996	-21.8	42.1	3.2	14.9	1
NAU	823.1	<i>Sylvilagus</i>	2	12-05-96	-20.8	42.9	3.6	15.3	1
NAU	827.1	<i>Sylvilagus</i>	2	14-05-97	-20.9	41.2	3.1	14.1	1
NAU	832.1	<i>Sylvilagus</i>	2	20-05-96	-21.9	39.9	2.8	13.9	1
NAU	834.1	<i>Sylvilagus</i>	2	20-05-96	-20.9	40.3	3.0	13.8	1
NAU	860.1	<i>Sylvilagus</i>	2	16-05-96	-17.8	42.3	5.1	14.7	1

CAR-ref, Center for Archaeological Research-reference; NAU, Northern Arizona University; Geochron, Geochron Laboratories (Chelmsford, MA, USA); na, not available. \*Analytical uncertainties (1 $\sigma$  standard deviation) for  $^{13}\text{C}$  data at NAU are  $\leq 0.10\%$ ; \*\*when present replicate results were averaged.

MacCraken and Hansen, 1984; Sparks, 1968; Uresk, 1978; Westoby, 1980). Cottontails have a similar pattern. Turkowski (1975) looked at the stomach content of 97 cottontails from Maricopa County in southern Arizona collected over 16 months. In terms of dietary bulk, grasses (37.9%) and forbs (41.3%) were the most commonly consumed plant groups, with 43 plant species identified as dietary items over the study period. Strong seasonal patterns, with increased grass consumption in the summers, and increased consumption of succulents or other moisture rich plants during dry periods, were also present in cottontails (Hoffman *et al.*, 1993; MacCraken and Hansen, 1984; Turkowski, 1975; Brown, 1947; Chapman *et al.*, 1982; deCalesta, 1979; Riegel, 1942; Scribner and Krysl, 1982).

Cottontail and jackrabbits occupy small lifetime home ranges. Their dietary signature should reflect the local vegetation. While there are reports of movements of small numbers of *Lepus* in excess of 5 km (*e.g.* Smith *et al.*, 2002), most jackrabbits spend their lives within an area less than 1 km<sup>2</sup> in size, with most estimates falling below 170 ha (Best, 1996; Farias *et al.*, 2006; French *et al.*, 1965; Lechleitner, 1958; Smith, 1990). Cottontails have even smaller lifetime home ranges. Chapman *et al.* (1982) and Trent and Rongstad (1974) summarise studies that suggest home ranges less than 15 ha for a variety of *Sylvilagus* species (Haugen, 1942).

Leporids have short lives. In most cases, their dietary signature reflects a temporal span of less than two years. Tiemeier and Plenert (1964) found that only 9 of 906 jackrabbits in southern Kansas were more than three years of age (French *et al.*, 1965; Feldhamer, 1979). Ingles (1941), in a study of *S. audubonii* in

California, notes that only seven of 29 rabbits (*ca.* 24%) survived after a single year, with 19 months being the maximum age observed (Chapman *et al.*, 1982; Allen, 1939; Bronson and Tiemeier, 1958).

Critically, the short-term, local vegetation patterns present in leporid diets should produce distinct <sup>13</sup>C<sub>collagen</sub> values (Munoz *et al.*, 2011). Experimental studies suggest that the <sup>δ13</sup>C of herbivore bone collagen reflects the

carbon isotopic composition of the diet and, in turn, the vegetation type. Collagen values are about 5‰ heavier than diet (DeNiro and Epstein, 1978; Tykot, 2004). As vegetation changes, either on a seasonal basis or directionally over time, different mixes of C<sub>3</sub> (<sup>δ13</sup>C range of -33 to -23‰), C<sub>4</sub> (<sup>δ13</sup>C range of -16 to -9‰) and crassulacean acid metabolism (CAM) (most range between -10 and -20‰) plants will be present in many instances

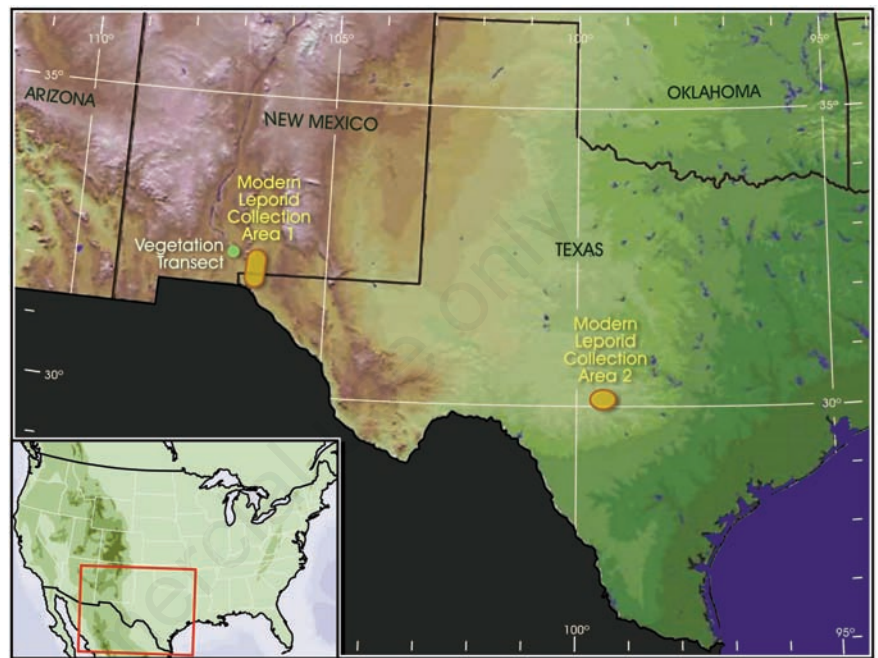


Figure 1. Map of Southwestern United States showing locations of modern leporid collection areas. Area 1 includes portions of El Paso County, Texas, and Dona Ana County, New Mexico. Area 2 is in Kerr County, Texas. Also shown is the location of the vegetation transect adjacent to Area 1.

Table 2. Carbon and nitrogen isotopic values for prickly pear (*Opuntia* sp.) stems from Texas counties.

County	Latitude (N)	Longitude (W)	Replicates	<sup>δ13</sup> C (‰)	<sup>δ15</sup> N (‰)*
Lubbock	33°37'12"	101°53'12"	1	-12.1	2.2
Hamilton	31°56'17"	98°04'07"	1	-11.2	2.9
Tom Green	31°41'30"	100°46'50"	1	-11.6	4.0
Lampasas	31°24'24"	98°10'25"	1	-13.2	5.9
Burnett	30°49'08"	98°13'34"	1	-12.5	4.4
Blanco	30°18'51"	98°24'32"	1	-12.8	2.6
Kendall	29°53'33"	98°38'36"	1	-11.7	1.5
Kendall	29°53'29"	98°38'37"	1	-12.0	3.4
Kendall	29°53'27"	98°38'37"	1	-12.5	1.5
Bexar	29°34'49"	98°37'54"	7	-12.6	2.8
Atascosa	28°57'45"	98°35'01"	1	-13.0	4.2
McMullen	28°36'17"	98°33'02"	1	-12.6	7.8
McMullen	28°13'51"	98°30'48"	1	-12.0	7.4
Kleberg	27°17'55"	97°49'19"	1	-12.9	4.9

\*Analytical uncertainties (1 standard deviation) for <sup>δ15</sup>N data at Northern Arizona University are  $\leq 0.20\%$ .

(Bender, 1968; O'Leary, 1988; Smith and Epstein, 1970). Given the wide diet of leporids, these different mixes of  $C_3$ ,  $C_4$ , and CAM plants should produce different  $\delta^{13}C_{\text{collagen}}$  values, depending on the proportions of these plants in the diet. For example, on the American Great Plains researchers have shown that increased summer rainfall in the context of sufficient temperatures should produce both more  $C_4$  grass and may increase the length of time that grass is available (Epstein *et al.*, 1997; Paruelo and Lauenroth, 1996). The  $\delta^{13}C$  of leporid bone collagen would reflect that shift. However, details between leporid collagen, vegetation regimes, and climate parameters are not well defined. Here we contrast collagen values derived from leporids in two locations that have different climate and vegetation regimes to better define the associated impacts.

## Materials and Methods

Jackrabbit and cottontail samples used in this analysis were collected from two locations in the American Southwest (Figure 1). Leporid collection Area 1 is located in far west Texas (El Paso County) and southern New Mexico (Dona Ana County) in the northern Chihuahuan Desert, east of El Paso, Texas ( $32^{\circ}00'N/106^{\circ}15'W$ ). Eight jackrabbits were collected from this area in late 1991 and 1992 (Mauldin, 1993). Eight additional samples were collected in the spring of 2009, along with 10 cottontails. Leporid Collection Area 2 is located in Kerr County in Central Texas (Figure 1;  $30^{\circ}05'N/99^{\circ}30'W$ ). Twenty-nine samples were collected between 1996 and 1999, with three additional leporids collected during 2008 and 2009.

All samples from Area 1 ( $n=26$ ), as well as the three most recent leporids samples gathered from Area 2, were collected as carcasses. For selected limbs, bones were broken and boiled to remove adhering tissue. Boiling also removes lipids (Ugan and Coltrain, 2011). The remaining 29 samples from Area 2 were recovered from museum collections at Texas Tech University. These samples were clean and dry at the time of our acquisition. The eight Area 1 samples collected in the early 1990s were analysed for  $\delta^{13}C$  collagen by Geochron Laboratories (Krueger, 1992). All other samples ( $n=50$ ) were prepared at the Center for Archaeological Research (CAR) at the University of Texas at San Antonio (UTSA) following methods developed by Longin and Ambrose (Longin, 1971; Ambrose, 1990), Hdescribed by Munoz and others (Munoz *et al.*, 2011). The carbon isotope ratios ( $\delta^{13}C$  values), along with the percentage of C and N in the leporid collagen samples, were measured

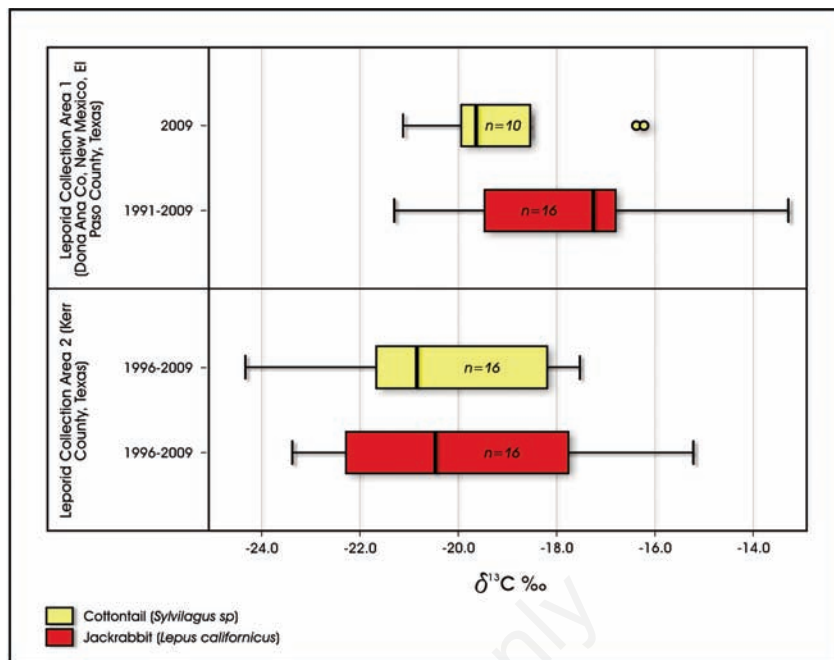


Figure 2. Box plots of  $\delta^{13}C$  collagen values from modern *Sylvilagus* sp. (yellow) and *Lepus* (red) by collection areas shown in Figure 1. A test of medians and comparison of distributions in Statistical Package for Social Science Version 19 show no significant difference between cottontail and jackrabbits (Area 1,  $n=26$ ; median test statistic=2.60, significance=.226; Mann-Whitney U statistic=107, significance=.155; Area 2,  $n=32$ ; median test statistics=2.00; significance=.157; Mann-Whitney U statistic=142, significance=.598). Comparisons of cottontail  $\delta^{13}C$  collagen values ( $n=26$ ) between the two areas showed no significant differences in distributions (Mann-Whitney U statistic=45, significance=.065), but significant differences in medians (test statistic=5.85, significance=.041). Comparisons of jackrabbit  $\delta^{13}C$  collagen median values were not significant ( $n=32$ ; median test statistic=2.00, significance=.157), but distributions were significantly different (Mann-Whitney U statistic=67, significance=.022).

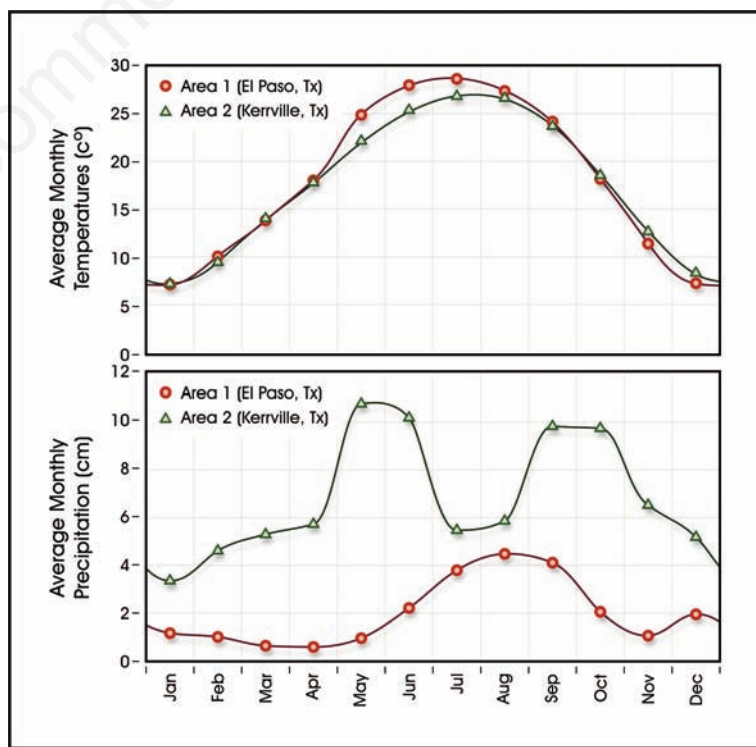


Figure 3. Average monthly temperature (top) and precipitation (bottom) values by area based on 1971-2000 records (44). Area 1 values are from El Paso International Airport (station ID 412797); Area 2 values are from Kerrville, Texas (station ID 414782).

using either a Carlo Erba NC2100 Elemental Analyzer or Costech ECS4010 Elemental Analyzer (Costech Analytical Technologies Inc., Valencia, CA, USA) attached on-line with a Thermo Finnigan Delta<sup>plus</sup> XP Stable Isotope Ratio Mass Spectrometer (IRMS) at the Colorado Plateau Analytical Laboratory, Northern Arizona University (NAU). All  $\delta^{13}\text{C}$  values are reported in permil relative to the VPDB scale.

For the 50 NAU samples, the weight percent nitrogen ranges from 12.21 to 16.26% with percent carbon falling between 35.5 and 45.27%

(Table 1). The atomic ratio of carbon to nitrogen is between 3.21 and 3.48. These ratios are consistent with good collagen integrity (Ambrose and Norr, 1992). The percent carbon and nitrogen values were not obtained for the eight Area 1 samples collected in the early 1990s. While Table 1 provides the  $\delta^{15}\text{N}$  values for the remaining 50 samples, the focus of our discussion is on variation in carbon isotopes and their relationship with vegetation and climate parameters. Causes of  $\delta^{15}\text{N}$  variability in leporids are not well understood. Recent work on jackrabbits (Ugan and Coltrain, 2011) sug-

gests that  $\delta^{15}\text{N}$  variability is primarily related to factors such as topography and soil salinity rather than directly reflecting climate variables (Ugan and Coltrain, 2011).

## Results and Discussion

Table 1 provides the  $\delta^{13}\text{C}$  values for the 58 samples, identified by genus and location (see Figure 1).  $\delta^{13}\text{C}_{\text{collagen}}$  of jackrabbit samples ( $n=32$ ) ranges from  $-23.38$  to  $-13.30\text{‰}$  with an average value of  $-18.79\text{‰}$ . Cottontail  $\delta^{13}\text{C}_{\text{collagen}}$  values ( $n=26$ ) range from  $-24.33$  to  $-16.23\text{‰}$  (average= $-19.90\text{‰}$ ), suggesting slightly higher proportions of  $\text{C}_3$  plants in their diet. Histograms (not shown) suggest that the cottontail  $\delta^{13}\text{C}_{\text{collagen}}$  values approximate normality, but the *Lepus* values are left skewed. As such, we focus on non-parametric comparisons.

Figure 2 presents box plots of  $\delta^{13}\text{C}_{\text{collagen}}$  values for each genus by collection areas (see Figure 1). Compared with cottontails, jackrabbit  $\delta^{13}\text{C}_{\text{collagen}}$  values are more positive in both locations, with differences of  $2.38\text{‰}$  in Area 1 median values and  $0.37\text{‰}$  in Area 2 medians. However, comparison of jackrabbits and cottontail medians (median test) as well as distributions (Mann-Whitney U) failed to show statistically significant differences. Comparison of  $\delta^{13}\text{C}_{\text{collagen}}$  values across the two areas by genus does show statistically significant differences on some variables. While the distributions of  $\delta^{13}\text{C}_{\text{collagen}}$  values for cottontails are not statistically different between areas (sig.=.065), median values are significantly different (sig.=.041). For jackrabbits, distributions of  $\delta^{13}\text{C}_{\text{collagen}}$  values between areas are significantly different (sig.=.022), but median values are not (sig.=.157). Overall, leporids in Area 1 clearly have a collagen signature that reflects more consumption of  $\text{C}_4$  and CAM plants relative to Area 2.

Monthly temperature and rainfall data (Figure 3) for two stations located within 30 km of the centers of Areas 1 and 2 show major differences in rainfall between the two areas (NOAA, 2004). The yearly Area 2 rainfall total (82.75 cm) is roughly 3.5 times that of Area 1 (23.95 cm). Area 2 has higher average rainfall in every month, with dramatic differences in the spring/summer and early fall during the growing season (Figure 3). Vegetation densities should be dramatically different between the two areas. While we lack information on specific plant growth patterns in Area 2, Figure 4 uses data in Kemp (1983) to monitor monthly vegetation changes in live, green tissue of the 44 most abundant plants along a transect west of Area 1 (Figure 1). Plants with green tissue are likely to be part of the leporid diet because of their higher moisture content

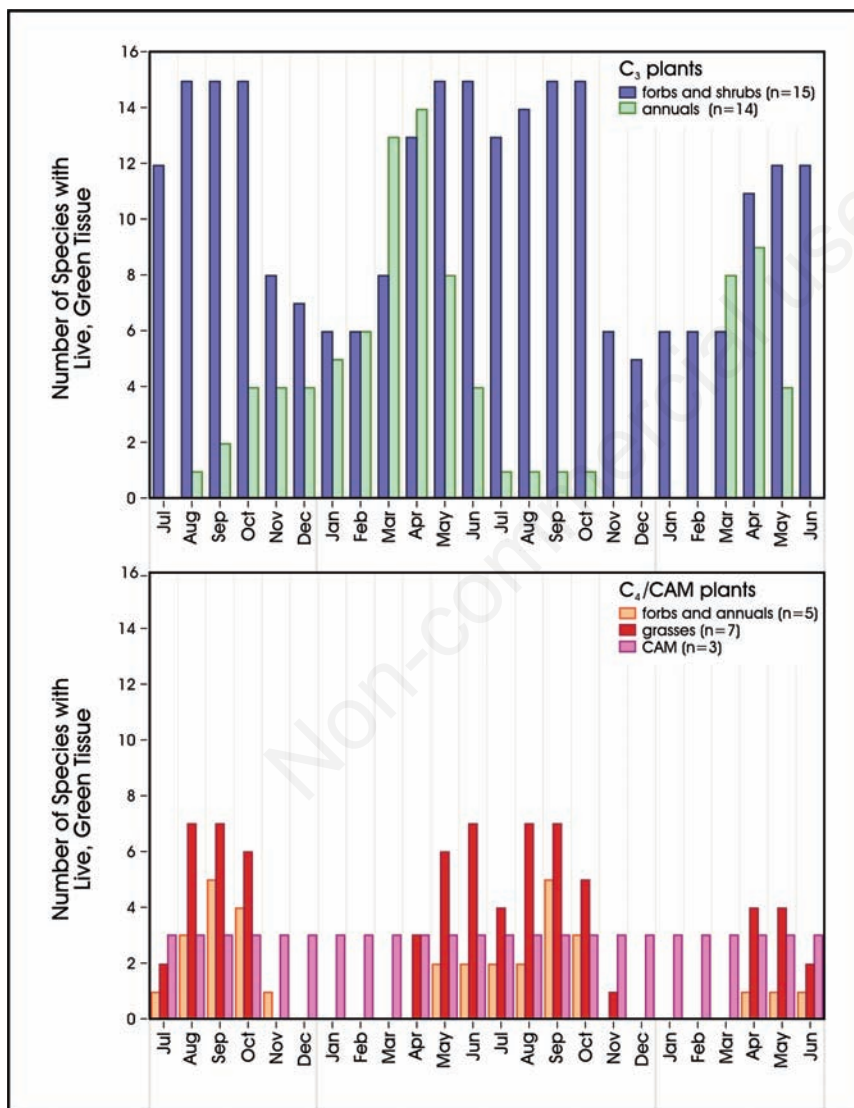


Figure 4. Monthly shifts in the number of species with live, green, above-ground tissue between July 1978 and June 1980 along a vegetation transect adjacent to Area 1. Data are from Kemp (1983) and include the 44 most abundant species. Forbs, shrubs, and annuals using a  $\text{C}_3$  photosynthetic pathway are grouped in the top bar graph, while  $\text{C}_4$  forbs, annuals and grasses are grouped with the crassulacean acid metabolism species in the bottom graph. Note that the values for December and January are estimated based on adjacent months and trends in the dataset.

(Uresk, 1978; Westoby, 1980).  $C_3$  plants are dominant during all periods (Figure 4, top panel). Production is highest during the late spring through the early fall. Availability of  $C_3$  plants declines over the late fall and winter months, though some  $C_3$  shrubs are present throughout the year. The seven types of  $C_4$  grasses,  $C_4$  forbs ( $n=2$ ) and  $C_4$  annuals ( $n=3$ ) are present only during the summer/early fall (Figure 4, bottom panel), probably in response to summer precipitation and temperatures (Figure 3). CAM plants, consisting here of prickly pear, cholla, and yucca (*torreyi*), are available year round and do not fluctuate in response to short-term rainfall or temperature shifts (Figure 4, bottom panel).

Linking the isotopic patterns in Figure 2 to the vegetation and climate patterns shown in Figures 3 and 4 are difficult given the lack of detailed vegetation data from Area 2. Clearly, the Area 1 vegetation data suggests that CAM resources may play an important seasonal dietary role. This is supported by a study on the impact of the grazing habits of rabbits on prickly pear in a region 35 km north of Area 1 (Hoffman *et al.*, 1993). That study shows two periods of heavy prickly pear stem use by leporids, with one feeding period occurring in June and a second during the months of December, January, and February. While reasons for the June feeding are unclear, the winter feeding spike correlates with a low number of alternative plants (Figure 4) and dry conditions (Figure 3). Moisture stress and low winter resource availability are unlikely in Area 2 given the greater precipitation and similarity in fall, winter, and spring temperatures. Compared to the  $\delta^{13}C_{\text{collagen}}$  of leporids in Area 2, higher values for Area 1 (Figure 2) may be related to increased Area 1 use of resources such as prickly pear. CAR-UTSA has processed and analysed, through NAU, samples from 14 prickly pear plants located in 11 Central and South Texas counties (Table 2). Stem  $\delta^{13}C$  values range from -11.22 to -13.17‰ (average = -12.35‰). These values are consistent with other studies of prickly pear (*e.g.* Eickmeir and Bender, 1976). Dietary intake of these succulents on a seasonal basis (Hoffman *et al.*, 1993) will result in higher  $\delta^{13}C_{\text{collagen}}$  values like those seen in the Area 1 samples.

## Conclusions

A comparison of  $\delta^{13}C$  values in bone collagen ( $\delta^{13}C_{\text{collagen}}$ ) of modern leporids from southern New Mexico and West Texas suggest that these areas have a stronger CAM/ $C_4$  signature (mean -18.20‰;  $n=26$ ) relative to Kerr County in Central Texas (mean -20.17‰;  $n=32$ ). Temperature and precipitation pat-

terns, along with vegetation transects data, suggest that key ecological differences reflected in the collagen are likely related to the different type of green forage available to leporids resulting from different amounts of rainfall, especially during the winter months. While research is ongoing into these relationships,  $^{13}C_{\text{collagen}}$  in modern leporid bone does track ecological differences in these two environments. This suggests that the  $^{13}C_{\text{collagen}}$  in leporid bone can be used as a high-resolution ecological proxy in archaeological research.

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