

Archaic and Late Prehistoric
HUMAN ECOLOGY IN THE
MIDDLE ONION CREEK VALLEY
Hays County, Texas

Volume 2:
Topical Studies

by
Robert A. Ricklis and Michael B. Collins

with contributions by

James T. Abbott	Mark W. Holderby
Thomas W. Boutton	Jeffery A. Huebner
Linda Scott Cummings	Thomas H. Loy
Boyce Driskell	Marilyn A. Masson
Charles D. Frederick	Raymond W. Neck
Wulf Gose	Kathryn Reese-Taylor
Jon Hageman	Dan K. Utley
Pamela J. Headrick	Carey Weber
Thomas R. Hester	

Texas Antiquities Committee Permit No. 0856
Principal Investigator: Michael B. Collins

Studies in Archeology 19
Texas Archeological Research Laboratory
The University of Texas at Austin
1994

The University of Texas at Austin
Texas Archeological Research Laboratory
J. J. Pickle Research Campus 5
Austin, Texas 78712-1100

Printed 1995, on acid-free, 60-pound paper.

ISBN 1-887072-04-7 (Volume 2)
ISBN 1-887072-05-5 (2 Volume Set)

CHAPTER 21

THE ISOTOPIC ECOLOGY AND NICHE SEPARATION OF GRASSLAND HERBIVORES IN A PREHISTORIC CENTRAL TEXAS ECOTONE

Jeffery A. Huebner and Thomas W. Boutton

The presence of contemporaneous bison (*Bison bison*), pronghorn antelope (*Antilocapra americana*) and deer (*Odocoileus virginianus*) skeletal remains at the Mustang Branch site demonstrates that environmental conditions which allowed these three herbivores to thrive in the vicinity of the Balcones Escarpment were different in Late Prehistoric times from those of today. Until the arrival of Spanish and later Euro-American settlers in Texas, environmental change was largely climate driven. With the introduction of such land-use practices as the moldboard plow to break prairie sod, grazing by domestic animals on fenced rangeland, reduction in fire frequency on rangelands, and unrestricted hunting of native wildlife species, culture, too, became a driving force in regional ecological change.

Present ecology of the Edwards Plateau, Blackland Prairie, and Balcones Escarpment bears little resemblance to that described by early settlers. One hundred fifty years ago these regions were described as expansive prairie grasslands, broken by mottes of oak and brush species in the uplands and gallery forests along the streams (Doughty 1983; Weniger 1984). Natural and anthropogenic wildfires checked the spread of woody plants in the grasslands (Smeins 1980).

Of the three species analyzed in this study, bison and antelope have been extirpated from the region. Deer have been forced into competition with cattle, goats, and other livestock as well as exotic species which have overlapping dietary preferences. Given the ecological changes that have taken place in Central Texas and elsewhere in the Southern Plains, modern studies of dietary habits are only of general utility in determining how these three species may have

partitioned available forage resources in late prehistory.

In this study, the collagen fraction of bone from prehistoric bison, antelope, and deer recovered from the Toyah component at the Mustang Branch and Barton sites (41HY209 and 41HY202), was analyzed by mass spectrometry for stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios to determine their dietary patterns. The isotopic analysis of multiple herbivore species for the purpose of dietary and paleoenvironmental reconstruction of grasslands has largely been restricted to Africa (Ambrose and DeNiro 1986; Vogel 1978). As in eastern and southern Africa, the prehistoric prairies of Central Texas were made up largely of C₄ grasses and C₃ forb and browse species which differ in carbon isotope composition, thereby allowing dietary preferences of herbivores to be identified. Nitrogen isotope values in plants vary with growth habitat and isotopic content of the soil. By using both isotopes it may be possible to further separate animals with similar $\delta^{13}\text{C}$ values. In addition, dietary data may contribute to a better understanding of the local paleoenvironment and the hunting strategies used by Late Prehistoric people who exploited the animal resources of this ecotone.

STABLE ISOTOPES IN NATURE

Terrestrial plants form the base of mammalian dietary webs and can be divided into three major photosynthetic types, each with unique carbon isotope fractionation patterns. For each photosynthetic type, $\delta^{13}\text{C}$ values are largely a result of: 1) the biochemical properties of the primary CO₂-fixing enzymes; and 2) limitations to CO₂ diffusion

into the leaf (O'Leary 1988). Plants with the C₃ photosynthetic pathway reduce CO₂ to phosphoglycerate, a C₃ compound, via the enzyme RuBP carboxylase. This enzyme discriminates against ¹³CO₂, resulting in relatively low $\delta^{13}\text{C}$ values for C₃ plants. C₃ plants have $\delta^{13}\text{C}$ values ranging from approximately -32 to -20‰, with a mean of -26.5‰.

C₄ plants reduce CO₂ to aspartic or malic acid, both C₄ compounds, via the enzyme PEP carboxylase. This enzyme does not discriminate against ¹³C, so that C₄ species have more enriched $\delta^{13}\text{C}$ values relative to C₃ plants. The $\delta^{13}\text{C}$ values for C₄ plants range from -17 to -9‰, with a mean of -12.5‰. Thus, the $\delta^{13}\text{C}$ values of C₃ and C₄ plants are distinct and nonoverlapping, with an isotopic separation of approximately 14‰ (Smith and Epstein 1971).

Crassulacean acid metabolism (CAM) plants (succulent plants such as cacti) have the ability to minimize water loss by fixing CO₂ at night via the enzyme PEP carboxylase. As a consequence, most CAM species have $\delta^{13}\text{C}$ values similar to C₄ plants. However, some facultative CAM species have the ability, under certain environmental and developmental circumstances, to switch to the C₃ mode of photosynthesis, fixing CO₂ during the day via RuBP carboxylase. The $\delta^{13}\text{C}$ values of these facultative CAM plants are dependent on the relative proportions of carbon fixed by RuBP carboxylase (daytime photosynthesis) and PEP carboxylase (nighttime photosynthesis). The $\delta^{13}\text{C}$ values for CAM species range between approximately -28 to -10‰ but are most commonly in the range of -20 to -10‰.

The majority of terrestrial plant species are C₃. Most temperate zone and all woodland and forest communities are dominated by C₃ species. C₄ and CAM species are significant components of many plant communities, and are particularly common in warm, arid or semiarid environments (Osmond et al. 1982). In the grasslands of South and Central Texas, the native grass species are almost exclusively C₄, except for needlegrass (*Stipa leucotricha*). In general, the proportion of C₄ species in a flora increases as latitude and altitude decrease (e.g., Boutton et al. 1980; Terri and Stowe 1976).

In herbivores, $\delta^{13}\text{C}$ values of the ingested plants undergo slight fractionation during biological synthesis into animal tissue (DeNiro and Epstein 1978). Bone collagen in herbivores is enriched by +5‰ relative to the diet (Vogel 1978; van der Merwe 1982; Krueger and Sullivan 1984). Bone collagen can be preserved for thousands of years in archeological sites (Armstrong et al. 1983). A bone collagen sample that retains an atomic C:N ratio of between 2.7-3.6 (DeNiro 1985) or at least 5% by weight of organic residue (Schwarcz and Schoeninger 1991) has not undergone diagenetic alteration of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and should provide reliable material for these measurements.

Stable nitrogen isotope values ($\delta^{15}\text{N}$) in most plants are

usually similar in range to the isotopic composition of the soil in which they grow. Shearer et al. (1978) analyzed 139 soil samples from widely varied environments in 20 states. Ninety percent of their samples fell within the +5.1‰ to +12.3‰ range, with surficial samples being slightly more enriched than those from deeper strata. They have further shown that there is no single environmental variable that is strongly correlated with the $\delta^{15}\text{N}$ values of soils. However, more recently Boutton et al. (1992) have demonstrated that soil $\delta^{15}\text{N}$ values in South Texas are affected by the plant communities. Soils from the center of mesquite (*Prosopis glandulosa*) mottes have lower mean $\delta^{15}\text{N}$ values (+6.1±0.7, n=18) than nearby soils supporting grasslands (+7.9±0.7, n=18).

Plants fall into two distinctive groups based on their mode of nitrogen acquisition. Plants in some higher plant families (e.g., Leguminosae, Rhamnaceae) can fix nitrogen from the air via a symbiotic relationship with a bacterium and have $\delta^{15}\text{N}$ values at or near 0‰. Nonnitrogen-fixing plants, which acquire mineral nitrogen from the soil, have $\delta^{15}\text{N}$ values which are similar to the soil nitrogen, commonly between +5 to +10‰. In South Texas, 64 samples of mesquite, which is a nitrogen-fixing species, had a mean $\delta^{15}\text{N}$ value of +2.0±1.1‰, while 27 samples from nonfixing plants had a mean of +4.0±1.6‰ (Boutton et al. 1992). In nonnitrogen-fixing plants, the $\delta^{15}\text{N}$ value can be affected by specific environmental conditions. In saline and arid areas plants have relatively enriched $\delta^{15}\text{N}$ values, while those in moist forests and mountains are generally depleted (Heaton 1987). Virginia and Delwiche (1982) found an increase in plant $\delta^{15}\text{N}$ in the sequence trees <shrubs <perennial herbs <annual herbs; however, it is not clear how common or widespread this trend might be.

The $\delta^{15}\text{N}$ values in bone collagen have also been found to reflect diet of animals (DeNiro and Epstein 1981). In bone collagen, $\delta^{15}\text{N}$ is enriched by +3‰ for each trophic level (Schoeninger and DeNiro 1984; Schwarcz and Schoeninger 1991). In addition to this step-wise trophic enrichment, the $\delta^{15}\text{N}$ of bone collagen of animals appears to be related to their drought-tolerance; $\delta^{15}\text{N}$ values of drought tolerant species are higher than would be expected for their trophic position. Enriched $\delta^{15}\text{N}$ values in bone collagen were first observed in two nondrinking rodent species by Schoeninger and DeNiro (1984). Later studies in South Africa (Heaton et al. 1986) and East Africa (Ambrose and DeNiro 1986) have identified the same pattern in drought-tolerant ungulate species. The retention and recycling of nitrogen by drought-tolerant animals (Ambrose 1991; Sealy et al. 1987) has been suggested as a mechanism to explain this $\delta^{15}\text{N}$ enrichment. Existing data suggests that the system is complex, and the exact mechanisms that determine $\delta^{15}\text{N}$ in animal tissue is poorly understood.

THE REGIONAL ENVIRONMENT

The Balcones Escarpment, in which the Mustang Branch site is situated, forms a narrow topographic, edaphic, and biologic ecotone between the eastern edge of the Edwards Plateau and the Blackland Prairie. Between Austin and San Antonio, the highly dissected escarpment, known as the Balcones Canyonlands, presents a varied topography of steep canyons and narrow divides that stand in contrast to the flatter plateau to the west and the prairies and forests to the east (Figure 228).

Soil series on the Edwards Plateau are numerous and varied. In the uplands, deeper soils located in valleys and on flats are commonly Mollisols, with shallower Inceptisols found on slopes. These soils are typically dark, rocky, and calcareous, with loamy or clayey texture formed over limestone (Godfrey et al. 1973). To the east of the escarpment, the soils of the Blackland Prairie are predominantly Vertisols followed by Alfisols and Mollisols, all with a clayey subsoil (Godfrey 1964).

Fortunately, disturbance to the natural vegetation patterns, while extensive, has not been complete. Analyses of remnant stands of native vegetation have documented the diversity and composition of these species on the landscape, albeit at a much smaller scale (Collins et al. 1975; Diamond and Smeins 1985; Diamond et al. 1987; Fowler and Dunlap 1986; Lynch 1971; Riskind and Diamond 1986). These studies, in conjunction with historical documentation, have identified native plant species and associations in each of the three natural regions.

The Balcones Canyonlands form a physical boundary between the mesic tallgrass Blackland Prairie and the more xeric mixed-grass prairie of the Edwards Plateau. Along this ecotone there is significant overlap of species; overlap decreases with distance from the ecotone. The C₄ tallgrasses, little bluestem (*Schizachyrium scoparium*), tall dropseed (*Sporobolus asper*), and sideoats grama (*Bouteloua curtipendula*) are found in all three regions, while more mesic species such as big bluestem (*Andropogon gerardii*) and Indiangrass (*Sorghastrum nutans*) are found only to the east. The more xeric short and midgrasses such as buffalo grass (*Buchloe dactyloides*), curly mesquite (*Hilaria belangeri*), and several grama species (*Bouteloua* sp.) are most common to the west.

Unlike the Blackland Prairie, the uplands of the Edwards Plateau were never open, treeless grasslands; however, grasslands were probably more extensive in the past (Riskind and Diamond 1986). In the southeastern portion of the plateau, Ashe juniper (*Juniperus ashei*), live oak (*Quercus virginiana*), and Texas persimmon (*Diospyros texana*) are the woody dominants in the uplands (Van Auken et al. 1979), with cedar elm (*Ulmus crassifolia*), Texas hickory (*Carya texana*) and other oak species (*Quercus* sp.)

becoming more common to the north (Riskind and Diamond 1986). Riparian gallery forests along perennial streams include bald cypress (*Taxodium distichum*) and sycamore (*Platanus occidentalis*) communities along the banks, with black walnut (*Juglans nigra*), pecan (*Carya illinoensis*), box elder (*Acer negundo*), cedar elm, and oak species on the floodplains. Beneath this canopy is an understory of smaller trees and shrubs such as dogwood (*Cornus drummondii*) and buttonbush (*Cephalanthus occidentalis*).

The Blackland Prairie was a tallgrass prairie containing all of the above-mentioned grass species in varying proportions in thin north-south belts (Collins et al. 1975). The prairie was dotted with mottes of oak and elm, and numerous deep cane breaks were interspaced between mesic gallery forests (Weniger 1984). On its southeastern flank, the post oak savannah separates the Blackland Prairie from the Coastal Prairies to the south, and the Piney Woods to the east.

HERBIVORE RANGE AND DIET

Bison, antelope, and deer were sympatric in Central Texas during the period A.D. 1200-1850. Only deer remain in the region, and due to environmental change precipitated by farming and ranching practices, their habitats and diets may have undergone significant alteration. Along with the long-term changes that have taken place, annual fluctuations in rainfall and the occurrence of range fires can significantly change the abundance and quality of forage plants from one year to the next, giving rise to significant variation in diet. These conditions make it difficult to use modern diet studies as direct analogs for prehistoric times.

While modern diet studies cannot identify the actual species consumed in prehistory, they can tell us the classes of vegetation that a particular herbivore will consume in a given setting. Knowing the approximate percentages of mast, browse, grass, and forbs that a herbivore consumes in a grassland or woodland environment gives us a set of expectations for how the animal may have foraged in prehistory.

Prehistoric Range

The Late Prehistoric ranges of bison, antelope, and deer can be defined with reasonable accuracy through the identification of their faunal remains from archeological sites in South and Central Texas. Deer were ubiquitous in the woodlands and savannahs of these regions. They are commonly the most abundant species in faunal collections for all Prehistoric time periods throughout the entire state. Deer are nonmigratory and spend their lives in a small territory, rarely more than 1.5 square miles (about 4 square kilometers), even during periods of food stress (Hahn 1945; Taylor

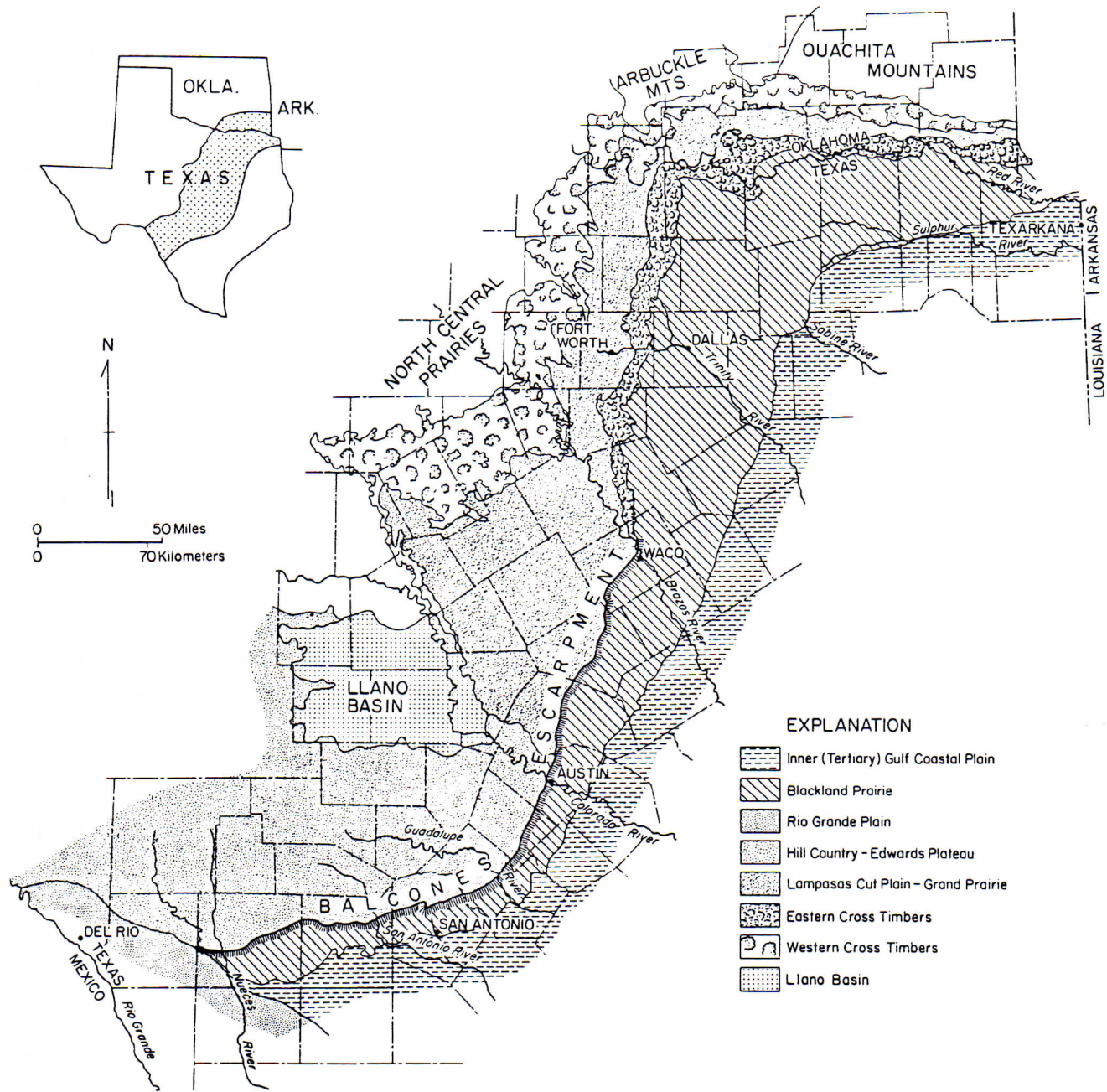


FIGURE 228. Map of physiographic provinces along the Balcones Escarpment, showing approximate location of the Mustang Branch and Barton sites within the Hill Country-Edwards Plateau section.

1956).

Antelope are gregarious and do not follow any regular pattern of yearly migration. Daily movements may amount to 3-4 linear miles (or 5-6 km) over a small home range, with the timing of range shifts dependent on forage quality (Buechner 1950). Antelope remains have been reported from 11 archeological sites in, or adjacent to, the grasslands of the western Edwards Plateau, Blackland and Coastal Prairies, and the Rio Grande Plain (Table 151). Antelope are probably underreported in faunal collections of this region due to the morphological similarity of their skeletal

remains with those of deer.

Bison were also present in these grasslands as well as in the eastern portion of the Edwards Plateau, spreading northward through the Rolling Plains (Lynott 1979), the Llano Estacado (Dillehay 1974), western and central Oklahoma (Baugh 1986), and points east (Neuman 1983). Sixty-five sites—including the Mustang Branch site—with Late Prehistoric components postdating A.D. 1200 in South and Central Texas contain bison faunal remains (Huebner 1991: Table 1). Roe (1970) marshals a broad body of historical evidence to demonstrate the irregular nature of bison "mi-

TABLE 151

LATE PREHISTORIC SITES WITH ANTELOPE REMAINS

Site	Reference
41JW8	Steele 1986b; Hester 1977
41ZV155	Hester and Hill 1975
41DM28	Hester 1975
41NU164	E. R. Mokry, personal communication 1992
41LK201	Steele 1986a
41MC222	Steele and Hunter 1986
41MC296	Steele and Hunter 1986
41BX228	Hulbert 1985
41TG91	Creel 1990
41GD21	Butler 1979
41BX300	Wooldridge 1987

gration." Bison move frequently and have been recorded as covering hundreds of miles in a single movement. However, these herd movements have no defined goals or end points such as would be expected with a migration, and can be more accurately described as movement in search of fresh range.

Modern Diets

Antelope exhibit great flexibility in dietary habits across their modern North American range. An annual diet of mostly forbs followed by browse, with negligible grass consumption, was observed in Alberta (Mitchell and Soliak 1971), eastern New Mexico (Beasom et al. 1982), the Panhandle (Koerth et al. 1984), and the Trans-Pecos (Buechner 1950) regions of Texas. In Oregon (Mason 1952), Saskatchewan (Dirschl 1963), and Utah (Beale and Smith 1970), antelope diets were found to contain more browse than forbs and little grass. From their analysis of antelope diet on the shortgrass prairie in northeast Colorado, Schwartz and Nagy (1976) reported that forbs and grass, but no browse, were consumed over the course of a year. In western Kansas, antelope subsist primarily on winter wheat from October through April and forbs the rest of the year (Sexton et al. 1981). These studies suggest that antelope are forb eaters in the southeastern portions of their range, with approximately 50-60% forbs and 36-41% browse in their diets (Koerth et al. 1984).

Both quantitative and qualitative studies indicate that bison consume mostly grass. Larson (1940) argued that bison were an important component in the maintenance of the shortgrass plains biome and that their eradication and replacement by cattle and sheep did much to destroy the climax vegetation by overgrazing. From observations of bison herds in Oklahoma and Arizona, Martin et al. (1951) identified an exclusively grass-based diet in the former location, and one primarily of salt bush in the latter. Quantitative analyses of bison diets on controlled ranges present more detailed data on foraging preferences. In the Henry

Mountains of southern Utah, summer and fall diets have been analyzed. Summer diets consisted of 99% grass and 1% forbs (Van Vuren 1984), and fall intake was composed of 96% grass and 4% forbs (Van Vuren and Bray 1983). On the shortgrass plains of northeastern Colorado, bison diets were studied on both heavily and lightly grazed pastures (Peden 1976; Peden et al. 1974). Under both grazing regimes, grass provided over 90% of fodder with forbs contributing 4% and shrubs 6% on the heavily grazed pasture. Of the grasses consumed by bison, 70% were warm season (C₄) species and 20% were cool season (C₃) species; C₄ forbs were consumed at a ratio of 10:1 over C₃ forbs.

The present-day economic importance of white-tailed deer in Central Texas has prompted studies of their diet and nutrition aimed at improving the overall quality of the animals. At the western edge of the Edwards Plateau, Bryant et al. (1981) observed deer feeding patterns under poor and excellent range conditions. On poor range, diets were largely browse (92%) with only small amounts of forbs (6%) and grass (2%). Under excellent conditions, diet was more balanced with 61% browse, 31% forbs, and 8% grass. Rumen contents from deer in a high density population in an enclosed mesquite-mixed grassland community in the Welder Wildlife Refuge were compared to those of a lower density population outside the preserve (Kie et al. 1980). Within the enclosure, annual diet averaged 76% forbs, 21% grass, and 3% browse, contrasted to a diet of 87% forbs, 10% grass, and 3% browse outside the enclosure. The authors hypothesized that the enclosed population overutilized the desirable forbs and was forced to eat more grass, which resulted in decreased nutrition levels and poor health and fitness. The most extensive studies of deer diets in Texas have been done at the Kerr Wildlife Management Area. These studies have examined deer diet under different range conditions, stocking densities, and degrees and types of competition. In one of the first investigations, Buechner (1944) noted that deer were in direct competition with goats for the available browse and that deer populations were affected more by the amount of available browse than any other class of forage. In a 1959 study, deer diet was observed under four different pasture conditions, both with and without competition from domestic stock (McMahan 1964). Yearly diets of 79% browse, 13% forbs and 7% grass were recorded in heavy-, moderate- and light-use pastures. With the competing stock removed browse dropped to 53% while forb consumption rose to 42%; grass accounted for only 5% of intake. Cross (1984) found that deer diet was different in burned versus unburned pastures. In the burned pasture, consumption of new growth grass and forbs increased at the expense of browse.

In summary, deer and antelope both tend to utilize small ranges, with the former being more localized than the latter. Bison are a more mobile species that will cover variable

amounts of range from year to year. Grass is the dietary preference of bison, while antelope and deer diets tend to reflect the quality and availability of browse and forb species in the local environment. Deer prefer browse and mast over forbs, but will increase their forb intake in the absence of competition. A diet high in grass can result in poor health and overall reduced fitness. In the southern portion of their range antelope subsist on forbs and browse and will consume grass by necessity. From these modern dietary patterns it is possible to estimate the isotopic range of prehistoric diet for each species from the classes of forage consumed. Within Central and southern Texas, bison diets are expected to be based on primarily C₄ grasses, with $\delta^{13}\text{C}$ values between -7.5‰ and -11.0‰. The forb, browse, and mast components of deer and antelope should produce an isotopic dietary signature in collagen of approximately -21.5‰. The amount of grass in the diet of these two species will be identified by the divergence from the exclusively C₃ signature (e.g., a 20% C₄ grass diet would produce a $\delta^{13}\text{C}$ value of -18.7‰). Stable nitrogen isotope values of native plants in the state have not been surveyed in a systematic manner. However, from the $\delta^{15}\text{N}$ values from herbivore bone collagen it may be possible to distinguish some broad plant groupings, such as nitrogen-fixers versus nonfixers or woody perennials versus herbaceous species.

METHODS

Cortical bone was selected from three localities in the project area. All samples except for 402 and 403, which were from 41HY209-M and 41HY202-A', were recovered from the Toyah interval occupation surface at 41HY209-T. Averaged ^{14}C assays strongly indicate contemporaneous occupations at these three sites circa 335±35 B.P. (A.D. 1615). Sample 402 is from a juvenile bison and 408 from a fetal deer; all others were adults. Isotopic analysis was performed at the Department of Rangeland Ecology and Management, Texas A&M University.

Bone samples were cleaned manually and ultrasonically in distilled water, then powdered in a Wiley mill to pass a 20-mesh screen. Collagen was extracted following the method of Boutton et al. (1984) using a 0.1 N HCl pretreatment for 6 hours to remove carbonates followed by a 0.1 N NaOH soak for 12 hours to remove soil humates. Collagen was then solubilized from the bone by incubation in distilled water at pH 3 at 90°C for 24 hours with occasional stirring. Carbon and nitrogen in the collagen were converted to CO₂, N₂, and H₂O by combustion in the presence of 2g CuO in an evacuated, sealed quartz tube at 900°C for 2 hours (Boutton 1991). Isotope ratios were measured on the resultant CO₂ with a VG-903 dual inlet, triple collector isotope ratio mass spectrometer and on N₂

with a Nuclide 3-60 dual inlet, double collector isotope ratio mass spectrometer. Results are reported using the δ notation relative to the international standards, PDB (Craig 1957) for carbon and atmospheric N₂ (Mariotti 1983) for nitrogen in ‰.

$$\delta^{13}\text{C}\text{‰} = \frac{(^{13}\text{C}/^{12}\text{C})_{\text{sample}} - 1 \times 1000}{(^{13}\text{C}/^{12}\text{C})_{\text{standard}}}$$

$$\delta^{15}\text{N}\text{‰} = \frac{(^{15}\text{N}/^{14}\text{N})_{\text{sample}} - 1 \times 1000}{(^{15}\text{N}/^{14}\text{N})_{\text{standard}}}$$

Analytical precision (machine error plus sample preparation error) for bone collagen was 0.1‰ for $\delta^{13}\text{C}$, and 0.2‰ for $\delta^{15}\text{N}$. Atomic C:N ratios were measured with a Carlo Erba NA-1500 elemental analyzer. Analytical precision based on five replicate samples was ±0.15% for carbon and ±0.11% for nitrogen.

Percentage of C₃ and C₄ plants in the diet of herbivores is determined by a simple mass balance equation using the average $\delta^{13}\text{C}$ values for the C₃ and C₄ photosynthetic pathways and $\delta^{13}\text{C}$ values of the bone collagen. Schwarcz et al. (1985) have placed the accuracy of this equation at ±8%.

RESULTS

Stable carbon and nitrogen isotope ratios and atomic C:N values for the 11 collagen samples are shown in Table 152 along with 6 additional $\delta^{13}\text{C}$ values from bison bone collagen ^{14}C assays. Atomic C:N ratios are a measure of the preserved *in vivo* dietary signature in bone collagen. Ratios outside the 2.7 to 3.6 range of modern collagen are indicative of diagenetic alteration of prehistoric samples (DeNiro 1985). All of the samples used in this study have C:N ratios of 3.11 to 3.33, typical of well-preserved collagen.

Bison have high $\delta^{13}\text{C}$ values relative to deer and antelope. Collagen $\delta^{13}\text{C}$ values from bison from the late Archaic period ($\bar{x} = -9.6 \pm 0.48\text{‰}$) and the Toyah interval ($\bar{x} = -9.5 \pm 1.14\text{‰}$) indicate that both consumed the same proportion of C₄ grasses (see Chapter 17); however the six Toyah-age $\delta^{13}\text{C}$ values are distributed bimodally. The $\delta^{13}\text{C}$ values of deer and antelope collagen indicate diets consistently high in C₃ species ($\bar{x}\delta^{13}\text{C} = -20.2 \pm 0.32\text{‰}$ and $-20.0 \pm 0.25\text{‰}$, respectively), with less breadth than shown by bison.

Stable nitrogen isotope values of the three species demonstrate lower interspecific variation than the stable carbon isotope values (see Table 152). Bison generally have the most enriched $\delta^{15}\text{N}$ values except for sample 402 which was an immature animal. Unlike the $\delta^{13}\text{C}$ values, $\delta^{15}\text{N}$ values for deer and antelope do not overlap which suggests that, while these two animals preferred C₃ plants, their diets may have consisted of different plant species.

TABLE 152

STABLE CARBON AND NITROGEN ISOTOPE RATIOS FOR THREE HERBIVORES
FROM MUSTANG BRANCH SITE AND BARTON SITE LOCALITIES

Species	Sample Number	Site/Area	C:N	$\delta^{15}\text{N}$ Per Mil	$\delta^{13}\text{C}$ Per Mil
Bison	401	41HY209-T	3.30	4.40	-10.0
	402	41HY209-T	3.15	3.50	-8.2
	403	41HY209-M	3.33	5.40	-10.5
	404	41HY202-A'	3.17	5.90	-8.5
	T1	41HY209-T			-10.9
	T2	41HY209-T			-8.7
	A1*	41HY209-T			-10.3
	A2*	41HY209-T			-9.6
	A3*	41HY209-T			-9.4
	A4*	41HY209-T			-9.2
Antelope	409	41HY209-T	3.16	4.10	-19.9
	410	41HY209-T	3.19	4.20	-20.0
	411	41HY209-T	3.12	4.20	-20.3
	412	41HY209-T	3.16	4.80	-19.7
Deer	406	41HY209-T	3.28	3.70	-20.6
	407	41HY209-T	3.11	3.30	-20.1
	408	41HY209-T	3.12	3.40	-20.0

* See Chapter 17.

DISCUSSION

Prehistoric Dietary Patterns

Results for these three herbivores show that dietary and habitat specialization produce discrete $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values separating grazers and mixed feeders (see Table 152). From the modern studies of foraging behavior and range preferences described above, it is possible to interpret the prehistoric dietary patterns of these animals by the isotopic signatures recorded in their bone collagen.

Bison, which are primarily grazers, exhibit a dietary range of between 75% to 95% C₄ plants with an average of 86% during the Toyah interval. This dietary intake falls within the expected isotopic range. Bison remains from the late Archaic have $\delta^{13}\text{C}$ values similar to those of the Toyah interval; however, their range (-10.3‰ to -9.2‰) is half that of the later animals. Since nearly all C₄ plants in Central Texas are grasses, this portion of the bison diet could only be grass. The remaining percentage of their diet could have been drawn from the few available C₃ grass species or forbs. It is also possible that some part of this diet was composed of browse species; however, given the biomass of grasses available in the region, the lack of any major competition for them, and the low density of bison herds, browse should have been an insignificant proportion of Late Prehistoric bison diets.

The wide distribution of $\delta^{13}\text{C}$ values during the Toyah interval at the project area sites is similar to the distribution of bison $\delta^{13}\text{C}$ values from five other grasslands in Texas

during the period A.D. 1200-1650 (Huebner and Boutton 1990, 1991), and from the two temporally discrete Late Prehistoric bison kills at the Gamsey site in southeast New Mexico (Speth 1983; Parry and Speth 1984). The breadth of the dietary pattern may have been a consequence of short term perturbations in the environment resulting from shifts in the seasonality or amounts of rainfall which permitted C₃ grasses and forbs a greater representation in the prairie biomass, and hence, bison diets (Huebner and Boutton 1991).

The $\delta^{13}\text{C}$ values of deer and antelope from the Mustang Branch site indicate a diet comprised mainly of C₃ plants, with a small percentage of C₄ grasses. Studies of deer diet on the Edwards Plateau today suggest that prehistoric deer in the Balcones Escarpment would have consumed primarily browse, with some forbs, and mast when in season. C₄ grasses on average account for roughly 9% of the diet which suggests that these animals were foraging more in the riparian woodland environment as opposed to open grassy uplands. Antelope, which tend to be mixed feeders in grassland settings, would have been consuming C₃ forbs along with some browse species as the major dietary components. Grass consumption by antelope is slightly higher than that of deer, with an average of 11%.

Stable nitrogen isotope values are within the range reported previously for terrestrial herbivores (Schoeninger and DeNiro 1984). The $\delta^{15}\text{N}$ values of bison are generally more enriched than those of antelope and deer. The different $\delta^{15}\text{N}$ values between deer and antelope indicate that dietary patterns which produced similar $\delta^{13}\text{C}$ values were

comprised of different classes of forage. Browse and forbs are predominantly C₃ plants, and both are components of deer and antelope diet. Eleven genera of native legumes, which often have low $\delta^{15}\text{N}$ values, are represented in forbs and browse plants in Central Texas (Table 153); six of those have been reported to be consumed by modern antelope (Buechner 1950; Koerth et al. 1984) and deer (Hahn 1945; Kie et al. 1980). Differential consumption of legume species may explain the lower $\delta^{15}\text{N}$ values in deer relative to antelope. Both deer and antelope are more depleted in ^{15}N than bison, which do not normally eat legumes.

Of these plants, deer tend to consume woody legumes while browsing, and antelope are recorded as consuming more herbaceous legumes. It is possible that this pattern of deer preferentially browsing and antelope selecting forbs held across a broader range dietary preference.

Based on these analyses, dietary niche overlap was minimal. On numerous occasions one species consumed a class of forage that another specialized in, but the only potentially real overlap was between antelope and deer over forbs and browse. Bison were alone in the grazing niche.

Previous Isotope Studies

Several studies have reported isotope ratios of bone collagen for one or more of the species reported here (Figure 229). Two studies have focused on modern deer. Land et al. (1980) analyzed $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of both organic and inorganic fractions of modern and archeological white-tailed deer bone from several North American locations. Those locations with three or more $\delta^{13}\text{C}$ values on the organic fraction of bone are Alaska ($\bar{x} = -23.8 \pm 1.40\text{‰}$), Arizona ($\bar{x} = -21.7 \pm 1.15\text{‰}$), and Texas ($\bar{x} = -21.3 \pm 1.79\text{‰}$). The archeological samples, primarily from Texas, were very depleted of ^{13}C and ranged between -27.5‰ and -22.1‰ . Diagenesis of the organic fraction is suspected as the cause of the depleted $\delta^{13}\text{C}$ values of the archeological samples.

A modern mule deer (*Odocoileus hemionus*) popula-

TABLE 153

NATIVE LEGUMES FOUND IN CENTRAL TEXAS

Genus	Consumption Type	Consumer	
		Deer	Antelope
<i>Acacia</i>	Browse	X	X
<i>Amorpha</i>	Browse		
<i>Astragalus</i>	Forb	X	X
<i>Cercis</i>	Browse		
<i>Dalea</i>	Forb		X
<i>Desmanthus</i>	Forb	X	X
<i>Galactia</i>	Forb		
<i>Lespedeza</i>	Forb		
<i>Prosopis</i>	Browse	X	X
<i>Psoraleidum</i>	Forb	X	X
<i>Senna</i>	Forb		

tion from a 1,368-km² area along the Cache La Poudre drainage in north central Colorado was analyzed by Hobson and Schwarcz (1986). In that group, 55 animals (19 males and 36 females, ranging in age from 1 to 11 years), showed no sex-related difference in diet with a mean $\delta^{13}\text{C}$ value of $-20.6 \pm 0.5\text{‰}$ (ca. 96% C₃). The diet of this population is primarily C₃ species, although two C₄ grass species are found in their range.

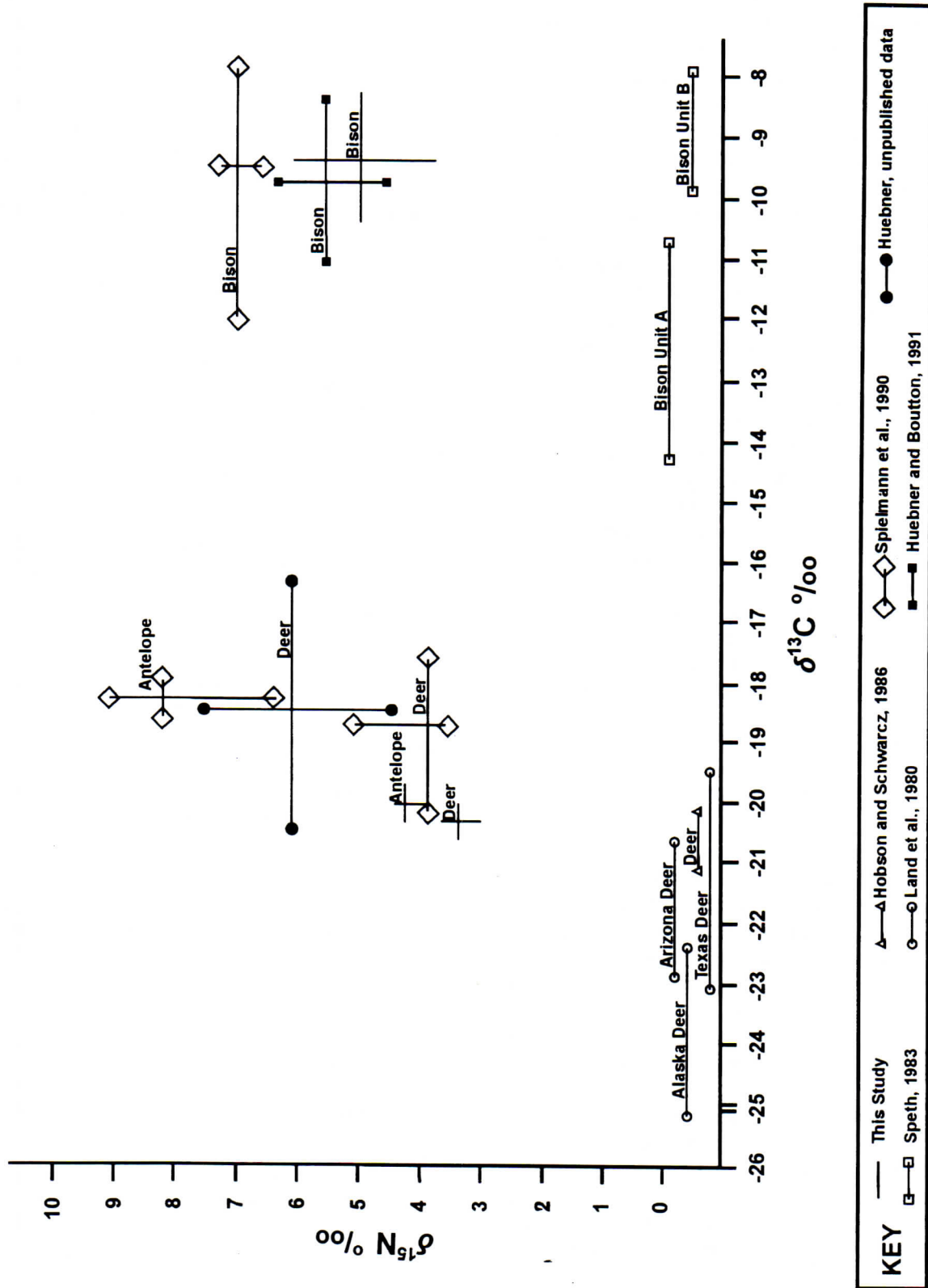
One of the first $\delta^{13}\text{C}$ analyses of bison was done by Speth (1983; see also Parry and Speth 1984). Two discrete lenses of bison bone were excavated from the Garnsey site in southeastern New Mexico. Bison bone collagen from the upper lens, Unit A, which postdates A.D. 1500, had a depleted mean $\delta^{13}\text{C}$ value of $-12.5 \pm 1.81\text{‰}$ (n=5). The lower lens, Unit B, dated to circa A.D. 1450-1500, was relatively enriched with a mean of $-8.9 \pm 0.92\text{‰}$ (n=16). Fossil pollen from the lower lens was typical of a grassy cienega environment while that of Unit A indicated a heavily grazed rangeland with a large number of weedy C₃ invader species (Hall 1984).

In a study of Pecos Pueblo, New Mexico, the same set of prehistoric animals was analyzed (Spielmann et al. 1990). Both the Pecos deer and antelope samples have more enriched $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, and a broader range of values while the bison had similar $\delta^{13}\text{C}$ values and more enriched $\delta^{15}\text{N}$ values than the Mustang Branch and Barton site samples.

Paleoenvironmental Implications

The dietary patterns of the animals which were killed in the vicinity of the Mustang Branch and Barton sites may be indicative of regional paleoenvironments of the seventeenth century. The stable isotope values of bone collagen reflect long-term dietary patterns of these animals, and should be related to the local environment. It can be inferred that the region had forage that the animals preferred. While this analysis cannot identify the actual plant species in that habitat, it does suggest that the distributions of native plant species (in particular the grasses) found in modern remnant stands are perhaps typical of latter stages of the prehistoric period. The limits of these habitats are large for a mobile species like bison and small for territorial species like deer. Bison and antelope both would have been found primarily on the open prairies, but competition between the two would have been negligible since antelope fed on forbs and bison on grass. The similarity in $\delta^{13}\text{C}$ values between the late Archaic bison and those from the Toyah interval indicate that the prairies on both sides of the ecotone were dominated by C₄ grass species during both these periods.

The distribution of $\delta^{13}\text{C}$ values in the Toyah interval bison samples appears bimodal. One explanation for this might be that one group was taken on the Edwards Plateau

FIGURE 229. Comparison of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of bison, antelope, and deer from several locations.

and the other on the Blackland Prairie. However, data from Huebner and Boutton (1991) shows no evidence for regional differences in bison diet in each of the different post-750 B.P. (A.D. 1200) grasslands of Texas. What may be causing the isotopic distribution is two age cohorts in the sample. Sample 402 (see Table 152) is from a "juvenile" (less than 3 years old) animal with a $\delta^{13}\text{C}$ of -8.2‰, which represents a 95% C₄ diet. Taphonomic and cultural factors prohibited an age assignment to the other bison samples, except to indicate they were adults. The juvenile animal shows a diet high in C₄ grass suggesting that during its short life the regional prairies were receiving typical late spring/summer rainfall. Some of the older animals lived during a period of increased winter rainfall which favored the growth and increased consumption of cool season C₃ grasses and forbs. Without the ages of the other animals this can only be speculation. Alternatively, the bimodal distribution may be a function of sampling error due to the very small sample size.

Sample 408 is from a fetal deer, near full term of gestation. Its $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values are within the range of the two adult samples. During *in utero* development a fetus draws its nutrition and bone collagen isotopic signature from the mother's diet. The winter and early spring dietary pattern passed on to the fetus during gestation is the same as the long-term diets recorded in the adult animals. This suggests that there was little seasonal variation in the isotopic content of deer diets. This assumes that there is no *in utero* isotopic fractionation. Nursing human neonates have more positive $\delta^{15}\text{N}$ values relative to their mothers because milk is enriched in ^{15}N relative to other body tissues (Fogel et al. 1989). However no studies have been done on fetal samples of any species.

SUMMARY

Through the use of stable isotope analysis of bone collagen, it has been possible to reconstruct the diets and habitats of three herbivores which are no longer sympatric in Central Texas. Prehistoric bison diets were primarily C₄ grasses, while deer and antelope consumed mostly C₃ browse and forbs and approximately 10% grass. Stable nitrogen isotope analysis suggests that different classes of C₃ forage were eaten by deer and antelope. The more depleted $\delta^{15}\text{N}$ values found in deer are interpreted as resulting from a diet with more legumes than that of antelope. There is little dietary niche overlap, with the possible exception of forbs and browse between deer and antelope. However, this was probably negligible since antelope prefer open grasslands habitats and deer prefer woodland settings.

The $\delta^{13}\text{C}$ values of modern deer analyzed by Land et al. (1980) and Hobson and Schwarcz (1986) were generally

more depleted than the archeological samples, including those samples from Texas. This may represent the decline in the acreage of native C₄ grasslands in the southwestern United States as a consequence of post-A.D. 1850 human land-use practices. The antelope and deer from New Mexico reported by Spielmann et al. (1990) had more C₄ forage in their diets, while the Pecos bison, as well as those from Unit B at the Garnsey site (Parry and Speth 1984), were similar in diet to those from the Mustang Branch site.

The animal diets identified by both stable isotopes can be used to support the interpretation that the floras reported from modern remnant stands are representative of the greater environment in Central and southern Texas during late prehistory.

REFERENCES CITED

- Ambrose, S. H.
1991 Effects of Diet, Climate, and Physiology on Nitrogen Isotope Abundances in Terrestrial Foodwebs. *Journal of Archeological Science* 18:293-318.
- Ambrose, S. H., and M. J. DeNiro
1986 The Isotopic Ecology of East African Mammals. *Oecologia* 69:395-406.
- Armstrong, W. G., L. B. Halstead, F. B. Reed, and L. Wood
1983 Fossil Protein in Vertebrate Calcified Tissues. *Philosophical Transactions of the Royal Society* B301:301-343, London.
- Baugh, S. T.
1986 Late Prehistoric Bison Distributions in Oklahoma. *Plains Anthropologist, Memoir* 21(31):83-96.
- Beale, D. M., and A. D. Smith
1970 Forage Use, Water Consumption, and Productivity of Pronghorn Antelope in Western Utah. *Journal of Wildlife Management* 34:570-582.
- Beasom, S. L., L. LaPlant, and V. W. Howard
1982 Similarity of Pronghorn, Cattle, and Sheep Diets in Southeastern New Mexico. In *Wildlife-Livestock Relationships Symposium Proceedings* 10, pp. 565-572. University of Idaho Forest, Wildlife, and Range Experimental Station, Moscow, Idaho.
- Boutton, T. W.
1991 Stable Carbon Isotope Ratios of Natural Materials: I. Sample Preparation and Mass Spectrometric Analysis. In *Carbon Isotope Techniques*, edited by D.C. Coleman and B. Fry, pp. 155-171. Academic Press, New York.
- Boutton, T. W., A. T. Harrison, and B. N. Smith
1980 Distribution of Biomass Species Differing in Photosynthetic Pathway Along an Altitudinal Transect in Southeastern Wyoming Grassland. *Oecologia* 45:287-298.

- Boutton, T. W., P. D. Klein, M. J. Lynott, J. E. Price, and L. L. Tieszen
1984 Stable Carbon Isotope Ratios as Indicators of Prehistoric Human Diet. In *Stable Isotopes and Nutrition*, edited by J. R. Turnlund and P. E. Johnson, pp. 205-220. ACS Symposium Series 258. American Chemical Society, Washington, D.C.
- Boutton, T. W., S. F. Zitzer, S. F. Archer, and L. A. Cifuentes
1992 Symbiotic N₂-Fixation in a Subtropical Thorn Woodland: Evidence from ¹⁵N Natural Abundance and Modulation Potential. *Bulletin of the Ecological Society of America* 73(2):117-118.
- Buechner, H. K.
1944 The Range Vegetation of Kerr County, Texas, in Relation to Livestock and White-Tailed Deer. *The American Midland Naturalist* 31:698-743.
- 1950 Life History, Ecology, and Range Use of the Pronghorn Antelope in Trans-Pecos, Texas. *The American Midland Naturalist* 43:257-354.
- Butler, B. H.
1979 Faunal Remains from Coletto Creek, Goliad County, Texas. In *Archeological Investigations of Two Prehistoric Sites on the Coletto Creek Drainage, Goliad County, Texas*, by D. E. Fox, pp. 83-99. Archeological Survey Report 69. Center for Archeological Research, The University of Texas at San Antonio.
- Bryant, F. C., C. A. Taylor, L. B. Merrill
1981 White-Tailed Deer Diets from Pastures in Excellent and Poor Range Condition. *Journal of Range Management* 34:193-200.
- Collins, O. B., F. E. Smeins, and D. H. Riskind
1975 Plant Communities of the Blackland Prairie of Texas. In *Prairie, A Multiple View*, edited by M. K. Wali, pp. 745-788. University of North Dakota Press, Grand Forks.
- Craig, H.
1957 Isotopic Standards for Carbon and Oxygen and Correction Factors for Mass Spectrometric Analysis of Carbon Dioxide. *Geochimica et Cosmochimica Acta* 12:133-149.
- Creel, D.
1990 *Excavations at 41TG91 Tom Green County, Texas 1978*. Publications in Archeology, Report 38. Texas State Department of Highways and Public Transportation, Highway Design Division, Austin.
- Cross, D. C.
1984 *The Food Habits of White-Tailed Deer on the Kerr Wildlife Management Area in Conjunction with Prescribed Burning and Rotational Livestock Grazing Systems*. Master's thesis, Southwest Texas State University, San Marcos, Texas.
- DeNiro, M. J.
1985 Postmortem Preservation and Alteration of In Vivo Bone Collagen Ratios in Relation to Paleodietary Reconstruction. *Nature* 317:806-809.
- DeNiro, M. J., and S. Epstein
1978 Influence of Diet on the Distribution of Carbon Isotopes in Animals. *Geochimica et Cosmochimica Acta* 42:495-506.
- 1981 Influence of Diet on the Distribution of Nitrogen Isotopes in Animals. *Geochimica et Cosmochimica Acta* 45:341-351.
- Diamond, D. D., D. H. Riskind, and S. L. Orzell
1987 A Framework for Plant Community Classification and Conservation in Texas. *The Texas Journal of Science* 29(3):203-221.
- Diamond, D. D., and F. E. Smeins
1985 Composition, Classification and Species Response Patterns of Remnant Tallgrass Prairies in Texas. *The American Midland Naturalist* 113:294-308.
- Dillehay, T.
1974 Late Quaternary Bison Population Changes on the Southern Plains. *Plains Anthropologist* 19:180-196.
- Dirschl, H. J.
1963 Food Habits of the Pronghorn in Saskatchewan. *Journal of Wildlife Management* 27:81-93.
- Doughty, R. W.
1983 *Wildlife and Man in Texas*. Texas A&M University Press, College Station.
- Fogel, M. L., N. Turross, and D. W. Owsley
1989 Nitrogen Isotope Tracers of Human Lactation in Modern and Archaeological Populations. *Annual Report of the Director Geophysical Laboratory of the Carnegie Institution of Washington* 89:111-117.
- Fowler, N. L., and D. W. Dunlap
1986 Grassland Vegetation of the Eastern Edwards Plateau. *American Midland Naturalist* 15:146-155.
- Godfrey, C. L.
1964 *A Summary of Soils on the Blackland Prairies of Texas*. Texas Agricultural Experimental Station Miscellaneous Publication MP-698. College Station.
- Godfrey, C. L., G. S. McKee, and H. Oaks
1973 *General Soil Map of Texas*. Texas Agricultural Experimental Station Miscellaneous Publication MP-1034. College Station.
- Hahn, H. C., Jr.
1945 The White-Tailed Deer in the Edwards Plateau Region of Texas. Report on file with the Texas Game, Fish, and Oyster Commission, Austin.
- =
- Hall, S. A.
1984 Pollen Analysis of the Garnsey Bison Kill Site, Southeastern New Mexico. In *The Garnsey Spring Campsite: Late Prehistoric Occupation in*

- Southeastern New Mexico*, by W. J. Parry and J. D. Speth, pp. 85-112. Technical Reports 15. Museum of Anthropology, University of Michigan, Ann Arbor.
- Heaton, T. H. E.
1987 The N-15/N-14 Ratios of Plants in South Africa and Namibia: Relationship to Climate and Coastal/Saline Environments. *Oecologia* 74:236-246.
- Heaton, T. H. E., J. C. Vogle, and G. von la Chevallierie
1986 Climatic Influence on the Isotopic Composition of Bone Nitrogen. *Nature* 322:822-823.
- Hester, T. R.
1975 Late Prehistoric Cultural Patterns Along the Lower Rio Grande of Texas. *Bulletin of the Texas Archeological Society* 46:107-125.
- 1977 *Archeological Research at the Hinojosa Site (41JW8), Jim Wells County, Southern Texas*. Special Report 6, Center for Archeological Research, The University of Texas at San Antonio.
- Hester, T. R., and T. C. Hill, Jr.
1975 *Some Aspects of Late Prehistoric and Protohistoric Archeology in Southern Texas*. Special Report 1. Center for Archeological Research, The University of Texas at San Antonio.
- Hobson, K. A., and H. P. Schwarcz
1986 The Variation in $\delta C-13$ Values in Bone Collagen for Two Wild Herbivore Populations: Implications for Palaeodiet Studies. *Journal of Archeological Science* 13:101-106.
- Huebner, J. A.
1991 Late Prehistoric Bison Populations in Central and Southern Texas. *Plains Anthropologist* 137:343-358.
- Huebner, J. A., and T. W. Boutton
1990 The Isotopic Ecology of Bison in Texas. Paper presented at the Forty-eighth Plains Anthropological Conference, Oklahoma City, Oklahoma.
- 1991 Stable Carbon Isotope Analysis of Prehistoric *Bison bison* Diet. *Bulletin of the Ecological Society of America* 72(2):147.
- Hulbert, R. C.
1985 Vertebrate Faunal Remains. In *The Panther Springs Creek Site: Cultural Change and Continuity Within the Upper Salado Creek Watershed, South-Central Texas*, by S. L. Black and A. J. McGraw, pp. 209-215. Archeological Survey Report 100. Center for Archeological Research, The University of Texas at San Antonio.
- Kie, J. G., D. L. Drawe, and G. Scott
1980 Changes in Diet and Nutrition with Increased Herd Size in Texas White-Tailed Deer. *Journal of Range Management* 33:28-34.
- Koerth, B. H., L. J. Krysl, B. F. Sowell, and F. C. Bryant
1984 Estimating Seasonal Diet Quality of Pronghorn Antelope from Fecal Analysis. *Journal of Range Management* 37:560-563.
- Krueger, H. W., and C. H. Sullivan
1984 Models for Carbon Isotope Fractionation Between Diet and Bone. In *Stable Isotopes and Nutrition*, edited by J. R. Tumlund and P. E. Johnson, pp. 205-220. ACS Symposium Series 258. American Chemical Society, Washington, D.C.
- Land, L. S., E. L. Lundelius, Jr., and S. Valastro, Jr.
1980 Isotopic Ecology of Deer Bones. *Paleogeography, Paleoclimatology, Paleoecology* 32:143-151.
- Larson, F.
1940 The Role of Bison in Maintaining the Shortgrass Plains. *Ecology* 21:113-121.
- Lynch, D.
1971 Phenology, Community Composition, and Soil Moisture in a Relic at Austin, Texas. *Ecology* 52:890-897.
- Lynott, M. J.
1979 Prehistoric Bison Populations of North Central Texas. *Bulletin of the Texas Archeological Society* 50:89-101.
- Mariotti, A.
1983 Atmospheric Nitrogen Is a Reliable Standard for Natural $15N$ Abundance Measurements. *Nature* 303:685-687.
- Martin, A. C., H. S. Zim, and A. L. Nelson
1951 *American Wildlife and Plants: A Guide to Wildlife Food Habits*. Dover, New York.
- Mason, E.
1952 Food Habits and Measurements of Hart Mountain Antelope. *Journal of Wildlife Management* 16:387-389.
- McMahan, C. A.
1964 Comparative Food Habits of Deer and Three Classes of Livestock. *Journal of Wildlife Management* 28:798-808.
- Mitchell, G. S., and S. Soliak
1971 Pronghorn Antelope Range Characteristics and Food Habits in Alberta. *Journal of Wildlife Management* 35:238-250.
- Neuman, R. W.
1983 The Buffalo in Southeastern United States Post-Pleistocene Prehistory. In *Southeastern Natives and Their Pasts*, edited by D. G. Wyckoff and J. L. Hoffman, pp. 261-280. Studies in Oklahoma's Past 11. Oklahoma Archeological Survey, Norman.
- O'Leary, M. H.
1988 Carbon Isotopes in Photosynthesis. *BioScience* 38:328-336.

- Osmond, C. B., K. Winter, and H. Ziegler
1982 Functional Significance of Different Pathways of CO₂ Fixation in Photosynthesis. In *Physiological Plant Ecology II. Water Relations and Carbon Assimilation*, edited by O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler, pp. 479-547. Springer-Verlag, New York.
- Parry W. J., and J. D. Speth
1984 *The Garnsey Spring Campsite: Late Prehistoric Occupation in Southeastern New Mexico*. Technical Reports 15. Museum of Anthropology, University of Michigan, Ann Arbor.
- Peden, D. G.
1976 Botanical Composition of Bison Diets on Shortgrass Plains. *American Midland Naturalist* 96:225-229.
- Peden, D. G., G. M. Van Dyne, R. W. Rice, and R. M. Hanson
1974 The Trophic Ecology of *Bison bison* L. on Shortgrass Plains. *Journal of Applied Ecology* 11:489-497.
- Riskind, D. H., and D. D. Diamond
1986 Plant Communities of the Edwards Plateau of Texas: An Overview Emphasizing the Balcones Escarpment Zone Between San Antonio and Austin with Special Attention to Landscape Contrasts and Natural Diversity. In *The Balcones Escarpment: Geology, Hydrology, Ecology and Social Development in Central Texas*, edited by P. L. Abbott and C. M. Woodruff, Jr., pp. 21-32. Published for the Geological Society of America Annual Meeting, San Antonio, November, 1986.
- Roe, F. G.
1970 *The American Buffalo*. University of Toronto Press, Toronto, Canada.
- Schoeninger, M. J., and M. J. DeNiro
1984 Nitrogen and Carbon Isotopic Composition of Bone Collagen from Marine and Terrestrial Animals. *Geochimica et Cosmochimica Acta* 48:625-639.
- Schwarcz, H. P., J. Melbye, M. A. Katzenberg, and M. Kryl
1985 Stable Isotopes in Human Skeletons of Southern Ontario: Reconstructing Palaeodiet. *Journal of Archaeological Science* 12:187-206.
- Schwarcz, H. P., and M. J. Schoeninger
1991 Stable Isotope Analyses in Human Nutritional Ecology. *Yearbook of Physical Anthropology* 34:283-321.
- Schwartz, C., and C. Nagy
1976 Pronghorn Diets Relative to Forage Availability in Northeastern Colorado. *Journal of Wildlife Management* 40:469-478.
- Sealy, J. C., N. J. van der Merwe, J. A. Lee Thorp, and J. L. Lanham
1987 Nitrogen Isotopic Ecology in Southern Africa: Implications for Environmental and Dietary Tracing. *Geochimica et Cosmochimica Acta* 51:2707-2717.
- Sexton, M. L., J. R. Choate, and R. A. Nicholson
1981 Diet of Pronghorn in Western Kansas. *Journal of Range Management* 34:489-493.
- Shearer, G., D. H. Kohl, and S. Chien
1978 The Nitrogen-15 Abundance in a Wide Variety of Soils. *Soil Science of America Journal* 42:899-902.
- Smeins, F. E.
1980 Natural Role of Fire on the Edwards Plateau. In *Prescribed Range Burning in the Edwards Plateau*, by L. D. White, pp. 4-16. Texas Agricultural Experiment Station Proceedings, College Station, Texas.
- Smith, B., and S. Epstein
1971 Two Categories of ¹³C/¹²C Ratios for Higher Plants. *Plant Physiology* 47:380-384.
- Speth, J. D.
1983 *Bison Kills and Bone Counts: Decision Making by Ancient Hunters*. Prehistoric Archeology and Ecology Series. University of Chicago Press, Chicago.
- Spielmann, K. A., M. J. Schoeninger, and K. Moore
1990 Plains-Pueblo Interdependence and Human Diet at Pecos Pueblo, New Mexico. *American Antiquity* 55:745-765.
- Steele, D. G.
1986a Analysis of Vertebrate Faunal Remains from 41LK201, Live Oak County, Texas. In *Archeological Investigations at 41LK201, Choke Canyon Reservoir, Southern Texas*, edited by C. L. Highley, pp. 200-250. Choke Canyon Series 11. Center for Archeological Research, The University of Texas at San Antonio.
- 1986b Analysis of Vertebrate Faunal Remains. In *The Clemente and Herminia Hinojosa Site, 41JW8: A Toyah Horizon Campsite in Southern Texas*, by S. L. Black, pp. 108-136. Special Report 18. Center for Archeological Research, The University of Texas at San Antonio.
- Steele, D. G., and C. A. Hunter
1986 Analysis of Vertebrate Faunal Remains from 41MC222 and 41MC296, McMullen County, Texas. In *The Prehistoric Sites at Choke Canyon Reservoir, Southern Texas: Results of Phase II Archeological Investigations*, by G. D. Hall, T. R. Hester, and S. L. Black, pp. 452-502. Choke Canyon Series 10. Center for Archeological Research, The University of Texas at San Antonio.
- Taylor, W. P. (editor)
1956 *The Deer in North America*. Stackpole, Harrisburg, Pennsylvania.
- Terri, J. A., and L. G. Stowe
1976 Climatic Patterns and the Distribution of C₄ Grasses in North America. *Oecologia* 23:1-12.
- Van Auken, O. W., A. L. Ford, and A. Stein
1979 A Comparison of Some Woody Upland and Riparian

- Plant Communities of the Southern Edwards Plateau. *The Southwestern Naturalist* 24:165-180.
- van der Merwe, N. J.
1982 Carbon Isotopes, Photosynthesis and Archeology. *American Scientist* 70:596-606.
- Van Vuren, D.
1984 Summer Diets of Bison and Cattle in Southern Utah. *Journal of Range Management* 37:260-261.
- Van Vuren, D., and M. P. Bray
1983 Diets of Bison and Cattle on a Seeded Range in Southern Utah. *Journal of Range Management* 36:499-500.
- Virginia, R. A., and C. C. Delwiche
1982 Natural ^{15}N Abundance of Presumed N_2 -Fixing and Non- N_2 -Fixing Plants from Selected Ecosystems. *Oecologia* 54:317-325.
- Vogel, J. C.
1978 Isotopic Assessment of the Dietary Habits of Ungulates. *South African Journal of Science* 74:298-301.
- Weniger, D.
1984 *The Explorer's Texas: The Lands and Waters*. Eakin Press, Austin.
- Wooldridge, H.
1987 Faunal Analysis. In *Archeological Mitigation at 41BX300, Salado Creek Watershed, South-Central Texas*, by P. R. Katz, pp. 89-96. Archeological Survey Report 130. Center for Archeological Research, The University of Texas at San Antonio.