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Modern Wyoming plant and pronghorn isoscapes and their implications for archaeology

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ABSTRACT

Stable isotope ratios obtained from pronghorn teeth recovered from archaeological sites in southwestern Wyoming may provide information on past climate and hunter behavior. However, the interpretation of archaeological isotope values depends on pronghorn isotopic correlations with the environment and geography. To investigate these correlations, a series of modern Wyoming carbon, oxygen and strontium isoscapes are compared with recent temperature, humidity and geological variation. Results indicate that both pronghorn and sagebrush carbon, and to a lesser degree oxygen, isotope ratios are tied to relative humidity. Temperature is correlated with oxygen isotope ratios in sagebrush, but not pronghorn. Strontium isotope ratios in both sagebrush and pronghorn vary with geography, which in turn reflects variation in geology.

1. Introduction

Pronghorn (*Antilocapra americana*) are medium-sized ungulates that live throughout the arid and semi-arid regions of western North America. Though often called antelopes, pronghorn are indigenous to North America and are not closely related to true Eastern Hemisphere antelopes. Prehistoric people hunted pronghorn throughout their range, occasionally resulting in substantial archaeological pronghorn bonebeds. Stable isotope analysis of pronghorn remains from these bonebeds may be informative of environmental conditions in specific areas during the years just prior to pronghorn death. This would be of interest to archaeologists investigating how prehistoric people responded to changing environmental conditions, as well as to other researchers interested in identifying past climatic conditions in western North America.

A number of investigators have proposed links between environmental conditions and stable isotope ratios in animal tissues (e.g., Koch, 1998; Hedges et al., 2005; Levin et al., 2006). The link between isotope ratios in pronghorn tissues and specific environmental conditions, however, has not been investigated previously. The current study analyzes the correlations between specific environmental or geographical conditions and isotope ratios within modern pronghorn in Wyoming, USA. Wyoming contains a number of different physiographic regions (Fig. 1) with varying environmental conditions (including humidity and temperature) and geological attributes such as soil type and underlying bedrock age (Knight, 1994). To ensure that the isotope ratios are in fact responding to environmental conditions rather than some aspect of pronghorn behavior or physiology, we also analyzed the correlations between environmental conditions and stable isotope ratios in the plants that constitute the bulk of pronghorn diet. Specifically, we evaluated in pronghorn, sagebrush, and rabbitbrush whether carbon isotope ratios are correlated with relative humidity, oxygen isotope ratios are correlated with temperature, and strontium isotope ratios are correlated with either soil type or underlying geology. For each case, we discuss the implications of our results for the use of stable isotope analysis of pronghorn remains in archaeological investigations.

2. Samples

Modern pronghorn incisors were obtained from the Wyoming Game and Fish Department, who collected them from hunters during the fall 2004 and 2005 pronghorn seasons. All sampled pronghorn are males killed in a known hunt area within Wyoming; Fenner (2008) provides additional information on pronghorn sample characteristics. The number of pronghorn isotope ratio samples per hunt area ranged from 1 to 24 (Table 1; see also Supplemental Table S1), with an average of 6.6 samples for carbon and oxygen analyses, and 4.1 samples for strontium analyses. Archaeological pronghorn incisors were obtained from six bonebed sites in southwestern Wyoming: Austin Wash, Boars Tusk, Eden–Farson, Firehole Basin, Gailiun, and Trappers Point. See Fenner (2007) for detailed discussion of sampling and isotope analysis of these archaeological materials.

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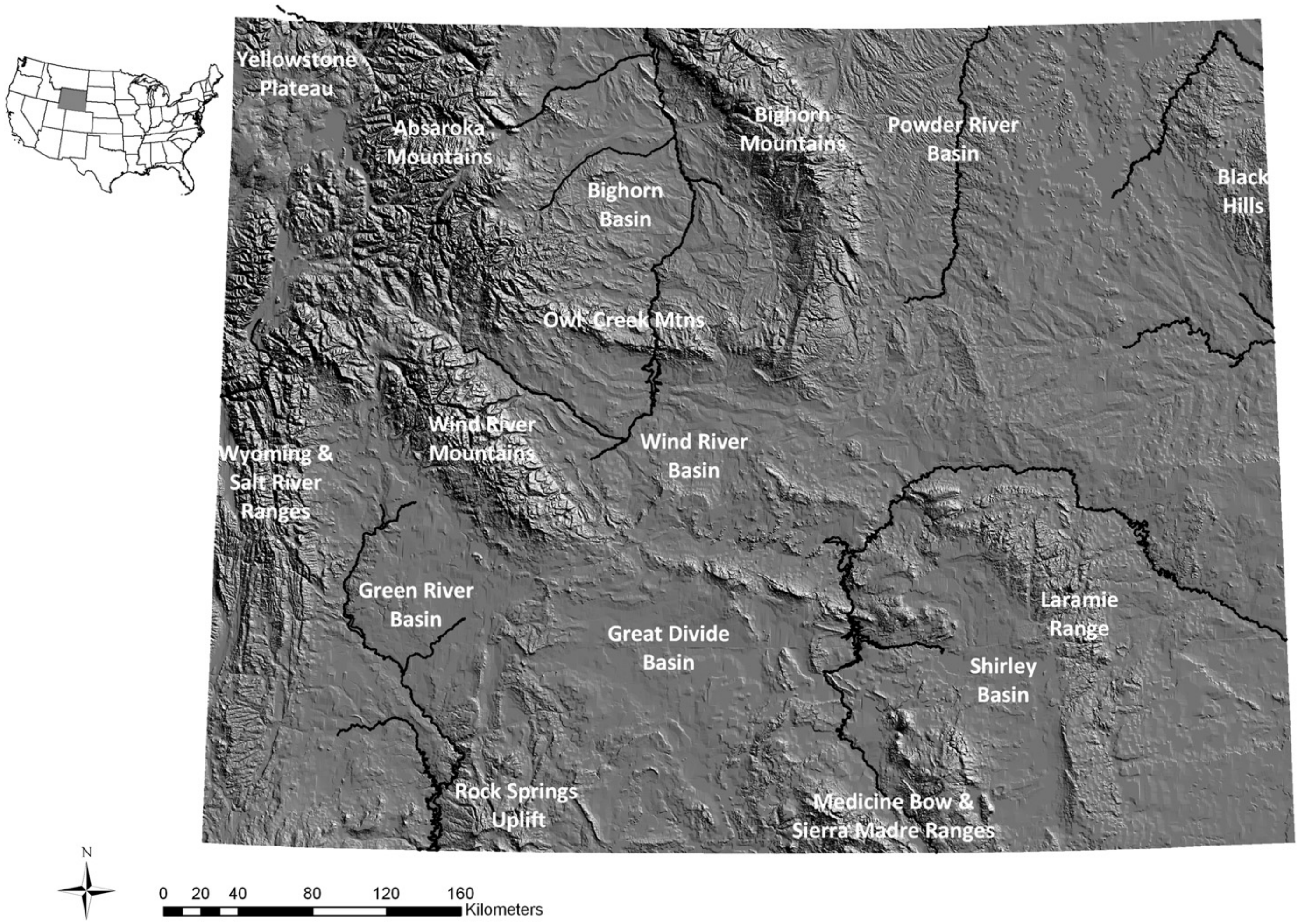

Fig. 1. Wyoming physiographic regions.

Plants were collected between June 28 and July 18, 2007. At each location, sagebrush samples were collected from one healthy Big Sagebrush (*Artemisia tridentata*) plant, and a nearby stunted Big Sagebrush plant. When present, leaves were collected from newly sprouted areas, and woody stem samples taken from less distal portions of the same branch. Rabbitbrush samples were taken from healthy-looking plants close to (within a few meters of) the sagebrush samples. The mean hunt area isotope ratio for each plant species was computed by averaging the measured isotope ratios of all samples for that species which were collected within the hunt area.

Chow tests of Douglas Rabbitbrush (*Chrysothamnus viscidiflorus*) and Gray Rabbitbrush (*Chrysothamnus nauseosus*) carbon and oxygen isotope ratio regressions against each environmental parameter (growing season and annual relative humidity and temperature) indicate that the regression slopes and intercepts were not significantly different between species (all $p>0.2$) so ratios from the two species were pooled prior to correlation analyses. Sagebrush plant material was collected from all reported locations (Fig. S2), but no rabbitbrush plants were found in the far northeastern portion of Wyoming so rabbitbrush samples are limited to southwestern and central Wyoming.

3. Methods

To avoid diagenesis concerns with archaeological samples, all pronghorn isotope ratios were obtained from enamel. Each tooth was mechanically cleaned using a Dremel drill with flapwheel sander, then enamel was collected by using a Dremel drill with diamond bit to carve a groove along the length of the buccal enamel surface of the tooth. The enamel was then pretreated to remove adhering materials using a slightly modified version of the procedure described by Koch et al. (1998:125; see Fenner, 2007 for details of the pretreatment procedures). Briefly, enamel was soaked in NaOCl overnight, rinsed in distilled water, soaked in 0.1 N acetic acid for 4 h, rinsed again, and dried in an oven. Carbon and oxygen isotope ratios in enamel carbonate were measured using continuous-flow isotope ratio mass spectrometry at the University of Wyoming Stable Isotope Facility and are reported in parts per mil (‰) with respect to the V-PDB standard. The average measured intra-individual carbon and oxygen isotope ratio difference in pronghorn was 0.17 ± 0.14‰, and the average intra-individual oxygen isotope ratio difference was 0.61 ± 0.33‰; similar values are expected for plant material analyses. Plant samples were prepared by grinding either by hand using a mortar and pestle or using a mechanical amalgamator, then dried overnight in an oven.

The carbon isotope ratio within atmospheric CO_2 has decreased by approximately 1.51‰ over the last century (Tieszen and Fagre, 1993). This decrease is likely due to the burning of fossil fuels with very low carbon isotope ratios. Because modern carbon ratios will be compared with archaeological ratios produced prior to this atmospheric change, 1.51‰ was added to all modern carbon isotope ratios to account for the modern carbon ratio offset. Note that adding this constant value this does not affect correlation or other analyses that compare only

Table 1
Mean hunt area environment and pronghorn incisor isotope ratio values.

Hunt area	May–Oct Mean relative humidity (%)	Annual mean relative humidity (%)	May–Oct mean temp. (°C)	Annual mean temp. (°C)	$\delta^{13}C$ sample count	Mean $\delta^{13}C$	$\delta^{13}C$ std dev	$\delta^{18}O$ sample count	Mean $\delta^{18}O$	$\delta^{18}O$ std dev	$^{87}Sr/^{87}Sr$ sample count	$^{87}Sr/^{87}Sr$ mean	$^{87}Sr/^{87}Sr$ std dev
17	53.5	58.6	15.5	6.9	2	−11.74	0.66	2	−9.01	1.35			
19	54.4	59.8	15.5	7.0	3	−11.98	0.33	3	−9.96	1.08	1	0.70967	
23	51.4	57.0	15.1	6.8	7	−11.55	0.45	6	−10.01	0.47			
24	52.6	57.8	15.3	7.0	8	−11.35	0.60	8	−8.27	1.17	2	0.71131	0.00148
32	50.0	55.6	14.4	6.5	1	−11.06		1	−9.78				
42	50.1	53.8	13.1	5.6	13	−11.07	0.45	13	−5.96	1.36	1	0.71039	
43	49.0	51.8	12.6	5.2	1	−10.91		1	−8.36				
46	48.5	54.8	12.9	5.6	4	−10.81	0.65	4	−6.98	0.44			
47	49.4	55.9	12.9	5.3	16	−10.83	0.40	17	−6.81	1.20	2	0.71022	0.00045
53	52.1	59.3	13.5	5.7	16	−10.99	0.51	17	−7.01	1.71			
57	47.0	56.6	13.4	5.6	12	−10.34	0.81	12	−2.81	1.18	3	0.71234	0.00071
59	45.5	55.7	13.4	5.5	3	−11.01	0.65	3	−6.05	1.12	3	0.71200	0.00153
61	48.3	58.0	13.6	5.6	1	−10.06		1	−7.04				
64	46.7	55.9	12.8	4.8	1	−11.64		1	−7.36				
65	48.7	54.6	10.4	3.0	2	−10.82	0.49	2	−5.43	0.53	1	0.71052	
66	45.0	52.2	15.0	6.6	4	−11.21	0.65	4	−7.44	1.05			
75	47.1	53.8	14.6	6.3	1	−11.53		1	−7.21				
87	47.7	52.8	7.2	−0.4	8	−10.56	0.53	8	−8.34	1.78	7	0.71200	0.00090
88	42.9	49.2	8.7	1.1	9	−10.55	0.87	9	−7.92	2.21	8	0.71114	0.00064
89	42.1	49.3	8.9	1.2	10	−10.28	0.75	9	−6.98	1.22	9	0.71086	0.00041
90	43.3	50.5	10.4	2.2	10	−10.17	0.90	10	−5.90	1.05	3	0.71261	0.00012
91	45.2	53.4	10.7	2.4	24	−10.37	0.68	24	−8.31	2.46	12	0.71286	0.00076
92	44.0	53.8	12.4	4.1	17	−10.18	0.66	17	−7.59	1.59	10	0.71381	0.00129
93	42.0	50.4	11.1	3.0	4	−9.47	0.86	4	−4.55	3.31	3	0.71041	0.00017
94	42.3	51.4	12.8	4.6	1	−9.31		1	−4.98		1	0.71037	
95	42.9	51.9	13.9	6.0	3	−10.45	0.33	3	−3.92	1.54	3	0.71008	0.00013
96	42.5	51.3	12.8	4.2	10	−10.09	0.99	10	−6.32	2.27	4	0.71121	0.00013
106	47.8	56.0	14.1	6.1	2	−10.99	0.61	2	−7.36	1.41			
107	46.4	54.1	10.3	2.3	6	−10.68	0.54	6	−7.85	0.91	6	0.71605	0.00189
112	46.0	55.3	13.1	5.4	1	−10.12		1	−5.92		1	0.71176	
115	49.3	55.0	13.4	56.8	4	−11.07	0.66	4	−7.29	1.12	2	0.71081	0.00106

See Methods section for discussion about calculation of the mean relative humidity and temperature figures. $\delta^{13}C$ and $\delta^{18}O$ values are relative to V-PDB. See Supplemental Table S1 for individual isotope ratio values.

modern ratios; it only is significant when comparing archaeological carbon isotope ratios to modern ratios.

Strontium isotope ratios were measured using thermal ionization mass spectrometry (TIMS) at the University of Wyoming Isotope Geology Laboratory. Results are reported as unitless $^{87}Sr/^{86}Sr$ ratios. Twelve NIST-987 strontium standards were also run, with measured values averaging 0.71026 ± 0.00001. Approximately 0.25 g of plant samples were ashed in quartz crucibles placed in a 450 °C furnace for 3 to 4 h, then dissolved in 7N HNO_3 on a hot plate overnight. Both plant and pronghorn samples were chemically separated using a Sr-Spec resin column as described in Fenner (2007).

Hunt area average relative humidity and temperature measures were computed using mean 1961 to 1990 monthly raster maps produced by the Spatial Climate Analysis Service at Oregon State University and obtained via Climate Source, Inc. For instance, computing the average growing season temperature value for a specific hunt area began with a map of the mean 1961 to 1990 May temperature within Wyoming. Each pixel within this map was added to the corresponding pixel on a mean 1961 to 1990 June temperature map, and the process repeated for July, August, September and October maps. The result for each pixel was then divided by the number of months (six). Those pixels representing areas with elevations above 3500 m were then identified and omitted from future calculations, since it is unlikely that there is significant pronghorn range above that elevation. The values of all remaining pixels within each hunt area were then averaged, and this value used to represent the hunt area's average growing season temperature (Table 1). Analogous computations were performed to determine average annual temperature, growing season relative humidity, and annual humidity for each hunt area.

Statistical computations were performed using SPSS 15. For correlations, the squared Pearson correlation coefficient (R^2) is reported. This statistic provides a measure of the strength of association, but is subject to parametric data requirements. Similar correlation results were obtained using Spearman's rho nonparametric calculations.

The plant-based $\delta^{13}C$, $\delta^{18}O$ and $^{87}Sr/^{86}Sr$ maps (Figs. S2, S5 and S7) were produced using inverse distance weighting in ArcGIS 9, with power equal to two. This approach is suited to the sparse and uneven nature of the sagebrush data, and is used to identify and compare general patterns.

4. Carbon isotopes

It is expected that growing season humidity acts as a basis for plant and pronghorn carbon isotope ratio variability in Wyoming because:

1. Almost all plants in the state, including sagebrush and rabbitbrush, use the C3 photosynthetic pathway. The exceptions are cacti and grasses that comprise a very low percentage of pronghorn diet (Yoakum, 2004). This means that there is little CAM or C4 contribution to pronghorn carbon isotope ratios, so differences in their ratios should be driven by environmental or physiological factors affecting plants rather than the much larger differences expected for a mixed C3/C4 diet.
2. $\delta^{13}C$ in C3 plants is commonly negatively correlated with humidity, because plants in low humidity environments close their stomata to conserve water and therefore process a greater percentage of CO_2, reducing heavy isotope discrimination (Barbour and Farquhar, 2000).

Qualitative assessment of a map of relative humidity shows a fairly strong increasing southwest-to-northeast trend across Wyoming (Fig. S1). Many of the exceptions to the general trend are high-humidity areas in mountain ranges that are outside of normal pronghorn habitat and therefore do not directly affect this study.

4.1. Carbon isotopic variation in plants

Sagebrush leaf $\delta^{13}C$ shows a fairly consistent decreasing southwest-to-northeast trend across Wyoming (Fig. S2; see Table S1 for all individual plant and modern pronghorn isotope results). Maps of sagebrush stems and, especially, rabbitbrush leaves do not show a consistent directional trend (data not shown). For sagebrush stems, this is probably because big sagebrush often live more than 50 years (Lesica et al., 2007) so their leaves and woody stems may reflect quite different average humidity conditions. The lack of rabbitbrush leaf $\delta^{13}C$ geographic structure is more surprising in that these C3 plants would be expected to respond to humidity similarly to sagebrush. No rabbitbrush was found in the most humid (northeast) area of the state, so perhaps rabbitbrush are specifically adapted to low humidity and do not require physiological responses. In any case, the lack of correlation of rabbitbrush leaf $\delta^{13}C$ with humidity ($R^2=0.023$, $p>0.60$) indicates that pronghorn $\delta^{13}C$ correlation with humidity will be weakened to the extent that rabbitbrush forms a part of the diet.

There is a fairly strong correlation between sagebrush leaf $\delta^{13}C$ and growing season humidity (Fig. 2). Note that the sagebrush leaves grew during the summer of 2007 while the growing season humidity values are an average of May through October data from 1961 to 1990. Likewise, the leaf isotope values are an average of ratios from one healthy plant and one nearby stunted plant, while the growing season humidity values are averaged over each entire hunt area (excluding high altitudes that are outside of likely pronghorn range). Despite these differences in time period and area represented, the correlation is significant and fairly strong. This suggests that the correlation is fairly robust to minor mean humidity changes. The correlation of sagebrush leaf $\delta^{13}C$ and annual humidity is slightly weaker but still statistically significant ($R^2=0.356$, $p=0.02$).

4.2. Carbon isotopic variation in pronghorn

Pronghorn $\delta^{13}C$ values show the same general southwest-to-northeast trend as in sagebrush, though offset from sagebrush by +14.2‰ (Fig. S3). This is a typical source-to-enamel fractionation offset for large herbivores (Cerling and Harris, 1999). Fig. S3 also shows mean $\delta^{13}C$ values in enamel from pronghorn remains recovered from six archaeological sites and the modern Reiser Canyon die-off. The coloring key for these sites is the same as for the modern hunt areas. Diagenesis is not expected to be a problem in Holocene tooth enamel, so the clear differences between pronghorn from archaeological sites and those from modern hunt areas must represent environmental changes, species behavior changes or carcass transport by prehistoric humans.

There is a strong negative correlation ($R^2=0.691$, $p<0.001$, $n=21$) between pronghorn enamel $\delta^{13}C$ and growing season humidity (Fig. 3). The correlation decreases somewhat ($R^2=0.570$, $p<0.001$, $n=31$) if samples with only 1 or 2 individuals are included, so there are minor sample size dependencies (a regression weighted by sample size has a correlation between these two values: $R^2=0.634$, $p<0.001$, $n=31$). The correlation is also reduced ($R^2=0.514$, $p<0.001$, $n=21$) if $\delta^{13}C$ is compared against annual humidity rather than growing season humidity.

The correlation with humidity is stronger for pronghorn than it is for sagebrush. This is unlikely to be explained by the presence of other plants in the diet, since sagebrush comprises a very large percentage of pronghorn diet and rabbitbrush, a common forb that also appears in pronghorn diets, had no correlation with humidity. Instead, it may be interpreted as indicating that sampling a wide swath of a hunt area improves the correlation. Collecting more sagebrush from a wider area within each hunt area would also likely improve the sagebrush correlation.

4.3. Carbon isotope variation archaeological implications

This analysis shows that, provided a set of uniformitarian assumptions hold, $\delta^{13}C$ in pronghorn enamel can be used to investigate past conditions, especially if at least 3 pronghorn individuals can be sampled per site. The necessary uniformitarian assumptions include consistency across time in plant and pronghorn carbon isotope physiology, atmospheric CO_2 isotope ratio, plant community distributions (particularly a consistent lack of C4 plants), and pronghorn feeding behavior. The time frame in question is typically one to several hundred years, though it is about 6000 calendar years at the Trappers

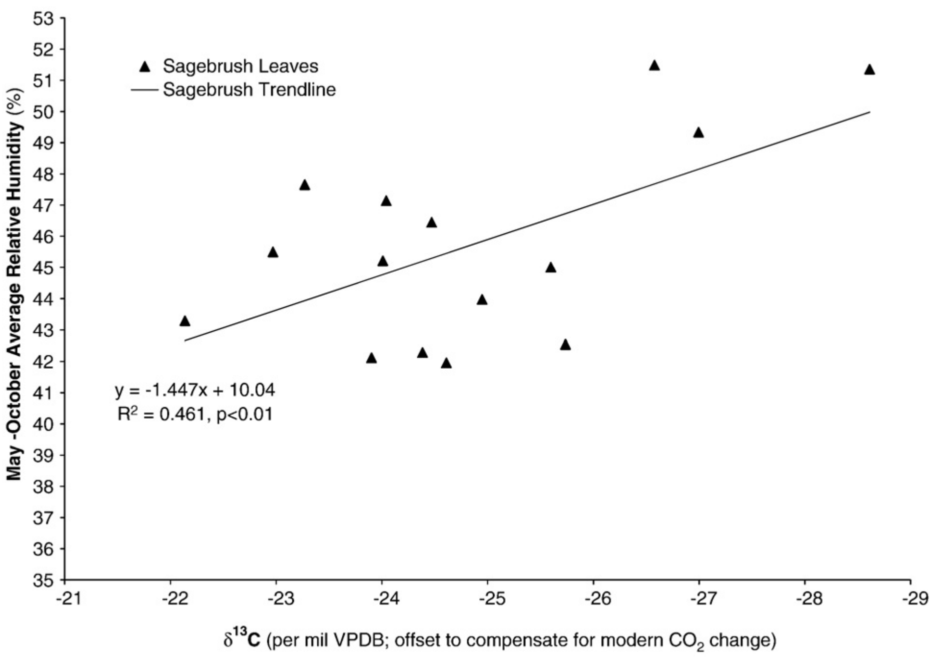

Fig. 2. Correlation between growing season relative humidity and $\delta^{13}C$ in big sagebrush leaves.

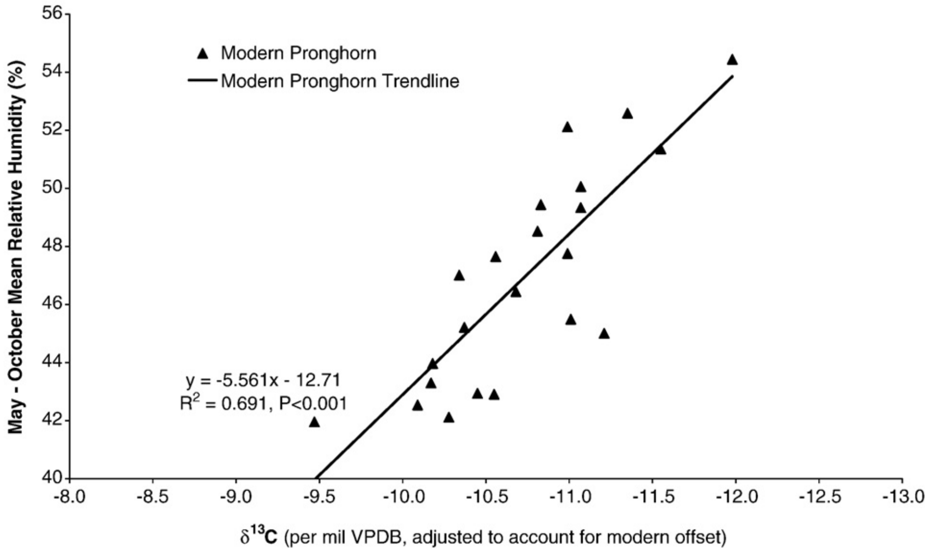

Fig. 3. Correlation between growing season humidity and $\delta^{13}C$ in modern pronghorn enamel. Only hunt areas with at least three sampled individuals are included. Outliers excluded.

Point site (Table 2). Except for a change in atmospheric CO_2 concentration (which has been accounted for as discussed in the Methods section), there is no apparent reason to expect significant anthropogenic or natural changes in these factors within the time frame in question. While change cannot be ruled out, the uniformitarian assumptions above seem reasonable.

Applying the correlation established using modern pronghorn enamel to archaeological samples produces projections of past relative humidity conditions (Table 2). Because of uncertainty related to the assumptions discussed above and imprecision of the modern correlations, these projections should be treated as rough estimates only. Four archaeological sites had $\delta^{13}C$ values that do not closely match modern values. The lowest mean modern growing season relative humidity within any sampled area of Wyoming is 42.0%, so the Eden–Farson, Gailiun and Firehole Basin sites had lower humidity than any modern hunt area. This suggests there was a period of reduced humidity in southwestern Wyoming, perhaps corresponding with the "Little Ice Age".

It is interesting that Eden–Farson and Boars Tusk had dramatically different relative humidity projections despite being within the same hunt area and close in time. Either relative humidity underwent very rapid changes, or some other process changed $\delta^{13}C$ at one or both of these sites. Boars Tusk seems to be the outlier, and it is probably a mass kill site (Fenner, 2007). Perhaps the Boars Tusk pronghorn came as a group from another area, either via pronghorn migration or human transport. The nearest area with a modern growing season relative humidity of at least 50% is in the Sierra Madre mountain range about 140 km to the southeast of Boars Tusk. Perhaps a more likely source pronghorn range, with 50.1% relative humidity, is in the Shirley Basin about 260 km due east of Boars Tusk. This scenario is supported by strontium ratios presented later in this article; the strontium ratios from Boars Tusk are substantially different from modern strontium ratios in its own hunt area, and similar to those in hunt areas to its east and west.

5. Oxygen isotopes

Temperature may be a basis for plant and pronghorn oxygen isotope ratio variability in Wyoming because:

1. Input $\delta^{18}O_{water}$ is presumably derived from precipitation (although both sagebrush and rabbitbrush are arid-adapted plants with fairly long root systems that may in some locations reach groundwater). Precipitation in Wyoming has a west-to-east $\delta^{18}O$ gradient that qualitatively appears to be almost identical to the temperature gradient shown in Fig. S3 (per www.waterisotopes.org modeled data not shown).
2. Structural $\delta^{18}O_{leaf}$ is derived from $\delta^{18}O_{leafwater}$, which per Craig–Gordon transpiration models is dependent on vapor pressure, which depends on temperature (and relative humidity, leaf physiology, and other conditions) (Ball, 1987; Zhang and Nobel, 1996; Roden and Ehleringer, 1999). Incorporation of $\delta^{18}O_{leaf}$ is thus complex but is expected to be related to temperature.

Growing season temperature shows a positive west-to-east trend in Wyoming, with the coldest region being the Yellowstone Plateau while the warmest areas are the Bighorn and Powder River basins (Fig. S4). Average annual temperature shows the same pattern, with a range of −4 to 9 °C.

5.1. Oxygen isotopic variation in plants

Sagebrush leaf $\delta^{18}O$ shows a consistent, negative southwest-to-northeast trend (Fig. S5). Sagebrush stem $\delta^{18}O$ shows a similar pattern, though not as pronounced (not shown). Rabbitbrush samples

Table 2
Archaeological site humidity projections.

Site	*n*	Site age	Mean $\delta^{13}C$	Hunt area Id	Hunt area modern growing season relative humidity	Projected arch. site relative humidity
Eden–Farson	12	~100 RCYBP	−8.84	92	44.0	36
Boars Tusk	6	100 RCYBP	−11.51	92	44.0	51
Gailiun	8	150 RCYBP	−9.19	91	45.2	38
Firehole Basin	7	630 RCYBP	−8.65	59	45.5	35
Austin Wash	7	1197 RCYBP	−10.15	94	42.3	44
Trappers Point	19	~5500 RCYBP	−10.02	87	47.7	43

n: number of samples. RCYBP: radiocarbon years before present. Humidity values in percent.

are limited to the southern half of the state and show a moderate negative west-to-east trend (not shown). Because there is only one sample from the southeast and none from the northwest, it is difficult to assess from the maps whether these patterns conflict with the temperature pattern.

Sagebrush leaf $\delta^{18}O$ is weakly correlated with growing season temperature (Fig. 4). The sagebrush leaf map shows a pattern more consistent with humidity than temperature, and the partial correlation of $\delta^{18}O$ with growing season temperature when growing season humidity is held constant is not significant (partial correlation = −0.390, $p = 0.15$, $n = 13$). So it appears that the southwest-to-northeast humidity trend dominates the northwest-to-southeast temperature trend in oxygen isotope incorporation into sagebrush leaves.

Rabbitbrush leaf structural $\delta^{18}O$ is weakly but not significantly correlated with temperature ($R^2 = 0.233$, $p = 0.10$). The lack of significant correlation may reflect rabbitbrush's restricted geographic distribution in Wyoming or a greater reliance on ground water than is the case for sagebrush.

5.2. Oxygen isotopic variation in pronghorn

Pronghorn enamel $\delta^{18}O$ shows a strong southwest-to-northeast trend (Fig. S6). The mean pronghorn $\delta^{18}O$ is −7.01‰, which is significantly different from the mean sagebrush $\delta^{18}O$ of −3.07‰, even after pronghorn values are increased by 1.4‰ to account for trophic fractionation (Bryant and Froelich, 1995; Podlesak et al., 2008) ($t = -5.4$, $p < 0.001$). This suggests that pronghorn are not obtaining most of their water from sagebrush. However, mean pronghorn $\delta^{18}O$ (after trophic correction) is not significantly different from mean rabbitbrush leaf $\delta^{18}O$ ($t = -1.7$, $p = 0.10$, equal variances not assumed). Forbs such as rabbitbrush probably have higher water content than does sagebrush, and likely obtain their water from nearer to the surface. $\delta^{18}O$ values indicate that Wyoming pronghorn are not obtaining a large percentage of their water from highly evaporated sources such as puddles.

There is no correlation between pronghorn enamel $\delta^{18}O$ and growing season temperature (Fig. 5). There is likewise no correlation if pronghorn $\delta^{18}O$ is compared against full-year mean temperature or if samples with less than 3 individuals are included. There is a statistically significant but small correlation when pronghorn $\delta^{18}O$ is regressed against growing season temperature using sample size weighting ($R^2 = 0.14$, $p = 0.04$, $n = 31$). The lack of strong correlation of pronghorn $\delta^{18}O$ with temperature is expected given the poor correlation of sagebrush and especially the non-correlation of rabbitbrush $\delta^{18}O$ with temperature.

5.3. Oxygen isotope variation archaeological implications

This analysis shows that $\delta^{18}O$ in pronghorn enamel cannot be used to investigate past temperature. Archaeologists need to select carefully the animal species used to investigate past environmental conditions. Evaporation sensitive species may be useful indicators of past aridity, but not temperature. Levin et al. (2006) proposed that a species be considered evaporation sensitive if it has a significant correlation between ε and water deficit, where $\varepsilon \approx \delta^{18}O_{enamel} - \delta^{18}O_{meteoric\ water}$. Relative humidity is expected to be strongly negatively correlated with water deficit, and so is substituted for water deficit in the following. The correlation is strong (Fig. 6), so pronghorn are evaporation sensitive. The south-west-to-northeast trend in pronghorn $\delta^{18}O$ clearly visible in Fig. S6 is due to correlation between $\delta^{18}O$ and growing season relative humidity ($R^2 = 0.230$, $p = 0.03$).

6. Strontium isotopes

Strontium isotope ratios in plants and, ultimately, pronghorn should depend on the $^{87}Sr/^{86}Sr$ ratios of geologic substrates, which in turn are a function of Rb/Sr ratio, initial $^{87}Sr/^{86}Sr$ ratio, and the age of geological materials (Faure and Powell, 1972). The substrate in question could be soil that developed from local bedrock or detritus that was transported from another area. Because of Wyoming's complex geologic history, both soil type and bedrock type vary substantially within the study area.

6.1. Strontium isotopic variation in plants

As expected, the mean strontium ratios in sagebrush ($n = 38$) and rabbitbrush ($n = 23$) are not significantly different ($t = 0.473$,

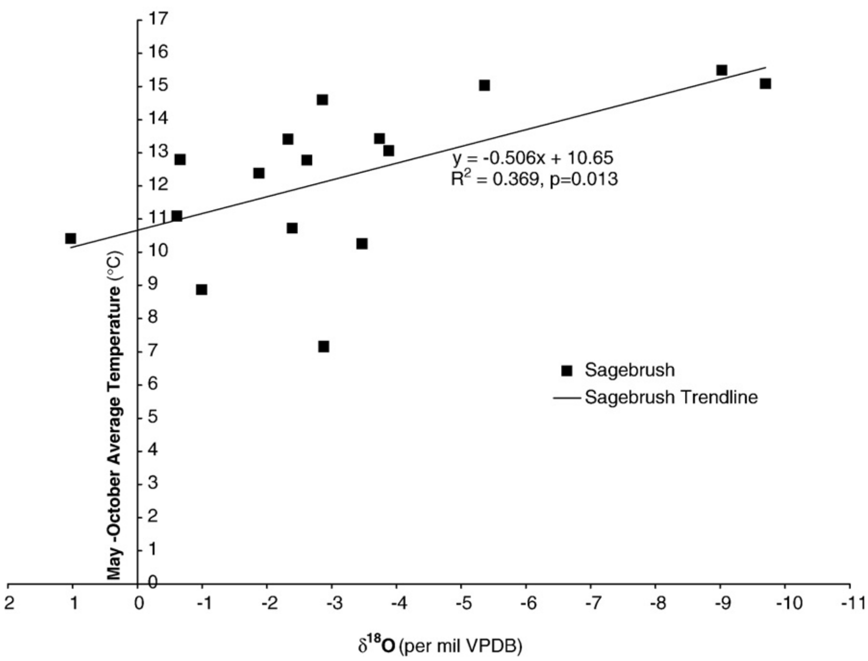

Fig. 4. Correlation between growing season temperature and $\delta^{18}O$ in big sagebrush leaves.

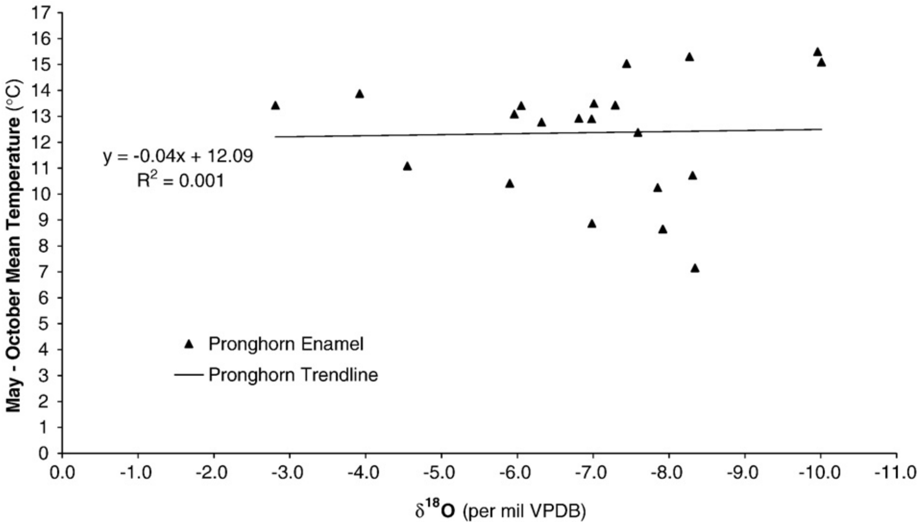

Fig. 5. Correlation between growing season temperature and $\delta^{18}O$ in pronghorn. Only hunt areas with at least three sampled individuals are included. Outliers excluded.

$p = 0.64$), so they are combined in Fig. S7 and in other analyses. Likewise, the slopes and intercepts of sagebrush and rabbitbrush regressions against bedrock age are not significantly different (Chow $F = 2.184$, $p = 0.15$) so all plants are combined in the bedrock correlation analysis. The highest $^{87}Sr/^{86}Sr$ values are found in a fairly restricted area just south and west of the Wind River Mountains. The eastern flank of the Wind River Mountains, however, does not show high strontium ratios nor does the eastern flank of the Wyoming Range or either flank of the Big Horn Mountains. These margins of the uplifts expose carbonate rocks with low $^{87}Sr/^{86}Sr$ ratios.

Plant $^{87}Sr/^{86}Sr$ values do not consistently vary by soil type in Wyoming. A particular soil type may have very different strontium ratios in different locations. For example, plants near the Gailiun site by the southwest tip of the Wind River Mountains have a mean strontium isotope ratio of 0.7188 (the red area with the highest value shown in Fig. S7) while those from Hunt Area 90 (a dark green spot about 50 km west of Gailiun) have a much different mean strontium isotope ratio of only 0.7108. Nevertheless, the soil type for both of the areas is WY17 (typic torriorthents, with loamy-skeletal, mesic and rock outcrops).

Likewise, plant strontium isotope ratio is not significantly correlated with underlying bedrock age ($p = 0.29$). This lack of correlation is not unanticipated because present-day $^{87}Sr/^{86}Sr$ depends both upon age and Rb/Sr ratio of the rock. Instead, mean plant strontium isotope ratios seem to correspond to $^{87}Sr/^{86}Sr$ values in the bedrock of nearby mountain ranges. The Wind River Mountains are an uplift that exposes granites with high Rb/Sr which are more than 2.6 billion years old and therefore contain high $^{87}Sr/^{86}Sr$ values. The Wyoming Range and the flanks of the Big Horn Mountains are composed of Paleozoic limestone containing low $^{87}Sr/^{86}Sr$ values.

6.2. Strontium isotopic variation in pronghorn

Pronghorn $^{87}Sr/^{86}Sr$ values (Fig. S8) show essentially the same geographical pattern as for plants. The highest pronghorn ratios are slightly to the east of the highest plant values, but this could be a

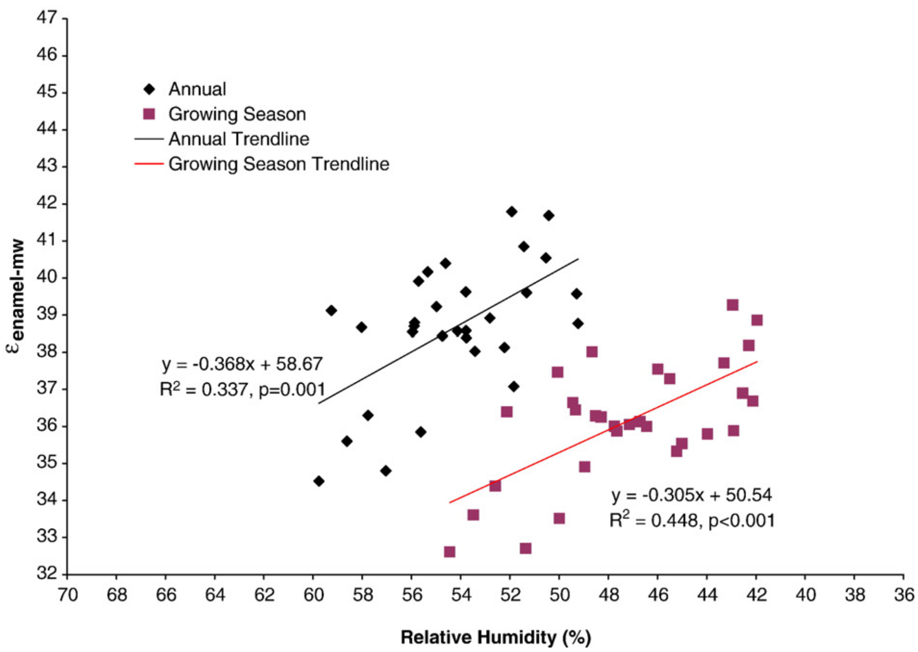

Fig. 6. Pronghorn evaporation sensitivity.

sampling artifact or related to minor pronghorn movements. Other areas show nearly identical pronghorn-plant patterns.

Fig. S9 shows strontium isotope ratios from suspended sediment in streams overlain on plant strontium data. Although data is only available from a few stream locations, they do appear to match the plant strontium ratios reasonably well. In particular, there are very high values in streams flowing west from the Wind River Mountains, but not in those flowing east. Likewise plants west but not east of the Wind Rivers have high strontium ratios. The values from the Powder River match the plant values from the Powder River Basin very well. These relationships reflect the derivation of strontium in streams from weathering of bedrock and soil in their watersheds.

6.3. Strontium isotope variation archaeological implications

Strontium ratios in pronghorn and plants vary consistently across Wyoming geography. Therefore strontium isotope ratios in archaeological specimens provide information about the geographical location of the animals when they were alive. It appears that the strontium ratios in pronghorn and plants are similar enough that approximate pronghorn isoscapes can be developed by collecting and measuring strontium ratios in plants. These isoscapes may indicate whether pronghorn migrated (or were transported) from their home range. River water suspended sediment provides another means of constructing strontium isoscapes. A project is currently underway to evaluate these relationships in more detail.

7. Conclusions

Stable isotope analysis of modern pronghorn and plants shows that isotope ratios do correlate with certain environmental or geographical conditions. Carbon isotope ratios show a strong correlation with relative humidity in both plants and pronghorn. This correlation may be used with archaeological pronghorn samples to estimate past humidity conditions. Oxygen isotope ratios are only weakly correlated with temperature in Wyoming sagebrush, and are not significantly correlated with temperature in rabbitbrush or pronghorn. It appears that oxygen isotope ratios are more strongly controlled by humidity than by temperature in Wyoming. Strontium isotope ratios do not seem to be controlled by soil type or underlying bedrock lithology. They seem instead to reflect a more complex interplay of bedrock composition, age, and presence of erosional debris from nearby mountain ranges. Further analysis of strontium isotope ratios in plants and stream-suspended sediment is needed to assess this hypothesis. In any case, strontium isotope ratios in both plants and pronghorn show geographic variability that supports using strontium isotope ratios in archaeological pronghorn enamel to trace past migration patterns or transport by humans across the landscape.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.gexplo.2008.09.003.

References

Ball, J.T., 1987. Calculations related to gas exchange. In: Zieger, E., Farquhar, G.D., Cowan, I.R. (Eds.), Stomatal Function. Stanford University Press, Stanford, pp. 445–476.
Barbour, M.M., Farquhar, G.D., 2000. Relative humidity- and ABA-induced variation in carbon and oxygen isotope ratios of cotton leaves. Plant, Cell and Environment 23, 473–485.
Brinck, E.L., Frost, C.D., 2007. Detecting infiltration and impacts of introduced water using strontium isotopes. Ground Water 45, 554–568.
Bryant, J.D., Froelich, P.N., 1995. A model of oxygen isotope fractionation in body water of large mammals. Geochimica et Cosmochimica Acta 59, 4523–4537.
Cerling, T.E., Harris, J.M., 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. Oecologia 120, 347–363.
Faure, G., Powell, J.L., 1972. Strontium Isotope Geology. Springer-Verlag, New York.
Fenner, J.N., 2007. Prehistoric Hunting On The Range Where the Antelope Play: Archaeological Pronghorn Bonebed Formation Analysis. Ph.D. Dissertation Thesis, University of Wyoming, Laramie, 217 pp.
Fenner, J.N., 2008. The use Of stable isotope ratio analysis to distinguish multiple prey events from mass kill events. Journal of Archaeological Science 35, 704–716.
Frost, C.D., Toner, R.N., 2004. Strontium isotopic identification of water–rock interaction and ground water mixing. Ground Water 42, 418–432.
Hedges, R.E.M., Stevens, R.E., Koch, P.L., 2005. Isotopes in bones and teeth. In: Leng, M.J. (Ed.), Isotopes in Palaeoenvironmental Research. Springer, Dordrecht, The Netherlands, pp. 117–145.
Knight, Dennis H., 1994. Mountains and Plains: The Ecology of Wyoming Landscapes. Yale University, New Haven.
Koch, P.L., 1998. Isotopic reconstruction of past continental environments. Annual Review of Earth and Planetary Sciences 26, 573–613.
Koch, P.L., Hoppe, K.A., Webb, S.D., 1998. The isotopic ecology of late Pleistocene mammals in North America: Part 1. Florida. Chemical Geology 152, 119–138.
Lesica, P., Cooper, S.V., Kudray, G., 2007. Recovery of big sagebrush following fire in southwest Montana. Rangeland Ecology and Management 60, 261–269.
Levin, N.E., Cerling, T.E., Passey, B.H., Harris, J.M., Ehleringer, J.R., 2006. A stable isotope aridity index for terrestrial environments. Proceedings of the National Academy of Science 103, 11201–11205.
Pietras, J.T., 2003. High-Resolution Sequence Stratigraphy and Strontium Isotope Geochemistry of the Lacustrine Wilkins Peak Member, Eocene Green River Formation, Wyoming, U.S.A. PhD Dissertation, University of Wisconsin - Madison, Madison.
Podlesak, D.W., Torregrossa, A., Ehleringer, J.A., Dearing, M.D., Passey, B.H., Cerling, T.E., 2008. Turnover of oxygen and hydrogen isotopes in the body water, CO_2, hair, and enamel of a small mammal. Geochimica et Cosmochimicia Acta 72, 19–35.
Roden, J.S., Ehleringer, J.R., 1999. Observations of hydrogen and oxygen isotopes in leaf water confirm the Craig–Gordon model under wide-ranging environmental conditions. Plant Physiology 120, 1165–1173.
Tieszen, L.L., Fagre, T., 1993. Carbon isotope variability in modern and archaeological maize. Journal of Archaeological Science 20, 25–40.
Yoakum, J.D., 2004. Foraging ecology, diet studies and nutrient values. In: O Gara, B.W., Yoakum, J.D. (Eds.), Pronghorn Ecology and Management. University Press of Colorado, Boulder, Colorado, pp. 447–502.
Zhang, H., Nobel, P.S., 1996. Dependency of c_i/c_a and leaf transpiration efficiency on the vapour pressure deficit. Australian Journal of Plant Physiology 23, 561–568.