

Mapping the origin of faunal assemblages using strontium isotopes

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Abstract.—One of the greatest challenges in using faunal assemblages to make ecological or paleoecological interpretations is determining the spatial scale over which such analyses are applicable. As a result, it has been difficult to use these assemblages to test hypotheses about spatial and temporal variability in populations. Here we show that it is possible to use strontium (Sr) isotopes from bones and vegetation to statistically constrain the area sampled in two Holocene predator accumulations in northeastern Yellowstone National Park, Wyoming. Previous studies have used these sites to elucidate local population responses to climatic change, by assuming that the specimens originated within ~5 km of the site. We used Sr analyses to construct a likelihood curve that describes the probability that our samples were collected within a given radius of each site. Our results indicate that the specimens in both sites were derived from non-overlapping populations and that the collection radius has not changed detectably over the past 3000 years. This work underscores the promise of this technique for ascribing source areas to paleontological, biological, and ecological specimens.

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Introduction

An extensive Holocene fossil record has been collected from Lamar Cave and Waterfall Locality (Hadly 1996, 1997, 1999; Hadly et al. 1998). Both sites are currently occupied wood rat (*Neotoma cinerea*) middens that contain specimens accumulated over the past 3000 years. Most of the specimens were originally the prey of raptors and carnivores. Raptor pellets and carnivore scats were subsequently gathered by wood rats and stored in their middens. Over 10,000 mammalian fossils have been excavated and identified from these two stratified deposits (Hadly 1996). Two of the most abundant organisms, voles (*Microtus montanus*) and pocket gophers (*Thomomys talpoides*), have been used to elucidate changes in abundance, body size, and genetic diversity as a function of climatic change (Hadly 1996, 1997, 1999; Hadly et al. 1998). Lamar Cave and Waterfall Locality are 24 km apart, and interpretation of these sites is based on the assumption that the specimens represent local, non-overlapping populations gathered from an area that has not changed through time. This assumption is supported by the obser-

vation that modern predator foraging ranges generally are <5 km from their roosts and dens, and that wood rats only range ~50 m from their middens (Vaughan 1990; Hadly 1996). However, studying the present does not rule out changes in the past, and it is possible that stratigraphic layers within a midden contain specimens collected from different areas. This problem is not unique to our sites. Taphonomy, the history of a specimen between its death and discovery, represents a significant challenge to those who base paleoecologic, paleoclimatic, or paleontologic interpretations on faunal assemblages (Allison and Briggs 1991; Brown and Lomolino 1998; Behrensmeyer et al. 2000).

Our goals were (1) to test the assumption that these sites represent local small-mammal populations that do not overlap spatially, (2) to determine whether the sampling area has changed through time, and (3) to constrain statistically the sampling area represented by these fossil sites. We analyzed the $^{87}\text{Sr}/^{86}\text{Sr}$ of small-mammal bones from these fossil localities and compared the results with $^{87}\text{Sr}/^{86}\text{Sr}$ analyses of local vegetation on which small

TABLE 1. $^{87}\text{Sr}/^{86}\text{Sr}$ of vegetation growing near Lamar Cave and Waterfall Locality. The SE of each measurement is 0.00003 (2σ).

Sample	Vegetation	Underlying rock type	$^{87}\text{Sr}/^{86}\text{Sr}$
SPLC 1b	Grasses	Granite-derived till	0.71237
SPLC 2a	Sagebrush	Granite-derived till	0.70948
SPLC 5b	Sagebrush	Granite-derived till	0.71208
SPLC 6a	Sagebrush	Granite-derived till	0.70897
SPLC 8b	Grasses	Granite-derived till	0.71024
SPLC 9b	Sagebrush	Granite-derived till	0.71089
SPLC 10b	Grasses	Granite-derived till	0.70971
SPLC 11c	Sagebrush	Granite-derived till	0.70940
SPLC 15b	Grasses	Granite-derived till	0.70911
SPLC 16a	Grasses	Granite-derived till	0.71155
SPLC 4a	Sagebrush	Precambrian granitic rocks	0.71276
SPLC 4d	Sagebrush	Precambrian granitic rocks	0.71320
SPLC 14b	Grasses	Precambrian granitic rocks	0.71147
SPLC 17b	Sagebrush	Eocene volcanic-derived sediments	0.70708
SPLC 18b	Grasses	Eocene volcanic-derived sediments	0.70690
SPWF 6a	Cottonwood	Eocene volcanic-derived sediments	0.70617
SPWF 7a	Cottonwood	Eocene volcanic-derived sediments	0.70833
SPWF 9b	Willow	Eocene volcanic-derived sediments	0.70752
SPWF 10c	Grasses	Eocene volcanic-derived sediments	0.70642
SPWF 10d	Grasses	Eocene volcanic-derived sediments	0.70730
SPWF 5b	Grasses	Paleozoic carbonate	0.70858
SPWF 10a	Grasses	Paleozoic carbonate	0.70839

mammals feed. Because predators collected these individuals, analyses of the bones of their small-mammal prey provide information about predator foraging habits at the time of collection, and thus the spatial component of taphonomy, which is critical for understanding these sites.

We addressed these goals with Sr isotopes because the study area contains a number of distinct geologic substrates (USGS 1972a,b, 1994; Prostka et al. 1975a,b; Berg et al. 1999; Lopez 2001) from which the isotopic signature of living organisms is derived. ^{87}Sr is a radioactive decay product of ^{87}Rb ; ^{86}Sr is stable. Thus, the $^{87}\text{Sr}/^{86}\text{Sr}$ in any given rock is dependent on the amount of Rb it contains (mineral composition) and its age (Faure 1986). Organisms do not measurably fractionate Sr, and as a result it is an ideal isotopic tool to address provenance issues (Koch et al. 1995; Hoppe et al. 1999; English et al. 2001). Small-mammal herbivores inherit the Sr signature of the vegetation they eat; the vegetation derives its Sr signature from the soil in which it grows. Our hypothesis is that the young, post-Pleistocene soils of Yellowstone will reflect the $^{87}\text{Sr}/^{86}\text{Sr}$ of the rock from which they are derived. We have direct evidence to support this hypothesis. Our analyses indicate that vegetation growing

directly on soil formed over an outcrop of Big-horn dolomite ($^{87}\text{Sr}/^{86}\text{Sr} = 0.70823$) has a signature similar (mean $^{87}\text{Sr}/^{86}\text{Sr} = 0.70849$; Table 1) to the rock itself. Vegetation growing 20 m away on alluvium derived from Eocene-aged andesites and basalts has a much lower Sr signature (0.70642) concordant with its younger, more mafic source rock. These results indicate that atmospheric inputs have slightly modified the bedrock Sr signature inherited by the soils, but that geologic contacts mark the borders between one soil Sr signature and another. This is expected given the low rates of atmospheric inputs (Junge and Werby 1958) and the relatively short duration of soil development on the Yellowstone plateau.

Methods

Bone samples were derived from multiple stratigraphic levels, and their age was constrained by ^{14}C -dated strata in both locations. In both sites the maximum age of the deposits was ~ 3000 years (Lamar Cave 2860 ± 70 [CAMS20356], Waterfall Locality 3020 ± 65 [AA7963]). Bone samples were prepared for Sr separation by ultrasonication in milliQ water, acetone, and hydrogen peroxide successively to remove adsorbed organic matter. They were

then dissolved in 7N HNO₃ and dried. Vegetation samples were ashed for four hours at 550°C in a muffle furnace, dissolved in a mixture of HNO₃ and HCl, and then dried. All samples were then redissolved in 2.5N HCl before separation by standard cation exchange techniques. Sr ratios were measured on a Finnigan MAT 262 thermal ionization mass spectrometer (TIMS). The mean value for NBS-987 during analysis of these samples was 0.71024 ± 0.00005 (2σ); data were normalized to ⁸⁶Sr/⁸⁸Sr = 0.1194.

GIS analysis used ArcView 3.2 (ESRI, Redlands, CA). Seven digital geologic maps (USGS 1972a,b, 1994; Prostka et al. 1975a,b; Berg et al. 1999; Lopez 2001) were combined in ArcView, and the percent coverage of each rock type was calculated for circular areas of different radii centered on each site. The percent coverage of each rock type was calculated at 1 km radial increments from 0 to 10 km, at 2.5 km increments from 10 to 20 km, and at 25 km.

Results and Discussion

We grouped the geologic formations, and the soils overlying them, by their Sr signature. Each formation was assigned a biologically relevant Sr signature by analysis of modern vegetation growing over the formation. This grouping results in three major geologic substrates within 25 km of our sites (USGS 1972a,b, 1994; Prostka et al. 1975a,b; Berg et al. 1999; Lopez 2001). To the north are the Bear-tooth Mountains, composed primarily of Precambrian granitic gneiss, schist, and amphibolite (⁸⁷Sr/⁸⁶Sr > 0.720), and to the east lie the Eocene-aged Absaroka Volcanic Supergroup, composed primarily of andesitic and basaltic volcanoclastics (⁸⁷Sr/⁸⁶Sr < 0.707) (Peterman et al. 1970; Doe et al. 1982; Hildreth et al. 1991). The third group, Quaternary sediments, are the most abundant rock type around either site. These sediments reflect the Sr signature of the rock from which they were derived. We drew the borders of sedimentary soil regions by geomorphologic analysis of provenance. There are two major types of Quaternary sediment in the area: glacial till, primarily derived from Precambrian gneiss and found close to Lamar Cave, and alluvial

and landslide deposits, primarily derived from Eocene volcanics, found close to Waterfall Locality. Where sediments were of undetermined origin, and the Sr signature of vegetation growing on them was not measured, the sediment was mapped as having an unknown signature. Vegetation growing on rock types that were not sampled, either because they were inaccessible or make up a small percentage of the rocks in the area, were also mapped as having an unknown signature. The data from the analyses of vegetation samples are presented in Table 1.

Lamar Cave sits in a small (~0.1 km²) outcrop of Eocene andesite surrounded by Precambrian gneiss and till derived from that gneiss. Seventy-three percent of the rock types found within 5 km of the site support vegetation with a ⁸⁷Sr/⁸⁶Sr > 0.710. In contrast, Waterfall Locality, which is only 24 km from Lamar Cave, sits in a band of Paleozoic carbonate surrounded primarily by Eocene basalts, andesites, and sediment derived from these volcanics. These Eocene rocks make up 90% of the substrate within 5 km of site, and vegetation growing over these rock types has a mean ⁸⁷Sr/⁸⁶Sr ~ 0.707. Thus, despite their proximity, the sites have easily distinguishable local Sr signatures. If the populations represented in the sites were collected locally, the ⁸⁷Sr/⁸⁶Sr of bones from the sites should be distinct and non-overlapping. If the sites contain specimens gathered from an area >25 km, bones from the two sites could exhibit overlapping Sr signatures, because the sites are 24 km apart.

The ⁸⁷Sr/⁸⁶Sr of the small-mammal specimens from the two sites do not overlap for any of the samples (Table 2). Small-mammal bones from Lamar Cave have an average ⁸⁷Sr/⁸⁶Sr of 0.7119 (SE = 4.8EE - 5), concordant with the hypothesis that the mammals were feeding locally on vegetation growing on glacial deposits derived predominantly from Precambrian granitic gneiss. The variation in isotopic signature among specimens from Lamar Cave is no greater than the variation in the ⁸⁷Sr/⁸⁶Sr of plant specimens growing on the local glacial deposits. Thus we think it likely that all of the specimens were gathered from over this substrate type. It is possible, however, that varia-

TABLE 2. Strontium isotope ratios and ages of small-mammal bones from Lamar Cave and Waterfall Locality. Each bone is from an animal no larger than a snowshoe hare.

Sample#	Stratigraphic level	Average depth below datum (cm)	Average calibrated age (cal. yr B.P.)*	$^{87}\text{Sr}/^{86}\text{Sr}$
EH-88-238	1	26	na	0.71186
EH-90-14	1	26	na	0.70969
EH-88-252	3	65	20	0.71021
EH-88-270	6	115	440	0.71184
EH-88-276	7	130	na	0.71258
EH-88-239	8	140	na	0.71193
EH-88-278	8	140	na	0.71201
EH-88-295	9	143	857	0.71130
EH-88-77	12	204	751	0.71185
EH-92-106	12	204	751	0.71157
EH-92-165	13	214	1419	0.71110
EH-92-156	13	214	1419	0.71139
EH-92-170	14	226	na	0.71165
EH-93-137	16	231	2421	0.71144
EH-88-165	16	241	2421	0.71191
EH-91-46	1b	25	na	0.70651
EH-91-57a	2a	50	495	0.70633
EH-91-57b	2a	50	495	0.70663
EH-91-66	3	50	na	0.70645
EH-91-87	4	50	na	0.70622
EH-91-105	6	59.2	1628	0.70626
EH-91-102	6	59.2	1628	0.70655
EH-91-110	8a	67	2230	0.70618
EH-91-156	9	70.8	2070	0.70696
EH-91-174	9c	75	na	0.70646
EH-91-158	10	75	2125	0.70653
EH-91-198	12	92.4	2515	0.70843
EH-91-203	13	103	2755	0.70692
EH-91-231	14	115.7	2878	0.70648
EH-91-231	14	115.7	2878	0.70637
EH-91-257	15a	130	No data	0.70646

* Average of the mean ages of radiocarbon dates from a given level. For age ranges and descriptions of methods of calibration for Lamar Cave, see Hadly 1996, 1999. Dates from Waterfall Locality are from unpublished radiocarbon data.

tion in small-mammal signatures is the result of particular animals averaging the signal from two or more discrete bedrock types. Small-mammal bones from Waterfall Locality have an average $^{87}\text{Sr}/^{86}\text{Sr}$ of 0.7066 (SE = 3.3EE - 5), demonstrating that these individuals were feeding locally on vegetation growing on soils derived from Eocene volcanics. The $^{87}\text{Sr}/^{86}\text{Sr}$ of one specimen from Waterfall Locality is higher than is compatible with Eocene volcanics, and it matches the $^{87}\text{Sr}/^{86}\text{Sr}$ of the Paleozoic carbonate outcrop that hosts the midden. The $^{87}\text{Sr}/^{86}\text{Sr}$ of small-mammal bones found in the two sites are significantly different (Mann-Whitney U -Test: $U = 497$, $p < 0.001$). Our results indicate that these populations of small-mammals have been isolated from each other for the past 3000 years. Predators have larger ranges than small mammals,

yet their range is also resolved by these data because they gathered these individuals as prey. These analyses present strong evidence that transport of prey did not occur between sites and that predators foraged locally.

We used the heterogeneous nature of the bedrock geology in the sites to constrain statistically the area represented in each site. Our method is based on five assumptions: (1) Sr passed from vegetation to the species feeding on that vegetation, (2) bedrock geology and geomorphology determine the boundaries between soils with different Sr signatures, (3) the $^{87}\text{Sr}/^{86}\text{Sr}$ of the vegetation on a given rock type has not changed during the Holocene soil formation process, (4) the Sr signatures of the specimens are not the result of diagenetic changes, and (5) the predators that collected the specimens picked prey at random over a

circular range. We have commented on the first two assumptions; the latter three merit further discussion. Given the fidelity of modern vegetation $^{87}\text{Sr}/^{86}\text{Sr}$ to rock $^{87}\text{Sr}/^{86}\text{Sr}$, and the relative youth of Yellowstone soils, we are confident that the vegetation $^{87}\text{Sr}/^{86}\text{Sr}$ over a given bedrock type has remained relatively constant during the Holocene, especially in comparison with the variation across bedrock contacts. As to diagenesis, we have ample evidence to support our assumption that diagenesis is not responsible for the signatures found in the specimens. First, both caves occur in rock types that do not have the same Sr signature as the bones found in them. Waterfall Locality sits in an outcrop of Paleozoic carbonate ($^{87}\text{Sr}/^{86}\text{Sr} = 0.70823$, our analysis), a signature that appears in only one of the 16 bone specimens analyzed from the site. Lamar Cave sits in an outcrop of Eocene volcanics, and sediment in the cave yields $^{87}\text{Sr}/^{86}\text{Sr} = 0.70684$ (our analysis), a signature that is not seen in any bone specimens from that cave. Second, if diagenesis was responsible for the observed signatures, we might expect to see a trend with time, older samples would have a signature closer to that of the cave, and that trend is notably absent. As to the assumption of random sampling, we use this to show that even without additional knowledge about the habits of taphonomic agents, it is possible to determine their range using our technique.

Given these assumptions, it is possible to calculate the probability that our specimens were collected from a given area. We ascertained which bedrock types could *not* have provided habitat for the small mammals we analyzed because the $^{87}\text{Sr}/^{86}\text{Sr}$ of vegetation growing on that rock type does not match that of the specimens. By measuring similar vegetation growing on different bedrock types, we minimized the potential effects of differences in strontium concentration on the calculated probabilities. For example, all of the specimens from Lamar Cave ($n = 15$) have a $^{87}\text{Sr}/^{86}\text{Sr} > 0.7096$ (Table 2). Therefore, these specimens could not have fed on vegetation growing in Eocene volcanic-derived soils; that vegetation has a $^{87}\text{Sr}/^{86}\text{Sr} < 0.7085$ (Table 1). The probability of randomly sampling an area underlain by $x\%$ Eocene volcanics and *not* de-

tecting an Eocene Sr signature is $p = (1 - x)^n$, where n is the number of samples. Analyses at different radii allow the construction of a likelihood curve that illustrates the change in probability with collection radius (Fig. 1). Only 8% of a 3-km radius circle around Lamar Cave is underlain by rocks with a Sr signature that is incompatible with the specimens from the cave. Thus the probability of sampling within 3 km of the site and not picking up a specimen from Eocene volcanics $= (1 - 0.08)^{15} = 0.24$, and thus we can assert that there is a 24% probability that our specimens came from within 3 km of our site. This probability is greater than 0.05 for each tested radius < 8 km. However, 19% of an 8-km radius circle around Lamar Cave is underlain by rocks with a $^{87}\text{Sr}/^{86}\text{Sr}$ too low to explain the signatures of the specimens. The probability of randomly sampling 15 specimens from a circle of this radius without picking a specimen from one of these incompatible rock types $= (1 - 0.19)^{15} = 0.04$ (the transition from compatible to incompatible rock types with distance from the sites can be seen in Fig. 2). We deem this an unlikely event and conclude that specimens from Lamar Cave are derived from an area within a radius of less than 8 km of the site.

A similar analysis can be performed for Waterfall Locality, but the spatial resolution is not as great because at small (< 15 km) radii the geology is relatively homogeneous. The large majority of the underlying rocks within 15 km of the site are Eocene volcanics, or alluvial sediments derived from those volcanics (USGS 1972b, 1994; Prostka et al. 1975b; Berg et al. 1999; Lopez 2001). All of these rock types could provide the $^{87}\text{Sr}/^{86}\text{Sr} \sim 0.7065$ of the bones from the deposit. However, at a radius > 15 km, the major Quaternary sediment type shifts to till derived from Precambrian gneiss in the Beartooth Mountains. The $^{87}\text{Sr}/^{86}\text{Sr}$ of the till is too high to match the signatures found in the Waterfall Locality specimens and thus can be used to constrain the most likely sampling radius around the site. Our analyses indicate that there is 95% probability that the samples in Waterfall Locality came from an area with a radius of less than 17.5 km is greater than 95%. Thus we statistically constrain the maximum area represented by our

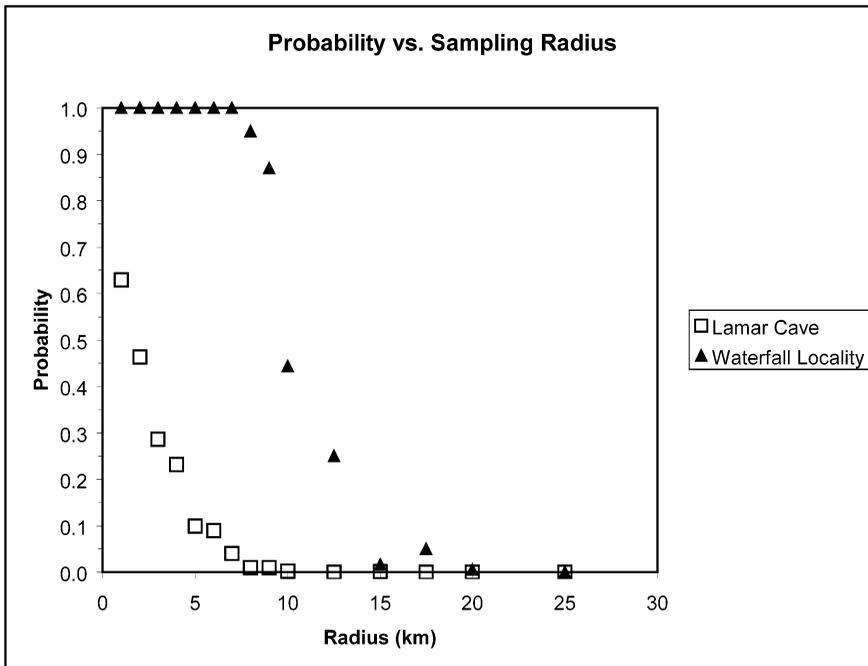


FIGURE 1. Probability that the specimens analyzed came from circular areas of different radii at Lamar Cave (squares) and Waterfall Locality (triangles). Probabilities are calculated using the equation: $p = (1 - x)^n$, where n is the number of specimens analyzed and x is the percent cover of rock types that have a $^{87}\text{Sr}/^{86}\text{Sr}$ that is incompatible with the signature of the specimens. Sr ratios of vegetation growing on Precambrian gneiss and till derived from that gneiss are compatible with the signature seen in small mammal bones from Lamar Cave. Sr ratios of vegetation growing of Eocene volcanics, sediment derived from those volcanics, and Bighorn Dolomite are compatible with the signature of the bones from Waterfall Locality. As a result of the relative homogeneity of Sr signature within 15 km of Waterfall Locality, the radius at which $p < 0.05$ is greater for Waterfall Locality than for Lamar Cave.

fossil assemblages and define the appropriate spatial scale for interpreting specimens from these sites.

Conclusions

The utility of these analyses lies both in their specific applications to the assemblages at Lamar Cave and Waterfall Locality and in their potential application to both past and present faunal accumulations. We demonstrate that each site contains distinct populations gathered from relatively small geographic areas. Because the majority of the bones in these sites were originally collected by raptors and mammalian carnivores, our data provide isotopic corroboration of modern observations that these predators generally forage within a small radius of their roosts or dens and have done so at least for 3000 years. Thus the faunal assemblages in these sites can be used to make interpretations about local

communities and are not artifacts of mixing of individuals derived from separate populations.

We also assert that the predators foraged over the same rock types through time, as indicated by the constancy of the Sr signature of bones at each site. The period represented by these deposits encompasses at least two significant climatic shifts, the Little Ice Age and the Medieval Warm Period (Porter 1986; Hughes and Diaz 1994). Neither of these events appears to have influenced the foraging territory of these predators. The analyses presented above would have detected marked shifts in foraging habitat by identifying the resulting change in Sr ratio. Thus we place constraints on the temporal variation in foraging range of both predators and prey. With greater sampling from each stratigraphic level it might be possible to constrain this variation further.

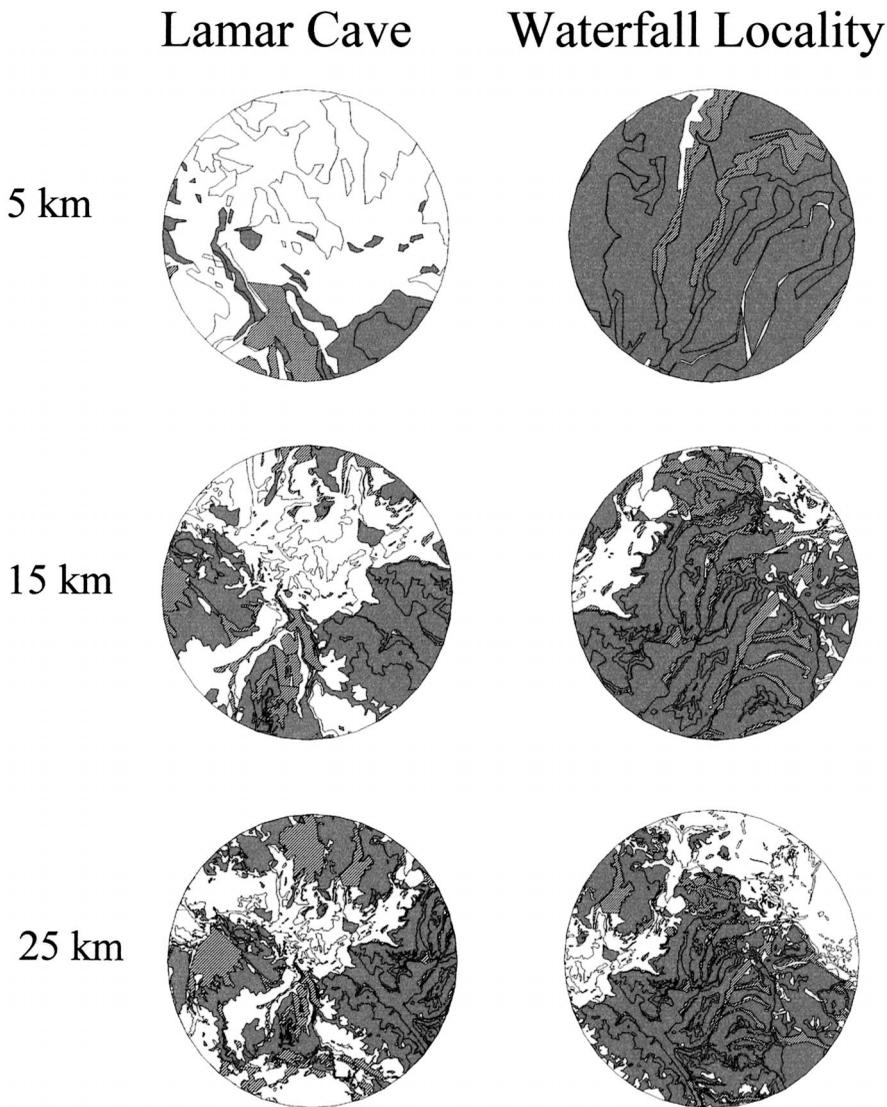


FIGURE 2. Modified geologic maps at 5, 15, and 25 km radii around Lamar Cave and Waterfall Locality. The sites are 24 km apart. Areas mapped in white are those that have vegetation with $^{87}\text{Sr}/^{86}\text{Sr}$ compatible with the values of bones in Lamar Cave. Areas mapped in dark gray are those in which vegetation has $^{87}\text{Sr}/^{86}\text{Sr}$ compatible with Waterfall Locality. Striped gray indicates areas of unknown $^{87}\text{Sr}/^{86}\text{Sr}$. Compatibility is based on analyses of modern vegetation and the boundaries are drawn according to rock type underlying the soil.

These analyses place a statistical constraint on what heretofore has been an untested assumption about sampling area. Such constraints are needed for a broad range of applications, including conservation, patterns of speciation, diet and migration histories, and biotic responses to climatic change. As genetic, behavioral, and physiologic analyses further our understanding of population responses to environmental variability, questions about provenance of individuals will become increas-

ingly important. Isotopic analyses may be critical for establishing the spatial origin of both ancient and modern assemblages.

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