

Determining landscape use of Holocene mammals using strontium isotopes

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Abstract The use of the landscape by animals is predicted to be a function of their body size. However, empirical data relating these two variables from an array of body sizes within a single mammalian community are scarce. We tested this prediction by assessing landscape use of mammals by analyzing strontium (Sr) isotope signatures found in mammalian hard tissues representing a 3,000-year record. We examined: (1) the Sr-determined landscape area of small (~100 g), medium (~1,500 g) and large (~100,000 g) mammals, and; (2) whether the area used by these mammals varied during periods of environmental change. Strontium isotope values were obtained from 46 specimens from the Holocene paleontological deposits of Lamar Cave and Waterfall Locality in Wyoming, USA, as well as from 13 modern ungulate specimens from the same area. Our data indicate that medium- and large-sized species use larger percentages of the landscape than do species of small body size. The isotope values for specimens from

each of the paleontological sites are similar across all stratigraphic levels, suggesting no change in home range over the last 3,000 years, even though climate is known to have fluctuated at these sites over this time period. Further, our study verifies that the fossil localities represent the local community. Where bedrock geology is appropriate, the use of strontium isotope analyses provides a valuable tool for discerning landscape use by vertebrate communities, an important though generally difficult aspect of an ancient species niche to identify.

Keywords Paleontology · Mammal · Body size · Home range · Climate · Yellowstone National Park

Introduction

Part of understanding the ecology of mammals involves identifying their home ranges by recognizing how individuals within a species utilize the landscape (Burt 1943; Hayne 1949; McNab 1963). Without assessing the landscape use of species, a thorough knowledge of resource use, competition and partitioning among species is not possible (Schoener 1974). Determining landscape use by extant mammals can be accomplished through direct observation during field studies and/or radio tracking (Millspaugh and Marzluff 2001). However, these methodologies are limited by the lifespan of the individuals studied and are not available for studies of prehistoric ranges, which may inform us about the stability of extant individual ranges over time and whether climatic and environmental changes have impacted these ranges.

Many mammalian ecological parameters, including home range, have been shown to correlate to body mass (Damuth 1981a, 1981b; Damuth and MacFadden 1990).

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Models predict that larger mammal species use more of the landscape than smaller ones (Bowman et al. 2002; Carbone et al. 2005; Giuggioli et al. 2006; Haskell et al. 2002; Jetz et al. 2004). Studies have generally supported these predictions, showing that larger taxa generally have larger home ranges and use more of the available landscape than do smaller ones (Damuth 1981a; Harestad and Bunnell 1979; Kelt and Van Vuren 2001; Lindstedt et al. 1986; McNab 1963). Variation in metabolic requirements, which depend on body mass, are suspected to be the cause of such differential use of the landscape (Damuth 1981a; Harestad and Bunnell 1979; Kelt and Van Vuren 2001; McNab 1963). Defining home ranges can show the movements of individuals in a particular area; however, it does not directly demonstrate where the individuals are obtaining resources to satisfy their metabolic requirements—these are mostly inferred. Additionally, direct tests for discriminating landscape use between species of different masses occupying the same geographic area are scarce.

One technique that has been particularly useful in analyzing the movements of both modern and ancient animals is the analysis of strontium isotope values within an individual's tissues. In animals, strontium isotopes arise from the food they consume, which in turn is related to the bedrock and soil on which an individual lives and eats (Faure 1986). Movement across the landscape and over bedrock with varying strontium isotope values results in the incorporation of different isotope values into an individual's tissues. This methodology has been applied primarily to examine the movements and migration patterns of ancient humans (Bentley et al. 2003; Ezzo et al. 1997; Hodell et al. 2004; Reynolds et al. 2005). Additionally, it has been used to understand the provenance of individuals within populations, as well as the origins of natural materials and mammal migration patterns (English et al. 2001; Ezzo et al. 1997; Hodell et al. 2004; Hoppe et al. 1999; Reynolds et al. 2005). Because the strontium isotope values derive from food, this technique can address whether larger species use larger areas to satisfy metabolic needs, or whether they roam larger areas for other needs, such as to encounter mates or avoid predation.

In this study we determine whether strontium isotope ratios corresponded to the expected landscape use of various mammals based on their size (e.g., larger home range for larger mammals). We also investigate whether these same animals altered their home ranges over time in response to known climatic fluctuations. We addressed these questions by examining Sr-isotope signatures in ancient mammals from two Holocene fossil sites located in Yellowstone National Park: Lamar Cave and Waterfall Locality.

Background and methods

Strontium isotopes and home range

Landscape $^{87}\text{Sr}/^{86}\text{Sr}$ values depend on the bedrock geology of the area as well as atmospheric inputs (Capo et al. 1998; Faure 1986). Individuals integrate the landscape $^{87}\text{Sr}/^{86}\text{Sr}$ ratios into their own tissues (Faure 1986), thus reflecting the values of the landscape where individuals foraged. Because of their relatively young age, which is a result of Pleistocene glaciation (Porder et al. 2003), the soils of Yellowstone National Park (YNP) have been shown to reflect primarily the $^{87}\text{Sr}/^{86}\text{Sr}$ values of local bedrock (Porder et al. 2003). The local bedrock in YNP around the two fossil study sites is heterogeneous with respect to strontium isotope values, permitting detection of the use of particular areas around the study sites (Porder et al. 2003).

The taphonomy of each of the paleontological localities influences how the provenance of fossils is interpreted. The cave deposits are wood rat (*Neotoma cinerea*) nests (middens) that have accumulated over the last 3,000 years (Hadly 1996, 1999). Wood rats make their nests from materials they gather from the immediate surroundings of their nest sites. Among the materials that wood rats utilize are carnivore scat and raptor pellets, containing the bones of scavenged and hunted prey; these remains accumulate in the nests over time. Consequently, our interpretations of landscape use depend on the foraging radius of the carnivores and raptors as well as the geographical range of their prey.

Study sites

The fossil deposits of Lamar Cave and Waterfall Locality are located in northern Yellowstone National Park, Wyoming (see “[Electronic supplementary material](#)”). More than 20,000 vertebrate fossils have been stratigraphically excavated and identified from these localities, and the fossil diversity represents 93% of the total modern mammalian diversity (Hadly 1996, 1999). Over the last 3,000 years, the sites have experienced warming and cooling trends, such as the Medieval Warm Period and the Little Ice Age, with temperature changes on the order of 1–2 °C (Hadly 1996; Whitlock 1993). Although both sites are in close proximity to one another, contemporaneous, and taphonomically similar, the deposits are surrounded by distinct habitats and underlain by different bedrock, which allows Sr-isotope values to be used to investigate individual home ranges (Porder et al. 2003).

Lamar Cave, formed in a small outcrop of Eocene andesite ($^{87}\text{Sr}/^{86}\text{Sr} = 0.70684$), is situated within a sagebrush grassland habitat. This habitat, except for Lamar Cave itself, is predominantly underlain by rocks and sediments of

Precambrian gneiss and schist, which yield much higher $^{87}\text{Sr}/^{86}\text{Sr}$ values. Isotopically, the dominant $^{87}\text{Sr}/^{86}\text{Sr}$ signal within an 8-km radius around the cave is >0.710 (Porder et al. 2003). Beyond 8 km, the strontium isotope signal becomes more heterogeneous, including rock types that have much lower $^{87}\text{Sr}/^{86}\text{Sr}$ values (<0.708) (Porder et al. 2003). Thus, individuals utilizing the landscape within 8 km of the cave are expected to have Sr-isotope values above 0.710, while individuals using larger ranges are expected to have lower $^{87}\text{Sr}/^{86}\text{Sr}$ values.

Waterfall Locality, surrounded by lodgepole pine forest, is situated in a narrow band of Paleozoic carbonate rock (Porder et al. 2003). The Paleozoic carbonate rock ($^{87}\text{Sr}/^{86}\text{Sr} = 0.70823$) is surrounded by Eocene volcanics (andesites and basalts), which dominate the bedrock and sediment. Thus, the $^{87}\text{Sr}/^{86}\text{Sr}$ signal of sediments within a 17.5-km radius of Waterfall Locality is low (<0.708) (Porder et al. 2003). We expected that individuals using the landscape within 17.5 km of this paleontological site to have Sr-isotope values below 0.708, while ranges beyond this vicinity would yield higher ratios.

Sample preparation

Holocene bone, dentine and enamel samples were obtained from 46 individuals of mammals collected from the various stratigraphic levels of Lamar Cave and Waterfall Locality in YNP. Species were divided into three size categories, small (~ 100 g), medium ($\sim 1,500$ g) and large ($\sim 100,000$ g). The small species category includes only *Thomomys talpoides*, a species common to both sites. The medium category includes Leporidae, *Lepus* sp., and *Marmota flaviventris*. The large category includes *Antilocapra americana*, Cervidae, and *Odocoileus* sp. Thirteen modern large-species enamel samples were obtained and analyzed from the Lamar area Yellowstone National Park collections of Dr. Peter Gogan (USGS), and include two species, *Bison bison* and *Cervus elaphus*.

Bone, dentine, and enamel were prepared for $^{87}\text{Sr}/^{86}\text{Sr}$ analysis following the general protocol of Porder et al. (2003). Briefly, teeth and bone were washed using a sonic cleaner and Milli-Q (Millipore, Billerica, MA, USA) water. Bone, dentine, and enamel powder were obtained from each sample using a variable speed Dremel (Racine, WI, USA) rotary tool and carbide drill bit. To remove any organic matter and/or diagenetic carbonate, the powdered samples were washed in 30% H_2O_2 overnight, decanted and rinsed with Milli-Q water, washed with 0.1 N acetic acid overnight, decanted and rinsed with Milli-Q water, then air-dried. The dried samples were dissolved in 2.5 N HCl, and Sr was separated using cation exchange techniques. $^{87}\text{Sr}/^{86}\text{Sr}$ ratios were analyzed using the Finnegan (Thermo Electron, Waltham, MA, USA) MAT 262 thermal ionization mass

spectrometer (TIMS) in the Department of Geological and Environmental Science at Stanford University. The mean $^{87}\text{Sr}/^{86}\text{Sr}$ value for NBS-987 was 0.71030 ± 0.00005 (2σ), and data were normalized to $^{86}\text{Sr}/^{88}\text{Sr} = 0.1194$ during the analyses. Sample data were corrected to the accepted $^{87}\text{Sr}/^{86}\text{Sr}$ value of 0.710235 for NBS-987.

Isotopic values were compared among body size categories at each locality using ANOVA and post hoc Tukey's HSD tests. Tukey's HSD tests are similar to *t*-tests but they take into account multiple comparisons. Statistics were run using JMP IN 5.1, and significance was set at $P < 0.05$.

Results

Diagenesis

Diagenesis (chemical modifications to specimens after the death of an animal) can be a major concern when analyzing isotopic ratios from fossils, especially when the ratios are obtained from bone (Hoppe et al. 2003; Schoeninger and DeNiro 1982; Sealy et al. 1991). Fossil diagenesis, generally a result of permeability of the specimen, can profoundly alter mineral composition, and thus transform the original Sr isotopic signature to that of the sediments in which it is entombed. Previous geochemical analysis of the specimens from these localities led us to predict that diagenesis was not likely to be significant because collagen and ancient DNA both were readily obtained from specimens deposited in these localities (Hadly 1996, 1999). To verify this prediction experimentally, we examined $^{87}\text{Sr}/^{86}\text{Sr}$ values from bone, dentine, and tooth enamel from single specimens containing all three. In total, seven individuals were used for our analysis, representing both fossil sites and obtained from multiple time slices. Enamel is more resistant to diagenetic alteration than dentine or bone because it is less permeable; bone is the most easily altered of the three substances. Thus, agreement of Sr ratios obtained from all three of these substances indicates negligible diagenetic alteration (Wang and Cerling 1994). As shown in Fig. 1, enamel isotope ratios derived from specimens representing the various localities and time intervals were identical to the individual's bone and dentine (Table 1). The similarity in $^{87}\text{Sr}/^{86}\text{Sr}$ ratios obtained from each substance (bone, dentine, and enamel) within an individual confirms that diagenesis is not a concern for these fossils, and thus Sr isotopes represent the original signature of the individual throughout its life. In addition, it is expected that diagenetic alteration will result in the incorporation of Sr from the surroundings in which the fossil was buried. At both sites the cave deposits are distinct from the area outside the cave and the Sr isotopes in our samples are different from the cave signatures.

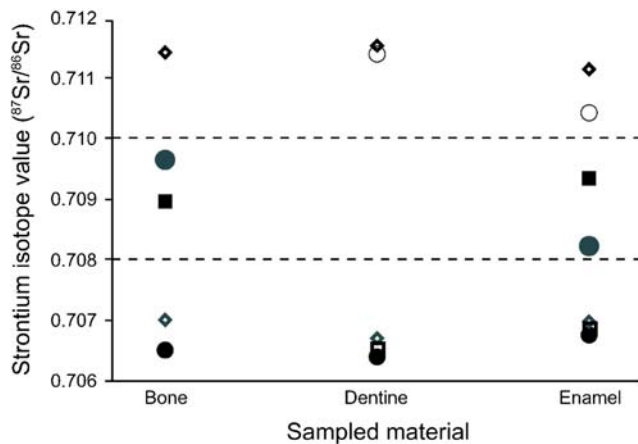


Fig. 1 Strontium isotope values from bone, dentine, and enamel of seven ancient mammalian individuals from Waterfall Locality and Lamar Cave, Wyoming, USA. *Identical symbols* in the bone, dentine, and enamel categories represent a sample from the same individual. Strontium isotope values above the *dashed line* at 0.710 are characteristic of substrate surrounding Lamar Cave, values below 0.708 are characteristic of substrate surrounding Waterfall Locality, and values between *dashed lines* indicate the use of mixed substrates. Standard error is included, but is not visible, since error is smaller than the data-point symbols

Use of the landscape

The granitic gneiss substrate in the vicinity of Lamar Cave is characterized by a $^{87}\text{Sr}/^{86}\text{Sr}$ value of >0.710 . The $^{87}\text{Sr}/^{86}\text{Sr}$ values for all 21 sampled individuals from Lamar Cave were concordant with the substrate, showing a mean of 0.71164 (range 0.70823–0.71352). While there were no trends or patterns over time (Table 1; Fig. 2), there were differences related to body size. Both medium and small size categories fall well within the range of the substrate for the Lamar Cave vicinity. The medium body mass category had a mean $^{87}\text{Sr}/^{86}\text{Sr}$ value of 0.71205. The small mass category exhibited a mean $^{87}\text{Sr}/^{86}\text{Sr}$ value of 0.71153. Individuals in the large body mass category, however, displayed a mean $^{87}\text{Sr}/^{86}\text{Sr}$ value of 0.70933, deviating from the mean of the local substrate (towards lower values). Statistically, the small and medium body size categories were significantly different from the large-sized category. Two individuals, one medium and one large, exhibit strontium isotope ratios <0.710 (Fig. 2). These values were recorded for a medium-sized jackrabbit (0.70934) and a large-sized pronghorn (0.70823). These particular values imply that these individuals used areas outside the 8-km vicinity of Lamar Cave. Alternatively, these individuals could have foraged more heavily on a small pocket of Eocene bedrock with a low strontium ratio adjacent to the cave itself. Our data show that the majority of the individuals, no matter what their size, confined their landscape use to within 8 km

of Lamar Cave (Porder et al. 2003), and that this has been the case for the past 3,000 years.

The landscape around Waterfall Locality holds a strontium signature of <0.708 . The 25 specimens from Waterfall Locality had a mean $^{87}\text{Sr}/^{86}\text{Sr}$ value of 0.70686 (range 0.70607–0.71042). Similar to Lamar Cave, there were no apparent trends or patterns in the Sr isotope data over time (Table 1; Fig. 2). However, again there were differences based on body size. The large body mass category had the highest mean $^{87}\text{Sr}/^{86}\text{Sr}$ value at 0.70859, greater than our expectations from a solely local source. Both small and medium body mass categories exhibited the same mean isotope value ($^{87}\text{Sr}/^{86}\text{Sr}$ value = 0.70671). Statistically, the large-sized category was significantly different from both the small- and medium-sized categories. One cervid individual ($^{87}\text{Sr}/^{86}\text{Sr}$ = 0.71042) displayed isotopic ratios well above 0.708, suggesting that this individual relied on extra-local foraging.

The modern specimens from the large body mass category displayed a mean $^{87}\text{Sr}/^{86}\text{Sr}$ value of 0.70838, but with high variance (range 0.70690–0.71164). The range in values for these specimens indicates that these individuals do not confine themselves to one particular bedrock type but rather roam throughout the area represented by both fossil localities.

Discussion

Based on the expectations of current models on mammal home ranges (Bowman et al. 2002; Carbone et al. 2005; Giuggioli et al. 2006; Haskell et al. 2002; Jetz et al. 2004), we predicted that large mammals should integrate the Sr isotope signatures of the various substrates present in the Park if they are using more of the landscape instead of confining themselves to one area (thus substrate type). In contrast, small mammals would show less variance in their values, and should demonstrate fidelity to one local substrate; medium-sized mammals should show intermediate values. Our analyses generally support these predictions. Our data showed that small mammals are well within expectations of local substrate use. None of the small mammals we sampled fell outside the local substrate values, demonstrating that they are exclusively local foragers. Large-body-sized individuals from both sites and from the modern data show $^{87}\text{Sr}/^{86}\text{Sr}$ values indicative of foraging on variable bedrock types, implying the utilization of a wider area around the fossil localities. However, surprisingly, not every individual did so; several large individuals showed smaller than expected foraging radii. Medium-sized individuals show a mostly local foraging signature, except for one specimen from Lamar (a jackrabbit). Because the Sr isotope values in mammal tissues are derived from food,

Table 1 Sample number, specimen number, Sr-isotope ratios, locality information, and radiocarbon age for specimens analyzed within this study

Sample no.	Specimen no.	Taxon	Material	Element	$^{87}\text{Sr}/^{86}\text{Sr}$	Locality	Level	^{14}C date
RSF04Sr01	206048	Artiodactyla	Dentine	Cheektooth	0.71138	LC	Undifferentiated	–
RSF04Sr02	206048	Artiodactyla	Enamel	Cheektooth	0.71042	LC	Undifferentiated	–
RSF04Sr04	EB91-20	<i>Odocoileus</i> sp.	Bone	M1	0.70650	WF	Undifferentiated	–
RSF04Sr05	EB91-20	<i>Odocoileus</i> sp.	Enamel	M1	0.70676	WF	Undifferentiated	–
RSF04Sr06	EB91-20	<i>Odocoileus</i> sp.	Dentine	M1	0.70639	WF	Undifferentiated	–
RSF04Sr07	205675	<i>Lepus townsendii</i>	Bone	Maxilla	0.70894	LC	3	20
RSF04Sr09	205675	<i>Lepus townsendii</i>	Enamel	Molar	0.70934	LC	3	20
RSF04Sr10	EB92-76	<i>Marmota flaviventris</i>	Bone	Dentary	0.71142	LC	12	751
RSF04Sr11	EB92-76	<i>Marmota flaviventris</i>	Dentine	m1	0.71152	LC	12	751
RSF04Sr12	EB92-76	<i>Marmota flaviventris</i>	Enamel	m1	0.71114	LC	12	751
RSF04Sr13	EB91-155	<i>Marmota flaviventris</i>	Bone	Dentary	0.70701	WF	Undifferentiated	–
RSF04Sr14	EB91-155	<i>Marmota flaviventris</i>	Dentine	Cheektooth	0.70670	WF	Undifferentiated	–
RSF04Sr15	EB91-155	<i>Marmota flaviventris</i>	Enamel	Cheektooth	0.70696	WF	Undifferentiated	–
RSF04Sr17	EB91-7	<i>Lepus americanus</i>	Dentine	Cheektooth	0.70652	WF	Undifferentiated	–
RSF04Sr18	EB91-7	<i>Lepus americanus</i>	Enamel	Cheektooth	0.70687	WF	Undifferentiated	–
RSF05Sr01	EB 90-139	<i>Antilocapra americana</i>	Enamel	m	0.70823	LC	9	857
RSF05Sr02	EB 90-139	<i>Antilocapra americana</i>	Bone	Jaw	0.70963	LC	9	857
RSF05Sr03	EB 91-155	Cervidae	Enamel	Incisor	0.71042	WF	Undifferentiated	–
RSF05Sr05	EB 92-46	<i>Marmota flaviventris</i>	Dentine	R incisor	0.71143	LC	12	751
RSF05Sr06	EB-90-61	<i>Marmota flaviventris</i>	Dentine	R incisor	0.71067	LC	3	20
RSF05Sr07	EB 90-122	<i>Marmota flaviventris</i>	Bone	L dentary	0.71179	LC	7	770
RSF05Sr08	EH 124	<i>Marmota flaviventris</i>	Bone	L dentary	0.71257	LC	3	20
RSF05Sr09	EB 92-87	<i>Marmota flaviventris</i>	Bone	Jaw	0.71211	LC	12	751
RSF05Sr10	EH 81	<i>Marmota flaviventris</i>	Bone	L dentary	0.71261	LC	7	770
RSF05Sr11	EB 90-61	<i>Marmota flaviventris</i>	Dentine	L incisor	0.71313	LC	3	20
RSF05Sr12	EH 82	<i>Marmota flaviventris</i>	Bone	L dentary	0.71352	LC	7	770
RSF05Sr13	EB 92-87	<i>Marmota flaviventris</i>	Dentine	Incisor	0.71286	LC	12	751
RSF05Sr16	EB 92-76	<i>Marmota flaviventris</i>	dentine	R Incisor	0.71238	LC	12	751
RSF05Sr20	EB 90-49	<i>Marmota flaviventris</i>	Dentine	LP4	0.71307	LC	3	20
RSF05Sr21	EB 91-83	Leporidae	Dentine	RM	0.70688	WF	2	495
RSF05Sr22	EB 91-94	Leporidae	Dentine	RM	0.70707	WF	2	495
RSF05Sr23	EB 91-83	Leporidae	Dentine	RM	0.70611	WF	2	495
RSF05Sr24	EB 91-157	Leporidae	Dentine	LM	0.70673	WF	9	2070
RSF05Sr25	EB 91-137	Leporidae	Dentine	LM	0.70607	WF	9	2070
RSF05Sr26	EB 91-204	Leporidae	Dentine	LM	0.70658	WF	13	2755
RSF05Sr27	EB 91-214	Leporidae	Dentine	LM	0.70659	WF	13	2755
RSF05Sr28	EB 91-157	Leporidae	Dentine	LM	0.70637	WF	9	2070
RSF05Sr29	EB 91-217	Leporidae	Dentine	LM	0.70663	WF	13	2755
RSF05Sr30	EB 91-83	Leporidae	Dentine	LM	0.70655	WF	2	495
RSF05Sr31	EB 91-157	Leporidae	Dentine	LM	0.70694	WF	9	2070
RSF05Sr32	EB 91-137	Leporidae	Dentine	LM	0.70699	WF	9	2070
RSF05Sr33	EB 91-137	Leporidae	Dentine	LM	0.70688	WF	9	2070
RSF05Sr34	EB 91-203	Leporidae	Dentine	LM	0.70708	WF	13	2755
RSF05Sr37	EB-88-264	<i>Thomomys talpoides</i>	Bone	Humerus	0.71203	LC	5	550
RSF05Sr38	EB 90-122	<i>Thomomys talpoides</i>	Bone	Humerus	0.71108	LC	7	770
RSF05Sr39	EB 91-157	<i>Thomomys talpoides</i>	Bone	Humerus	0.70668	WF	9	2070
RSF05Sr40	EB 88-292	<i>Thomomys talpoides</i>	Bone	Humerus	0.71197	LC	9	857
RSF05Sr41	EB 91-136	<i>Thomomys talpoides</i>	Bone	Humerus	0.70668	WF	9	2070

Table 1 continued

Sample no.	Specimen no.	Taxon	Material	Element	$^{87}\text{Sr}/^{86}\text{Sr}$	Locality	Level	^{14}C date
RSF05Sr42	EB 91-421	<i>Thomomys talpoides</i>	Bone	Humerus	0.71175	LC	10	751
RSF05Sr43	EB 92-92	<i>Thomomys talpoides</i>	Bone	Humerus	0.71086	LC	12	751
RSF05Sr44	EB 92-92	<i>Thomomys talpoides</i>	Bone	Humerus	0.71148	LC	12	751
RSF05Sr45	EB 91-231	<i>Thomomys talpoides</i>	Whole tooth	Tooth fragment	0.70667	WF	14	2878
RSF05Sr46	EB 91-137	<i>Thomomys talpoides</i>	Whole tooth	Tooth fragment	0.70661	WF	9	2070
RSF05Sr47	EB 91-19	<i>Thomomys talpoides</i>	Whole tooth	Tooth fragment	0.70651	WF	Undifferentiated	–
RSF05Sr48	EB 91-83	<i>Thomomys talpoides</i>	Whole tooth	Tooth fragment	0.70698	WF	2	495
RSF05Sr49	EB 91-80	<i>Thomomys talpoides</i>	Whole tooth	Tooth fragment	0.70681	WF	9	2070
Sr02YP26	95–03	<i>Cervus elaphus</i>	Enamel	Incisor	0.70839	YNP	Modern	0
Sr02YP19	96–100	<i>Cervus elaphus</i>	Enamel	Incisor	0.70912	YNP	Modern	0
Sr02YP24	98–242	<i>Cervus elaphus</i>	Enamel	Incisor	0.71034	YNP	modern	0
Sr02YP25	95–34	<i>Cervus elaphus</i>	Enamel	Incisor	0.70827	YNP	Modern	0
Sr02YP22	96–50	<i>Cervus elaphus</i>	Enamel	Incisor	0.71164	YNP	Modern	0
Sr03186	02046	<i>Bison bison</i>	Enamel	Incisor	0.70690	YNP	Modern	0
Sr03181	02154	<i>Bison bison</i>	Enamel	Incisor	0.70806	YNP	Modern	0
Sr03187	02047	<i>Bison bison</i>	Enamel	Incisor	0.70782	YNP	Modern	0
Sr03184	02150	<i>Bison bison</i>	Enamel	Incisor	0.70738	YNP	Modern	0
Sr02YP15	96–153	<i>Cervus elaphus</i>	Enamel	Incisor	0.70815	YNP	Modern	0
Sr02YP16	96–176	<i>Cervus elaphus</i>	Enamel	Incisor	0.70728	YNP	Modern	0
Sr02YP10	95–52	<i>Cervus elaphus</i>	Enamel	Incisor	0.70756	YNP	Modern	0
Sr02YP25	95–34	<i>Cervus elaphus</i>	Enamel	Incisor	0.70801	YNP	Modern	0

Radiocarbon age represents the average for bone date in levels where ^{14}C was analyzed (Hadly 1996; Porder et al. 2003). In levels where ^{14}C was not analyzed, dates are estimated through regression analysis (level vs. ^{14}C date)

our results support the conclusion that large animals gather resources from a larger geographic area than do smaller body-sized animals.

Adjustments in the size of a species' home range might be expected for a particular species with the changes in climate and the environment that have occurred in YNP over the last 3,000 years (Hadly 1996, 1999; Whitlock 1993). Specifically, foraging range is expected to increase during colder times to obtain the necessary resources. The major climatic changes at YNP occurred during the Medieval Warm Period [1,150–650 years before present (ybp)] and the Little Ice Age (650–50 ybp). Climatically, temperature changes during these two events are on the order of $\pm 1^\circ\text{C}$, with the Medieval Warm Period being dry and the Little Ice Age having variable precipitation levels (Barnosky et al. 2003; Hadly 1996, 1999). The lack of differences in $^{87}\text{Sr}/^{86}\text{Sr}$ value across levels (representing various time intervals) within either Lamar Cave or Waterfall Locality indicates that the climatic changes that occurred during the Holocene had no demonstrable effect on the utilization of landscape by these mammals, no matter what their size. Further, because the species within the small and medium body mass categories were likely the prey of either raptors or mammalian carnivores (e.g., coyotes) and do not show $^{87}\text{Sr}/^{86}\text{Sr}$ differences over time in the fossil localities, these

results support the assertions that the foraging radii of predators did not change over time and that the deposits derive from fauna that lived in close proximity to these sites (Porder et al. 2003).

More broadly, there has been debate recently over whether or not the niches of species are conserved (Peterson et al. 1999; Weins and Graham 2005). Many studies analyzing niche conservatism compare characteristics of extant species or use models to determine whether niches are maintained over time (Peterson et al. 1999; Weins and Graham 2005). Understanding whether or not these characteristics are conserved implies temporal context, and the analysis of particular niche axes over time appears to be a more straightforward way to assess niche conservatism. Home range is a significant component of a species niche. Our data clearly show that these mammalian niches have been conserved over the past 3,000 years of environmental variation in the ecosystem.

Conclusions

Identifying how individuals use the landscape is important if we are to gain complete understanding of the niches of species. Our study analyzed the effects of body size on

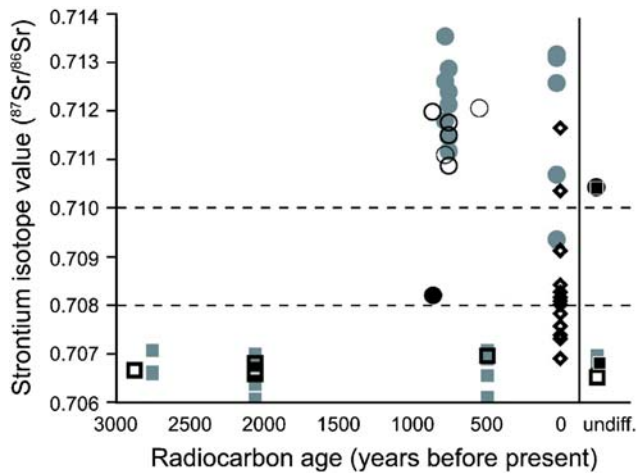


Fig. 2 Strontium isotope values of small (*hollow symbols*), medium (*gray symbols*), and large (*black symbols*) body mass mammals from modern Yellowstone National Park (*diamonds*), Waterfall Locality (*squares*), and Lamar Cave (*circles*) plotted by radiocarbon age (years before present). Radiocarbon age represents the average of bone dates in levels where ^{14}C was analyzed (Hadly 1996; Porder et al. 2003). In levels where ^{14}C was not analyzed, dates are estimated through regression analysis (level vs. ^{14}C date). Specimens were categorized as undifferentiated (*undiff.*) if they had been excavated but could not later be placed into a specific level. Modern specimens were taken from carcasses of animals that had recently died. Strontium isotope values above the *dashed line* at 0.710 are characteristic of substrate surrounding Lamar Cave, values below 0.708 are characteristic of substrate surrounding Waterfall Locality, and values between *dashed lines* indicate the use of mixed substrates. Standard error is included, but is not visible since the error is smaller than the datapoint symbols

landscape use of mammals collected from samples covering the past 3,000 years. We examined fossils from two paleontological sites and investigated strontium isotope ratios of specimens to determine whether there was a discernible relationship between body size and foraging range and how foraging range changed in response to climate variability. Our results show that medium- and large-sized mammals used more of the landscape than individuals of smaller-sized species. In support of niche conservatism, we found that this pattern did not change over the past 3,000 years, despite recorded climatic fluctuation. Lastly, our study corroborates previous evidence suggesting that these two fossil sites derive from the local community of mammals. More generally, our data suggest that where there is suitable bedrock, the analysis of $^{87}\text{Sr}/^{86}\text{Sr}$ values appears to be a useful approach to studying how organisms, both extant and extinct, use the landscape around them.

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