PALEOZOOLOGICAL STABLE ISOTOPE DATA

FOR MODERN MANAGEMENT OF HISTORICALLY EXTIRPATED

MISSOURI BLACK BEARS (*URSUS AMERICANUS*)

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by

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The undersigned, appointed by the dean of the Graduate School, have examined the thesis entitled

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and hereby certify that, in their opinion, it is worthy of acceptance.

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PALEOZOOLOGICAL STABLE ISOTOPE DATA FOR MODERN MANAGEMENT OF HISTORICALLY EXTIRPATED MISSOURI BLACK BEARS (*URSUS AMERICANUS*)

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ABSTRACT

Human population growth and intensification of resource extraction during the 19th century changed the American landscape. Deforestation, residential sprawl and hunting activities impacted the behavior and sometimes the existence of native species. By the early 1900s, North American black bears (*Ursus americanus*) were extirpated from Missouri. Modern efforts to restore this species to the region are guided by the assumption that extant extra-local black bear ecology accurately depicts native Missouri ursid ecology. Paleozoological data provide the only means to test this assumption. Stable carbon and nitrogen isotope analysis of skeletal remains of ten late Holocene black bears from Lawson Cave in central Missouri reveals three aspects of native black bear diet: 1) Lawson Cave black bears are isotopically distinct from herbivores and carnivores; 2) There is no clear trend in black bear diet over the past 600 years; and 3) Lawson Cave black bear diet is not significantly different from that of modern black bears. Native Missouri black bears, as reflected by the Lawson Cave ursids, are no different from extra-local modern black bears in terms of diet. Therefore, these ecological data can be applied to future management and conservation planning regarding Missouri black bears by indicating appropriate regions (which can support the resource-use habits of black bears) for relocation programs.

CHAPTER 1: INTRODUCTION

Prior to the 20th century, *Ursus americanus* (North American black bear) was widespread throughout North America, reaching as far north as Alaska and as far south as Mexico (Pelton 2000). However, human population growth, expansion across the landscape and increased resource extraction during the 19th century took its toll. By the early 1900s, *U. americanus* was all but eliminated from the state of Missouri due to large-scale, unregulated hunting and deforestation by Industrial-aged human populations. Grayson and Delpech (2001, 2003) termed this competition between humans and bears for habitats and resources the Kurtén Response, after vertebrate paleontologist Björn Kurtén who first suggested Neanderthals and extinct European cave bears (*Ursus* [subgenus *Spelearctos*] spp.) competed for scarce (living and hibernation, respectively) cave space.

Growing awareness of the dramatic historic decrease in *U. americanus* numbers and geographic range by wildlife conservationists highlights the need for ecological data on this species. Relevant ecological data include habitat range, social behaviors and diet. While zoologists and ecologists can glean this information from modern populations, paleozoology offers the unique time perspective particularly relevant to future attempts to rejuvenate this species in the state of Missouri. Paleozoological analysis of pre- and periextirpation *U. americanus* remains from the region can reveal if there have been changes in *U. americanus* behavior and diet over the past several hundred years. If differences are observed then it is likely that modern behaviors do not reflect native ursid behaviors in the region. Fortunately, paleodata can illuminate pre-extirpation native ursid behaviors, and thus can indicate how best to approach future restoration efforts. For example, paleozoology can identify the historic range of *U. americanus*, their preferred habitat and general diet. This knowledge can be used to determine where a future relocation program would be most successful. Rejuvenation of this species in Missouri may yield positive social and economic consequences for residents, including restoration of a sense of state pride and identity and encouragement of ecotourism, which could bring considerable revenue to the state.

Having been extirpated from Missouri by about A.D. 1900 (Pelton 2000; Schwartz and Schwartz 1981), *U. americanus* has received much attention from wildlife advocates. Recent wildlife management activities have involved the investigation of small (recent immigrant or old relic) populations in southern Missouri (McKinley 1962; Schwartz and Schwartz 1981; Smith and Clark 1994). The paleontological Lawson Cave collection analyzed herein is relevant to current and future attempts to manage this species in Missouri because it dates to the period just prior to local *U. americanus* extirpation. Patterns in ursid diet and habitat use prior to extirpation can help guide future management efforts. How successful might relocation programs for black bears be in Missouri? What food resources did native Missouri black bears consume? Where in Missouri are sufficient populations of these resources located today and would these regions be able to support black bear populations today?

Dietary data are critically important for identifying suitable habitats for management of local Missouri black bear populations. We know that black bears are flexible consumers, but investigations for future conservation programs should concern questions about what native black bears should eat (or what they did eat prior to Industrial-aged anthropogenic effects), and not what black bears can eat (i.e., human refuse composed largely of corn [C_4] products). Due to extirpation of Missouri black bears, we have no modern reference data or benchmarks with which to assess native Missouri black bear diet. Thus any sort of conservation, management, or restoration activity must assume that native Missouri black bears had the same ecology as extant extra-local (non-Missouri) black bears. Fortunately, analysis of paleozoological remains can answer questions about native Missouri black bear diet and habitat use that allow this assumption to be tested.

Paleozoology and Conservation Biology

Paleozoology is the study of paleontological (ancient faunal remains without associated human artifacts) and zooarchaeological (faunal remains with associated human artifacts) materials (Grayson 1984; Lyman 2008). Paleozoological data describe the structure and composition of faunal assemblages, and include measures of taxonomic abundance (number of individuals per taxon), richness (number of taxa) and evenness (distribution of individuals across taxa) (Lyman 2008). Thus, paleozoology is simply the study of past faunal populations, and its goals include reconstruction of past environments and animal (including human) behavior (i.e., subsistence, migration and social systems). Recently, paleozoological data have contributed to conservation and management of modern species because such data offer unique insight into long-term ecological patterns (Etnier 2004; Harpole 2004; Hughes 2004; Lyman 1996, 2006; Newsome et al. 2007). Paleozoological specimens analyzed herein belong to an assemblage from Lawson Cave in central Missouri.

During a preliminary study in Fall 2008, stable carbon and nitrogen isotope values were measured for bone collagen samples from three taxa: North American black bear (*Ursus americanus)*, wolf/dog (*Canis* spp.), and white-tailed deer (*Odocoileus virginianus*). The black bear was a paleontological specimen from Lawson Cave (LCB001) and the canid and deer were modern specimens from Missouri. Despite the lack of temporal control on these specimens, results indicated high reproducibility of stable carbon ($\delta^{13}C$) and stable nitrogen ($\delta^{15}N$) isotope values for individual specimens, as well as identifiable isotopic differences between taxa occupying different trophic positions: herbivores (*O. virginianus*), omnivores (*U. americanus*) and carnivores (*Canis* spp.) (Table 1).

Table 1. Average stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values and standard deviations (σ) of replicate measurements (N_r) for specimens analyzed during the pilot study. All specimens were collected from Missouri and are curated in the University of Missouri Department of Anthropology Zooarchaeology Laboratory.

Taxon	**Common Name**	N_r	$\delta^{13}C$	σ_C	$\delta^{15}N$	σ_N
Odocoileus virginianus	White-tailed deer	5	-21.23	2.30	4.31	0.37
Ursus americanus	N. American black bear	6	-19.51	0.31	4.44	0.28
Canis spp.	Wolf/dog	2	-15.16	0.08	7.18	0.05

As expected the lowest $\delta^{13}C$ and $\delta^{15}N$ values were obtained for *O. virginianus*, which indicated a diet rich in C_3 plants and little to no meat. Conversely, the highest $\delta^{13}C$ and $\delta^{15}N$ values were obtained for *Canis* spp., and indicated a diet of mixed C_3-C_4 plants and plant consumers (meat). Stable carbon and nitrogen isotope values for *U. americanus* fell between those of *O. virginianus* and *Canis* spp. These $\delta^{13}C$ and $\delta^{15}N$ patterns indicated a potential to answer questions about *U. americanus* diet in Missouri: Where do these animals fall on a continuum of omnivory; and, are modern Missouri black bears similar to 200 to 600 year old Missouri black bears with regard to diet? This thesis expands upon the preliminary study and investigates *U. americanus* diet in Missouri over the past several hundred years using paleozoological remains in an attempt to elucidate patterns of *U. americanus* habitat use that are relevant to modern conservation and *U. americanus* restoration and relocation efforts.

Paleozoological specimens (i.e., approximately 200 yr B.P. to 600 yr B.P.) collected from Lawson Cave in southern Boone County, Missouri, are analyzed for stable carbon and nitrogen isotopes. Stable carbon and nitrogen isotope values are measured from extracted bone collagen to determine relative contributions of C_3 and C_4 plant constituents and meat to late prehistoric/early historic period *U. americanus* diet. Given that *U. americanus* is omnivorous, stable nitrogen isotope values for this taxon should be lower than those of carnivorous taxa (i.e., *Canis* spp. and *Lynx rufus*) and higher than those of herbivorous taxa (i.e., *Marmota monax* and *Sylvilagus floridanus*). However, given that *U. americanus* eats a primarily vegetarian diet I suspected that Lawson Cave ursid isotope values would be most similar to the isotope values of Lawson Cave herbivores. If *U. americanus* individuals consumed more meat on average than omnivorous Lawson Cave taxa (i.e., *Didelphis virginiana* and *Sus scrofa*) then stable nitrogen isotope values for ursids would be higher than those of omnivorous Lawson Cave taxa; if the Lawson Cave ursids consumed less meat on average than the omnivorous taxa, then I expected the measured stable nitrogen isotope values to be lower than those of Lawson Cave omnivores. High stable nitrogen isotope values are expected for carnivorous taxa given that meat composed a large portion of their diet. I expected the highest observed stable carbon isotope values to be measured in *S. scrofa* because these specimens, if farm-raised, likely consumed high quantities of corn, a C_4 plant. If *U.*

americanus individuals primarily consumed nuts and berries (C_3 plant material), I expected to observe low stable carbon isotope values in their collagen.

In addition to comparing 200 to 600 year old *U. americanus* with contemporaneous herbivores, omnivores and carnivores from Lawson Cave, they were also compared to one another and to modern (<150 year old) *U. americanus* specimens to investigate black bear diet through time. If Lawson Cave *U. americanus* individuals consumed a diet similar to that of modern black bears then stable isotope values of the two groups should be statistically indistinguishable. If *U. americanus* diet has changed over the last 600 years bone collagen isotope values for (geologically) old specimens and (geologically) young specimen should be significantly different. This test was enhanced by comparing fluorine (F) concentrations, which give a relative order of deposition (and by implication, the relative calendric age) of individual bears, and isotope values from the same individual. A correlation between F concentration and stable carbon or stable nitrogen isotope values could indicate change in black bear diet through time.

Thesis Structure

In chapter 2 I describe the materials and methods used to answer three research questions and to test the critical assumption regarding similarity of black bear ecology in Missouri and elsewhere. Chapter 3 presents the results of my analysis, including the reliability of the method, trophic-level differences, temporal variation in ursid diet, and comparison of Lawson Cave and modern ursids. Statistical analyses of stable isotope data indicate: 1) There is more variation among individuals than among replicates of the same individual; 2) There is more variation among taxa than within taxa; 3) All three trophic levels have unique isotope signatures; 4) Lawson Cave black bears are distinguishable from contemporaneous herbivores; and 5) Lawson Cave black bears are no different from modern black bears in terms of isotopic values.

Chapter 4 discusses patterns observed in the data, including elevated stable nitrogen isotope values, inter-element variation, and black bear diet. The highest stable nitrogen isotope values were observed in carnivores and nutritionally stressed individuals. The highest stable carbon isotope values were observed in pig specimens and one canid, and they likely indicate consumption of some C_4 (corn and herbaceous plants) materials or C_4-consuming herbivores. In contrast, all other specimens analyzed had stable carbon isotope values within the expected range for C_3 (tree) consumption. Lawson Cave black bears also had carbon isotope values within the range expected for C_3 consumption; nitrogen isotope values for ursids indicated meat consumption at the secondary consumer (omnivore) level.

Chapter 5 concludes the study by contextualizing the significance of my results and highlighting their significance for conservation biology. This study lends support to the ecological assumption that native Missouri black bears had the same ecology as non-Missouri black bears. Therefore, given that some deciduous forests still exist in the state and that many of these once decimated forests are being revived, non-Missouri black bears should be able to successfully re-populate regions of the state. Whether current black bears in Missouri are immigrants from adjacent states or relict natives, dietary data will be critically important for understanding how best to manage these populations and any future populations. Future efforts to rejuvenate black bears in Missouri will have positive social and economic consequences for the state and its residents. Presence of black bears will strengthen the sense of Show-Me state identity of residents, and they may provide future prospects for ecotourism and new revenue for the state.

CHAPTER 2: METHODS AND MATERIALS

Today wildlife managers, conservation biologists and restoration ecologists assume that non-Missouri black bear ecology accurately reflects native Missouri black bear ecology. In order to test this assumption, I measured stable carbon and nitrogen isotopes and fluorine concentrations in an assemblage of paleontological bone specimens with the goal of answering three questions. First, are there observable differences in diet among omnivores, herbivores, and carnivores from Lawson Cave, and more specifically, was Lawson Cave ursid diet isotopically different from that of co-occurring herbivores? Second, is there evidence that native Missouri *U. americanus* diet changed through time, as reflected by the Lawson Cave ursids? And third, do Lawson Cave bears differ from modern Missouri black bears in terms of diet? These questions could be answered any number of ways *if* native Missouri black bears still existed. Our best evidence suggests they do not (Schwartz and Schwartz 1981). Therefore, to produce answers, we must examine paleozoological remains of Missouri black bears, and thus, the kinds of analytical techniques that can be successfully used are constrained.

Lawson Cave

Lawson Cave (Figure 1) is a natural trap cave located approximately 8 kilometers (5 miles) south of Columbia, Missouri, in Three Creeks Conservation Area (Wolverton 1996, 2001). The conservation area receives its name for the three creeks (Turkey Creek, Bass Creek, and Bonne Femme Creek) that run through the deciduous forest, which today consists primarily of eastern red cedar trees (*Juniper virginiana*). A team of University of Missouri—Columbia (MU, hereafter) zoology professors and students excavated Lawson Cave from 1954 to 1960. They recovered the skeletal remains of 16 taxa, including several representatives of *Ursus americanus*, *Marmota monax* (woodchuck), *Didelphis virginiana* (opossum), *Sciurus* spp. (squirrel), *Canis* spp. (dog or coyote), *Sus scrofa* (domestic pig) and *Sylvilagus floridanus* (cottontail rabbit).

After excavation the Lawson Cave faunal collection sat virtually untouched for thirty years, though a brief report was published incorrectly suggesting the ursid remains represented grizzly bears (*Ursus arctos*) because of their seemingly large tooth-sizes (Wells 1959). The collection, currently curated in the MU Department of Anthropology Zooarchaeology Laboratory, was analyzed in the late 1990s by MU Anthropology graduate student Steve Wolverton (Wolverton 1996, 2001, 2006). The Lawson Cave collection is particularly interesting because faunal analysis indicates that (1) Lawson Cave is a natural trap cave, (2) faunal accumulation was largely, if not entirely, during the historic period, (3) the ecozone during accumulation was (as it is today) a deciduous-forest habitat, and (4) there is a large number of *U. americanus* individuals represented ($n \geq 10$, determined by frequency of right femora). Furthermore, the ursid accumulation is biased with a high representation of young-adult and prime-adult males, likely an artifact of black bear ecology and behavior (i.e., males emigrate from the natal territory to establish new territories) (Wolverton 1996, 2001). Wolverton (2001) submitted three Lawson Cave *U. americanus* ilia for radiocarbon dating. All three dates indicated historic period accumulation (AA38931, 233 ± 39; AA38932, 207 ± 34; CAMS-27141, 170 ± 60 C14 yr B.P.) (Wolverton 2001).

Once the site and collection were fully characterized, Wolverton used these data to investigate temporal and regional variation observed in Midwestern ursids. Wolverton and Lyman (1998) investigated the long-held assumption of continent-wide gradual and continuous size diminution of *U. americanus* throughout the Holocene, and concluded that *U. americanus* body-size is not a valid chronometer. Instead, morphometric variation is more likely linked to phenotypic plasticity and geographic differences due to resource availability (Wolverton and Lyman 1998). Additionally, Wolverton (2006) used the Lawson Cave collection to test the Kurtén Response proposed by Grayson and Delpech (2001, 2003). He found that paleozoological and historical data support the idea that North American black bears were out-competed for land and resources during the 19th century as human population and resource extraction expanded. The Lawson Cave collection was an appropriate test for this phenomenon due to its age (approximately 200 to 600 yr B.P.), location, and composition.

Subsequently, MU Anthropology graduate student Corey Hudson (2009) selected the Lawson Cave ursid collection for analysis of ancient DNA (aDNA). Working with professors in the MU Department of Biological Sciences, Hudson (2009) investigated the relatedness of Lawson Cave black bears and modern black bears in southeastern Missouri to determine whether the modern population is a relictual population or made up of recent immigrants from Arkansas that are descendants of individuals translocated from Manitoba and Minnesota. While aDNA could not give a definitive answer to this question, Hudson's results bear directly on current conservation efforts involving *U. americanus*. Furthermore, his techniques and results can be applied in any modern conservation campaign.

Realizing that our efforts served similar goals (to improve our understanding of a historically extirpated population of *U. americanus*), Hudson and I pooled our efforts and limited financial resources to develop a greater understanding for the geologic age of the Lawson collection. Ten *U. americanus* right femora (used to determine the minimum number of individuals [MNI]) were selected for fluorine-concentration determination by neutron activation analysis (NAA). NAA was conducted at the MU Research Reactor (MURR) by Rosania and Boulanger (2009) to determine the concentration of fluorine (F) in each Lawson Cave black bear specimen. Based on the well-demonstrated fact that fluorine from groundwater is absorbed by buried bone (Lal 1975; McConnell 1962; Van de Water 1953), we determined the relative order of deposition for the ten *U. americanus* individuals. *U. americanus* femora were rank-ordered from least to greatest fluorine content; bones with lower fluorine content indicated a more recent depositional event and higher fluorine content indicated an earlier depositional event. The depositional event is assumed to correspond with the time of death.

Subsequently, Hudson and I subsampled three *U. americanus* femora (one with low F-content, one with average F-content, and one with high F-content) for direct accelerator mass spectrometry (AMS) radiocarbon dating at the University of Arizona. The fluorine concentrations and AMS radiocarbon dates indicate that the previous assumption, that the ursid remains were all deposited roughly contemporaneously, is false (AA84746, 229 ± 41; AA84747, 206 ± 41; AA84748, 630 ± 42 C14 yr BP) (Appendix, Table 1). Flourine content of both and a radiocarbon age of one suggest that two individuals (LCB008 and LCB010) are about 400 years older than the other Lawson cave *U. americanus* specimens. Consistent replicate testing of these two individuals by both dating methods indicates that this observation is not due to sampling or instrument error. These two geologically older individuals extend the time span for which I can explore potential changes in diet. Have black bears in Missouri consumed roughly consistent diets for the past 600 years? Or has black bear diet in the region changed? In this thesis, stable isotope analysis of ten paleontological (Lawson Cave) and two modern (Missouri) black bears provides answers to these and other questions.

Ursus americanus Ecology

In the Linnean system of taxonomy *Ursus americanus* is in the order Carnivora and the family Ursidae (Lariviere 2001). But not all members of Carnivora are carnivores. Ursidae (bear family) and Procyonidae (raccoon family) contain omnivorous and herbivorous species. For example, within Ursidae, *Ailuropoda melanoleuca* (giant panda), which is found throughout southern and central China, subsists almost entirely on bamboo, and is thus an herbivore (Chorn and Hoffman 1978). The opposite extreme (full carnivory) is represented by *Ursus maritimus* (polar bear), which primarily subsists on seal (DeMaster and Stirling 1981; Pasitschniak-Arts and Messier 2000). Where does *U. americanus* fall on this dietary continuum from herbivory to carnivory? In comparison with other ursids, black bears are the most herbivorous of the omnivorous ursids (Boileau et al. 1994); therefore, black bears are one step above *A. melanoleuca* on the trophic-level dietary continuum. Interestingly, diet is linked to both the physiology and behavior of organisms; therefore, diet is a critical component to understanding black bear habitat use and distribution.

Extant black bears exhibit exploded polygyny, a mating system wherein one male mates with several females. This mating system influences residential patterns, and thus, habitat use of black bears. Females occupy solitary regions based on resource availability (i.e., larger territory in less resource-rich areas), and males roam much larger territories that encompass the ranges of multiple females (Landers et al. 1979; Lariviere 2001; Whitaker and Hamilton 1998). Extant black bears have few offspring that mature slowly, thus requiring significant maternal investment during the first two years of life (Doan-Crider and Hellgren 1996). Therefore, primary productivity strongly influences black bear behavior, including residential and mating patterns, because it influences what is available for consumption (Mosnier et al. 2008).

Modern black bears are opportunistic feeders, and eat a variety of foods including berries, grass, tree bark and seeds. Although plant material usually constitutes the majority of their diet (Boileau et al. 1994; Schullery 1986), *U. americanus* also consume animal foods, such as ants, crickets, fish, frogs, small rodents and carrion (Schwartz and Schwartz 1981). Diet of modern bears is drastically affected by deforestation and urban sprawl; many bears today are found living on the periphery of modern suburbs and have been increasingly observed eating human refuse. *U. americanus* will rummage through human trash in search of edible materials. Access to alternative (non-natural) resources and increased interaction with people has caused a noticeable change in *U. americanus* behavior and diet (Beckmann and Berger 2003). Determination of black bear diet prior to the modern significant contribution from human refuse requires analysis of an assemblage that predates the Industrial era. Fortunately, analysis of paleozoological ursid remains from Lawson Cave can answer questions about black bear diet prior to their consumption of excessive human waste, which may be observed in modern individuals.

Paleozoology can indicate what was available on the landscape for black bear consumption, and particularly, what plant and animal materials were included in their diet. For example, analysis of coprolites can identify plant seeds and taxonomically specific skeletal specimens included in an organism's diet, quantification and distribution of skeletal elements on the landscape and tooth marks on those elements can be used in conjunction with known behavioral patterns to identify taxa responsible for creating skeletal assemblages, and stable isotope analysis can indicate an organism's trophic position and distinguish between photosynthetically distinct types of plants included in their diet. Dietary data will be critically important for identifying suitable habitats for management of local Missouri black bear populations. We know that black bears are flexible consumers, but it is necessary to determine what Missouri black bears should eat. Due to extirpation of Missouri black bears, we have no modern reference data with which to assess native Missouri black bear diet. Thus any sort of conservation, management, or restoration activity necessarily assumes that native Missouri black bears had the same ecology as extant extra-local (non-Missouri) black bears. Fortunately, analysis of paleozoological remains can answer questions about native Missouri black bear diet and habitat use that allow this assumption to be tested. How might the requisite data be gleaned from paleozoological remains?

Stable Isotope Analysis

Stable isotopes in an organism's tissues allow one to reconstruct the organism's diet. They do not allow one to determine the actual constituents of a meal, but instead indicate the relative proportions of meat and vegetation, as well as allow distinction between two groups of plants (C_3 and C_4) that utilize different photosynthetic systems. Therefore, stable isotopes can be used to determine if late Holocene *U. americanus* in Missouri were as vegetarian as their modern counterparts. And if so, we can determine which of the two general types of plants they consumed.

Stable carbon isotope values can reveal the relative contribution of C_3 and C_4 plants to an organism's diet (Cerling and Harris 1999; DeNiro and Epstein 1978). Stable nitrogen isotope values indicate the amount of meat consumed, and thus the trophic position of an organism (DeNiro and Epstein 1978). These dietary signatures can be found in many tissues, including bone, enamel, hair, feather, liver, and fingernail/claw. The material chosen for analysis is dependent upon the research questions being asked and the nature of the study. For example, teeth, hair, and nails offer small windows into the period of the organism's life in which the material formed, while other materials, like liver and bone, record an average isotopic value based on the most recent dietary constituents and the tissue replacement rate of the material (i.e., bone remodeling rate). The annual turnover rate for cortical bone is approximately 2.5%; therefore, cortical bone records a long-term average of dietary constituents (Chrisholm et al. 1982; Harkness and Walton 1972; Libby 1964; Pate 1994; van der Merwe and Vogel 1978). Taphonomic factors often limit investigation of dietary behaviors of extinct taxa to analysis of apatite (inorganic material) in enamel because collagen (organic material) preserves less frequently. Analysis of live organisms, though, requires tissues that can be extracted noninvasively, such as fingernails, hair, and feathers (Buchardt et al. 2007; Codron et al. 2007; Schoeninger et al. 1999). Fortunately, historic period studies often have several tissues to choose from, including both organic and inorganic material. The material chosen should reflect the research question. For this study, I required a measure of the average diet of each individual during the last several years of life to minimize fluctuations due to seasonal variation in resource acquisition. Stable isotope values measured in bone collagen offer this long-term average dietary information.

Since the early dietary studies of Vogel and van der Merwe (1977) and DeNiro and Epstein (1978, 1981) carbon and nitrogen isotopes have been increasingly used in subsistence reconstruction studies. In order to understand how carbon and nitrogen isotopes are used in such studies, it is first necessary to understand the isotopic systems involved and the effects of different nutrient sources on the isotopic signatures recorded in the tissues of an organism. The photosynthetic pathway utilized by a plant determines its $\delta^{13}C$ signature, and there are two isotopically distinct photosynthetic pathways (C_3 and C_4). Another photosynthetic pathway, CAM (Crassulacean acid metabolism), alternates between the C_3 and C_4 pathways. Thus CAM plants are not isotopically distinct from C_3 and C_4 plants (O'Leary 1988). CAM plants live in extremely hot, dry climates (i.e., deserts) and are primarily succulents; thus, they are not a major vegetation type in Missouri.

Stable Carbon Isotopes

Until roughly 8 mya the C_3 (Calvin-Benson) photosynthetic pathway dominated the ecosphere. Subsequent changes in temperature, precipitation, atmospheric carbon dioxide levels (Royer et al. 2004), fire frequency (Osborne 2008), and possibly changes in the galactic cosmic ray flux (Shaviv and Veizer 2003) encouraged the expansion of C_4 (Hatch-Slack) photosynthesizing plants. C_4 plants, such as grasses and some forbs, generally thrive in hot, dry, and/or carbon dioxide-deficient environments. They function as relatively closed systems, closing their stomata during the hottest period of the day and using internal CO_2 more efficiently than C_3 plants. Thus, they make use of both light and heavy carbon isotopes (^{12}C and ^{13}C, respectively), which results in high $\delta^{13}C$ values ranging between -14‰ and -9‰. In contrast, C_3 plants, such as trees, shrubs, bushes, and most forbs, generally occupy temperate, moist, and/or carbon dioxide-rich environments. Consequently, they function as open systems, keeping their stomata open and selectively using the lighter carbon isotope (^{12}C) during photosynthesis. Therefore, C_3 plants are depleted in ^{13}C and have low $\delta^{13}C$ values ranging between -30‰ and -22‰. Isotopic signatures of C_3 and C_4 plants do not overlap, making their identification possible from only carbon isotope values (Bender 1971; Cerling et al. 1993; Cerling et al. 1997; Farquhar 1983; Farquhar et al. 1989; Winter et al. 1976).

Stable carbon isotope values in a consumer's tissues reflect the average $\delta^{13}C$ value of that consumer's diet. The old proverb *you are what you eat* mostly holds true, with the addition of a tissue specific fractionation factor. Buchardt et al. (2007) determined that compared to diet, fingernails are enriched in ^{13}C by approximately 3‰. Therefore, $\delta^{13}C$ values measured in an organism's fingernails are roughly 3‰ higher than the individual's average diet. Cerling and colleagues (1997) have shown that tooth enamel is enriched in ^{13}C by roughly 9‰ to 14‰ compared to the organism's diet; therefore, the $\delta^{13}C$ value for an individual's enamel will be approximately 9‰ to 14‰

higher than its diet. As for bone collagen, the tissue analyzed herein, carbon isotope values are enriched by approximately 5‰ to 6‰ (Bumsted 1983; van der Merwe 1982). This means that the isotopic values measured in Lawson Cave bone collagen will be enriched by 5‰ to 6‰ compared to each organism's diet.

Stable Nitrogen Isotopes

In contrast to carbon isotopes, which differentiate between C_3 and C_4 plants, nitrogen isotopes distinguish between trophic positions. Plants absorb their nutrients through soil and obtain nitrogen through soil ammonium (NH_4^+) and/or nitrate (NO_3^-) (Pate 1994). Consequently, high-nutrient soil will grow plants with heavy nitrogen content in their tissues. When such producers (plants) are consumed, their nitrogen content enters the consumer's body, and is subsequently fractionated by approximately 3‰ because of selective use of the lighter isotope (^{14}N) in metabolic reactions (Minagawa and Wada 1984). Therefore, each consecutive trophic level in a given environment is enriched in ^{15}N (relative to ^{14}N) by approximately 3‰. For example, omnivores will exhibit $\delta^{15}N$ values approximately 3‰ higher than herbivores and carnivores will exhibit $\delta^{15}N$ values roughly 3‰ higher than omnivores.

There are some confounding factors to acknowledge when using stable nitrogen isotopes for dietary inference. Nitrogen content is highly influenced by the nutrient source (i.e., soil), and is therefore site specific. It would be invalid to compare $\delta^{15}N$ values for taxa living in different environmental contexts. If such a study were necessary, a full range of $\delta^{15}N$ values for representative taxa would be necessary to allow for analysis of relative differences between source values for each site. This would be possible since the 3‰ isotopic-enrichment occurs independently of the environment.

Besides nutrient-source differences, Minagawa and Wada (1984) investigated possible differences in $\delta^{15}N$ values according to biological age of an animal. They determined that $\delta^{15}N$ values do not vary with age unless the individual consumes a distinctly different diet at different stages of life. For example, infant mammals that have not been weaned from their mother's milk reveal high $\delta^{15}N$ values making it look as though juvenile individuals were consuming food one trophic level above that of their mother (Fogel et al. 1989; Nelson et al. 1998). An individual's health and body size have also been found to influence $\delta^{15}N$ values. The metabolic response of a nutritionally stressed individual involves more efficient use of heavy nitrogen (^{15}N), thus elevating $\delta^{15}N$ values of their tissues (Hobson et al. 1993; Nelson et al. 1998). With reference to body size differences, Lee-Thorp et al. (1989) and Cerling and Harris (1999) demonstrated that metabolic differences between small and large mammals create slightly different nitrogen isotope signatures. Large-bodied mammals are consequently slightly heavy isotopically compared to smaller-bodied mammals. Despite these factors, stable nitrogen isotopes can be used to compliment stable carbon isotope values so long as the investigator diligently examines factors relevant to his/her study.

Any study attempting to reconstruct diet via chemical analyses must be attentive to possible diagenetic factors that could alter the chemical signatures found in the tissues analyzed (DeNiro 1985; DeNiro and Epstein 1981; Ezzo 1994; Krueger 1991; Pate 1994; van Klinken and Hedges 1995). Tooth enamel is relatively resistant to diagenetic factors and preserves most effectively in the fossil record; therefore, it is generally the tissue of choice in fossil hominid studies. While cortical bone is more susceptible to diagenesis, it is often chosen (when available) over tooth enamel because (1) it offers a window into the organism's average diet over a longer time span, (2) much more material can be extracted from the sample for initial analyses and reliability testing, and (3) teeth are the most diagnostic skeletal part for identification of taxa and are saved from destructive analyses whenever possible.

Sample Preparation

To determine the relative contribution of meat and vegetation, and the proportion of C_3 and C_4 plants in the contribution from vegetation, to *U. americanus* diet, stable carbon and nitrogen isotope concentrations were measured on ten Lawson Cave black bear right femora. Three replicates were analyzed for each black bear individual to measure reliability and replicability of the technique. Additionally, 14 specimens from five different taxa were sampled from the Lawson Cave collection (Table 2). Two taxa, *Marmota monax* (woodchuck) and *Sylvilagus floridanus* (cottontail rabbit), were selected to establish the herbivory end of the dietary isotope continuum. *M. monax* was represented by three specimens (one left femora and two left mandibles) and *S. floridanus* was represented by five specimens (five right femora). Two omnivorous taxa, *Didelphis virginiana* (opossum) and *Sus scrofa* (pig), were selected for comparison with the omnivorous ursids. *D. virginiana* was represented by one specimen (left femur) and *S. scrofa* was represented by four specimens (four left femora). Lastly, one taxon, *Canis* spp. (dog or coyote), was selected to establish the carnivory end of the continuum, and was represented by one specimen (left femur).

Because carnivorous taxa are underrepresented in the Lawson Cave collection, two additional carnivore specimens were selected from another collection to firmly establish the isotope signatures for carnivores and the boundary distinguishing this trophic group on the continuum of omnivory. Two *Lynx rufus* (bobcat) left femora, curated in the MU Department of Anthropology Zooarchaeology Laboratory, were selected for analysis. I did not have access to carnivore specimens from Missouri, therefore, these two individuals are modern specimens from Oklahoma. Lastly, two modern *U. americanus* specimens (one left mandible and one left femur) were examined for dietary isotope signatures. These specimens (also in the MU Zooarchaeology Laboratory) were collected from Cedar County and Reynolds County in southwest and southeast Missouri, respectively (Figure 1), and are of unclear age but given their preservation condition and associated collection notes, it is likely that they are no older than 100 to 150 years.

Table 2. List of bone specimens from which collagen was extracted for stable isotope analysis. Modern specimens are denoted with an asterisk (*). All other specimens are paleontological.

Trophic level	**Species**	**Common name**	**N**	**Location**
Omnivores	*Ursus americanus**	North American black bear	1	Cedar Co., MO
	*Ursus americanus**	North American black bear	1	Reynolds Co., MO
	Ursus americanus	North American black bear	10	Lawson Cave, MO
	Didelphis virginiana	Opossum	1	Lawson Cave, MO
	Sus scrofa	Pig	4	Lawson Cave, MO
Herbivores	*Marmota monax*	Woodchuck	3	Lawson Cave, MO
	Sylvilagus floridanus	Cottontail rabbit	5	Lawson Cave, MO
Carnivores	*Canis* spp.	Dog/coyote	1	Lawson Cave, MO
	*Lynx rufus**	Bobcat	2	Oklahoma
Total			28	

Sample sizes of all taxa were limited by three factors: 1) the paleontological nature of the Lawson Cave assemblage limited the number of individual organisms and the number of taxa, 2) black bear extirpation prior to modern analyses limited the number of modern Missouri black bear skeletons, and 3) population size and distribution of large carnivores on the landscape are constrained by ecological requirements (i.e., large carnivores require large quantities of space and calories).

Bone samples were cut using a diamond-blade rock saw. For femora, two mid-diaphyseal cross section cuts enabled selection of small samples of thick cortical bone. For mandibles, small triangular chunks of cortical bone were removed from the anteriodistal portion of the specimens. A series of acid digestions was necessary prior to isotope analysis to dissolve inorganic and exogenous materials, and to extract lipids from the bone samples. In the years prior to the research reported here, the Lawson Cave specimens were treated with an unknown epoxy or resin, likely in an attempt to inhibit deterioration. Unfortunately, many preservation materials contain trace amounts of carbon and nitrogen (Moore et al. 1989); therefore, I treated all bone samples with a chloroform-methanol solution ($CHCl_3$ and CH_3OH) at a ratio of 2:1 before beginning the ABA (acid, base, acid) pretreatment adopted from Evin et al. (1971) and Newsome et al. (2007). Samples soaked in the chloroform-methanol mixture at room temperature for 24 hours. They were then rinsed three times with deionized water, and put in 1 M hydrochloric acid (HCL) for 72 hours to demineralize, or dissolve the inorganic components of the bones. Next, samples were rinsed three times with deionized water, and put in 0.1 M sodium hydroxide (NaOH) for 24 hours. This base treatment removed potential contaminants such as humic acids and fatty acids. Following the NaOH soak, samples were again rinsed three times with deionized water and put in 1 M HCL for 72 hours. When this last demineralization soak was completed, samples were rinsed three times with deionized water and put in another chloroform-methanol (2:1) solution for 24 hours. This solvent was selected to extract any lipids that may not have been able to escape from the bones during the first chloroform-methanol soak. Once this last soak was completed, samples were rinsed three times in deionized water and dried for three days in a dessicator.

The remaining material (clean collagen) was used for isotope analysis. Approximately one and a half milligrams of each dried collagen sample was weighed into tin vessels for isotope analysis. Stable carbon and nitrogen isotope analysis was conducted at the MU Geological Sciences' Stable Isotope Laboratory. Tin vessels containing collagen samples were flash combusted at 1020 degrees centigrade in a Carlo Erba 1500 Elemental Analyzer coupled to a Thermo Finnigan DeltaPlus mass spectrometer, which measured the isotope ratios of nitrogen (N_2) and carbon dioxide (CO_2) for each sample.

Stable carbon and nitrogen isotope values were used to evaluate *U. americanus* diet prior to historic extirpation from Missouri. Three kinds of analyses were performed: (1) stable carbon and nitrogen isotope values from 10 Lawson Cave black bears were compared to isotope values for contemporaneous taxa from the same paleontological deposit, (2) stable carbon and nitrogen isotope values and relative geological ages of the individual paleontological black bears were compared to identify temporal patterns (if any), and (3) stable carbon and nitrogen isotope values for the paleontological black bears were compared to isotope values for modern black bears.

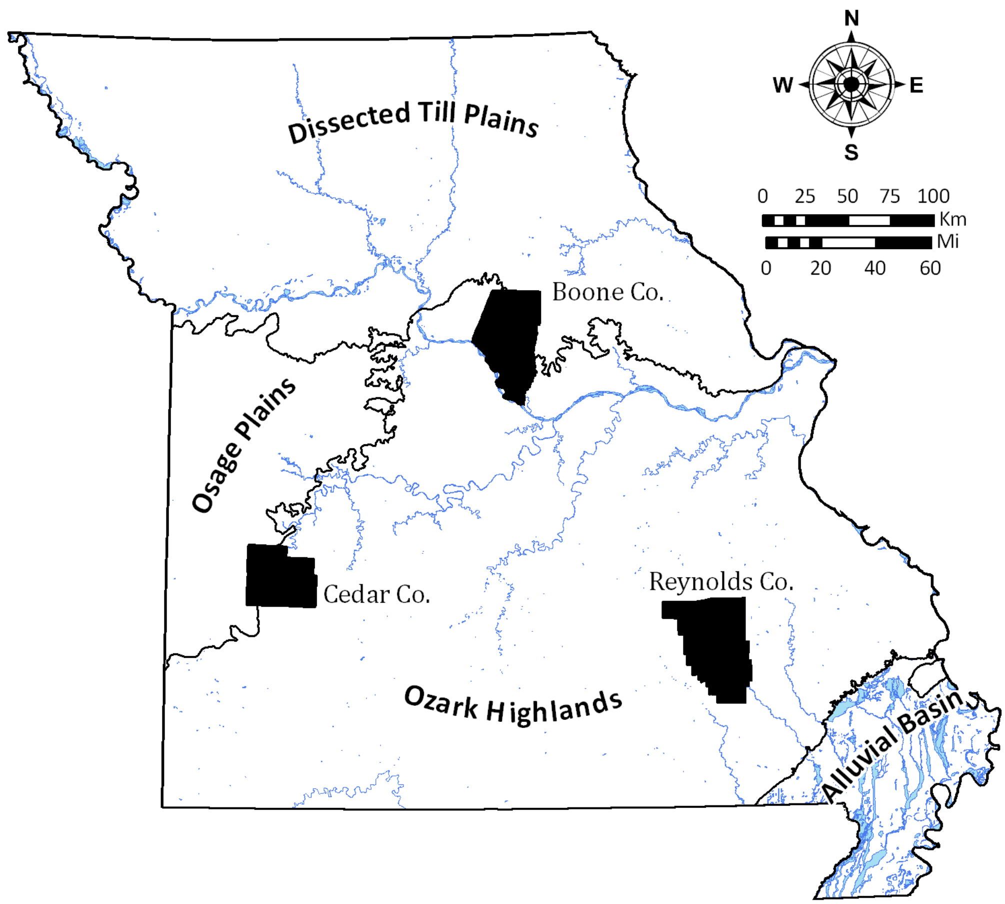

Figure 1. Geographic regions of Missouri. Lawson Cave is located in Boone County. Modern *U. americanus* specimens were surface collected from Cedar County and Reynolds County. Spatial data available at Missouri Spatial Data Information Service (MSDIS) online, http://www.msdis.missouri.edu (accessed Feb. 2, 2010). M. Boulanger aided in production of this figure.

CHAPTER 3: RESULTS

Recall that wildlife managers, conservation biologists and restoration ecologists are forced to assume that non-Missouri black bear ecology accurately reflects native Missouri black bear ecology. In order to test this assumption, I sought answers to three questions. First, are there observable differences in diet among omnivores, herbivores, and carnivores from Lawson Cave and are Lawson Cave black bears distinguishable from Lawson Cave herbivores? Second, did native *U. americanus* diet change through time in Missouri, as reflected by the Lawson Cave ursids? And third, does Lawson Cave black bear diet differ from that of modern Missouri black bears?

Carbon:Nitrogen Ratios

Atomic ratios of carbon to nitrogen were determined for each specimen in order to demonstrate two things (Appendix, Table 2): First, I needed to determine whether the state of preservation for each specimen was adequate for dietary interpretation of stable isotope results; and second, I needed to determine whether the collagen extraction technique successfully dissolved all lipids, inorganic material and exogenous material. Atomic ratios of carbon to nitrogen and consistency across replicate samples from each individual ensured that these two conditions were met for nearly all samples analyzed. Fresh bone collagen ($C_2H_5NOC_5H_9NOC_5H_{10}NO_2$) from modern specimens has an atomic C/N ratio of 3.2 (DeNiro 1985). DeNiro (1985) determined that archaeological/paleontological bone specimens have C/N ratios between 2.9 to 3.6. Deviations from this expected range indicate contamination of bone collagen with exogeneous material, such as epoxy resin used to preserve bones or improper extraction of collagen, which can occur if lipids and/or inorganic materials are not adequately extracted or dissolved. All, but one individual (LCM003) sampled in this study had C/N ratios within the expected range of values for clean collagen. All three replicates for LCM003 were above the expected C/N ratio (Appendix, Table 2), indicating contamination or inadequate collagen extraction. Lipids have more carbon than collagen; therefore, high C/N ratios likely indicate that lipids were inadequately extracted from this specimen. Given that collagen is enriched in the heavy carbon isotope (^{13}C) as compared to lipids, it would be inappropriate to compare lipid-containing specimens to lipid-free specimens (DeNiro 1985). For this reason, LCM003 (a *Marmota monax* specimen) was removed from all statistical tests. Specimen LCS003 (a *Sylvilagus floridanus* specimen) was also removed from all statistical tests because each replicate had abnormally high stable nitrogen isotope values. High nitrogen values indicate that this specimen was either degraded in quality or that the individual to whom it belonged was nutritionally stressed (Hobson et al. 1993; Nelson et al. 1998). This issue will be addressed in the Discussion section.

Analytical Precision

The DeltaPlus mass spectrometer measured the isotopic ratios of nitrogen (N_2) and carbon dioxide (CO_2) for each sample, including 24 acetanilide standards. The analytical precision for $\delta^{15}N$ for this instrument was based on 24 acetanilide samples and was better than 0.13‰. The analytical precision for $\delta^{13}C$ was based on the same 24 acetanilide samples and was better than 0.05‰. This means that the variability observed in stable isotope values is not the result of instrument error.

Reliability of Method

Reliability of the method used to determine stable carbon and nitrogen isotope values for bone collagen was determined by comparison of three replicates for each individual. I was interested in determining whether there was more variation in isotopic values among individuals than within individuals. Additionally, I wanted to know if there was more variation among taxa than among individuals within the same taxon. Results from a nested ANOVA for carbon indicated higher variance among taxa (F_s=6.01, df=7, 20, P<0.001) than among individuals within the same taxon (Table 3). Therefore, stable carbon isotope values for bone collagen from different taxa were more variable than carbon isotope values from individuals within the same taxon. Additionally, there was greater variation among individuals than among replicates of the same individual (F_s=35.82, df=20, 56, P<0.001). Therefore, stable carbon isotope values for bone collagen from different individuals varied more than replicate carbon isotope values from the same individual. Thus, this test demonstrates the reliability of the isotope determination. Stable carbon isotopes can successfully distinguish taxa and individual black bear specimens found in Lawson Cave.

Patterns exhibited by stable nitrogen isotope values mimic those of the stable carbon isotope values. Results from a nested ANOVA indicate higher variance among taxa (F_s=4.64, df=7, 20, P=0.003) than among individuals within the same taxon, and higher variance among individuals than among replicates of the same individual

(F_s=63.36, df=20, 56, P<0.001) (Table 4). Therefore, stable nitrogen isotope values from different taxa were more variable than nitrogen isotope values from individuals belonging to the same taxon. Additionally, there was greater variation among individuals than among replicates of the same individual. Thus, this test demonstrates that stable nitrogen isotopes can reliably distinguish taxa and individual black bear specimens found in Lawson Cave.

Table 3. A nested ANOVA evaluating the variability of carbon isotope values for replicates of each individual and identifying any differences among taxa and individuals within those taxonomic groups.

Source of variation	**SS**	**df**	**MS**	**Fs**	**F_{cv}**	**P**	**Variance (%)**
Among taxa	547.21	7	78.17	6.01	2.51	<0.001	59.87
Within taxa	259.95	20	13.00	35.82	1.77	<0.001	36.95
Within individual	20.32	56	0.36				3.18
Total	**827.47**	**83**					**100.00**

Table 4. A nested ANOVA evaluating the variability of nitrogen isotope values for replicates of each individual and identifying differences among trophic groups and individuals within those trophic groups.

Source of variation	**SS**	**df**	**MS**	**Fs**	**$F_{critical}$**	**P**	**Variance (%)**
Among taxa	197.28	7	28.18	4.64	2.51	0.003	52.56
Within taxa	121.53	20	6.08	63.36	1.77	<0.001	45.27
Within individual	5.37	56	0.10				2.18
Total	**324.18**	**83**					**100.00**

Trophic-Level Differences

A few patterns are apparent in the isotopic data based on typical stable carbon and nitrogen isotope values for consumer tissues. Recall that there is a 3‰ increase in nitrogen values with each consecutive trophic level and stable carbon isotope values range between -25‰ and -17‰ for C_3-consumers and between -9‰ and -5‰ for C_4-consumers. Carnivore bone collagen had the highest stable nitrogen isotope values, followed by omnivores and then herbivores, which as a whole had the lowest measured nitrogen values (Figure 2). Specifically, high stable nitrogen isotope values (greater than 6‰) were measured for *Didelphis virginiana* (LCD001), *Canis* spp. (LCC001) and *Lynx lupus* (OKL001). Conversely, low nitrogen isotope values (less than 3‰) were measured for two *S. floridanus* (LCS004 and LCS005) and two *M. monax* (LCM001 and LCM002). Modern *U. americanus* had stable nitrogen isotope values greater than those of Lawson Cave herbivores, but slightly less than those of Lawson Cave omnivores. Stable nitrogen isotope values from Lawson Cave *U. amerianus* are similar to modern *U. americanus* values, but are slightly more ^{15}N-heavy.

Herbivore bone collagen had the lowest stable carbon isotope values, followed by omnivores and carnivores, which had similar average values. Both modern and Lawson Cave *U. americanus* had stable carbon isotope values similar to those measured for Lawson Cave omnivores and carnivores (Figure 3). All specimens analyzed in this study (including Lawson Cave and modern specimens) plot within the stable carbon isotope range for dominantly C_3 consumption (-25‰ and -17‰), except the canid (LCC001) and two pigs (LCP003 and LCP004) which had carbon isotope values between -17‰ and -9‰. No specimens had carbon isotope values above -9‰. Therefore, all animals consumed primarily C_3 materials, except LCC001, LCP003 and LCP004; these individuals consumed mixed C_3-C_4 diets (Appendix, Table 1). Some C_4 materials could have contributed to each individual's diet, but recall that bone collagen records a long-term average, and thus reflects the isotope signature of the primary dietary constituent(s).

The nested ANOVA indicated that replicate samples for each individual were consistent (more variation among individuals than within individuals), and there was more variation among taxa than within taxa. Therefore, I sought to evaluate whether there was more variation among trophic groups (i.e., herbivores, omnivores and carnivores) than within trophic groups. A Kruskal-Wallis nonparametric comparison of Lawson Cave herbivore, omnivore and carnivore stable isotope values identified differences in stable carbon ($H=10.77$, $df=2$, $p=0.005$) and stable nitrogen ($H=13.59$, $df=2$, $p=0.001$) isotope values among the three trophic groups. Two-sample Mann-Whitney nonparametric comparisons indicated where differences existed among the three groups. Stable carbon isotope values for herbivores and omnivores were significantly different ($U=9$, $n_1=6$, $n_2=17$, $p=0.002$). Stable nitrogen isotope values for herbivores and omnivores were also different ($U=6$, $n_1=6$, $n_2=17$, $p=0.001$). Significant differences in stable nitrogen isotope values were also apparent between herbivores and carnivores ($U=0$, $n_1=3$, $n_2=6$, $p=0.010$). Thus, herbivores and omnivores consumed different proportions of C_3 and C_4 vegetation, and as expected, herbivores relative to omnivores and relative to carnivores exhibited significantly different degrees of carnivory.

Mann-Whitney nonparametric comparisons of herbivore and ursid stable isotope values for the Lawson Cave sample were used to investigate whether the two groups were distinguishable. Both stable carbon ($U=6$, $n_1=6$, $n_2=10$, $p=0.005$) and nitrogen ($U=4$, $n_1=6$, $n_2=10$, $p=0.002$) isotope values for *U. americanus* from Lawson Cave were different than those of Lawson Cave herbivores. Lawson Cave *U. americanus* and contemporary herbivores had different diets; the ursids consumed a different proportion of C_3 and C_4 plants and more meat than the herbivores (Figure 4).

Standard deviations for each taxon were calculated to identify differences among individuals of the same taxon, and thus to determine which taxa had the most variable stable carbon and nitrogen isotope values (diet) (Table 5). Stable carbon isotope values measured in Lawson Cave *S. scrofa* (LCP) were more variable ($\sigma = 4.45$) than any other taxon. Stable nitrogen isotope values measured in Lawson Cave *S. floridanus* (LCS) were more variable than any other taxon ($\sigma = 1.91$) (Table 5). F-tests of variance were used to evaluate whether the differences in variability among the taxa analyzed in this study were significantly different from one another. Significant differences in variance for carbon isotope values were observed between Lawson Cave *U. americanus* and four other taxa, including *S. scrofa* ($F=102.29$, $n_1=3$, $n_2=9$, $p<0.001$), *M. monax* ($F=43.74$, $n_1=1$, $n_2=9$, $p<0.001$), Modern *U. americanus* ($F=9.55$, $n_1=1$, $n_2=9$, $p=0.013$), and *S. floridanus* ($F=11.31$, $n_1=3$, $n_2=9$, $p=0.002$) (Table 6). Significant differences in variance for nitrogen isotope values were observed between *S. floriandus* and *S. scrofa* ($F=16.51$, $n_1=3$, $n_2=3$, $p=0.023$) and *S. floridanus* and Lawson Cave *U. americanus* ($F=5.17$, $n_1=9$, $n_2=3$, $p=0.024$) (Table 7).

Table 5. Average stable carbon and nitrogen isotope values and standard deviations for each taxon.

Taxon	**n**	$\bar{X}_{carbon}$	σ_c	$\bar{X}_{nitrogen}$	σ_n
Sus scrofa	4	-17.19	4.45	5.08	0.47
Marmota monax	2	-24.36	2.91	1.71	1.09
Sylvilagus floridanus	4	-21.64	1.48	2.41	1.91
Modern *Ursus americanus*	2	-19.27	1.36	4.09	0.31
Lawson *Ursus americanus*	10	-19.84	0.44	4.74	0.84
Lynx rufus	2	-19.30	0.40	5.76	0.44
Canis spp.	1	-11.17	-	6.97	-
Didelphis virginiana	1	-19.14	-	8.91	-

Therefore, the answer to my first question is yes; there are isotopically observable differences in the diets of Lawson Cave carnivores, herbivores and omnivores. Dietary differences include the proportion of C_3 and C_4 plants, the level of carnivory and the variability of species' diets within each trophic group. Additionally, Lawson Cave ursids are distinguishable from contemporaneous herbivores. Thus the ecological assumption that native Missouri black bears are no different from extra-local modern black bears in terms of position in the trophic pyramid is supported.

Temporal Variation in Ursid Diet

Rank-ordered stable carbon and nitrogen isotope values for Lawson Cave *U. americanus* were compared with fluorine concentrations from the same skeletal specimens to identify temporal patterns (Figures 5 and 6). Though there appears to be an increase in the isotopic ratios over time, Spearman's rank order analysis for both stable carbon (r_s= -0.27, df=8, p>0.10) and nitrogen (r_s= -0.43, df=8, p>0.10) isotope measurements indicate no significant correlation between the isotopes and fluorine concentrations. Thus, the answer to my second question is no; there is no clear (statistically detectable) trend in *U. americanus* diet (C_3 and C_4 plant and meat consumption) through time.

Difference between Lawson Cave and Modern Ursids

Stable carbon and nitrogen isotope values for Lawson Cave *U. americanus* were compared to those of modern *U. americanus* from two locations (Cedar County and Reynolds County) in Missouri. Small sample sizes require conservative interpretation, but non-parametric Mann-Whitney U-tests failed to identify differences between stable carbon isotope values (U=8, n_1=2, n_2=10, p=0.334) and between stable nitrogen isotope values (U=4, n_1=2, n_2=10, p=0.099) for modern and Lawson Cave *U. americanus*.

Despite small differences in variability, the Mann-Whitney U-test failed to identify major differences in the isotopic composition of modern and Lawson Cave black bears. Therefore, the answer to my third question is no; late Holocene *U. americanus* from Lawson Cave did not consume an isotopically different diet than modern *U. americanus.* Thus the assumption that native Missouri black bears were no different from extra-local modern black bears in terms of diet is supported.

Standard deviations were calculated to identify differences among Lawson Cave ursids and modern ursids, and to determine the variability of each sample's diet (Table 5). Stable carbon isotope values were more variable in modern ursids ($\sigma = 1.36$) than in Lawson Cave ursids ($\sigma = 0.44$), and this difference was statistically significant ($F=9.55$, $n_1=1$, $n_2=9$, $p=0.013$) (Table 6). Conversely, stable nitrogen isotope values were more variable in Lawson Cave ursids ($\sigma = 0.84$) than in modern ursids ($\sigma = 0.31$), but this difference was not statistically significant ($F=7.34$, $n_1=9$, $n_2=1$, $p=0.279$) (Table 7). Small sample sizes may have influenced the patterns in isotope variability, but I cannot ignore that there is a statistical difference in carbon isotopes between Lawson Cave and modern ursids, and that this data might still bear some ecological significance. The results indicate that modern ursids consumed more variable proportions of C_3 and C_4 plant materials than Lawson Cave ursids, and Lawson Cave ursids may have consumed more variable proportions of meat and vegetation than modern ursids. Why this might be the case is presently unclear, but I hypothesize that these changes in diet variability were the result of 19th century anthropogenic habitat modification. Hardwood forest destruction and human population expansion reduced black bear habitat. Black bears that survived this change likely did so due to dietary plasticity; as opportunistic omnivores, they likely encountered and consumed more diverse plant materials (including corn and other non-deciduous forest plants) than previous black bears as they searched for new habitats. High variability in the relative amount of meat and vegetation consumed by Lawson Cave black bears is likely an artifact of a more diverse selection of dietary materials from which black bears could choose. Lawson Cave black bears were less restricted by resources that were available for consumption, as compared to modern black bears. Further analyses on more paleontological and modern Missouri black bears are required to test this hypothesis.

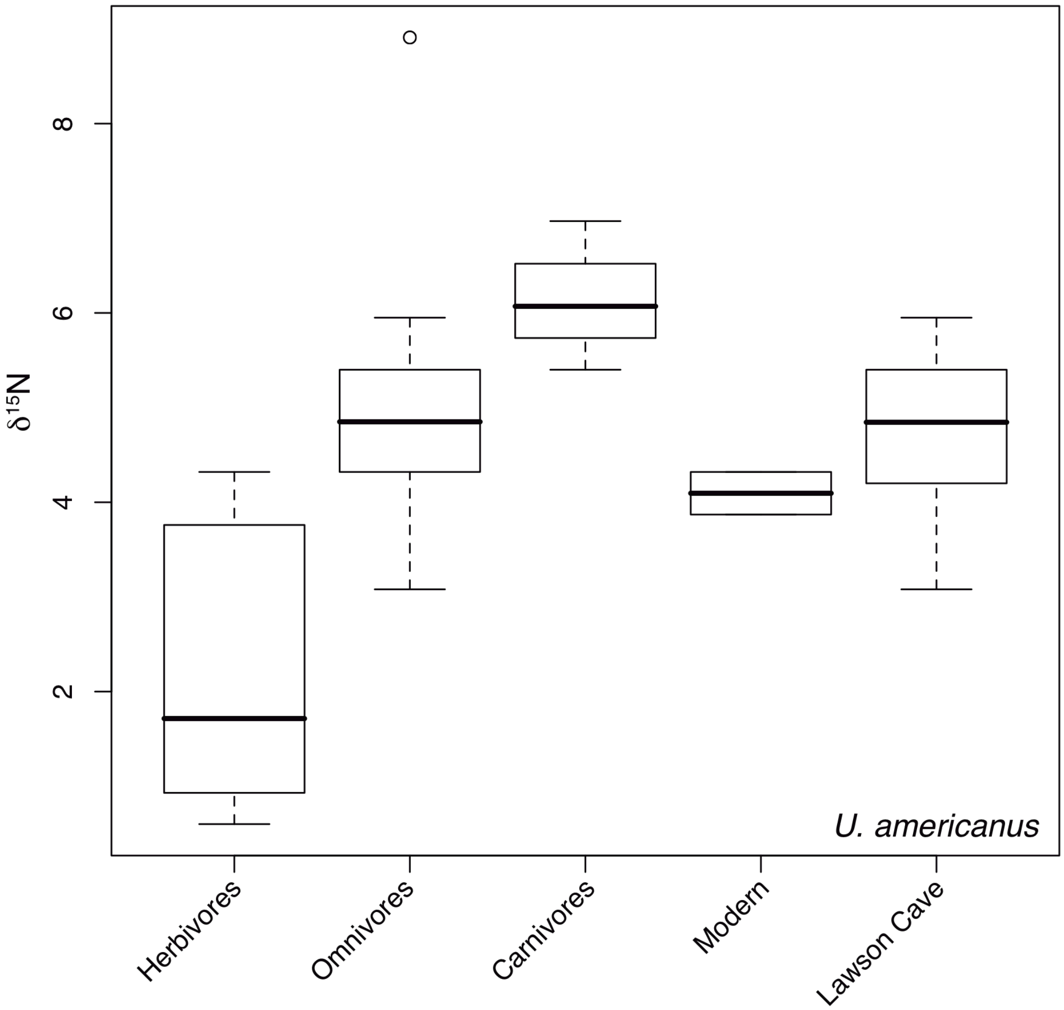

Figure 2. Box and whisker plot of stable nitrogen isotope values for herbivores, omnivores, carnivores, and modern and Lawson Cave ursids. Central marks are medians, box edges are the 25th and 75th percentiles, whiskers extend to samples within one standard deviation of the central mark, and open circles mark extreme outliers (greater than two standard deviations from the central mark).

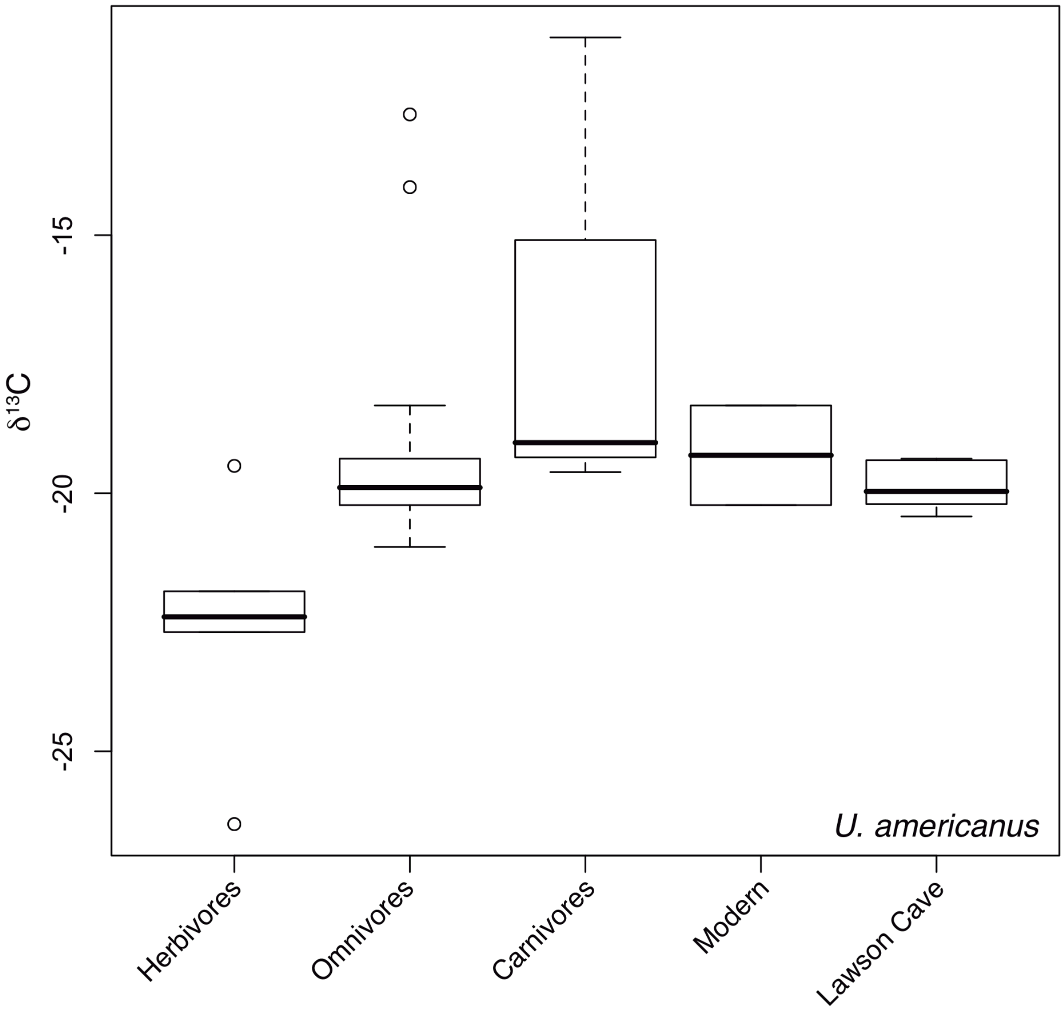

Figure 3. Box and whisker plot of stable carbon isotope values for herbivores, omnivores, carnivores, and modern and Lawson Cave ursids. Central marks are medians, box edges are the 25th and 75th percentiles, whiskers extend to samples within one standard deviation of the central mark, and open circles mark extreme outliers (greater than two standard deviations from the central mark).

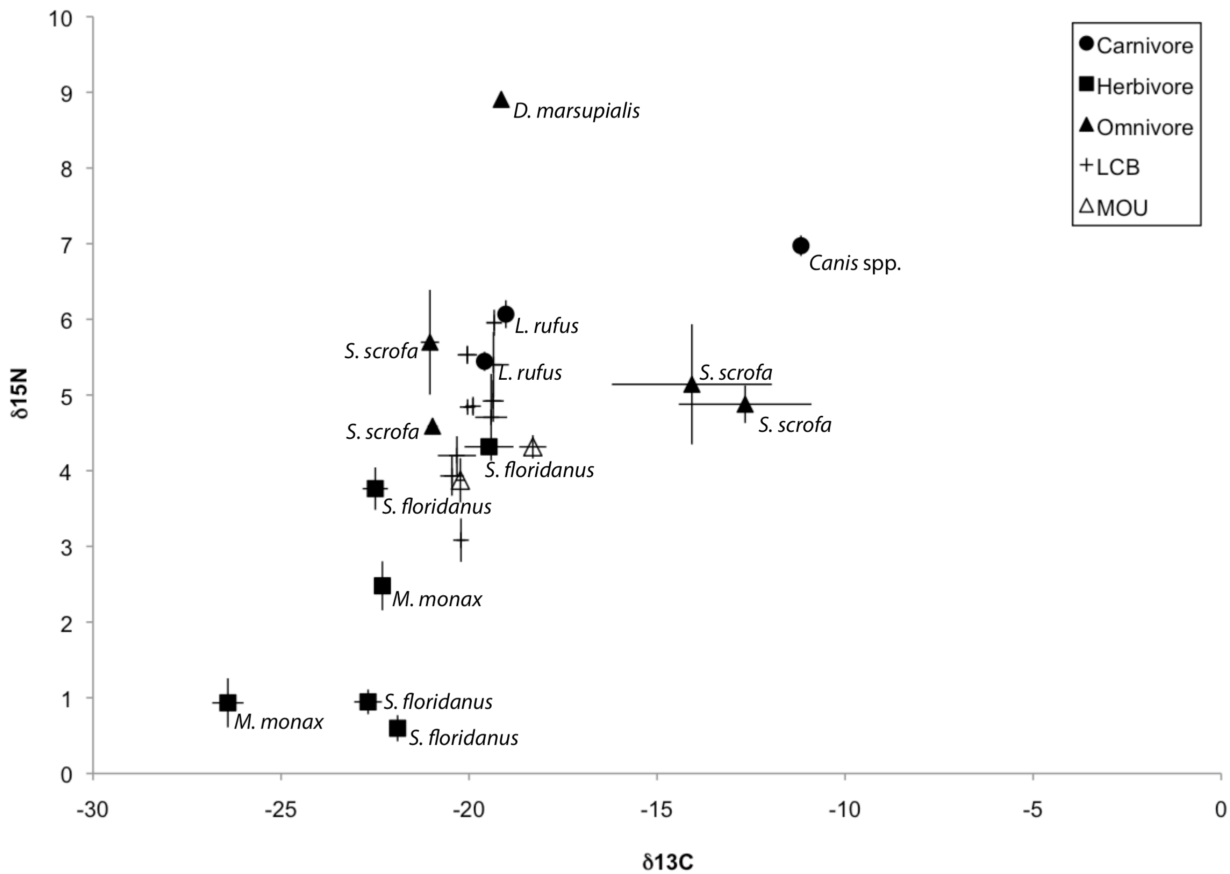

Figure 4. Stable carbon and nitrogen isotope values for carnivores, herbivores, omnivores, Lawson Cave black bears (LCB) and modern black bears (MOU). Each point is an average for each individual based on three replicates and error bars represent the variation among replicates.

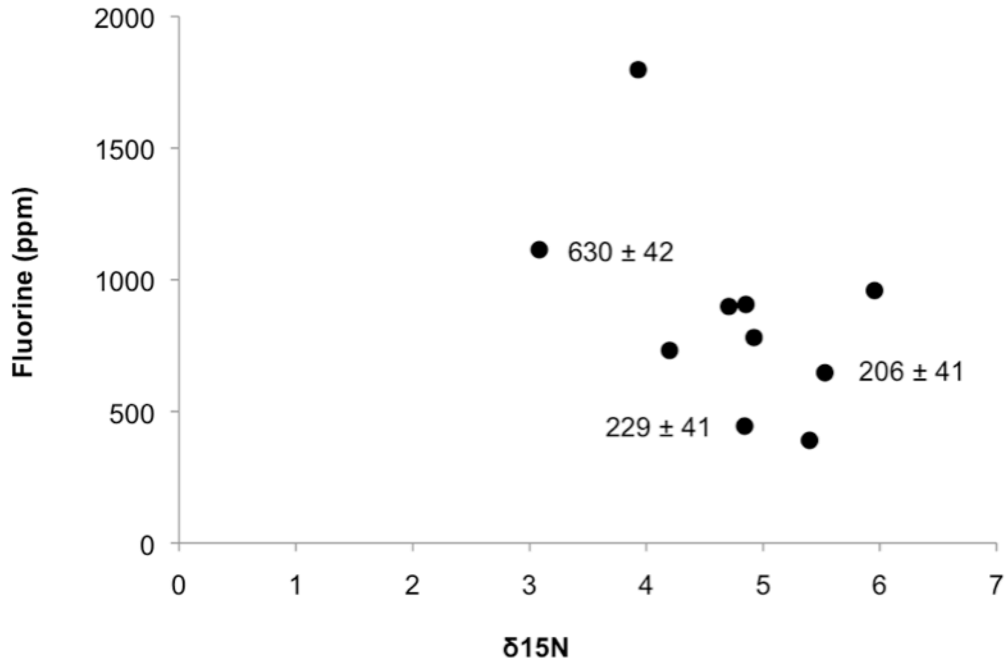

Figure 5. Average stable nitrogen isotope values for Lawson Cave black bears plotted against fluorine concentrations measured from the same ten ursids and radiocarbon dates for three ursids (LCB002, LCB005, and LCB008) (Appendix, Table 1).

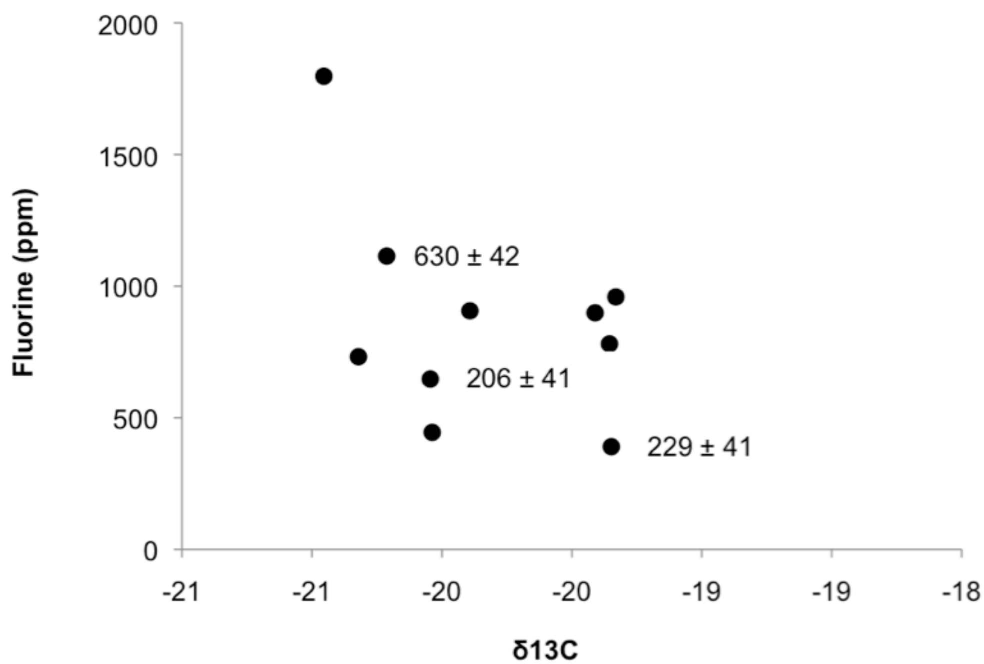

Figure 6. Average stable carbon isotope values for Lawson Cave black bears plotted against fluorine concentrations measured from the same ten ursids and radiocarbon dates for three ursids (LCB002, LCB005, and LCB008) (Appendix, Table 1).

Table 6. F-tests of variance and associated probabilities indicate differences in stable carbon isotope variability among taxa. Probabilities significant at an alpha level of 0.05 are in bold.

	M. monax		Modern *U. americanus*		*S. floridanus*		*L. rufus*		Lawson *U. americanus*	
	F	p	F	p	F	p	F	p	F	p
S. scrofa	2.34	0.440	10.71	0.220	9.04	0.052	123.77	0.066	102.29	**0.000**
M. monax	-	-	4.58	0.278	3.87	0.144	52.93	0.087	43.74	**0.000**
Modern *U. americanus*			-	-	1.18	0.574	11.56	0.182	9.55	**0.013**
S. floridanus					-	-	13.69	0.196	11.31	**0.002**
L. rufus							-	-	1.21	0.613
Lawson *U. americanus*									-	-

Table 7. F-tests of variance and associated probabilities indicate differences in stable nitrogen isotope variability among taxa. Probabilities significant at an alpha level of 0.05 are in bold.

	M. monax		Modern *U. americanus*		*S. floridanus*		*L. rufus*		Lawson *U. americanus*	
	F	p	F	p	F	p	F	p	F	p
S. scrofa	5.38	0.103	2.30	0.443	16.51	**0.023**	1.14	0.582	3.19	0.184
M. monax	-	-	12.36	0.176	3.07	0.392	6.14	0.244	1.68	0.227
Modern *U. americanus*			-	-	37.96	0.119	2.01	0.391	7.34	0.279
S. floridanus					-	-	18.84	0.167	5.17	**0.024**
L. rufus							-	-	3.64	0.387
Lawson *U. americanus*									-	-

CHAPTER 4: DISCUSSION

As expected, low stable nitrogen isotope values were measured for *S. floridanus* and *M. monax*, indicating a largely herbivorous diet, and providing a local expected value for herbivores. Stable carbon isotope values were low for all taxa, except *Canis* spp. and *S. scrofa*, indicating consumption of C_3 plant material by nearly all taxa (Figure 4; Appendix, Table 1). This result is expected given that the majority of these taxa subsisted in a deciduous-forest environment. Conversely, particularly high carbon isotope values measured in *Canis* spp. and *S. scrofa* indicate a mixed diet, including both C_3 and C_4 plant consumption. Consumption of corn (a C_4 plant), other C_4 plants and C_4 consumers (i.e., grazers) will elevate stable carbon isotope signatures of an organism's tissues. Thus, *Canis* spp. likely consumed some C_4 consumers available on the landscape and *S. scrofa* likely consumed corn and/or other C_4 plants available in the region (i.e., grasses and forbs). Interestingly, two groups of *Sus* are evident based on stable carbon isotope values (Figure 4); high $\delta^{13}C$ values indicate C_4 consumption and low $\delta^{13}C$ values indicate C_3 consumption. A t-test indicates that this difference is not statistically significant at an alpha level of 0.05 (t=4.30, df=1, p=0.056), but this distinction likely indicates differences in corn (C_4) consumption between the two groups. It is possible that two *Sus* (LCP003 and LCP004) were domesticated hogs (*Sus scrofa domestica*) that escaped from local farmlands, whereas the other two *Sus* (LCP001 and LCP002) may have been feral pigs (*Sus scrofa*) that ate less corn than the recently escaped domestic pigs.

Elevated Stable Nitrogen Isotope Values

High stable nitrogen isotope values generally indicate significant meat consumption. Therefore, high nitrogen values measured for *Canis* spp., *L. rufus* and *D. virginiana,* likely indicate significant contributions of meat to these species' diets. *Canis* spp., *L. rufus*, and *D. virginiana* all have stable nitrogen isotope values above 6‰, indicating levels of carnivory at the tertiary consumer level (carnivores) (Table 8). In contrast, modern and Lawson Cave *U. americanus* and *S. scrofa* fall within the range for secondary consumers (omnivores) (3‰ to 6‰). *S. floridanus* and *M. monax* have nitrogen isotope values below 3‰; thus, they are classified as primary consumers (herbivores) (Table 8).

Table 8. Trophic-level classification of taxa based on stable nitrogen isotope values.

$\delta^{15}N$ value	Taxon	Trophic-Level
< 3‰	woodchuck, rabbit	Primary consumer (herbivore)
3‰ to 6‰	black bear, pig	Secondary consumer (omnivore)
> 6‰	canid, opossum, bobcat	Tertiary consumer (carnivore)

High nitrogen values (a=7.42‰, b=7.72‰, c=7.29‰) measured in the collagen of one *S. floridanus* (LCS003) initially seemed to indicate an anomaly: Do the values indicate a flaw in the analytical method? Is this a rare example of a hypercarnivorous cottontail rabbit? Or could there be a physiological explanation? The first explanation, that high values are a result of the method, seems unlikely given the consistent values obtained for all three replicate samples (Appendix, Table 3). And since general knowledge of *S. floridanus* diet indicates strict herbivory (Chapman et al. 1980), a physiological explanation seems most plausible. Heavy nitrogen values are observed in two types of individuals: (1) juveniles and (2) malnourished individuals (Fogel et al. 1989; Hobson et al. 1993; Nelson et al. 1998). Tissues of juvenile mammals consuming

^{15}N-rich milk from their mothers have elevated δ^{15}N values; thus, the stable nitrogen isotope signature of a suckling juvenile mimics the isotope signature of an organism that feeds one trophic level above the lactating mother (Fogel et al. 1989). Likewise, the metabolic response of a starving individual involves more efficient use of heavy nitrogen (^{15}N), which elevates δ^{15}N values in their tissues (Hobson et al. 1993; Nelson et al. 1998). Both the proximal and distal femoral epiphyses of LCS003 are fused; thus, the individual was likely weaned from breast milk for a significant amount of time prior to death. Therefore, prolonged malnutrition is the best explanation for the observed elevation in δ^{15}N values. Regardless of the physiological explanation responsible for the values measured in LCS003, the specimen was an outlier, and thus was removed from statistical analyses.

D. virginiana is an omnivore (Austad 1988; McManus 1974), yet as stated above stable nitrogen isotope values for the Lawson Cave specimen fall within the expected range for carnivores (Figure 4; Table 8). Three replicates gave consistent results (a=8.85‰, b=8.85‰, c=9.02‰) (Appendix, Table 3), ruling out a methodological error as the cause of the elevated values. Additionally, opossums do not have large home ranges; therefore, I can rule out the possibility that this stable isotope signature was acquired from a distant region. Interestingly, early reports by students involved in the initial excavation of Lawson Cave indicated that some bones had been gnawed, and inspection of the remains confirms a low degree of gnawing damage (Wolverton 2001). Given the evidence of gnawing, combined with the known potential causes for elevated stable nitrogen isotope values discussed above (i.e., nutritional stress and carnivory), it seems reasonable to suggest that the opossum may have survived the fall into the natural trap cave and subsisted on limited food resources (some of which may have been carrion) until it died. Nutritional stress and consumption of carrion while in the natural trap cave would have contributed to the elevated nitrogen values observed in the Lawson Cave opossum, but it is unclear whether there would have been sufficient amount of time for this signature to be observed in the collagen specimen analyzed.

Inter-Element Variation

Samples from two *M. monax* (LCM002 and LCM003) and one modern *U. americanus* (MOU001) were measured from mandibles instead of femora. Interestingly, these mandibular values were consistently lighter than femoral values for both stable carbon and nitrogen. This may explain the high standard deviation calculated for *M. monax* (Table 5). Despite this apparent pattern in stable isotope values based on the skeletal element analyzed, a nested ANOVA indicated greater variation between taxonomic groups than within and greater variation between individuals than within replicates of the same individual. Therefore, I concluded that it was valid to compare stable isotope values from mandibles and femora. When possible, though, samples should be taken from the same skeletal element, as well as the same position (i.e., mid-shaft) on the element to minimize inter- and intra-element variation that can result from different bone remodeling rates.

Black Bear Diet

On average, Lawson Cave *U. americanus* ($\delta^{13}C$=-19.84) have stable carbon isotope values similar to those of Lawson Cave *D. virginiana* ($\delta^{13}C$=-19.14), modern *U.*

americanus ($\delta^{13}C$=-19.27) and modern *L. rufus* ($\delta^{13}C$=-19.30) (Appendix, Table 1). Each of these taxa falls within the distribution of expected values for C_3 consumption. Interestingly, they each fall at the high end of the range for C_3 consumers. Remember that stable isotope values measured in bone collagen give a long term average of the organism's diet; therefore, it is likely that each of these species consumed a diet of primarily C_3 materials, but I cannot rule out a small contribution from C_4 materials. The Three Creeks Conservation Area has been and still is dominated by C_3 vegetation (i.e., deciduous trees); therefore, combined with the stable carbon isotope values it is safe to assume that the main constituents of Lawson Cave black bear diet were C_3 materials. Remember, though, that the stable carbon isotope signature can be the result of plant or meat consumption. Identifying the proportion of each material (plant and meat) that contributed to *U. americanus* diet was a primary goal. Therefore, stable nitrogen isotopes were used to determine whether the stable carbon isotope signature measured in *U. americanus* collagen was the result of plant consumption only, or a combination of plant and meat consumption. Lawson Cave *U. americanus* have stable nitrogen isotope values similar to those of Lawson Cave *S. scrofa* and modern *U. americanus*. An average stable nitrogen isotope value of 4.74‰ indicates meat consumption at the secondary consumer trophic level (i.e., omnivore). Lawson Cave *U. americanus* likely consumed meat on a regular basis, but meat consumption by them was far less than that of Lawson Cave *Canis* spp. (6.97‰), which would be classified as a tertiary consumer (true carnivore) (Table 8).

Lastly, I was interested in evaluating change in native Missouri *U. americanus* diet through time. Spearman's rank order analysis indicated no significant linear patterns in stable carbon or stable nitrogen isotope values over 600 years. Additionally, a Mann-

Whitney U test comparing Lawson Cave and modern *U. americanus* diet in Missouri indicated no significant differences in stable carbon and nitrogen isotopes (diet). These results indicate a static diet (within the resolution of $\delta^{13}C$ and $\delta^{15}N$) for *U. americanus* in Missouri over the past several hundred years. Interestingly, study of change has been dominant in many realms of study, but recently (beginning in the 1970s) the importance of stasis in the fossil record has been recognized by archaeologists, paleontologists and paleoecologists alike (e.g., DiMichele et al. 2004). Evidence of stasis in the fossil record is as important as change and can be directly applicable to ecological concerns today. The evidence for stasis herein confirms the ecological assumption used by conservationists managing modern populations; native Missouri black bears are no different from extra-local modern black bears, at least in terms of diet as reflected by stable isotopes. Therefore, ecological data from modern extra-local black bears and native paleontological black bears can be applied to future management and conservation planning regarding black bears in Missouri.

CHAPTER 5: CONCLUSIONS

Analysis of stable isotopes in the bone collagen of 10 early historic native Missouri black bears indicates that: 1) Lawson Cave carnivores, omnivores, and herbivores are isotopically different from one another, and Lawson Cave black bears are isotopically distinct from herbivores; 2) there is no clear trend in black bear diet over the past 600 years; and 3) Lawson Cave black bear diet is not significantly different from that of modern black bears. In order to contextualize the significance of these results and highlight their significance, in this concluding chapter I describe the pertinent social milieu and the implications of my results for conservation biology.

Who Really Cares about Ecological Conservation?

In Spring 2009, I conducted an ethnographic study to assess the amount of knowledge Central Missouri residents had about local environment and wildlife management policies, how residents perceived these policies to impact their daily behaviors, such as visiting government protected lands and participating in environment and wildlife management programs (i.e., recycling, conservation and hunting activities), and whether or not they felt that current policies were adequate for managing local environmental resources. Additionally, I assessed whether attitudes, perceptions and knowledge of the environment and wildlife management varied according to particular demographic variables (age, sex, occupation level, and residence). My study involved three methods of analysis: Personal interviews and an anonymous online survey were conducted to develop a baseline of self-reported attitudes, perceptions and knowledge;

and direct observation was used to test whether the majority of peoples' daily behaviors actually reflect the self-reported data. Samples for each component of the study were selected from University of Missouri, Columbia, faculty, staff and students.

On the whole, informants expressed interest in the environment, including interest in local wildlife, and interest in recycling and the effects of pollution on the environment. While intergroup variation was low for two demographic groups (age and occupation), several patterns were apparent when comparing responses between gender groups and residence groups. When asked whether special laws should be created to protect wildlife, the responses were generally positive (i.e., yes, laws should be created to protect wildlife). I found it interesting, though, that the only negative responses were from semi-rural individuals. This difference could be due to sampling error, but it would be interesting to explore this apparent pattern because a related pattern emerged when informants were asked whether or not wildlife management programs should involve transplanting animals into the native regions from which they were historically extirpated. Most informants (61%, n=16) agreed on some level or reported neutral feelings (27%, n=7) regarding such animal translocations, but the remaining 12% (n=3) that disagreed lived in semi-rural or suburban communities. This result suggests that communities on urban peripheries are more inclined to disagree with transplanting wildlife into previously occupied regions. Perhaps this response results from the fact that these communities are much more likely to be disrupted by wildlife, such as black bears, and because they are more familiar with myths and realities about dangerous behaviors of large semi-carnivorous mammals (Virginia Department of Game and Inland Fisheries 2007). For example, much conflict often occurs in peripheral communties because animals, such as North American black bears, have been displaced by human activities (Pelton 2000).

This ethnographic study is directly pertinent to the implications of my isotopic study of native Missouri black bears. Many Central Missouri residents are interested in the environment and are interested in species conservation. Obviously, some residents may feel more strongly about these environmental issues and some may feel apathetic to them. Any campaign to rejuvenate an animal population to a region must contend with the feelings and desires of local human residents. Some residents interviewed during my ethnographic study indicated interest in Missouri black bears, and acknowledged that they were aware of the decline in Missouri black bears over the last century. This indicates that wildlife enthusiasts may be able to initiate an ecological movement to re-establish black bears in Missouri and to better manage existing ones. Rejuventation of black bears in the state may be a promising avenue for ecotourism, and thus a way to bring revenue into the state. If and when rejuvenation of black bears occurs, behavioral information on native Missouri black bears will be of the utmost importance. The lack of native black bears on the landscape today necessessitates the study of paleozoological remains.

Management Implications

North American black bears once roamed the North American landscape in great abundance. But by the early 20th century, cumulative anthropogenic effects on the landscape, including human population expansion and increased resource extraction, hunting, and habitat modification decimated the black bear population. Black bears were all but eliminated from the state of Missouri. Modern interest in rejuvenating the local black bear population demands that research be done to elucidate the ecological requirements of Missouri black bears. Unfortunately, without modern Missouri black bears on the landscape, conservation ecologists must look elsewhere for populations to study. Modern black bears recently transplanted in Arkansas (from Manitoba and Minnesota), and populations in other regions of North America offer (what until now had to be assumed is) important information, but none that is specific to the Missouri landscape. The current assumption that modern extra-local black bears are no different from native Missouri black bears had not been tested prior to this study. In order to test this assumption, modern conservation efforts must make use of data gleaned from past Missouri black bear populations. Study of paleozoological assemblages consisting of pre- and peri-extirpation black bears can be used to expand our knowledge of black bear behavior in Missouri and stretches the temporal depth of that knowledge. A key element of that knowledge base includes the study of black bear diet.

Black bears were extirpated from Missouri by the early 20th century. Therefore, modern attempts to manage this species in the region have no modern local references. The Lawson Cave ursids provide answers to questions about *U. americanus* diet in Missouri obtainable in no other way. Results from this study indicate that in terms of isotopic composition late Holocene *U. americanus* diet is not significantly different from modern *U. americanus* diet. Therefore, ecologists may supplement modern dietary data with those for past black bears.

Ethnographic research and enactment of wildlife ordinances concerning ursids indicate that many Missourians recognize that local black bear numbers have drastically changed over time, and many of them are interested in protecting and rehabilitating the species (Cowan 1970; Etling 2000). Fifty years ago, the Arkansas Game and Fish Commission developed the same concern over dwindling black bear populations (Smith and Clark 1994). Therefore, in 1958 wildlife officials began transplanting *U. americanus* from Minnesota and Manitoba to Arkansas (Etling 2000; Smith and Clark 1994). These relocations were successful, and the population grew and expanded into southeastern Missouri. Consequently, *U. americanus* numbers in Missouri increased over the last several decades. But while wildlife conservationists and wildlife enthusiasts have enjoyed this unintended success, it has not been without consequence. Curious black bears (no doubt in search of food and homes) now come into contact with residential areas. Some residents, fearing these animals, shoot them. For these reasons, wildlife management programs must find suitable regions to which individual *U. americanus* may be relocated, and simultaneously consider the needs of local human residents.

Wildlife conservationists should look for regions interspersed with trees and reasonably separated from areas with high human population densities. Suitable regions likely exist in the Ozark Highlands (Figure 1), which offer some of the most biologically diverse habitats in the state. Ample plant and animal species are available for *U. americanus* consumption. The Ozark Highlands occupy much of the state south of the Missouri River, and are characterized by ample tree and shrub (C_3) genera, including *Acer* (maple), *Carya* (hickory), *Cornus* (dogwood), *Quercus* (oak), *Ulmus* (elm), *Platanus* (plane), *Juniperus* (juniper), and *Fraxinus* (ash), *Campsis* (trumpet creeper), *Viburnum* (viburnum), and *Vitis* (grape) (Zimmerman and Wagner 1979). Species within each of these genera produce products for *U. americanus* consumption, including flowers, fruits, leaves and nuts. In addition to these C_3 plants, grasses and forbs (C_4 plants) are also available in between heavily forested areas, as are animals that dwell within these habitats.

Regions can be evaluated for suitability based on habitat and food availability, but successful wildlife management programs must also include public outreach and education programs designed specifically for the species being relocated. Teaching the public to coexist with "new" species and helping them to see the importance or benefits of coexisting with these species are important aspects of conservation today. The combination of past, present, and future knowledge of people, the landscape and the organisms living on the landscape will ensure successful wildlife conservation programs. Interestingly, case studies similar to the Lawson Cave research can be used on any species in any state. Without paleozoological data wildlife conservationists make decisions with limited knowledge, and potentially incomplete data (Lyman and Cannon 2004). Thus, paleozoologically derived data, which can expand our knowledge to create a more comprehensive understanding of ecological systems, is an essential component of future wildlife management decisions.

REFERENCES

Austad, S. N.

1988 The Adaptable Opossum. *Scientific American* 258(2):98-104

Beckmann, Jon. P. and Joel Berger

2003 Rapid Ecological and Behavioural Changes in Carnivores: The Responses of Black Bears (*Ursus americanus*) to Altered Food. *Journal of Zoology* 261:207-212.

Bender, Margaret M.

1971 Variations in the 13C/12C Ratios of Plants in Relation to the Pathway of Photosynthetic Carbon Dioxide Fixation. *Phytochemistry* 10:1239–1245.

Boileau, F., M. Crete and J. Huot

1994 Food Habits of the Black Bear, *Ursus americanus*, and Habitat use in Gaspesie Park, Eastern Quebec. *Canadian Field-Naturalist* 108:162-169.

Buchardt, Bjorn, Vibeke Bunch and Pekka Helin

2007 Fingernails and diet: Stable Isotope Signatures of a Marine Hunting Community from Modern Uummannaq, North Greenland. *Chemical Geology* 244:316-329.

Bumsted, M. Pamela

1983 Adult Variation in d13C: Pre-Columbian North America. *American Journal of Physical Anthroplogy* 60:178-179.

Cerling, Thure E. and J. M. Harris

1999 Carbon Isotope Fractionation Between Diet and Bioapatite in Ungulate Mammals and Implications for Ecological and Paleoecological Studies. *Oecologia* 120:347-363.

Cerling, T. E., Yang Wang and Jay Quade

1993 Expansion of C4 Ecosystems as an Indicator of Global Ecological Change in the Late Miocene. *Nature* 361:344-345.

Cerling, Thure E., John M. Harris, Bruce J. MacFadden, Meave G. Leakey, Jay Quade, Vera Eisenmann and James R. Ehleringer

1997 Global Vegetation Change through the Miocene/Pliocene Boundary. *Nature* 389:153-158.

Chapman, J. A., J. G. Hockman and M. M. Ojeda

1980 *Sylvilagus floridanus. Mammalian Species* 136:1–8.

Chorn, John and Robert S. Hoffman
1978 *Ailuropoda melanoleuca. Mammalian Species* 110:1-6.

Chrisholm, B. S., D. E. Nelson and Henry P. Schwarcz
1982 Stable-Carbon Isotope Ratios as a Measure of Marine versus Terrestrial Protein in Ancient Diets. *Science* 216:1131-1132.

Codron, Daryl, Jacqui Codron, Julia Lee-Thorp, Matt Sponheimer, Darryl de Ruiter and James S. Brink
2007 Stable Isotope Characterization of Mammalian Predator-Prey Relationships in a South African Savanna. *European Journal of Wildlife Research* 53:161-170.

Cowan, Ian McTaggart
1970 The Status and Conservation of Bears (Ursidae). In *Bears-Their Biology and Management*, edited by S. Herrero, pp. 343-367. International Union for Conservation of Nature and Natural Resources, Morges, Switzerland.

DeMaster, D. P., and I. Stirling
1981 *Ursus maritimus*. *Mammalian Species* 145:1-7.

DeNiro, Michael J.
1985 Postmortem Preservation and Alteration of In Vivo Bone Collagen Isotope Ratios in Relation to Palaeodietary Reconstruction. *Nature* 317:806-809.

DeNiro, Michael J. and Samuel Epstein
1978 Influence of Diet on the Distibution of Carbon Isotopes in Animals. *Geochimica et Cosmochimica Acta* 42:495-506.

1981 Influence of Diet on the Distribution of Nitrogen Isotopes in Animals. *Geochimica et Cosmochimica Acta* 45:341-351.

DiMichele, W. A., A. K. Behrensmeyer, T. D. Olszewski, C. C. Labandeira, J. M. Pandolfi, S. L. Wing, and R. Bobe
2004 Long-Term Stasis in Ecological Assemblages: Evidence from the Fossil Record. *Annual Review of Ecology, Evolution and Systematics* 35:285–322.

Doan-Crider, Diana L. and Eric C. Hellgren
1996 Population Characteristics and Winter Ecology of Black Bears in Coahuila, Mexico. *Journal of Wildlife Management* 60:398-407.

Etling, Kathy
2000 The Bear Truth. *Missouri Conservationist* 61. Electronic document, http://mdc.mo.gov/conmag/2000/04/40.htm, accessed February 3, 2010.

Etnier, Michael A.
2004 The Potential of Zooarchaeological Data to Guide Pinniped Management Decisions in the Eastern North Pacific. In *Zooarchaeology and Conservation Biology*, edited by R. L. Lyman and K. P. Cannon, pp. 88-102. University of Utah Press, Salt Lake City.

Evin, J., R. Longin, G. Marien and C. Pachiaudi
1971 Lyon Natural Radiocarbon Measurements II. *Radiocarbon* 13:52-73.

Ezzo, Joseph A.
1994 Putting the "Chemistry" Back into Archaeological Bone Chemistry Analysis: Modeling Potential Paleodietary Indicators. *Journal of Anthropological Archaeology* 13:1-34.

Farquhar, Graham D.
1983 On the Nature of Carbon Isotope Discrimination in C4 Species. *Australian Journal of Plant Physiology* 10:205-226.

Farquhar, Graham D., James R. Ehleringer and Kerry T. Hubrick
1989 Carbon Isotopic Discrimination and Photosynthesis. *Annual Review of Plant Physiology and Molecular Biology* 40:503-537.

Fogel, Marilyn L., Tuross, Noreen & Owsley, D. W.
1989 Nitrogen Isotope Tracers of Human Lactation in Modern and Archaeological Populations. Annual Report of the Director, Geophysical Laboratory 2150:111-117.

Grayson, Donald K.
1984 *Quantitative Zooarchaeology: Topics in the Analysis of Archaeological Faunas*. Academic Press, Orlando.

Grayson, Donald K. and Francoise Delpech
2001 The Upper Paleolithic at Grotte XVI (Dordogne, France): Richness, Evenness, and Cave Bears. In *Questioning the Answers: Resolving Fundamental Problems of the Early Upper Paleolithic,* edited by M. A. Hays and P. Thacker, pp. 187-197. British Archaeological Reports International Series 1005. Oxford.

2003 Ungulates and the Middle-to-Upper Paleolithic Transition at Grotte XVI. *Journal of Archaeological Science* 30:1633-1648.

Harkness, D. D. and A. Walton
1972 Glasgow University Radiocarbon Measurements IV. *Radiocarbon* 14:111-113.

Harpole, Judith L.
2004 Zooarchaeological Implications for Missouri's Elk (*Cervus elaphus*) Reintroduction Effort. In *Zooarchaeology and Conservation Biology*, edited by R. L. Lyman and K. P. Cannon, pp. 103-115. University of Utah Press, Salt Lake City.

Hobson, Keith A., Ray T. Alisauskas and Robert G. Clark
1993 Stable-Nitrogen Isotope Enrichment in Avian Tissues Due to Fasting and Nutritional Stress: Implications for Isotopic Analyses of Diet. *The Condor* 95:388-394.

Hudson, Corey M.
2009 *Mitochondrial Ancient DNA Analysis of Lawson Cave Black Bears* (Ursus americanus). Unpublished Master of Arts thesis, University of Missouri, Columbia.

Hughes, Susan S.
2004 Postcontact Changes in the Behavior and Distribution of Rocky Mountain Bighorn Sheep (*Ovis canadensis*) in Northwestern Wyoming. In *Zooarchaeology and Conservation Biology*, edited by R. L. Lyman and K. P. Cannon, pp. 116-135. University of Utah Press, Salt Lake City.

Krueger, H. W.
1991 Exchange of Carbon with Biological Apatite. *Journal of Archaeological Science* 18:355-361.

Lal, S. B.
1975 Bone Fluorine as a Measure of Archaeological Antiquity. *Geophytology* 5:105-109.

Landers, J. Larry, Robert J. Hamilton, A. Sydney Johnson and R. Larry Marchinton
1979 Foods and Habitat of Black Bears in Southeastern North Carolina. *Journal of Wildlife Management* 43:143-153.

Lariviere, Serge
2001 *Ursus americanus*. *Mammalian Species* 647:1-11. vol. 647.

Lee-Thorp, Julia, Judith C. Sealy and N. J. van der Merwe
1989 Stable Carbon Isotope Ratio Differences Between Bone Collagen and Bone Apatite, and Their Relationship to Diet. *Journal of Archaeological Science* 16:585-599.

Libby, W. F., R. Berger, J. F. Mead, G. V. Alexander and J. F. Ross
1964 Replacement Rates for Human Tissue from Atmospheric Radiocarbon. *Science* 146:1170-1172.

Lyman, R. Lee

1996 Applied Zooarchaeology: The Relevance of Faunal Analysis to Wildlife Management. *World Archaeology* 28:110-125.

2006 Paleozoology in the Service of Conservation Biology. *Evolutionary Anthropology* 15:11-19.

2008 *Quantitative Paleozoology*. Cambridge University Press, New York.

Lyman, R. L., and K. P. Cannon (editors)

2004 *Zooarchaeology and Conservation Biology.* University of Utah Press, Salt Lake City.

McConnell, Duncan

1962 Dating of Fossil Bones by the Fluorine Method. *Science* 136:241-244.

McKinley, Daniel

1962 The History of Black Bear in Missouri. *Bluebird* 29:3-17.

McManus, J. J.

1974 *Didelphis virginiana. Mammalian Species* 40:1-6.

Minagawa, Masao and Eitaro Wada

1984 Stepwise Enrichment of 15N Along Food Chains: Further Evidence and the Relation Between d15N and Animal Age. *Geochimica et Cosmochimica Acta* 48:1135-1140.

Moore, Katherine M., Matthew L. Murray and Margret J. Schoeninger

1989 Dietary Reconstruction from Bones Treated with Preservatives. *Journal of Archaeological Science* 16:437-446.

Mosnier, Arnaud, Jean-Pierre Ouellet and Réhaume Courtois

2008 Black Bear Adaptation to Low Productivity in the Boreal Forest. *Ecoscience* 15:485-497.

Nelson, D. E., A. Angerbjorn, K. Lidén and I. Turk

1998 Stable Isotopes and the Metabolism of the European Cave Bear. *Oecologia* 116:177-181.

Newsome, Seth D., Michael A. Etnier, Diane Gifford-Gonzalez, Donald L. Phillips, Marcel van Tuinen, Elizabeth A. Hadly, Daniel P. Costa, Douglas J. Kennett, Tom P. Guilderson and Paul L. Koch

2007 The Shifting Baseline of Northern Fur Seal Ecology in the Northeast Pacific Ocean. *Proceedings of the National Academy of Sciences* 104:9709-9714.

Osborne, Colin P.
2008 Atmosphere, Ecology and Evolution: What Drove the Miocene Expansion of C4 Grasslands? *Journal of Ecology* 96:35-45.

O'Leary, Marion O.
1988 Carbon Isotopes in Photosynthesis. *BioScience* 38:328-366.

Pasitschniak-Arts, Maria, and Francois Messier
2000 Brown (Grizzly) and Polar Bears. In *Ecology and Management of Large Mammals in North America*, edited by S. Demarais and P. R. Krausman, pp. 409-428. Prentice Hall, Upper Saddle River, NJ.

Pate, F. Donald
1994 Bone Chemistry and Paleodiet. *Journal of Archaeological Method and Theory* 1:161-209.

Pelton, Michael R.
2000 Black Bear. In *Ecology and Management of Large Mammals in North America*, edited by S. Demarais and P. R. Krausman, pp. 389-408. Prentice Hall, Upper Saddle River, NJ.

Rosania, Corinne N. and Matthew T. Boulanger
2009 *Fluorine Analysis of North American Black Bear (Ursus americanus) Bones from Lawson Cave, Boone County, Missouri*. Unpublished report on file, University of Missouri Research Reactor (MURR), Columbia.

Royer, Dana L., Robert A. Berner, Isabel P. Montanez, Neil J. Tabor and David J. Beerling
2004 CO2 as a Primary Driver of Phanerozoic Climate. *GSA Today* 14:4-10.

Schoeninger, M. F., J. Moore and J. M. Sept
1999 Subsistence Strategies of Two Savanna Chimpanzee Populations: The Stable Isotope Evidence. *American Journal of Primatology* 49:297-314.

Schullery, Paul
1986 *The Bears of Yellowstone*. 2 ed. Roberts Rinehart, Boulder, CO.

Schwartz, Charles W. and Elizabeth R. Schwartz
1981 *The Wild Mammals of Missouri*. University of Missouri Press, Columbia.

Shaviv, Nir J. and Ján Veizer
2003 Celestial Driver of Phanerozoic Climate? *GSA Today*:4-10.

Smith, Kimberly G. and Joseph D. Clark
1994 Black Bears in Arkansas: Characteristics of a Successful Translocation. *Journal of Mammalogy* 75:309-320.

Van de Water, Marjorie
1953 How Old Is It? *The Science News-Letter* 64:10-12.

van der Merwe, Nikolaas J.
1982 Carbon Isotopes, Photosynthesis, and Archaeology. *American Scientist* 70:596-606.

van der Merwe, Nikolaas J. and John C. Vogel
1978 13C Content of Human Collagen as a Measure of Prehistoric Diet in Woodland North America. *Nature* 276:815-816.

van Klinken, Gert J. and Robert E. M. Hedges
1995 Experiments on Collagen-Humic Interactions: Speed of Humic Uptake, and Effects of Diverse Chemical Treatments. *Journal of Archaeological Science* 22:263-270.

Virginia Department of Game and Inland Fisheries
2007 Living with Black Bears in Virginia (Video Transcript). Electronic document, http://www.dgif.virginia.gov/video/living-with-black-bears/living-with-black-bears-transcript.pdf, accessed April 19, 2009.

Vogel, John C. and N. J. van der Merwe
1977 Isotopic Evidence for Early Maize Cultivation in New York State. *American Antiquity* 42:238-242.

Wells, P. H.
1959 Bear Bones from a Boone County Cave. *Bulletin of the National Speleological Society* 21:13-14.

Whitaker, John O. Jr and William J. Jr. Hamilton
1998 *Mammals of the Eastern United States*. 3 ed. Comstock Pub. Associates, Ithaca.

Winter, K., J. H. Troughton and K. A. Card
1976 d13C Values of Grass Species Collected in the Northern Sahara Desert. *Oecologia* 25:115-123.

Wolverton, Steve
1996 *Morphometry and Taphonomy of the Lawson Cave Ursids.* Unpublished Master of Arts thesis, University of Missouri, Columbia.

2001 Caves, Ursids, and Artifacts: A Natural-Trap Hypothesis. *Journal of Ethnobiology* 21:55-72.

2006 Natural-Trap Ursid Mortality and the Kurtén Response. *Journal of Human Evolution* 50:540-551.

Wolverton, Steve and R. Lee Lyman
1998 Measuring Late Quaternary Ursid Diminution in the Midwest. *Quaternary Research* 49:322-329.

Zimmerman, Michael and Warren L. Wagner
1979 A Description of the Woody Vegetation of Oak-Hickory Forest in the Northern Ozark Highlands. *Bulletin of the Torrey Botanical Club* 106:117-122.

APPENDIX

Table 1. Contextual data for specimens analyzed in this study. Includes species, common name, site from which specimen was recovered, skeletal element analyzed, average stable carbon (δ13C) and nitrogen (δ15N) isotope values, diet inferred from stable isotope values, fluorine concentrations (F) and AMS radiocarbon ages (C14) obtained for each individual.

Sample	**Species**	**Common Name**	**Site**	**Element**	**δ13C**	**St dev**	**δ15N**	**St dev**	**Diet**	**F (ppm)**	**St dev**	**C14**	**St dev**
LCB001	*Ursus americanus*	North American black bear	Lawson Cave, MO	Femur	-20.32	0.51	4.20	0.26	C3	731.69	28.14		
LCB002	*Ursus americanus*	North American black bear	Lawson Cave, MO	Femur	-19.35	0.41	5.40	0.43	C3	390.1	34	229	41
LCB003	*Ursus americanus*	North American black bear	Lawson Cave, MO	Femur	-19.41	0.43	4.71	0.57	C3	898.55	48.56		
LCB004	*Ursus americanus*	North American black bear	Lawson Cave, MO	Femur	-20.04	0.11	4.84	0.05	C3	444.34	16.41		
LCB005	*Ursus americanus*	North American black bear	Lawson Cave, MO	Femur	-20.04	0.26	5.53	0.12	C3	646.98	11.59	206	41
LCB006	*Ursus americanus*	North American black bear	Lawson Cave, MO	Femur	-19.89	0.06	4.85	0.12	C3	906.3	5.9		
LCB007	*Ursus americanus*	North American black bear	Lawson Cave, MO	Femur	-19.33	0.21	5.95	0.17	C3	959.17	171.08		
LCB008	*Ursus americanus*	North American black bear	Lawson Cave, MO	Femur	-20.21	0.12	3.08	0.29	C3	1114.14	35.63	630	42
LCB009	*Ursus americanus*	North American black bear	Lawson Cave, MO	Femur	-19.36	0.28	4.92	0.28	C3	780.6	23.36		
LCB010	*Ursus americanus*	North American black bear	Lawson Cave, MO	Femur	-20.45	0.31	3.93	0.26	C3	1797.61	71.11		
LCC001	*Canis* spp.	Dog/coyote	Lawson Cave, MO	Femur	-11.17	0.16	6.97	0.14	C3/C4				
LCD001	*Didelphis virginiana*	Opossum	Lawson Cave, MO	Femur	-19.14	0.04	8.91	0.10	C3				
LCM001	*Marmota monax*	Woodchuck	Lawson Cave, MO	Femur	-22.30	0.18	2.48	0.32	C3				
LCM002	*Marmota monax*	Woodchuck	Lawson Cave, MO	Femur	-26.41	0.42	0.93	0.32	C3				
LCM003	*Marmota monax*	Woodchuck	Lawson Cave, MO	Femur	-25.36	0.14	0.75	0.20	C3				
LCP001	*Sus scrofa*	Pig	Lawson Cave, MO	Femur	-20.97	0.14	4.59	0.10	C3				
LCP002	*Sus scrofa*	Pig	Lawson Cave, MO	Mandible	-21.04	0.24	5.70	0.69	C3				
LCP003	*Sus scrofa*	Pig	Lawson Cave, MO	Mandible	-12.66	1.77	4.88	0.25	C3/C4				
LCP004	*Sus scrofa*	Pig	Lawson Cave, MO	Femur	-14.07	2.13	5.14	0.79	C3/C4				
LCS001	*Sylvilagus floridanus*	Cottontail	Lawson Cave, MO	Femur	-19.47	0.65	4.32	0.09	C3				
LCS002	*Sylvilagus floridanus*	Cottontail	Lawson Cave, MO	Femur	-22.49	0.34	3.76	0.28	C3				
LCS003	*Sylvilagus floridanus*	Cottontail	Lawson Cave, MO	Femur	-18.51	0.62	7.48	0.22	C3				
LCS004	*Sylvilagus floridanus*	Cottontail	Lawson Cave, MO	Femur	-21.90	0.18	0.60	0.17	C3				
LCS005	*Sylvilagus floridanus*	Cottontail	Lawson Cave, MO	Femur	-22.69	0.37	0.95	0.16	C3				
MOU001	*Ursus americanus*	North American black bear	Cedar Co., MO	Mandible	-20.23	0.13	3.87	0.29	C3				
MOU002	*Ursus americanus*	North American black bear	Reynolds Co., MO	Femur	-18.30	0.36	4.32	0.15	C3				
OKL001	*Lynx rufus*	Bobcat	Oklahoma	Femur	-19.02	0.04	6.07	0.18	C3				
OKL002	*Lynx rufus*	Bobcat	Oklahoma	Femur	-19.59	0.13	5.45	0.13	C3				

Table 2. Atomic ratios of carbon and nitrogen for each replicate sample. Samples outside the range for collagen (defined by DeNiro 1985) are in bold.

Sample	% C	% N	Atomic Ratio
LCB001a	46.81	17.55	3.11
LCB001b	44.88	17.07	3.07
LCB001c	46.19	17.50	3.08
LCB002a	45.04	16.40	3.20
LCB002b	46.17	16.55	3.25
LCB002c	45.33	15.74	3.36
LCB003a	46.33	17.02	3.18
LCB003b	44.30	16.73	3.09
LCB003c	45.39	16.67	3.18
LCB004a	47.15	17.97	3.06
LCB004b	44.46	17.00	3.05
LCB004c	43.01	16.40	3.06
LCB005a	43.04	15.45	3.25
LCB005b	45.62	17.32	3.07
LCB005c	48.61	18.51	3.06
LCB006a	47.18	17.99	3.06
LCB006b	48.23	18.35	3.07
LCB006c	44.89	17.04	3.07
LCB007a	46.40	16.30	3.32
LCB007b	46.59	16.87	3.22
LCB007c	47.23	17.04	3.23
LCB008a	47.23	17.25	3.20
LCB008b	45.75	17.12	3.12
LCB008c	42.96	15.73	3.19
LCB009a	43.10	15.65	3.21
LCB009b	43.26	15.68	3.22
LCB009c	43.51	15.76	3.22
LCB010a	44.03	16.33	3.14
LCB010b	39.64	14.95	3.09
LCB010c	41.21	15.54	3.09
LCC001a	45.71	17.27	3.09
LCC001b	45.43	17.33	3.06
LCC001c	43.35	16.44	3.08
LCD001a	43.79	15.69	3.25
LCD001b	44.10	15.86	3.24
LCD001c	41.18	14.72	3.26
LCM001a	40.20	15.40	3.05
LCM001b	40.90	15.50	3.08
LCM001c	39.80	15.41	3.01
LCM002a	41.75	15.54	3.14
LCM002b	42.47	15.92	3.11
LCM002c	41.82	15.85	3.08
LCM003a	41.82	12.74	**3.83**
LCM003b	35.74	10.82	**3.85**
LCM003c	31.76	8.89	**4.17**
LCP001a	40.28	14.99	3.14

LCP001b	41.58	15.55	3.12
LCP001c	35.93	13.19	3.18
LCP002a	43.47	16.06	3.16
LCP002b	42.95	15.90	3.15
LCP002c	44.21	16.36	3.15
LCP003a	43.07	16.19	3.10
LCP003b	42.08	15.58	3.15
LCP003c	41.80	15.57	3.13
LCP004a	43.25	15.94	3.17
LCP004b	43.43	16.13	3.14
LCP004c	43.69	16.12	3.16
LCS001a	42.55	15.68	3.17
LCS001b	42.60	15.72	3.16
LCS001c	42.02	15.42	3.18
LCS002a	41.21	14.56	3.30
LCS002b	40.59	14.70	3.22
LCS002c	40.41	14.48	3.26
LCS003a	41.85	14.39	3.39
LCS003b	39.19	13.95	3.28
LCS003c	38.93	13.71	3.31
LCS004a	42.27	15.85	3.11
LCS004b	42.13	15.76	3.12
LCS004c	41.79	15.52	3.14
LCS005a	41.60	15.73	3.08
LCS005b	42.32	15.89	3.11
LCS005c	41.74	15.74	3.09
MOU001a	42.65	16.02	3.11
MOU001b	43.44	16.20	3.13
MOU001c	41.36	15.51	3.11
MOU002a	41.26	15.48	3.11
MOU002b	44.22	16.71	3.09
MOU002c	42.80	16.23	3.08
OKL001a	43.24	16.34	3.09
OKL001b	48.36	18.64	3.03
OKL001c	38.94	14.88	3.05
OKL002a	46.40	18.00	3.01
OKL002b	44.73	17.37	3.00
OKL002c	46.05	18.02	2.98
		avg	**3.17**
		stdev	**0.17**
		max	**4.17**
		min	**2.98**

Table 3. Stable carbon and nitrogen isotope values for replicate samples (columns a, b, and c) of each individual included in this study.

	δ13C					δ15N				
Sample	**a**	**b**	**c**	**Average**	**St Dev**	**a**	**b**	**c**	**Average**	**St Dev**
LCB001	-19.76	-20.75	-20.45	**-20.32**	**0.51**	4.49	4.01	4.10	**4.20**	**0.26**
LCB002	-18.91	-19.72	-19.41	**-19.35**	**0.41**	5.78	4.93	5.49	**5.40**	**0.43**
LCB003	-19.88	-19.04	-19.32	**-19.41**	**0.43**	4.05	5.07	5.00	**4.71**	**0.57**
LCB004	-19.91	-20.07	-20.13	**-20.04**	**0.11**	4.83	4.89	4.80	**4.84**	**0.05**
LCB005	-20.26	-19.76	-20.11	**-20.04**	**0.26**	5.63	5.57	5.40	**5.53**	**0.12**
LCB006	-19.82	-19.95	-19.90	**-19.89**	**0.06**	4.85	4.98	4.73	**4.85**	**0.12**
LCB007	-19.11	-19.37	-19.52	**-19.33**	**0.21**	6.15	5.87	5.84	**5.95**	**0.17**
LCB008	-20.18	-20.11	-20.35	**-20.21**	**0.12**	3.19	3.30	2.76	**3.08**	**0.29**
LCB009	-19.29	-19.11	-19.66	**-19.36**	**0.28**	4.96	5.18	4.63	**4.92**	**0.28**
LCB010	-20.10	-20.59	-20.68	**-20.45**	**0.31**	4.23	3.73	3.84	**3.93**	**0.26**
LCC001	-11.20	-11.01	-11.32	**-11.17**	**0.16**	6.98	6.84	7.11	**6.97**	**0.14**
LCD001	-19.18	-19.10	-19.16	**-19.14**	**0.04**	8.85	8.85	9.02	**8.91**	**0.10**
LCM001	-22.11	-22.46	-22.34	**-22.30**	**0.18**	2.14	2.79	2.51	**2.48**	**0.32**
LCM002	-26.53	-26.76	-25.95	**-26.41**	**0.42**	0.71	0.78	1.31	**0.93**	**0.32**
LCM003	-25.47	-25.41	-25.20	**-25.36**	**0.14**	0.58	0.69	0.98	**0.75**	**0.20**
LCP001	-21.08	-20.82	-21.01	**-20.97**	**0.14**	4.48	4.68	4.61	**4.59**	**0.10**
LCP002	-20.91	-21.32	-20.88	**-21.04**	**0.24**	5.09	6.45	5.55	**5.70**	**0.69**
LCP003	-14.70	-11.70	-11.58	**-12.66**	**1.77**	4.62	5.11	4.91	**4.88**	**0.25**
LCP004	-12.40	-13.35	-16.47	**-14.07**	**2.13**	5.71	5.48	4.23	**5.14**	**0.79**
LCS001	-19.50	-20.10	-18.80	**-19.47**	**0.65**	4.30	4.42	4.24	**4.32**	**0.09**
LCS002	-22.71	-22.10	-22.67	**-22.49**	**0.34**	3.96	3.89	3.44	**3.76**	**0.28**
LCS003	-18.77	-18.97	-17.80	**-18.51**	**0.62**	7.42	7.72	7.29	**7.48**	**0.22**
LCS004	-22.01	-21.70	-21.99	**-21.90**	**0.18**	0.40	0.69	0.70	**0.60**	**0.17**
LCS005	-22.89	-22.26	-22.91	**-22.69**	**0.37**	1.13	0.87	0.84	**0.95**	**0.16**
MOU001	-20.14	-20.17	-20.37	**-20.23**	**0.13**	3.95	4.12	3.55	**3.87**	**0.29**
MOU002	-18.70	-18.00	-18.21	**-18.30**	**0.36**	4.39	4.42	4.14	**4.32**	**0.15**
OKL001	-18.98	-19.02	-19.06	**-19.02**	**0.04**	6.28	5.99	5.94	**6.07**	**0.18**
OKL002	-19.73	-19.48	-19.56	**-19.59**	**0.13**	5.59	5.35	5.39	**5.45**	**0.13**