SCIENCE ADVANCES | RESEARCH ARTICLE

ANTHROPOLOGY

Mammoth featured heavily in Western Clovis diet

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Ancient Native American ancestors (Clovis) have been interpreted as either specialized megafauna hunters or generalist foragers. Supporting data are typically indirect (toolkits, associated fauna) or speculative (models, actualistic experiments). Here, we present stable isotope analyses of the only known Clovis individual, the 18-month-old Anzick child, to directly infer maternal protein diet. Using comparative fauna from this region and period, we find that mammoth was the largest contributor to Clovis diet, followed by elk and bison/camel, while the contribution of small mammals was negligible, broadly consistent with the Clovis zooarchaeological record. When compared with second-order consumers, the Anzick-1 maternal diet is closest to that of scimitar cat, a mammoth specialist. Our findings are consistent with the Clovis megafaunal specialist model, using sophisticated technology and high residential mobility to subsist on the highest ranked prey, an adaptation allowing them to rapidly expand across the Americas south of the Pleistocene ice sheets.

INTRODUCTION

To answer questions about the mode, tempo, and human ecology involved in the peopling of the Americas, we must understand subsistence economies, strategies, and diets of the first Americans. These issues are hotly contested, with multiple hypotheses that enjoy some level of support. Some researchers contend that Clovis populations were megafaunal specialists to some extent, focusing particularly on mammoth (*Mammuthus columbi*) (*1*–*8*), while others have argued that such an adaptation was not viable, and thus, Clovis populations were more likely broad-spectrum foragers, regularly incorporating in their diet small game, plants, and perhaps fish (*9*–*14*). The resolution of this debate has profound implications for reconstructing the adaptive strategies that allowed rapid expansion of Paleoindians throughout the Western Hemisphere and assessing the impact of that expansion on megafaunal extinctions during the terminal Pleistocene (*15*–*17*). However, to date, all attempts to resolve the diets of the first Americans have relied on secondary datasets, such as faunal remains from archaeological sites [(*3*) versus (*9*)], modern experimentation to determine weapon function [(*18*) versus (*19*)], models of potential foraging behaviors and diet based in part on modern ecosystems [(*13*) versus (*3*)], and hypothetical notions of expected numbers of kill sites per taxon in relation to abundance of various taxa in the paleontological record (*12*, *20*–*21*). There is also disagreement whether the spatial association of megafaunal remains and artifacts within archaeological sites is sufficient to infer hunting [(*12*) versus (*7*, *22*)]. Contributing to the problem is uncertainty relating to mere association versus utilization, taphonomic bias favoring larger bodied species, and differing excavation methods (*23*). In sum, these lines of evidence have not provided definitive answers about Clovis Paleoindian diets and no consensus has emerged within the archaeological community.

In contrast, more direct evidence of paleodiets can be gleaned from stable isotope analyses of human remains (*24*–*25*). At present, only three Clovis and Clovis-age individuals are known in the record: Anzick-1 from Montana [~12,800 calibrated years before the present (cal yr B.P.)] (*26*–*28*), Arlington Springs from the southern California coast (~12,920 cal yr B.P.) (*29*), and Hoyo Negro from the Yucatan Peninsula, Mexico (~12,870 cal yr B.P.) (*30*–*31*). While neither the Hoyo Negro nor Arlington Springs individuals have yielded stable isotope information from bone collagen, extensive published information is available for Anzick-1 (*28*, *32*) (Fig. 1). Although some archaeologists have hypothesized about the existence of pre-Clovis populations, the current consensus is that the Clovis complex represents the earliest widespread cultural manifestation south of the glacial ice sheets (*15*, *33*–*34*). Ancient DNA extracted from the Anzick-1 infant shows that he (and by secure inference, other people of the Clovis cultural complex) belonged to the Southern Native American (SNA) clade, the only Native American genetic group that expanded south of the ice sheets into North, Central, and South America in a rapid, star-like radiation after ~14,900 to 13,900 years ago (*17*, *32*, *35*–*36*). Therefore, isotopic data from the Anzick-1 child and contemporary potential food resources from the same geographic and ecological region can provide critical direct data on Western Clovis diet and, by extension, early Paleoindian adaptive strategies. Western Clovis comprises Clovis populations in North America west of the Mississippi River.

Here, we report stable isotope measurements on (i) a suite of spatially relevant and Clovis-contemporary (Late Glacial) potential prey resources and (ii) a wide range of comparative secondary consumers (carnivores/omnivores) that fed on megaherbivores and smaller mammals to reconstruct the protein diet of the mother of Anzick-1. A dietary mixing model was produced to assess relative contributions of various prey species to the Anzick-1 diet. We consider implications of the results for the current debate on Paleoindian adaptive strategies.

THE STABLE ISOTOPE RECORD

Anzick-1 was a ~18-month-old male child found in direct association with a large assemblage of over 100 Clovis lithic and osseous artifacts near Wilsall, Montana (*26*–*27*, *37*). Numerous radiocarbon assays have been previously obtained from Anzick-1 bone collagen (*27*, *32*, *38*–*39*), but the most accurate age appears to be 10,915 ± 50 ^{14}C yr B.P. (12,905 to 12,695 cal yr B.P.) obtained on the bone

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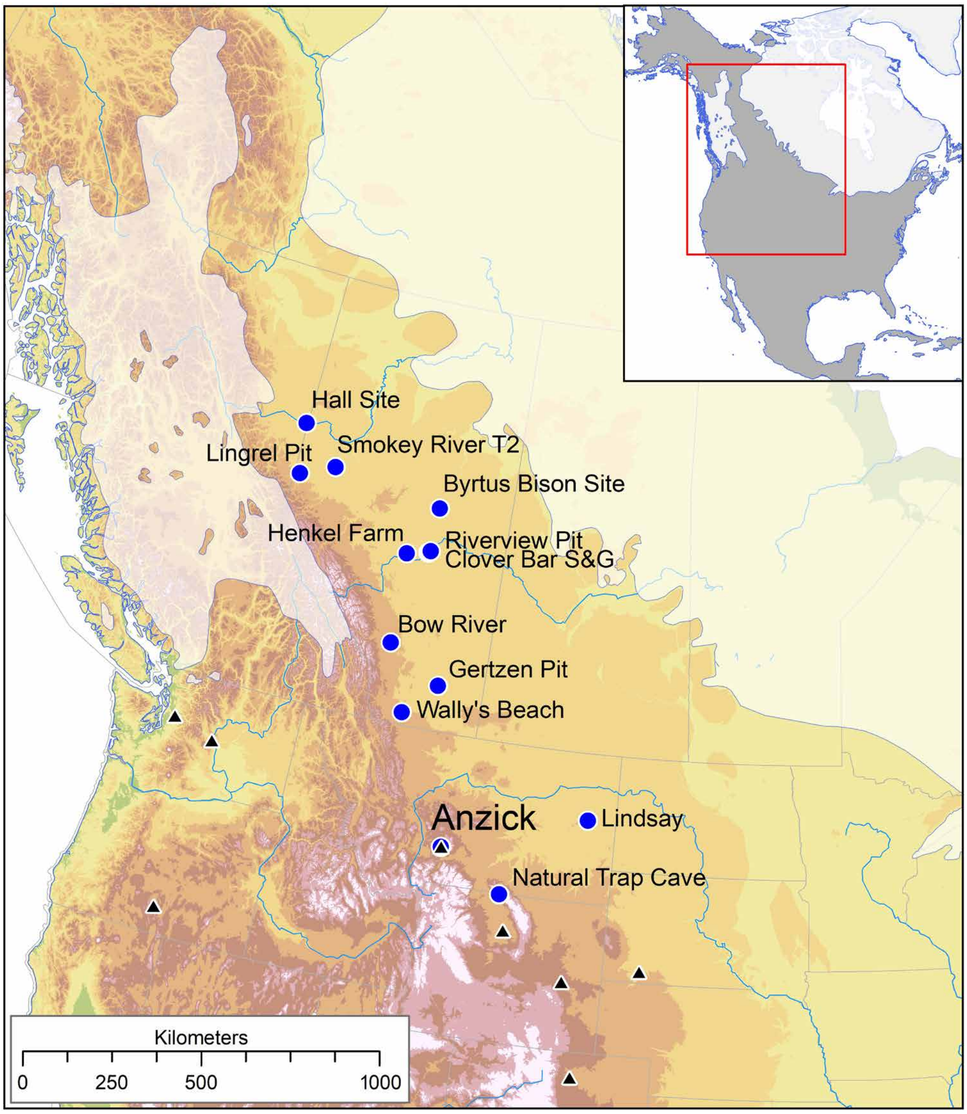

Fig. 1. Location of Anzick site, faunal samples (circles) used in this study, and major Clovis sites (triangles). Glacial ice at 12,800 cal yr B.P. (*72*).

collagen–specific amino acid, hydroxyproline (*28*). This age is consistent with radiocarbon dates on associated worked elk antler rods (12,990 to 12,840 cal yr B.P.) (*27*–*28*, *32*). Table S1 lists all stable isotope measurements and their associated radiocarbon ages from Anzick-1. From these data, we selected δ^{13}C and δ^{15}N values for our mixing model [Stable Isotope Mixing Model in R (SIMMR); (*40*–*41*)] based on the following criteria: (i) both δ ^{13}C and δ^{15}N measurements were reported; (ii) the ^{14}C ages obtained from the same sample and pretreatment were within the accepted age range of the Anzick-1 individual (i.e., 10,500 to 11,000 ^{14}C yr B.P.); and (iii) the measurements were derived from whole collagen or gelatin, rather than isolated amino acids (section S1). We used these criteria to minimize the impact of potential contaminants (indicated by younger or older radiocarbon ages) and to facilitate direct comparison with whole collagen isotope measurements from potential prey resources. The CAMS-80535 to CAMS-80537 series provided the best set of isotopic measurement data, fulfilling all three criteria. The SR-8149 to SR-8151 series did not have associated ^{14}C ages, so we could not assess their accuracy (and therefore potential contamination). The SR-8151 OxA series was rejected because the ^{14}C ages were outside of the acceptable age range, suggesting contamination that might also affect the stable isotope measurements. Finally, the SR-8151 hydroxyproline sample (OxA-X-2739-54), being from a single amino acid, is not comparable to food resource data.

We averaged the three whole collagen data pairs, resulting in a δ^{13}C value estimate of −17.9 ± 0.3‰ and δ^{15}N value estimate of 9.3 ± 0.8‰. We then applied a correction for the nursing signal for the Anzick-1 infant. The standard nursing effects are +3‰ for the δ^{15}N value and +1‰ for the δ^{13}C value (*42*). Given the estimated age of Anzick-1 at 18 months (*26*), we estimated that two-thirds of the diet was obtained from nursing and one-third was from solid foods (see section S2). This resulted in a correction of −2‰ for the δ^{15}N values and −0.7‰ for the δ^{13}C values. This yielded a corrected maternal values of −18.6 ± 0.3‰ for the δ^{13}C values and 7.3 ± 0.8‰ for the δ^{15}N values. To directly compare maternal diet values with potential food resources in our mixing model, we applied a standard trophic discrimination factor (TDF) correction of 1.1‰ for the δ^{13}C value and 3.8‰ for the δ^{15}N value (*43*). This yielded corrected maternal diet δ^{13}C and δ^{15}N values of −19.7‰ and +3.5‰, respectively. Our study focused on the application of bulk (total organic carbon and nitrogen) isotope analyses. We were not able to perform compound-specific isotope analyses, which have yielded dietary insights into the lives of other humans, because the Anzick-1 remains have been reburied and are unavailable.

The Anzick-1 stable isotope data were then compared to a potential food source dataset derived from newly reported analyses and published sources, including megafaunal herbivores and small mammals from the site and region (tables S2 to S5). To more precisely situate Clovis diets relative to other contemporary second-order consumers, we also compared Anzick-1 maternal diet to other secondary consumer diets in the local foodwebs. Potential food source taxa were selected on the basis of presence in the archaeological/paleontological record for the northwestern Great Plains during the terminal Pleistocene [e.g., (*44*)]. Many of these taxa also commonly occur in Clovis faunal assemblages (see table S3) (*2*–*3*, *9*–*10*).

Because stable isotopic baselines can vary by region and through time (*45*), we focused on data from the region of Anzick-1: Northwestern Great Plains, encompassing eastern Montana and southern Alberta (Fig. 1). This region represents the eastern edge of the Mammoth Steppe, comprising a relatively uniform faunal community across Beringia and into Alberta during much of the late Pleistocene (*44*). Therefore, we focused on samples from the terminal Pleistocene period (~14,000 to 12,400 cal yr B.P.), resulting in 36 measurement pairs, 31 from published sources and 5 specimens from the Royal Alberta Museum newly analyzed here (table S2), including *Bison* (bison) (*n* = 10), *Bootherium bombifrons* (helmeted muskox) (*n* = 1), *Camelops hesternus* (yesterday's camel) (*n* = 3), *Cervus canadensis* (elk/wapiti) (*n* = 2), *Equus* (horse) (*n* = 15), *Homotherium serum* (scimitar-toothed cat) (*n* = 1), *Mammuthus* (mammoth) (*n* = 2), *Panthera atrox* (American lion) (*n* = 1), and *Rangifer tarandus* (caribou) (*n* = 1). These isotopic data fell into distinct clusters based on taxon (Fig. 2 and fig. S4). To expand the sample of secondary consumers and to increase herbivore species diversity, we included 41 measurement pairs from Natural Trap Cave (NTC) fauna, located in Wyoming ~200 km from the Anzick site [reported in (*46*)] (Fig. 1). The NTC assemblage is restricted in time and location and represents a single animal community with the same isotopic baseline, including several species from the terminal Pleistocene dataset, allowing us to compare the datasets. NTC taxa included carnivores: *Aenocyon dirus* (dire wolf, formerly *Canis dirus*) (*n* = 1), *Arctodus simus* (short-faced bear) (*n* = 1), *Canis lupus* (gray wolf) (*n* = 9), *Miracinonyx inexpectata* (American cheetah) (*n* = 3), and *P. atrox* (*n* = 3), as well as additional herbivores: *Antilocapra americana* (pronghorn) (*n* = 1), *Bison* (*n* = 5), *C. hesternus* (*n* = 1), Equini (*Equus* or *Haringtonhippus*) (horse or stilt-legged horse) (*n* = 15), and *Ovis canadensis* (bighorn sheep) (*n* = 2). Because the NTC fauna we used dates to just before the Last Glacial Maximum (LGM; ~26,400 to 23,300 cal yr B.P.), and the taxa that overlap between the two datasets are systematically offset, we computed a transfer function to bring them into the same isotopic baseline as the terminal Pleistocene assemblages (see section S3 and figs. S1 and S2).

No late Pleistocene or pre-LGM small mammals were available or reported in the literature, so we obtained samples representing four species from NTC [*Lepus* (hare), *Marmota* (marmot), *Neotoma* (packrat), and *Sylvilagus* (cottontail rabbit)] that date to the early Holocene (~8000 to 4000 cal yr B.P.). We conducted radiocarbon and stable isotope analyses on all four individuals using the same procedures applied to the megafauna reported here. While these are younger than the other specimens, their stable isotope baseline is consistently higher than that of pre-LGM fauna, allowing us to include them here by using the same transfer function mentioned above (section S3 and fig. S3). Our entire comparative faunal dataset comprises 81 measurement pairs of megaherbivores (*n* = 58 from 9 taxa), secondary consumers (*n* = 19 from 6 taxa), and small mammals (*n* = 4 from 4 taxa). We were not able to obtain stable isotope information on ground sloths (suborder: Folivora), as no specimens of suitable age were available from this region for stable isotope analysis. We did not include fishes or birds because they are absent from nearly all Clovis faunal assemblages and their exploitation is inconsistent with Clovis technology and settlement behavior (Supplementary Text).

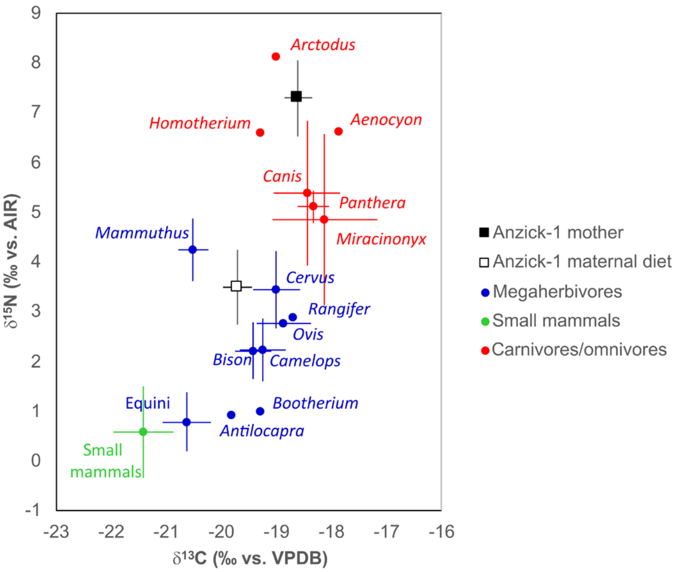

Fig. 2. Isospace plot showing mean faunal collagen δ^{13}C and δ^{15}N values for Anzick-1 and regional fauna. Small mammals is average of *Lepus*, *Marmota*, *Neotoma*, and *Sylvilagus*. Anzick-1 mother diet is corrected for TDF (*43*). Error bars show ±1 SD.

RESULTS

Stable carbon and nitrogen isotope values of potential food resources cluster by taxon as expected, and results are broadly similar to previous studies (*24*, *44*–*45*) (Fig. 2 and fig. S4), with small terrestrial mammals having relatively lower δ^{13}C and δ^{15}N values compared to megafauna. Equini had relatively low δ^{15}N values compared to other megaherbivores. *Mammuthus* had relatively low δ^{13}C values and high δ^{15}N values. *Bison* and other herbivores had relatively high δ^{13}C values. Secondary consumers show higher δ^{15}N values compared with the herbivores, as expected for consumers. The Anzick-1 maternal δ^{13}C and δ^{15}N values fall within this secondary consumer cluster (Fig. 2).

Biplots of the Anzick-1 and faunal δ^{15}N and δ^{13}C values show that the maternal values fall within the dietary mixing space bounded by the faunal isotope values, demonstrating that their isotopic compositions can be explained by a mixture of the selected food sources in the maternal diet (Fig. 2). The most proximal potential food sources are *Cervus*, *Mammuthus*, *Bison*, and *Camelops* (the last two with overlapping isotopic values). *Rangifer* and *Ovis* are slightly more distant, while *Antilocapra*, *Bootherium*, and Equini are far distant. *Mammuthus* occupy a distinctive isotopic space that does not overlap with other grazers or megaherbivore mixed feeders or browsers (Fig. 2), suggesting that they contributed substantially to Anzick-1's maternal diet. Except for *Mammuthus*, no other potential prey species is positioned in the regional isospace in such a way that would shift Anzick's maternal diet to higher δ^{15}N and lower δ^{13}C values. The Anzick-1 isotopic values are distant from small mammals, suggesting that this latter contributed very little to the overall protein diet for Anzick-1.

Three Bayesian mixing models were used to estimate the proportional contributions of the different items to Anzick-1 maternal diet: (1) all megaherbivores, (2) all megaherbivores and small mammals, and (3) a subset of megaherbivores with the highest diet contributions from models 1 and 2 and Clovis zooarchaeological assemblages to more precisely discriminate importance to the Anzick-1 maternal diet (results shown in Fig. 3, figs. S6 to S8, and table S7). While two-biomarker analyses should be used on seven or fewer sources given potential overlap in isospace (*47*), we cannot arbitrarily exclude sources across the sample of the Anzick-1 mother and secondary consumers because it would inhibit comparisons. For this reason, we developed model 3, the four-source model.

The results from model 1 indicate that although the Anzick-1 mother derived her dietary protein from multiple megaherbivores, *Mammuthus* contributed a substantial proportion (mean of 39 ± 12%, median of 40%). All other herbivores provide much lower contributions, ranging from 15% (*Cervus*) to 4% (Equini). The inclusion of small mammals (model 2) did not make any substantive difference to the model, with *Mammuthus* contribution remaining the highest (35 ± 15%, median of 37%). All non-*Mammuthus* megaherbivores contributed low percentages to the overall diet (15 to 4%), and small mammals contributed only 4% to the overall diet. Mixing model output cannot clearly resolve the relative importance of other (non-mammoth) megaherbivores, given their overlap in isospace and similar distance from the Anzick-1 isotopic values. To provide more fine-grained detail, model 3 was based on only four sources encompassing the highest potential contributors based on ubiquity in Clovis faunal assemblages [*Bison*/*Camelops*, Equini, *Mammuthus*; (*2*)] and presence at the Anzick site (*Cervus*). For model 3, mean dietary contribution estimates for Anzick-1 were *Mammuthus* (35 ± 15%), *Cervus* (35 ± 17%), *Bison*/*Camelops* (21 ± 15%), and Equini (10 ± 6%). Bayesian 95% credible intervals (CIs) for all models indicate that there are no credible solutions that do not have substantial mammoth contributions (table S7).

In comparison to other secondary consumers, Anzick-1 maternal isotopic values are most proximal and similar to *Homotherium*, more distant from *Arctodus* and *Aenocyon*, and farther distant from *C. lupus*, *Panthera*, and *Miracinonyx* (Figs. 2 and 4 and fig. S5). *Homotherium* is considered a mammoth specialist (*48*), while less is known about *Arctodus* diet and behavior. *Aenocyon* preyed on megafauna, primarily horse, ground sloth, mastodon, bison, and camel (*45*). In contrast, *C. lupus* can be a proxy for broader-spectrum diets that included more small mammal hunting and less megafaunal predation (*49*). *Canis* has lower δ^{15}N values than Anzick-1, consistent with consumption of food resources with lower δ^{15}N values, such as small mammals. *Ursus arctos* is estimated with lower δ^{15}N and higher δ^{13}C values than *Canis*, and is farther distant from Anzick-1 (see discussion in section S5 and fig. S8). In sum, Anzick-1 mother's placement is most similar to *Homotherium*, providing independent evidence of mammoth focus consistent with the Anzick-1 maternal paleodiet estimates.

DISCUSSION

Western Clovis were megafaunal specialists

Our results provide direct evidence for Western Clovis diets at ~12,800 cal yr B.P. Rather than suggesting a broad-spectrum lifeway utilizing many small- and medium-sized mammals, these analyses indicate a strong megafaunal focus, primarily on *Mammuthus*, followed by *Cervus* and *Bison*/*Camelops*. While *Bison* and *Camelops* cannot be distinguished given their overlapping isotopic values, *Camelops* (and probably Equini) may have been rare by the time Anzick-1's mother was foraging in western Montana (*50*), suggesting that this portion of the diet (~21%) was primarily *Bison*. The very low proportion (4.2 to 9.7%) of Equini in the reconstructed paleodiet is consistent with decreasing horse populations at the time of Anzick-1

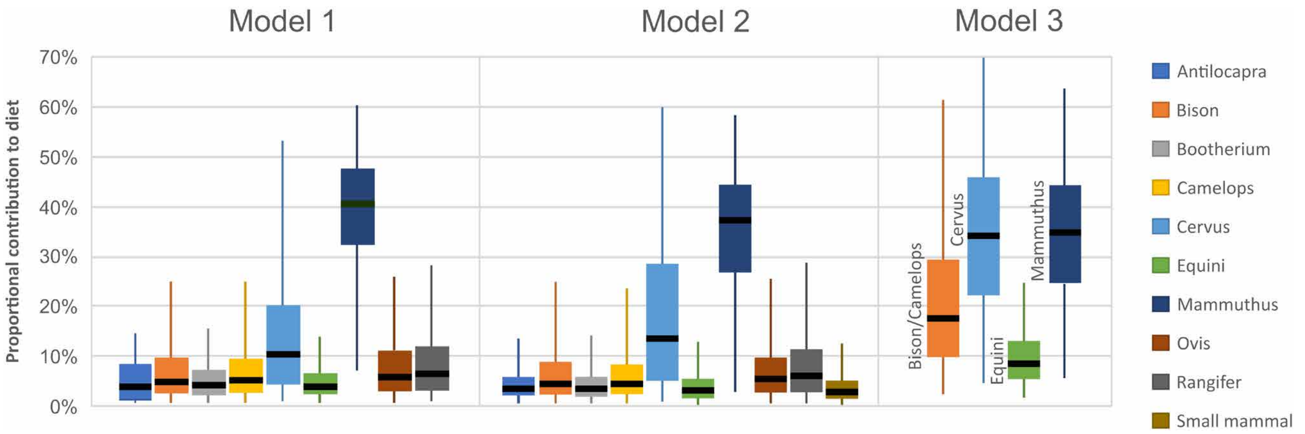

Fig. 3. Models of Anzick-1 maternal diet based on bone collagen δ^{13}C and δ^{15}N values. Estimated contributions (%) of food sources to maternal diet were determined using a 9-source (model 1), 10-source (model 2), and 4-source (model 3) and 2-biotracer ($\delta^{13}C_{collagen}$ and $\delta^{15}N_{collagen}$) mixing model in SIMMR. Box plots showing median (center line), 50% credible interval (CI) (box edges), and 95% CI (error bars) for estimated contributions.

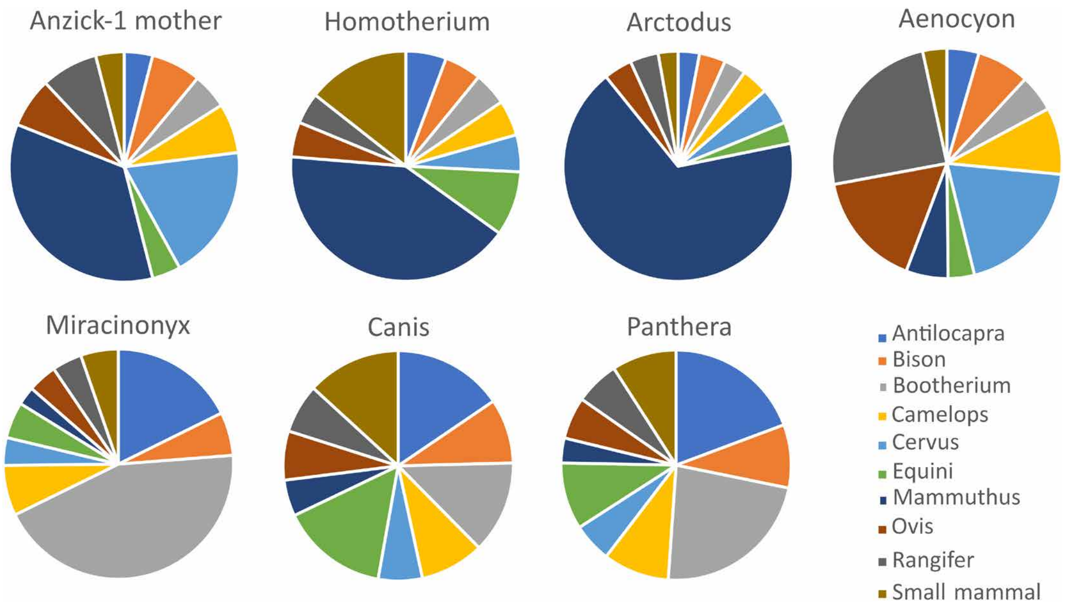

Fig. 4. Anzick-1 maternal and other secondary consumer diets (mean proportional contribution to diet per taxon) using model 2 (10-source model) in SIMMR.

(*51*). *Mammuthus* and *Bison* are the most common taxa in Clovis faunal assemblages (*2*), and this broad agreement between the zooarchaeological record and our stable isotope models reinforces these results. *Cervus* is relatively uncommon in the Clovis record, having been a postglacial immigrant to temperate North America, but the presence of elk antler rods in association with the burial implies that elk almost certainly were hunted by this Clovis group. In view of the relatively late age of Anzick-1 within Clovis site chronologies and Anzick's location in the Northwestern Great Plains, this finding suggests either temporal changes in Clovis diets and/or regional variation. Broader trends in Early Paleoindian faunal assemblages support this. The relatively low importance of *Camelops* and Equini in both our analyses and Clovis faunal assemblages in general raises a question about the health of those populations in the terminal Pleistocene. Equids and *Camelops* were hunted at Wally's Beach, just before the onset of the Clovis interval (*52*–*55*). It is possible that both species had become extirpated (at least regionally) by the later part of the Clovis era, represented by Anzick. *Mammuthus*, *Bison*, and the newly arrived *Cervus* (*56*) may have represented remaining options for consumers of the largest megaherbivores available.

Small mammals comprised a very small part of Anzick-1's maternal diet (~4%) and were likely even less important than our results show, since Clovis-age small mammals should have lower δ^{15}N values than the Early Holocene samples we analyzed (section S3). While rodents and other small mammals appear in Clovis sites, they are not as common as megafauna, and considering body mass (and inferred edible portions of meat and fat), assemblages are overwhelmingly dominated by megafauna, particularly *Mammuthus* and *Bison* (*2*). Seasonal collection of berries and fruits by Eastern Clovis people is documented (*6*), but no Clovis assemblage includes any groundstone tools suitable for bulk processing of nuts and seeds. The extent of such plant use is difficult to directly ascertain; however, we can infer relatively little plant contribution to Clovis diet given the similarity in isotopic values between Anzick-1's mother and hypercarnivores such as *Homotherium* and *Aenocyon*, and dissimilarity from generalists such as *C. lupus* and omnivores such as *U. arctos*. Had Anzick-1's maternal diet included a substantial contribution of plants, the δ^{15}N values would be considerably lower than observed (e.g., ~1 to 3‰ instead of 7.3‰).

Anzick-1's maternal diet can be directly compared with diets of other secondary consumers that occupy specific niches and have preferred prey. She is most similar to *Homotherium*, the scimitar-tooth cats, widely interpreted as juvenile mammoth specialists (*48*, *57*–*60*), although Fox-Dobbs *et al.* (*45*) suggested a wider range of prey (but still overlapping with mammoth). More recently, Smith *et al.* (*49*) found that *Homotherium* exhibited a high level of prey specialization, exclusively on grazers (bison and mammoth) and potentially focusing on juvenile nursing mammoths, consistent with other research (*46*). *Aenocyon* are more constrained than *C. lupus*, overlapping in δ^{13}C values with some extinct cats (*49*). *Arctodus* is more difficult to interpret, as isotope values vary depending on region, and some have argued that it had a more flexible diet (*45*, *49*). In contrast, Anzick-1 mother was quite distant from *Panthera*, *Canis*, *Miracinonyx*, and estimated *Ursus*. *Canis* and *Panthera* were more generalist, consuming both grazers and mixed feeders (*45*, *49*). Canidae tend to be generalists, with a broader carbon isotope niche than other carnivores (*49*), consistent with our results. *Miracinonyx* have long been argued to be *Antilocapra* specialists, but also preyed to a lesser extent on horse, bison, and sheep (*61*). Collectively, these data suggest that Western Clovis people (represented by Anzick-1) were more focused on larger-bodied megafaunal grazers, primarily *Mammuthus*, and were not generalists who regularly consumed smaller bodied herbivores.

Proboscidean hunting is a contentious issue, but our data demonstrate that *Mammuthus* were a substantial part of Anzick-1's maternal diet and the isotope values cannot be explained by consuming another taxon. Furthermore, in contrast to individual zooarchaeological assemblages, which represent a brief dietary snapshot, our stable isotope analyses of bone collagen reflect a longer period of cumulative diet represented by the period of tissue formation in Anzick-1, likely over a year. This reconstructed Western Clovis paleodiet at Anzick has broader implications, given consistency with a wide variety of data, including the bulk of Clovis zooarchaeological data, suggesting that, with caveats, this focus on megafauna, particularly *Mammuthus*, was likely practiced by Clovis more broadly.

Independent proxies consistent with *Mammuthus* consumption

Zooarchaeological analyses of Clovis sites provide independent proxies for paleodiets during the Early Paleoindian period. There exists strong agreement between (i) our estimated mammoth contributions to diet, (ii) dietary comparison with other secondary consumers considered here, and (iii) the broader Clovis zooarchaeological record. Syntheses of the Clovis faunal record (*3*) consistently find that proboscideans, primarily *Mammuthus*, but also *Mammut* and highland gomphothere (*Cuvieronius hyodon*) (*62*), dominate the assemblages in multiple ways: in terms of minimum number of individuals, frequency of occurrence, presence in multiple assemblages, and mass of meat obtainable. *Bison*, *Camelops*, and Equini also frequently occur in Clovis faunal assemblages (*2*). *Cervus*, a recent arrival south of the glacial ice, is found in fewer assemblages, but its presence at the Anzick site in the form of 11 antler foreshafts (*27*, *37*) attests to its importance to that particular Clovis band. This pattern, evincing an emphasis on mammalian megafauna, is consistent with the results we obtained through dietary analysis based on stable isotopes.

A wide variety of other independent datasets are consistent with our isotopic results, including Clovis technology and toolkits, mobility patterns, and site placement, and provide proxies for paleodiets during the Early Paleoindian period. Large and robust lithic and bone projectile points, sturdy, thick bone or antler foreshafts, end scrapers, bifacial and backed-blade knives, bone/antler/wood-working gravers and burins, and massive butchering tools have long been interpreted as a hunting toolkit directed primarily at megafauna (*19*, *63*). Extensive residential mobility of Clovis complex peoples, directly indicated by great distances between lithic toolstone sources and the sites where they were used, is more consistent with foragers focused on megafauna that tend to migrate seasonally over large distances rather than broad-spectrum foragers of primarily endemic small game and fish (*1*). Such a vast range of movement is comparable to that seen in recent reconstructions of mammoth movement patterns in late Pleistocene Alaska (*64*–*65*). In that instance, it even appears that late Pleistocene Beringians were situating their seasonal hunting camps to coincide with regions frequented by mammoth herds (*64*). At Swan Point in Eastern Beringia (Alaska), predating Clovis by almost 1000 calendar years, remains of three mammoths were recovered along with horse, other megafauna, and waterfowl (*7*, *64*, *66*). In North America south of the continental ice sheets, early hunter-gatherers are also associated with landscapes frequented by mammoth (*67*). This behavior continued a pattern that began in northern Eurasia where Upper Paleolithic peoples appear to have been expanding across the mammoth steppe, subsisting on proboscideans and other megafauna common to that extensive biome. From this perspective, Clovis antecedents were tracking familiar habitat from Siberia through Beringia and deeper into North America as glacial ice receded.

Western Clovis diet and megafaunal extinctions

Western Clovis people, represented by Anzick-1's mother, were focused on the largest megaherbivores on the landscape (*Mammuthus*, *Cervus*, *Bison*) with very little contribution from small mammals. The closest secondary consumer analog to Clovis hunter-gatherer diets was the mammoth specialist *Homotherium*. While we do not interpret the results from this one individual as bearing directly on the cause(s) of widespread megafaunal extinctions in the Americas at the Pleistocene/Holocene boundary, we do suggest that predation of some megafaunal species by Clovis populations with effective distance weapons may have played a role [see (*19*)], in conjunction with climate and vegetation shifts. A similar trajectory is represented in South America, where the arrival of Clovis-derived fluted fishtail projectile points marks the onset of rapid megafaunal decline (*68*). Ultimately, by the beginning of the Younger Dryas, at the transition between Clovis and later, more regional Paleoindian complexes (e.g., Folsom, Western Stemmed), *Mammuthus*, an important resource for Clovis as shown by this study, became extinct. The loss of this taxon may have played a role in behavioral shifts and the end of Clovis as a distinct cultural tradition in the Americas.

Dietary analysis of the Anzick-1 Clovis child and derived maternal diet, based on his stable carbon and nitrogen isotope composition, demonstrates that his band, and probably Western Clovis populations in general, focused on *Mammuthus*. Consumption of small mammals and plants was negligible and use of smaller bodied herbivores like *Antilocapra* and *Ovis* was relatively low, while *Cervus* and *Bison* consumption was more common. This suggests a clear megafaunal specialization rather than a broad-spectrum foraging strategy, consistent with Clovis residential mobility patterns and technological organization (*1*). Anzick-1's maternal diet was most similar to *Homotherium*, a juvenile mammoth specialist, and dissimilar from diets of *C. lupus* and *U. arctos*, which reflected a broader dietary spectrum. These results are consistent with faunal patterns within Clovis sites, where proboscideans, particularly *Mammuthus*, are the most common in terms of biomass, followed by other megaherbivores. The temporal position of Anzick-1 near the end of the Clovis period suggests some shifts in Clovis diet, including reduction of *Equus* and *Camelops*, which were probably already in decline, and increase in *Cervus,* likely in response to dynamics of prey availability and abundance during the terminal Pleistocene. Nonetheless, *Mammuthus* was still a substantial component of Western Clovis diet throughout the Clovis period.

MATERIALS AND METHODS

Ethics statement

This research is published after consultation with and support of regional Native American tribes in Montana and Wyoming. This research does not include any new destructive analysis or handling of human remains (Anzick-1), relying on existing isotope data and new analyses from non-human faunal specimens.

Anzick-1 child

The Anzick-1 stable carbon and nitrogen isotope values were obtained from previously published literature (*28*, *32*), and no destructive or intrusive analysis was undertaken for this study. The Anzick infant's burial was discovered accidentally in 1968 on the Anzick property in Wilsall, Montana. Eyewitness accounts verify that the infant's bones were closely associated with a lithic assemblage of 68 bifaces, 8 projectile points, 1 blade, 9 flakes, and 11 elk antler rods, typical of the Clovis complex, all covered with red ochre powder (*26*, *37*). The materials represent items interred with the child in a single burial episode (*26*–*27*). The autosomal genome of this infant was reported in 2014, indicating that he (and the Clovis population to which he belonged) was representative of a major clade of ancestral Native Americans (SNA) that rapidly spread through North America south of the ice sheets and into South America (*32*). The infant bones were repatriated and reinterred in an inter-tribal ceremony on 28 June 2014.

Faunal remains

All faunal bone samples were either previously published or newly analyzed by us (tables S4 and S5). All new specimens came from existing collections curated at the Royal Alberta Museum and University of Wyoming Geological Museum. We selected faunal taxa based on their ubiquity in the local region surrounding Anzick, the Northwestern Great Plains, and their occurrence within the same deglaciation period, 14,000 to 12,000 cal yr B.P. We relied on existing descriptions for taxonomic identification. We selected specific taxa to encompass the suite of potential faunal resources used by the Western Clovis band associated with Anzick-1's mother and to capture food source isotopic variation (table S2). To expand the sample both taxonomically and numerically, we used pre-LGM specimens from nearby NTC and utilized a transfer function to bring these datasets to the same isotopic baseline (section S3). To minimize interlaboratory error, we focused on obtaining published data following similar collagen extraction methods (*32*, *39*, *44*, *46*). For samples run for this study ($n = 9$), we used the Longin method (*69*).

We considered three sets of faunal food sources. Model 1 (megaherbivores) included fauna commonly found in the Northwestern Great Plains ecosystem in the terminal Pleistocene (*Antilocapra*, *Bison*, *Camelops*, Equini, *Mammuthus*, *Ovis*, *Rangifer*), and taxa found at the Anzick site itself, namely, *C. canadensis*. Model 2 (megaherbivores and small mammals) included all model 1 taxa but included an averaged small mammal category, encompassing four taxa with similar isotopic values (*Lepus*, *Marmota*, *Neotoma*, and *Sylvilagus*). Because of the overlap of many taxa in similar isospatial positions, we produced model 3 (likely primary diet sources) based on the highest potential contributors as indicated by frequency in Clovis faunal assemblages (*2*), presence at the Anzick site, and high contributions in models 1 and 2. Model 3 included *Mammuthus*, *Cervus*, a combined *Bison*/*Camelops* group given their nearly identical isotopic values, and Equini. The dataset of comparable carnivores/omnivores (*Aenocyon*, *Arctodus*, *C. lupus*, *Homotherium*, *Miracinonyx*, and *Panthera*) was analyzed relative to model 2 herbivore fauna. Additional data on faunal sample composition and included and excluded taxa are found in sections S3 to S5.

Sample pretreatment and stable isotope measurements

All carbon and nitrogen stable isotope measurements are expressed in delta notation (as δ^{13}C and δ^{15}N values, respectively) relative to internationally accepted standards (*70*). By convention, δ^{13}C and δ^{15}N values are reported in parts per thousand (‰). The international standard for carbon is Vienna Pee Dee Belemnite (VPDB) and that for nitrogen is atmospheric N_2 (AIR). The standard reference materials used to calibrate raw isotopic measurements to the internationally accepted scales are described below.

Bone collagen (δ^{13}C and δ^{15}N values)

All newly reported faunal bone collagen extractions were conducted in the same laboratory (DirectAMS) using the modified Longin protocol (*69*). Fragmented bone was demineralized in HCl (1.0 M) at room temperature, followed by treatment in KOH (1.0 M), and gelatinized at 70°C in dilute HCl (0.001 M, pH 3). Bone collagen samples were submitted to the Cornell University stable isotope laboratory for carbon and nitrogen stable isotope measurement, where they were measured, along with isotopic standards, on a Thermo Delta V isotope ratio mass spectrometer interfaced to an NC2500 elemental analyzer. The carbon and nitrogen stable isotope compositions are expressed relative to VPDB and AIR, respectively, using the internal standard "DEER," which had been previously calibrated against internationally certified standards. All sample sequences included the same quality control check standard, "KCRN" -corn and "CBT" -trout, as a check of the normalization. Precision was calculated as the pooled SD of all repeated measures of calibration and check standards over the relevant analytical runs following (*71*) and was 0.09‰ for δ^{13}C and 0.05‰ δ^{15}N values. All bone collagen samples used in this study met well-accepted quality standards (%N > 5%, %C > 13%, an atomic C/N ratio of 2.9 to 3.6, and a collagen yield of >1%) (table S6). Further, our δ^{13}C and δ^{15}N values for ungulates and one carnivore are generally comparable to those previously reported for paleontological and archaeological specimens in the region.

Trophic discrimination factors

We used the following collagen source–to–collagen consumer TDFs (TDFs with associated SDs) following (*43*): $\Delta^{13}\mathrm{C}_{\text{consumer collagen}-\text{source collagen}} = 1.1 \pm 0.2‰$ and $\Delta^{15}\mathrm{N}_{\text{consumer collagen}-\text{source collagen}} = 3.8 \pm 1.1‰$. We assume a nursing signal of +3‰ for δ^{15}N values and +1‰ for δ^{13}C values (*42*), modified by estimated two-third nursing and one-third solid food, resulting in −2‰ for δ^{15}N values and −0.7‰ for δ^{13}C values to yield a corrected maternal value.

Stable isotope mixing models and diet estimation

To estimate the proportional contributions of food sources to Anzick-1's maternal diet, we used SIMMR, a Bayesian stable isotope mixing model framework available as an open-source package in R. Bayesian mixing models assume that all sources included in the model contributed to the diet. Table S7 provides means and SDs, medians, and 50% CIs for each potential food source's contributions to Anzick-1's maternal diet (see also Fig. 3).

Supplementary Materials

This PDF file includes:

Supplementary Text
Figs. S1 to S9
Tables S1 to S7
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