Using stable isotopes as an additional tool to understand ancient human environments

Utilización de isótopos estables como una herramienta adicional para el conocimiento de ambientes humanos del pasado

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INTRODUCTION

Ecological dynamics among fauna in ecosystems is contingent upon prior biotic and abiotic interaction. Therefore, to get a complete understanding of ecology in modern ecosystems as well as adequate predictions for ecology in future ecosystems, it is important to obtain an accurate idea of relationships among ancient animals and the environments in which they lived. Traditionally, paleontologists have focused on examining morphology and comparisons to modern analogs to address the ecology of ancient animals. One recent technique that has proven useful to examine ecology in ancient animals, including humans, is through examination of stable isotope values found in tooth enamel (Bocherens, 2003; Bocherens et al., 1996; Cerling et al., 1998; Drucker et al., 2003; Koch, 1998; Kohn et al., 2005; Quade et al., 1992). Isotopic analyses can reveal information about resource use and partitioning among fauna, being able to determine diet and habitat use, for example. In this lecture I will present work done in collaboration with Nuria Garcia Garcia and others on Pleistocene sites in Spain. We have analyzed stable carbon and oxygen isotope values found in the tooth enamel of mammalian carnivores and herbivores with the overall aim of understanding the ecological context in which ancient humans lived during the Pleistocene in Spain. We will address: (1) whether stable isotope values permit identification of resource use and partitioning among taxa? (2) If resource use and partitioning are determined, do the results corroborate the ecology predicted by other methodologies (e.g., morphology)? While isotopic analyses generally have concentrated on examining herbivorous taxa where there is a mixture of plants using either the C₃ or C₄ photosynthetic pathways, recent studies, including my own at Yellowstone National Park, have shown resource use and partitioning in areas containing only C₃ plants (Bocherens, 2003; Bocherens et al., 1996, 2004; De Niro & Epstein, 1978; Feranec, 2007; Feranec & Macfadden, 2006; Koch et al., 1998, 2005; Macfadden & Cerling, 1996; Vogel, 1978). The analysis of stable isotopes from ancient mammals provides another technique to determine the autecological and synecological relationships among fauna in ancient ecosystems enabling an accurate portrayal of the setting in which humans lived.

BACKGROUND

ISOTOPES IN PALEOECOLOGY

Isotopic results are expressed in the standard δ-notation: X = [(R_{sample}/R_{standard}) - 1] x 1000, where X is the δ^{13}C or δ^{18}O value, and R = ¹³C/¹²C and ¹⁸O/¹⁶O, respectively. The δ^{13}C and δ^{18}O values are reported relative to the VPDB standard. Animals that feed on dif-
ferent kinds of plants will reflect the carbon isotope value of their food in their tissues (De Niro & Epstein, 1978; Tieszen et al., 1979; Vogel, 1978). Studies utilizing differences in the carbon isotope values from mammals generally focus on communities containing a mixture of C3 and C4 plants, which enables taxa to be distinguished based on the predominant forage included in the diet, where grass feeders generally display more positive (C4) δ13C values, and browsers display more negative (C3) δ13C values (Cerling et al., 1998; Koch et al., 1998; Kohn et al., 2005; MacFadden & Cerling, 1996; Tieszen, 1994; Vogel, 1978).

Based on previous studies and where Spain is geographically situated, it has been shown that the late Pleistocene and modern flora is dominated by C3 plants (Collins & Jones, 1985; Flynn et al., 1984; Pamlqvist et al., 2003; Sage et al., 1999). Different processes, besides photosynthetic pathway, such as variation in light intensity, temperature, nutrient availability, and water stress, can produce measurable variation in the δ13C value in C3 plants (Bocherens, 2003; Ehleringer & Monson, 1993; Farquhar et al., 1989; Heaton, 1999; Koch, 1998; O’Leary, 1988). C3 plants typically have more negative values in closed, forested habitats; while in more open, drier habitats more positive isotope values are typical (Bocherens, 2003; Cerling et al., 2004; Ehleringer & Monson, 1993; Farquhar et al., 1989; Heaton, 1999; O’Leary et al., 1992; Van der Merwe & Medina, 1991). Animals that eat these C3 plants will reflect the carbon isotope ratio ingested. While herbivores do reflect the carbon isotope values of plants ingested, the δ13C value of the tooth enamel is enriched by a consistent amount, about +14.0‰ for medium to large-bodied mammals (Cerling & Harris, 1999; Passey et al., 2005). Assuming a fractionation from plant material to tooth enamel at +14.0‰, extant taxa that feed solely on modern C3 plants will display enamel carbon isotope values between 21.0‰ and 8.0‰. In Pleistocene taxa, a diet of pure C3 plants would range from 19.5‰ to –6.5‰. The difference between Pleistocene and modern is due to fossil fuel burning over the last few hundred years. Isotope values more positive than –6.5‰ would imply incorporation of either C4 or CAM plants into the diet (Cerling & Harris, 1999; Cerling et al., 2004; MacFadden & Cerling, 1996).

Similar to the herbivores, carnivore carbon isotope values within tooth enamel will reflect the isotopic value of prey. Based on the portion of prey ingested (e.g. muscle, organs), and the fractionation of isotope values between the food and the tooth enamel, carnivores display similar carbon isotope values as is found in the tooth enamel of their prey (Bocherens et al., 1994; Grocke, 1997; Kohn et al., 2005; Lee-Thorp et al., 2000). For example, a specialist carnivore that consumes only herbivores whose tooth enamel δ13C value is -10‰, will have a tooth enamel δ13C value of 10‰.

OXYGEN ISOTOPES IN MAMMALS

The oxygen isotopes in mammal tooth enamel depends on the isotopic composition of ingested water, the consistent fractionation of oxygen isotopes between body water and the tooth enamel, and the metabolism of the particular animal (Koch et al., 1989; Kohn, 1996; Kohn et al., 1996, 1998; Land et al., 1980; Longinelli, 1984; Luz & Kolodny, 1985; Luz et al., 1984). Mammals ingest water from two sources, either through drinking meteoric water or from what they consume. Meteoric water is affected by climatic influences such as temperature and humidity, such that δ18O values are more positive where and when it is warmer and more negative where and when it is colder (Dansgaard, 1964; Dansgaard et al., 1982; Fricke & O’Neil, 1996; Kohn & Welker, 2005; Rozanski et al., 1992, 1993).

METHODS

To collect tooth enamel, sampling involved drilling about 1020 mg of pristine enamel powder off the tooth along a non-occlusal surface parallel to the growth axis and across its
entire length using a 0.5 mm inverted cone carbide drill bit and a variable speed Dremel®TM rotary tool. The powder was first collected and treated with 30% hydrogen peroxide for 24 hours to remove organics. The hydrogen peroxide was then decanted and the enamel powder was then washed with distilled water, and soaked in 0.1N acetic acid for another 24 hours to remove any diagenetic carbonate. The following day the acetic acid was decanted and the enamel powder was washed with distilled water and dried.

After treatment, the samples were analyzed using an ISOCARB automated carbonate preparation system attached to a Micromass Optima gas source mass spectrometer within the Geology Department at the University of California, Davis. The ~ 1 mg samples were dissolved in 100% phosphoric acid at 90ºC to create CO2. Mean differences among species within localities were compared by ANOVA and post hoc Tukey HSD tests, which are similar to t-tests, but take into account multiple comparisons. Statistical analyses were run on JMP IN 5 for students, with significance set at $p < 0.05$. Precision was 0.1‰ for $\delta^{13}C$ and 0.1‰ for $\delta^{18}O$.

RESULTS AND DISCUSSION

So far we have analyzed three different ecosystems in Spain including: middle Pleistocene deposits from the Sierra de Atapuerca, the late Pleistocene deposits of Valdegoba Cave, and the late Pleistocene deposits of Pinilla del Valle. At each locality, tooth enamel from both carnivores and herbivores was analyzed. Results from each locality show that there are significant differences in $\delta^{13}C$ values implying the use of different resources within each guild.

Specifically, within the sampled deposits in the Sierra de Atapuerca, Fallow deer (Dama dama) isotope values are significantly different from Red deer (Cervus elaphus) and horses (Equus sp.) and show that this species likely did not eat in open environments. Red deer and horses show similar feeding strategies with less negative carbon values implying use of open environments. For the carnivores, carbon isotope values for Ursus deningeri are significantly different from either lions (Panthera leo) or canids (Vulpes vulpes) and support the contention that this species is herbivorous. Special metabolic mechanisms involved in hibernation in Ursus deningeri might also have influenced its isotope values. The carbon isotope values of remaining carnivores were similar and suggest that each was an opportunistic carnivore, eating a wide variety of prey items.

At Valdegoba Cave, Capra pyrenaica displayed the most positive value for herbivores, while Canis lupus was the most positive carnivore. The most negative herbivore value was displayed by a grassland indicator species, Stephanorhinus hemitoechus, while the negative value for S. hemitoechus is not unusual for eating of a diet of C3 grasses. Ursus spelaeus had the most negative values for the carnivores. All the carnivores at Valdegoba cave, except Canis lupus, are significantly more negative than the herbivores. This may result from the carnivores having rarely used the analyzed herbivores as primary prey, or isotopic fractionation differences based on the portion of food ingested. Species like Vulpes vulpes and Lynx pardinus likely consumed smaller mammals that were not sampled for this study. Further, the $\delta^{13}C$ values of Ursus arctos and Ursus spelaeus species imply resource partitioning, with more negative $\delta^{13}C$ values on cave bears, U. spelaeus. This is consistent with “classical” paleontological interpretations based on anatomical traits.

At Pinilla del Valle, similar to the other localities, individuals within a particular species generally group together. Fallow deer (Dama dama) displayed the most positive $\delta^{13}C$ values, while hyenas (Crocuta crocuta) displayed the most negative values. Brown bears (Ursus arctos) and pigs (Sus scrofa) show great variability in values suggesting ecological generalism or opportunism. Curiously, there are 7 individuals that show values indicative of consuming a large percen-
tage (up to 100%) of C4 grasses. This result is unexpected, as the flora in Spain has been shown to be nearly 100% C3 plants. Further analyses are currently underway to test these results to confirm or reject the presence of C4 plants at Pinilla during the late Pleistocene.

**CONCLUSIONS**

The results gathered from the three localities show that it is possible to understand the ecology of taxa within ancient ecosystems through the examination of stable carbon and oxygen isotope values, even those ecosystems dominated by C3 plants. In general, the isotopic results corroborate conclusions from previous studies that analyzed morphology or comparisons to modern analogs, but in some circumstances the isotopic results imply a different ecology than previous suggestions. Because of these analyses at the three different localities, a framework has been created to understand the ecosystems in which ancient humans lived over the Pleistocene in Spain.

**REFERENCES**


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