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Stable carbon isotope values reveal evidence of resource partitioning among ungulates from modern C_3-dominated ecosystems in North America

Robert S. Feranec *

Department of Integrative Biology, University of California, Berkeley, CA 94720, United States
New York State Museum, 3140 Cultural Education Center, Albany, NY 12230, United States

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Abstract

Resource use and niche partitioning has rarely been shown in ancient C_3-dominated environments through analysis of stable isotope values, even though before 7 million years ago worldwide environments were predominantly composed of C_3 plant taxa. This study explores whether the analysis of stable carbon isotopes from ungulate tissues can accurately identify resource use and niche partitioning in a modern C_3-dominated ecosystem in North America, in order to lay the groundwork for application to more ancient ecosystems. $\delta^{13}C$ values were obtained from the scat, collagen, and tooth enamel from populations of *Antilocapra americana*, *Bison bison*, *Cervus elaphus*, *Odocoileus hemionus*, and *Ovis canadensis* in Yellowstone National Park, and used to trace isotopic uptake and incorporation from the diet into herbivore hard tissues. Significant differences were observed among taxa in $\delta^{13}C$ values from all three of the sample materials. Scrutinizing the carbon isotope values further showed that elk and mule deer had the widest range in isotopic values, implying the widest range of resource use. Similarities among taxa in the $\delta^{13}C$ of scat concur with other studies that attribute the similarities to winter habitat use. Because (1) significant differences were observed in the $\delta^{13}C$ values of scat, collagen and ultimately tooth enamel and (2) the isotopic inputs of carbon are relatively well understood, and (3) carbon isotope values can be obtained from non-altered fossil material, this methodology appears practicable for objectively examining ecological relationships, such as resource use and niche partitioning, among taxa in ancient C_3-dominated ecosystems of North America and elsewhere, and suggests the technique will be valuable in investigating resource use and niche partitioning among taxa prior to the C_4 global carbon shift.

Keywords: C3-ecosystems; Carbon-13; Diet; Modern; Ruminantia; Yellowstone National Park

1. Introduction

Analysis of stable isotope values from the tissues of mammals has proven to be a useful method for examining resource use and niche partitioning among taxa within modern and ancient environments (DeNiro and Epstein, 1978; Vogel, 1978; Teeri and Schoeller, 1979; Tieszen et al., 1979; Ambrose and DeNiro, 1986a,b; Ambrose,

* New York State Museum, 3140 Cultural Education Center, Albany, NY 12230, United States. Tel.: +1 518 474 5819; fax: +1 518 486 2034.
E-mail address: rferanec@mail.nysed.gov.

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1991; Bocherens et al., 1996; MacFadden and Cerling, 1996; Bocherens et al., 1997; Cerling et al., 1997; Koch, 1998; MacFadden et al., 1999; Bocherens et al., 2001). These studies have generally concentrated on the analysis of carbon isotopes in environments where both C_3 and C_4 plant taxa are present due to the large differences in $^{13}C/^{12}C$ taken up by the different photosynthetic pathways (Farquhar et al., 1982; Farquhar et al., 1989; Ehleringer et al., 1991; Ehleringer and Monson, 1993). Partitioning in ancient ecosystems has rarely been shown in C_3-dominated environments even though before 7 million years ago worldwide, prior to the rapid increase in C_4 ecosystems (RICE; Kohn and Cerling, 2002), environments were largely composed of C_3 plant taxa (Cerling et al., 1997; Fox and Koch, 2003). Even today, environments above 45° N latitude in North America almost entirely consist of C_3 plants (Teeri and Stowe, 1976; Stowe and Teeri, 1978; Ehleringer et al., 1991; Tieszen et al., 1997; Sage et al., 1999). It therefore is important to understand whether resource use and niche partitioning can be robustly identified using isotopic values in C_3-dominated environments, inasmuch as that would expand both the geographic and temporal application of the technique. Isotopic studies have shown that there are intra-ecosystem variations in carbon isotope values even where only one type of photosynthetic pathway is present (van der Merwe and Medina, 1991; Fizet et al., 1995; Bocherens et al., 1995, 1997; Ben-David et al., 1997; Cerling et al., 1999; Bocherens, 2003; Drucker et al., 2003; Stewart et al., 2003; Cerling et al., 2004; Urton and Hobson, 2005) and these variations may be used to identify niche partitioning among taxa within a C_3-dominated environment.

Resource use and niche partitioning in ancient C_3-dominated ecosystems has been inferred from isotopic analyses, generally through analysis of two or more isotopic systems, commonly carbon combined with either oxygen or nitrogen (Fizet et al., 1995; Bocherens et al., 1995, 1997; Cerling et al., 1999; Bocherens et al., 2001; Bocherens, 2003; Drucker et al., 2003), as derived from fossil ungulate teeth or bones. Difficulties can arise in interpreting the results from these studies for a number of reasons. First, there have been very few modern studies examining the range of isotopic variation in modern ungulates within C_3-dominated ecosystems, making it difficult to determine if the observed differences from one area, such as Europe or Africa, are comparable to those of another area, such as North America (Bocherens et al., 1997; Cerling et al., 1999; Heaton, 1999; Bocherens et al., 2001; Cerling et al., 2004). Second, usually few samples per ancient taxon are obtained, making it difficult to assess the robustness of the conclusions and whether the results are unique for the particular ecosystem or far-reaching. Third, the influences on the isotopic values of nitrogen and oxygen (e.g., metabolism) are incompletely understood (Luz et al., 1984; Ambrose and DeNiro, 1987; Yakir et al., 1990; Ambrose, 1991; Bryant et al., 1996; Kohn, 1996; Kohn et al., 1996; Koch, 1998; Kohn, 1999), such that variations in nitrogen or oxygen isotope values can be observed even if the same resource is utilized at the same time by different taxa. This creates a problem in interpreting niche partitioning if too much emphasis is placed on the differences observed in those isotopes.

Here I address some of these complications by examining whether the analysis of stable isotopes from ungulates can accurately identify resource use and niche partitioning in a modern C_3-dominated ecosystem in North America, Yellowstone National Park. I present data to evaluate whether resource use by individual taxa is specialized enough that intra-ecosystem isotopic variation can identify niche differences. I compare the stable isotope values of carbon in the diet of several species (as inferred from observations of what they ate and isotopic analysis of their scat), with the isotopic compositions that are ultimately incorporated into their collagen and tooth enamel. Results are interpreted in terms of potential application of the method to fossil ecosystems, where, due to taphonomic constraints, not all isotopic systems are available.

2. Background information

2.1. Yellowstone National Park

Yellowstone National Park (YNP) provides an ideal location to study if the analysis of stable isotopes can distinguish resource partitioning among ungulates in a C_3 ecosystem. The park, which is located predominantly in the northwestern-most corner of Wyoming but extends into Idaho and Montana to the west and north (Fig. 1) lies above 1600 m and has distinct vegetation types (Despain, 1990). Forests, dominated by lodgepole pine (*Pinus contorta*), comprise 80% of the park, shrub (especially sagebrush)–grassland occupies 15%, while the remainder of the park consists of lakes and rivers with Yellowstone Lake being the largest body of water (Duckworth and Young, 2003). Nearly all the known plant taxa within the park (up to 97%) use the C_3 photosynthetic pathway (Despain, 1990; Watson and Dallwitz, 1992 onwards; Sage et al., 1999). The park has been a focus of ecosystem preservation since 1872 and is arguably one of the largest relatively undisturbed temperate-latitude ecosystems in the world. Thus, it