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ORIGINAL RESEARCH

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Within trophic level shifts in collagen–carbonate stable carbon isotope spacing are propagated by diet and digestive physiology in large mammal herbivores

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Abstract

Stable carbon isotope analyses of vertebrate hard tissues such as bones, teeth, and tusks provide information about animal diets in ecological, archeological, and paleontological contexts. There is debate about how carbon isotope compositions of collagen and apatite carbonate differ in terms of their relationship to diet, and to each other. We evaluated relationships between $\delta^{13}C_{collagen}$ and $\delta^{13}C_{carbonate}$ among free-ranging southern African mammals to test predictions about the influences of dietary and physiological differences between species. Whereas the slopes of $\delta^{13}C_{collagen}$–$\delta^{13}C_{carbonate}$ relationships among carnivores are ≤1, herbivore $\delta^{13}C_{collagen}$ increases with increasing dietary $\delta^{13}C$ at a slower rate than does $\delta^{13}C_{carbonate}$, resulting in regression slopes >1. This outcome is consistent with predictions that herbivore $\delta^{13}C_{collagen}$ is biased against low protein diet components (^{13}C-enriched C_4 grasses in these environments), and $\delta^{13}C_{carbonate}$ is ^{13}C-enriched due to release of ^{13}C-depleted methane as a by-product of microbial fermentation in the digestive tract. As methane emission is constrained by plant secondary metabolites in browse, the latter effect becomes more pronounced with higher levels of C_4 grass in the diet. Increases in $\delta^{13}C_{carbonate}$ are also larger in ruminants than nonruminants. Accordingly, we show that $\Delta^{13}C_{collagen\text{-}carbonate}$ spacing is not constant within herbivores, but increases by up to 5 ‰ across species with different diets and physiologies. Such large variation, often assumed to be negligible within trophic levels, clearly cannot be ignored in carbon isotope-based diet reconstructions.

KEYWORDS
browse, C_3, C_4, grass, methane, protein

1 | INTRODUCTION

Stable carbon isotope analysis is routinely used to reconstruct consumer resource use patterns in modern, archeological, and paleontological contexts (Ben-David & Flaherty, 2012; Cerling & Harris, 1999; Cerling et al., 2015; Crawford, McDonald, & Bearhop, 2008; Hare & Sealy, 2013). Indeed, the approach provides arguably the most direct evidence for diet and habitat use among fossil animals. For this purpose, two phases of skeletal material may be analyzed: the collagen (protein) or carbonate (mineral apatite) phase, either from bone or from teeth (typically using dentine for the former, and tooth enamel for the latter). Whereas collagen typically degrades within a