The confounding effects of source isotopic heterogeneity on consumer–diet and tissue–tissue stable isotope relationships

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Abstract: Stable isotope analysis of consumer tissues document patterns of resource use because data are linearly related to isotope compositions of their source(s) (i.e., food, water, etc.). Deviations in parameters estimated for these relationships can arise from variations in consumer tissue–diet spacing (DTS) and the level of isotopic heterogeneity in the source(s). We present a set of simple hypotheses that distinguish between the effects of DTS and source isotope heterogeneity. The latter may arise via mixed diets, during tissue turnover, or by isotopic routing of dietary components. We apply these concepts to stable carbon and nitrogen isotope relationships between gut contents and body tissues of large mammal herbivores from mixed C3/C4 South African savannas and test predictions based on the compound- and/or time-specific data archived within each material. Predicted effects of source isotope heterogeneity are readily detected in carbon isotope relationships between materials representing different time periods or comprising bulk versus protein-only diet components. Differences in DTS of carbon isotopes across mammal herbivore species with very different feeding niches (and diet isotope compositions) are likely to be small or non-existent in these habitats. Variations in DTS estimated for nitrogen isotopes are much greater, leading to inconsistencies that cannot be explained by diet or trophic level effects alone. The effects of source heterogeneity on isotopic relationships generate numerical artefacts that have been misinterpreted as variations in DTS. We caution against generalized application of hypotheses based on assumptions of source isotopic homogeneity, even for single diets commonly used in laboratory studies. More careful consideration of how heterogeneity affects consumer–diet relationships is needed for many field and laboratory systems.

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The models used to generate predictions assume $\delta S$ is distributed normally, with a true mean of zero and standard deviation of 1.0. This is not true for at least half of our empirical dataset, since food sources for herbivores in southern African savannas have a bimodal $\delta^{13}\text{C}$ distribution because of difference between C$_3$ (dicots) and C$_4$ (grass) photosynthetic pathways. Although residuals from all our analyses were normally distributed, the bimodal distributions of $\delta^{13}\text{C}$ values amongst browsers and grazers could raise concerns about the validity of parameters estimated for regression models using such datasets. Here we show that the general principles outlined in the main text are robust to the bimodal distribution of $\delta S$ in these cases, repeating the same simulations as used for Fig. 1. However, we now used $\delta S_1$ and $\delta S_2$ values drawn from either of two distinct, non-overlapping ranges for $\delta S$, for which the means differ by 15‰. Individuals are randomly allocated diets from either source, so that some utilize two values from either range whereas others use two isotopically distinct sources. Results are shown in fig. S1 below.
Figure S1. Simulated hypothetical relationships between stable isotope composition of consumers (δT) and their sources/diets (δS) under different scenarios (left hand columns), where available δS values are bimodally distributed to mimic the δ\textsuperscript{13}C difference between C\textsubscript{3} and C\textsubscript{4} vegetation. Panels on the right show corresponding relationships between consumer-diet spacing (ΔTS, i.e. δT-δS) and δS. Each scenario corresponds to equations 1 through 5 in the main text. In (a), δT varies with δS of a single source, plus a constant ΔTS. In (b and c), changes to ΔTS are assumed to influence the relationship: first due to differences in ΔTS between two species (b – two intercepts); and next if ΔTS varies as a negative linear function of δS (c). In (d and e), relationships assume heterogeneity in δS: due to consumption of different diets or compound-specific differences in δS of a single diet, and/or nutrient routing (d); and due to non-equilibrium between consumer and diet isotope compositions following a diet switch (e). In (d and e), only a single source value is plotted on the x-axis, reflecting common practice of ignoring heterogeneity, e.g. within laboratory feeds. Note the difference in slopes (b) between the single-(a-c) and multiple-source (d, e) models (the solid line depicts the linear regression, the dashed line depicts a 1:1 relationship), and the increased variation around the regression when multiple sources are included. Axis units and model parameters are not shown as only regression parameters are relevant here.