
Oxygen Isotopes Indicate That Rocky Mountain Mule Deer (*Odocoileus hemionus hemionus*) Can Be Seasonally Nonobligate Drinkers

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ABSTRACT

Understanding seasonal water budgets of wildlife is critical, as climate change alters water availability. Rocky Mountain mule deer (*Odocoileus hemionus hemionus*) mainly obtain water from their diet and drinking water; however, winter access to these resources varies with snow cover. To assess reliance on water sources by mule deer during winter, we longitudinally sampled female deer in Utah's Bear River Mountains, a montane region with deep snow and ample drinking water sources, and Pine Valley, a semiarid region with little snow. We implanted physiological biologgers to record heart rate and collected serum samples at the onset and end of winter over 2 yr. We measured the triple oxygen stable isotope composition of a body water sample ($\Delta^{17}\text{O}_{\text{BW}}$) dis-

tilled from serum. We then compared measured $\Delta^{17}\text{O}_{\text{BW}}$ to predictions generated from two isotope models of water and oxygen fluxes that differed in their estimates of metabolic rate, based on either heart rate or body mass. Close agreement between measured and predicted $\Delta^{17}\text{O}_{\text{BW}}$ validated our assumptions, although estimating metabolic rate via heart rate did not improve model predictions. Our results indicate that in the Bear River Mountains, deer increased their water drinking when snow cover limited foraging but that in Pine Valley, they relied on consistent food water input because of minimal snow cover. Estimates suggest that some deer in Pine Valley were seasonally independent from drinking water. Applying $\Delta^{17}\text{O}_{\text{BW}}$ modeling enhances wildlife conservation by providing novel inferences about how individuals obtain water, informing proactive management in the face of climate change.

Keywords: stable isotope analysis, metabolic water, hydrogen isotope, triple oxygen isotopes, animal water balance, ^{17}O excess, heart rate, plant water.

Introduction

Animals require water for essential life functions such as facilitating metabolic reactions and expelling waste (Nagy and Peterson 1988). In some regions, warming temperatures are leading to aridification and increased drought frequency and intensity, making it more difficult to obtain water (Yuan et al. 2023) while simultaneously increasing thermoregulatory water losses (Fuller et al. 2021). These negative impacts on water balance can be fatal, especially for animals with substantial water demands, such as many large ungulates (Fuller et al. 2021). As such, there is an increasing demand for methods to assess water balance in free-ranging animals to inform wildlife managers regarding which species are most susceptible to reductions in water sources and potential increases in water effluxes.

Assessing water fluxes is difficult in free-ranging animals, typically requiring multiple capture events and sample collections within a short time frame, including injection of an inert isotope tracer (Nagy 1983; Speakman 1997; Butler et al. 2004). However, recent studies have documented that water influxes and effluxes can be estimated by measuring the triple oxygen stable isotope composition of a body water sample ($\Delta^{17}\text{O}_{\text{BW}}$; Feng et al. 2022, 2024; Hu et al. 2023; Steele et al. 2025). $\Delta^{17}\text{O}$ is the residual of the

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expected relationship between oxygen isotope values: $\delta^{17}\text{O}$ and $\delta^{18}\text{O}$ (the prime symbol indicates linearized values; see “Methods”). $\Delta^{17}\text{O}$ has the unusual property of being relatively insensitive to many mass-dependent fractionation processes that cause substantial variation in $\delta^{18}\text{O}$ (Thiemens and Heidenreich 1983; Thiemens 1999; Sharp 2007), making $\Delta^{17}\text{O}$ a valuable tracer of water sources used by animals (Pack et al. 2013; Whiteman et al. 2019). Animals use atmospheric oxygen to produce oxidase water as a by-product during energy metabolism (Garrett and Grisham 2017). Atmospheric oxygen, and thus oxidase water, has a substantially lower $\Delta^{17}\text{O}$ value (-441 per meg [10^{-6} ; ppm]; -0.441%) than many drinking water and food water sources, which are derived from meteoric water (water originating from precipitation; 0 – 40 per meg; Whiteman et al. 2019; Wostbrock et al. 2020).

The stark difference in $\Delta^{17}\text{O}$ between oxidase water and other water inputs enables interpretation of this variable based on animal physiological processes (Hu et al. 2023; Steele et al. 2025). Estimated oxygen and water fluxes (e.g., rates of oxidase water production and drinking water intake) can be used to model a predicted value of $\Delta^{17}\text{O}_{\text{BW}}$ (Steele et al. 2025). If this prediction closely matches the measured $\Delta^{17}\text{O}_{\text{BW}}$, the estimated fluxes are likely accurate. A recent controlled study of deer mice (*Peromyscus maniculatus*) demonstrated that $\Delta^{17}\text{O}_{\text{BW}}$ could consistently be predicted as <30 per meg different from measured $\Delta^{17}\text{O}_{\text{BW}}$ (mean absolute difference = 11 ± 9 per meg) and that variation in $\Delta^{17}\text{O}_{\text{BW}}$ clearly tracked variation in drinking water intake (Steele et al. 2025). This close agreement between measured and predicted $\Delta^{17}\text{O}_{\text{BW}}$ is striking, as typical instrument error is 5 – 15 per meg (Voigt et al. 2022; Steele et al. 2024) and the total reported range of $\Delta^{17}\text{O}_{\text{BW}}$ across all measured modern animal taxa is ~ 300 per meg (Pack et al. 2013; Whiteman et al. 2019; Sabat et al. 2021; Feng et al. 2022, 2024, 2025; Lehmann et al. 2022; Hu et al. 2023; Navarrete et al. 2023; Steele et al. 2024, 2025). Thus, predicting and measuring $\Delta^{17}\text{O}_{\text{BW}}$ has high potential for revealing seasonal water dynamics of free-ranging wildlife, including those of management importance like game species.

Mule deer (*Odocoileus hemionus*) are one of the most abundant wide-ranging ungulates in North America (Combe et al. 2022), occurring from Alaska to Mexico in a variety of ecosystems (e.g., deserts, forests, agricultural and urban areas) at elevations from sea level to $>4,000$ m (Blood 2000; Combe et al. 2022). They are popular for game and ecotourism, giving them economic and social importance in North America (deVos et al. 2003). Mule deer predominantly browse on forbs and the leaves of woody plants, using grasses when these preferred browse items are seasonally limited (Kufeld et al. 1973). Compared to white-tailed deer (*Odocoileus virginianus*), mule deer typically occupy drier regions in western North America with lower annual precipitation and thus reduced vegetation cover and forage availability and can also consume lower-quality vegetation than the white-tailed deer (Heffelfinger 2006; Staudenmaier et al. 2022). However, since they are selective foragers with a smaller bite size, stomach volume, and digestive capacity than many other ungulates, like elk (*Cervus canadensis*), they typically cannot persist solely on low-quality vegetation to meet their nutritional needs (Collins and Urness 1983; Schuyler et al. 2021). Because of these sensi-

tivities, mule deer population dynamics are strongly correlated with annual variation in winter snowpack, where applicable, and summer forage production (Stoner et al. 2016).

It is debated whether mule deer can be nonobligate drinkers (Anderson 1949; Hervert and Krausman 1986; UDWR 2019). The water content of their diet (“food water”) depends on the hydration status of forage plants, which is dependent on precipitation and humidity (Marshall et al. 2005, 2008). For ruminants with similar diets and body mass, such as bighorn sheep (*Ovis canadensis*), high food water content may allow them to fulfill their water needs without having to drink (Gedir et al. 2016), and as a result, their habitat use is constrained by forage availability and quality rather than access to drinking water (Cain et al. 2008). However, in arid and semiarid environments, mule deer often select habitats near permanent water sources because vegetation contains insufficient food water (Sánchez-Rojas and Gallina 2000; McKee et al. 2015). In these dry environments, mule deer drink 2 – 10 L of water a day (Elder 1954; Hervert and Krausman 1986; Hazam 1987), with females typically consuming more water than males, likely due to the demands of lactation. Furthermore, water intake nearly doubles in summer compared to winter (Longhurst et al. 1970; Hazam 1987), likely related to thermoregulatory water losses (Fuller et al. 2021).

During winter, heavy snowfall can reduce access to vegetation and dramatically increase the metabolic cost of locomotion, and in mountainous regions, this may drive deer to descend to lower elevations (Parker et al. 1984; Hobbs 1989; DeCesare et al. 2021; Knight 2022). Resident deer that remain at higher elevations seek habitat close to water sources and canopy cover to provide shelter from wind and snow and minimize their movement to conserve energy (Wood 1988; Nicholson et al. 1997; Serrouya and D'Eon 2008). Like other ungulates (Degen and Young 1990; Crater and Barboza 2007), deer may consume snow when access to other resources is limited (Knight 2022), and there seems to be only a small increase in metabolic demand despite the energy required to melt ingested snow when utilizing this as a source of water (Degen and Young 1990; Crater and Barboza 2007).

Like other animals, mule deer also endogenously synthesize their own metabolic water via two processes, which differ in their source of oxygen: (1) by combining atmospheric oxygen with hydrogen in the mitochondria, yielding oxidase water, and (2) by transferring bound oxygen from food molecules (e.g., glucose) to hydrogen via dehydration-condensation reactions, yielding “condensation water” (Garrett and Grisham 2017; Steele et al. 2025). Previous studies of ruminants in (semi)arid regions found that combined, these two sources of endogenously synthesized water typically contribute up to 15% of their total water influx, including pronghorns (*Antilocapra americana*), hartebeests (*Alcelaphus buselaphus*), and impalas (*Aepyceros melampus*; Maloiy and Hopcraft 1971; Whisler 1984). Illustrating the contribution from these “hidden” endogenous water sources is a key advantage to using triple oxygen isotope analysis.

The use of $\Delta^{17}\text{O}$ as a tool to study water balance is new, and other data can support analysis and interpretation. Synthesis of oxidase water depends on metabolic rate, which can be estimated via allometric equations using body mass or proxies such as heart

rate (Butler et al. 2004). Consumption of food, and thus food water, can be inferred from stable isotope measurements of hydrogen, carbon, and nitrogen. Transpiration fractionates plant water, causing tissues like leaves to have elevated hydrogen isotope ($\delta^2\text{H}$) values (Cernusak et al. 2016); thus, substantial food water input could cause elevated $\delta^2\text{H}_{\text{BW}}$ if there is high consumption of fractionated plant water. The carbon isotope ($\delta^{13}\text{C}$) values of animal tissues can, in some contexts, reflect diet selection between forbs, shrubs, and trees that use the C_3 photosynthetic pathway ($\delta^{13}\text{C}$: -28‰ to -24‰) versus grasses that use the C_4 pathway ($\delta^{13}\text{C}$: -16‰ to -10‰ ; O'Leary 1988). Consuming more leaves may signify a higher input of fractionated plant water, which typically has a low $\Delta^{17}\text{O}$ (typically -200 to -50 per meg; Aron et al. 2021), as opposed to consuming more roots and xylem, which would increase the contribution from nonfractionated plant water with $\Delta^{17}\text{O}$ values similar to local meteoric water (Cernusak et al. 2016). Finally, tissue nitrogen isotope ($\delta^{15}\text{N}$) values can be used as a proxy of trophic level or can indicate periods of reduced food intake and nutritional stress (Martínez del Río and Wolf 2005; Ben-David and Flaherty 2012), potentially important for understanding seasonal changes in resource availability.

To better understand variation in the water flux of free-ranging Rocky Mountain mule deer (*Odocoileus hemionus hemionus*) during winter, we collected deer serum samples from two study sites in Utah: the Bear River Mountains, a montane region with substantial freshwater drinking sources and seasonal snow cover, and Pine Valley, a semiarid region with fewer freshwater drinking sources and minimal snow cover. We predicted that deer from the Bear River Mountains obtain most of their water from drinking because of the abundant water availability and reduced food water intake (due to snow cover reducing foraging), while Pine Valley deer would rely more on food water because of fewer drinking water sources and greater foraging opportunities (due to reduced snow cover). We tested this prediction by estimating influxes and effluxes to the body water pool for each deer, covering the time frame of body water turnover before sampling, then using these fluxes to predict $\Delta^{17}\text{O}_{\text{BW}}$, which we compared to the $\Delta^{17}\text{O}_{\text{BW}}$ measured in serum samples. We compared two approaches for estimating influxes and effluxes related to metabolism: the first estimated field metabolic rate (FMR; kJ/d) via allometric scaling based on body mass, and the second estimated FMR via heart rate data collected from biologgers. We predicted that using the bilogger heart rate data would yield more accurate predictions of $\Delta^{17}\text{O}_{\text{BW}}$. We also used measurements of $\delta^{13}\text{C}$ and $\delta^2\text{H}_{\text{BW}}$ of serum samples to further constrain estimates of oxygen influxes and effluxes (e.g., food water).

Methods

Study Area and Environmental Data

Pine Valley (common elevation: 1,000–2,000 m; 37°N) is ~50 km northwest of Zion National Park, Utah, and the Bear River Mountains (common elevation: 1,500–3,000 m; 41.6°N) are located ~30 km southeast of Logan, Utah. Both regions have isolated peaks $>3,000$ m (Wells 1960; Hull and Hull 1974). Vegetation in Pine Valley includes sagebrush (*Artemisia* spp.), rabbitbrush

(*Chrysothamnus* spp.), juniper (*Juniperus* spp.), hopsage (*Grayia* spp.), buckwheat (*Eriogonum* spp.), and single-leaf pinyon (*Pinus monophylla*; Yorks et al. 1992, 1994). The Bear River Mountains feature sagebrush, juniper, bigtooth maple (*Acer grandidentatum*), buckbrush (*Ceanothus* spp), Douglas fir (*Pseudotsuga menziesii*), and bitterbrush (*Purshia tridentata*; Pederson and Harper 1978; Peterson and Messmer 2007).

We sampled female deer longitudinally in November/December 2021, March 2022, and December 2022. During these time frames, the Bear River Mountains were consistently colder by a mean of 8°C and had greater snow cover by a mean of 13 cm per period (table 1). Major drinking water sources in the Bear River Mountains include Bear Lake (28,230 ha), Blacksmith Fork, Logan River, Otter Creek, Rock Creek, and Curtis Creek, whereas Pine Valley has only one major water feature (Santa Clara River). To examine vegetation availability and further assess snow cover, we used normalized difference vegetation index (NDVI) data. The NDVI uses near-infrared and red-light reflectance as an index of photosynthetic biomass and thus availability of forage (Hamel et al. 2009; Stoner et al. 2016). Abundant vegetation results in NDVI values ≥ 0.6 , whereas sparse vegetation results in values ≤ 0.3 (Weier and Herring 2000). The NDVI has also been used as predictor of various components of biological fitness for different cervid species (Pettorelli et al. 2006, 2011), including mule deer (Hurley et al. 2014; Stoner et al. 2016). The NDVI also negatively correlates with snow cover, with values ≤ 0.2 suggesting that snow is deep enough to hide vegetation (Weier and Herring 2000; Kaufmann et al. 2003). Mean NDVI values were 0.26 in the Bear River Mountains during November 2021 but then dropped to ~0 in March and December 2022, reflecting snow cover during these time frames (table 1). NDVI values were consistently between 0.21 and 0.28 in Pine Valley across sampling periods, reflecting the lack of snow cover and suggesting more consistent foraging availability than in the Bear River Mountains. For full details of how NDVI data were collected, please see appendix S1 (apps. S1–S4 are available online).

Deer Captures and Measurements

Deer were captured using a net gun from a helicopter (Brigham Young University Institutional Animal Care and Use Committee protocol 150110; for details, see Van de Kerk et al. 2020). Deer were then processed by measuring body mass to the nearest kilogram with a spring scale (Hersey 2025), checked for lactation status, and given a body condition score based on palpation methods developed by Cook et al. (2007). Age was estimated using tooth wear and eruption patterns (Hinton et al. 2023). Blood samples were collected via the cephalic, saphenous, or jugular veins (Roug et al. 2022). Deer were then fitted with a global positioning system collar (model GS-2DH, Advanced Telemetry Systems, Isanti, MN) and implanted with subcutaneous heart rate biologgers using aseptic techniques (LINQ II, Medtronic, Mounds View, MN; Utah State University Institutional Animal Care and Use Committee protocol 13045). Heart rate was measured continuously and reported as average beats per minute within 2-min sampling periods. We then calculated the median of all 2-min

Table 1: Results of longitudinal mule deer sampling efforts and average ambient temperature, snow depth, and normalized difference vegetation index data across time in the two capture locations

Variable	Bear River Mountains			Pine Valley		
	November 2021	March 2022	December 2022	December 2021	March 2022	December 2022
Deer (<i>n</i>)	7	7	4	9	9	6
Ambient temperature (°C)	2.6 ± .3	−11.5 ± 1.0	−1 ± .5	8.9	−.5 ± 2.7	5.6 ± 2.1
Snow depth (cm)	6	18	15	0	0	0
NDVI	.26 ± .04	.02 ± .04	.00 ± .01	.21 ± .04	.28 ± .05	.27 ± .04

Note. NDVI = normalized difference vegetation index.

averages that occurred 7 d before each capture date when associated blood samples were collected. The biologists also provided measurements of core body temperature, which was sampled every 4 h and used to generate a median value for isotope modeling. If deer were previously implanted with a biollogger, data were retrieved by transcutaneous telemetry (CareLink 2090 programmer with software model SW007, Medtronic). All sampling was part of routine processing by the Utah Division of Wildlife Resources (UDWR), and all animal handling and sample collections were done under the direct supervision of a veterinarian (V. Stout) within the UDWR.

To assess the influence of seasonal differences in environmental conditions, we compared longitudinal differences in body mass and condition of individual deer that were sampled at all three time points (November/December 2021, March 2022, and December 2022) with Friedman tests followed by a post hoc Conover-Iman test using a Holm-Bonferroni correction. We compared longitudinal differences in median heart rate of individual deer that were sampled in March and December 2022 with either a paired-samples *t*-test or a Wilcoxon signed-ranks test.

Stable Isotope Measurements

Deer blood samples were centrifuged, and serum was stored at −20°C and then shipped to Old Dominion University (Norfolk, VA), where samples were thawed and cryogenically distilled to obtain body water (Steele et al. 2024). We analyzed 42 distilled body water samples, each representing a unique combination of a deer and a sampling period. Depending on volume, replicates of samples were distilled, thus samples were measured twice (*n* = 4) or 3–8 times (*n* = 38; tables S1, S2 [tables S1–S10 are available online]). Stable isotopes were measured in distilled body water samples via cavity ring-down spectroscopy (L2140-*i*, Picarro, Santa Clara, CA), yielding values of $\delta^{17}\text{O}$, $\delta^{18}\text{O}$, and $\delta^2\text{H}$. Protocols for the cavity ring-down spectroscopy instrument followed Steele et al. (2024). Each distilled replicate of a sample was injected into the analyzer 5–13 times depending on sample volume. Analysis runs included standards (USGS50 and USGS47; Qi et al. 2014; Coplen et al. 2015) and more than five control waters that had been measured against Vienna Standard Mean Ocean Water and Standard Light Antarctic Precipitation Water (Sharp 2007). Standards bracketed sample $\delta^{18}\text{O}$ values and were used to calculate correction factors for $\delta^{17}\text{O}$, $\delta^{18}\text{O}$, and $\delta^2\text{H}$ (corrected

value = stretching value × raw value + offset value; Sharp 2007; Steele et al. 2024). After correcting raw measurements, we calculated $\Delta^{17}\text{O}$ as

$$\Delta^{17}\text{O} = \delta^{17}\text{O} - 0.528 \times \delta^{18}\text{O}. \quad (1)$$

Here, the prime symbol indicates linearization ($\ln(\delta^x\text{O} + 1)$, where *x* is 17 or 18) of the curvilinear relationship between $\delta^{17}\text{O}$ and $\delta^{18}\text{O}$. We then calculated means and standard deviations of $\delta^2\text{H}$, $\delta^{17}\text{O}$, $\delta^{18}\text{O}$, and $\Delta^{17}\text{O}$ for control waters and distilled samples; removed outliers; and recalculated means using an automated postprocessing script (Steele et al. 2024) in R (ver. 4.4.3). We excluded data from analysis runs with more than two measurements of controls that differed from known values by these thresholds: $\delta^{17}\text{O} \geq 0.15\text{‰}$, $\delta^{18}\text{O} \geq 0.3\text{‰}$, and $\Delta^{17}\text{O} \geq 15$ per meg. Corrected measurements of replicates of a single sample were averaged to generate a final value. Final values were used to generate maps showing variation of isotope values across geographic ranges using global positioning system location data from capture events in ArcGIS Pro (ver. 3.1.2).

To assess whether stable oxygen and hydrogen isotope values differed over time or between regions, we compared $\delta^{18}\text{O}_{\text{BW}}$, $\Delta^{17}\text{O}_{\text{BW}}$, and $\delta^2\text{H}_{\text{BW}}$ of individual deer that were sampled at all three time points with Friedman tests followed by a post hoc Conover-Iman test using a Holm-Bonferroni correction and regional differences in measured oxygen and hydrogen isotopes using either an independent *t*-test or a Mann-Whitney test.

Samples with adequate serum volume for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis (*n* = 31) were dried for >48 h at 60°C and loaded (~1 mg) into tin capsules, which were analyzed at the University of New Mexico Center for Stable Isotopes (Albuquerque, NM) using a Costech 4010 elemental analyzer (Costech Analytical Technologies, Valencia, CA) coupled to a Delta V Plus isotope ratio mass spectrometer (Thermo Fisher Scientific, Waltham, MA). Within-run analytical precision of $\pm 0.2\text{‰}$ (SD) for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values was confirmed by analyzing two protein-based internal reference materials. We compared differences in measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between regions using either an independent *t*-test or a Mann-Whitney test.

Oxygen Isotope Modeling

For each sample, we compared the measured $\Delta^{17}\text{O}_{\text{BW}}$ to a predicted $\Delta^{17}\text{O}_{\text{BW}}$ that was based on modeling of deer body water

oxygen fluxes, consisting of estimates of seven oxygen inputs and eight outputs (table 2). The inputs were: (1) drinking water, (2) condensation water, (3) oxidase water, (4) inhaled water vapor, (5) decarboxylation water (oxygen in waste CO₂ that is exchanged with body water before exhalation), (6) unfractionated plant water, and (7) fractionated plant water. The outputs were: (1) exhaled CO₂, (2) fecal water loss, (3) nasal water vapor loss, (4) oral water vapor loss, (5) transcutaneous water vapor loss, (6) oxygen loss in urea, (7) urinary water loss, and (8) bound oxygen in fecal waste (assumed to be zero). For each flux, we defined moles of oxygen, $\delta^{18}\text{O}$ and $\Delta^{17}\text{O}$ of the oxygen source, and the applicable fractionation values ($^{18/16}\alpha$, $^{17/16}\alpha$, or θ). Like Steele et al. (2025), both approaches assumed that the total inputs and outputs were equal, such that over the time frame of body water turnover the animal was assumed to have a net steady state of body water content.

We compared two flux modeling approaches, based on estimating FMR using heart rate data (“heart rate model”) versus body mass data (i.e., allometric scaling; “body mass model”). The heart rate model used an equation from a captive mule deer study to convert heart rate (HR) and body mass (m ; in kg) to FMR (kcal/d; Kautz et al. 1981):

$$(3.6 \times \text{HR} - 21.3) \times m^{0.75}. \quad (2)$$

FMR was then converted to kilojoules per day by multiplying it by 4.184 (Moen 1976). In contrast, the body mass model estimated FMR (kJ/d) using body mass alone (Kohn 1996):

$$10^{2.96} \times m^{0.73}. \quad (3)$$

The heart rate model was applied only to deer sampled in March and December 2022 because they had biollogger data, whereas the body mass model was applied to all deer in all sampling seasons. Aside from the estimation of FMR, the heart rate model and body mass model were identical in their approaches to estimating oxygen fluxes. However, we expected that the difference in FMR estimation between these models could be influential because 13 of 15 oxygen inputs and outputs are directly or indirectly estimated using FMR. Specifically, substantial differences in FMR could particularly impact estimated intake of food and drinking water and urinary water loss.

We followed the modeling steps in Steele et al. (2025) with several modifications. First, we estimated fluxes based on a 24-h period, aligning with our FMR estimates (kJ/d). Second, because we did not measure food intake, we estimated each deer’s food consumption based on estimated FMR and food energy. We adjusted this food consumption to reflect foraging availability and the influence of snow cover via NDVI data. NDVI values ≤ 0.2 indicate sparse vegetation availability or that snow was likely covering vegetation (Weier and Herring 2000); thus, we decreased or increased plant consumption based on whether the NDVI was ≤ 0.2 or > 0.2 , respectively.

Third, we divided food water into two categories based on consumption of plants (Hu et al. 2023). Fractionated plant water occurs in tissue with extensive stomata such as leaves; evaporation through these stomata can fractionate water oxygen isotopes during transpiration (Farquhar et al. 2007; Kirkham 2023). Non-fractionated plant water occurs in tissues that often lack stomata and experience less evaporation and transpiration, such as stems and roots, resulting in water isotope values similar to local soil water (Yakir 1992; Landais et al. 2006; Cernusak et al. 2016). We defined the ratio of fractionating plant tissue as

$$\frac{\text{fractionating tissue}}{\text{nonfractionating tissue} + \text{fractionating tissue}}. \quad (4)$$

This ratio is influential because consumption of nonfractionating plant tissue provides food water that will mirror the isotope values (e.g., $\delta^2\text{H}$, $\delta^{18}\text{O}$, and $\Delta^{17}\text{O}$) of local meteoric water whereas consumption of fractionating plant tissue provides food water that will have increased $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values and decreased $\Delta^{17}\text{O}$ values, depending on the extent of transpiration. We adjusted this ratio to reflect seasonal food availability, based on the NDVI, $\delta^2\text{H}_{\text{BW}}$, and snow depth (tables 1, 3). In November–December, many graminoids and forbs have senesced, and mule deer primarily consume leaves of evergreen trees and shrubs (Willms et al. 1976; DeCesare et al. 2021); thus, we used an estimated ratio of 0.75 (mean NDVI ≥ 0.15 , mean $\delta^2\text{H}_{\text{BW}} \geq 35\text{‰}$ [compared to local drinking water], mean snow depth ≤ 7 cm). In March, the beginning of the growing season produces more graminoids and forbs (Willms et al. 1976), and consumption of these plants

Table 2: List of oxygen fluxes for the body mass model and the heart rate model

Input	Output
1. Inhaled water vapor ^{a,b}	1. Bound oxygen in fecal waste ^a
2. Condensation water ^{b,c}	2. Fecal water loss ^a
3. Decarboxylation oxygen ^{a,b}	3. Transcutaneous water vapor loss ^{b,c}
4. Oxidase water ^{b,c}	4. Oral water vapor loss ^{a,b}
5. Fractionated plant water ^{b,c}	5. Nasal water vapor loss ^{a,b}
6. Nonfractionated plant water ^c	6. Exhaled CO ₂ ^{b,c}
7. Drinking water ^c	7. Oxygen bound in excreted urea ^a
	8. Urinary water loss ^a

^aEstimated using the methods described in Steele et al. (2025).

^bIndicates that flux is fractionating.

^cEstimated using methods that either differed or were not included in Steele et al. (2025).

Table 3: Variation in measured oxygen and hydrogen isotopes (± 1 SD) and average mass, heart rate, and age in mule deer across three periods in the two capture locations

Variable	Bear River Mountains			Pine Valley		
	November 2021 (<i>n</i> = 7)	March 2022 (<i>n</i> = 7)	December 2022 (<i>n</i> = 4)	December 2021 (<i>n</i> = 9)	March 2022 (<i>n</i> = 9)	December 2022 (<i>n</i> = 6)
$\delta^{17}\text{O}_{\text{BW}}$ (‰)	-2.53 $\pm$.34	-4.92 $\pm$.53	-5.82 $\pm$.10	1.25 $\pm$ 1.20	.64 $\pm$ 1.25	-2.33 $\pm$.99
$\delta^{18}\text{O}_{\text{BW}}$ (‰)	-4.60 $\pm$.65	-9.17 $\pm$.99	-10.86 $\pm$.18	2.64 $\pm$ 2.30	1.45 $\pm$ 2.41	-4.23 $\pm$ 1.90
$\Delta^{17}\text{O}_{\text{BW}}$ (per meg)	-100 $\pm$ 11	-66 $\pm$ 13	-57 $\pm$ 13	-147 $\pm$ 19	-127 $\pm$ 22	-89 $\pm$ 15
$\delta^2\text{H}_{\text{BW}}$ (‰)	-62.89 $\pm$ 2.64	-95.69 $\pm$ 6.66	-98.91 $\pm$ 4.60	-28.43 $\pm$ 11.87	-29.37 $\pm$ 8.77	-44.15 $\pm$ 10.03
Mass (kg)	64.7 $\pm$ 9.0 ^a	57.0 $\pm$ 4.3 ^{a,b}	68.0 $\pm$ 4.5 ^b	58.9 $\pm$ 5.1	57.2 $\pm$ 5.6	59.3 $\pm$ 4.0
Body condition score (1.0–6.0)	4.6 $\pm$ 1.3 ^c	2.0 $\pm$.3 ^{c,d}	4.2 $\pm$ 1.3 ^d	2.6 $\pm$.6	2.0 $\pm$.2	2.5 $\pm$.5
Heart rate (bpm)	...	65 $\pm$ 15	71 $\pm$ 12	...	70 $\pm$ 11	76 $\pm$ 14
Age (yr)	...	6 $\pm$ 2	8 $\pm$ 3	...	6 $\pm$ 2	6 $\pm$ 2

Note. Ellipses indicate that the variable was not measured during this time frame. BW = body water sample.

^aSignificant difference between November 2021 and March 2022 ($t = -3.37$, $P = 0.008$).

^bSignificant difference between March 2022 and December 2022 ($t = 3.44$, $P = 0.011$).

^cSignificant difference between November 2021 and March 2022 ($t = -5.68$, $P < 0.001$).

^dSignificant difference between March 2022 and December 2022 ($t = 3.56$, $P = 0.006$).

should include more stems (i.e., nonfractionating plant tissue); thus, we reduced the estimated ratio to 0.60 (mean NDVI ≥ 0.25 , mean $\delta^2\text{H}_{\text{BW}} \geq 25\text{‰}$ [compared to local drinking water], mean snow depth ≤ 3 cm). Deep snow cover, regardless of the time period, could bury and nearly eliminate access to most graminoids and forbs, causing deer to heavily rely on the leaves of evergreen trees and shrubs, which we reflected with a ratio of 0.90 (mean NDVI ≤ 0.05 , mean $\delta^2\text{H}_{\text{BW}} \geq 35\text{‰}$ [compared to local drinking water], mean snow depth ≥ 15 cm).

Fourth, since we did not directly measure oxygen intake, we converted FMR (kJ) to milliliters of oxygen consumed. Fifth, we adjusted the estimation of drinking water intake to account for the total daily water turnover for deer. We used percentages of body water content ($w\%$) and water turnover rate ($t\%$), with the latter derived from an initial baseline (16.7%; Nagy and Peterson 1988) and adjusted based on regional differences and measured isotope data:

$$\frac{m \times 1,000 \times w\% \times t\%}{18}. \quad (5)$$

Here, mass is converted to grams and then to moles. If daily water turnover exceeded the sum of the other water inputs (i.e., all water inputs other than drinking water), this difference became the drinking water input (Kohn 1996). If the sum of the inputs other than drinking water exceeded the estimated daily water turnover, then the drinking water value was set to zero, and the daily water turnover was changed to match the sum of the nondrinking water inputs (Kohn 1996). All other estimations of oxygen inputs followed Steele et al. (2025). For full details of modeling parameters and the estimation of all oxygen inputs, please refer to appendix S2 and tables S3–S6.

All seven oxygen inputs were combined into a total input. We then calculated absolute ratios of $^{18}\text{O}/^{16}\text{O}$ and $^{17}\text{O}/^{16}\text{O}$ using the $\delta^{18}\text{O}$ and $\Delta^{17}\text{O}$ values for oxygen sources and multiplied the fractional contribution of each input (i.e., moles input/moles total input) by their respective $^{18/16}\alpha$ and $^{17/16}\alpha$ values, and the results were summed together and multiplied by the absolute ratio of the oxygen source.

Regarding outputs, unlike Steele et al. (2025), we did not have direct measures of exhaled CO_2 data. Thus, we estimated exhaled CO_2 using the moles of H_2 per kilogram of food (Kohn 1996; Hu et al. 2023). This value was then converted to moles and compared with the moles of bound oxygen to assign a “food H_2/O_2 ratio,” which was used to calculate exhaled CO_2 (Kohn 1996). In addition, we adjusted the calculation of transcutaneous water vapor loss to account for a single day. All other estimations of oxygen outputs followed the approach described in Steele et al. (2025). For full details of modeling parameters and the estimation of all oxygen outputs, please refer to appendix S3 and tables S3–S6.

After estimating all eight outputs, we then summed them together to determine total outputs, which were used to estimate the fractional contribution of each individual output. Unlike the inputs, outputs were all derived from the same source (body water), so the absolute ratios of $^{18}\text{O}/^{16}\text{O}$ and $^{17}\text{O}/^{16}\text{O}$ were determined by multiplying the fractional contribution and the re-

spective $^{18/16}\alpha$ and $^{17/16}\alpha$ values, and then these totals were summed together. The different absolute ratios of the inputs (e.g., atmospheric oxygen) for ^{18}O and ^{17}O were then summed and divided by the outputs. The absolute ratios of $^{18}\text{O}/^{16}\text{O}$ and $^{17}\text{O}/^{16}\text{O}$ were then used to calculate $\delta^{18}\text{O}_{\text{BW}}$ and $\delta^{17}\text{O}_{\text{BW}}$ (using Vienna Standard Mean Ocean Water) and in combination to calculate $\Delta^{17}\text{O}_{\text{BW}}$.

Model Comparison

To compare performance between our two modeling approaches for predicting $\delta^{18}\text{O}_{\text{BW}}$ and $\Delta^{17}\text{O}_{\text{BW}}$, we calculated prediction error (i.e., measured values – predicted values) and root mean square error (RMSE). Comparison was not possible for November/December 2021 because deer in this period lacked heart rate data. We then compared the RMSE generated for each approach and conducted Friedman tests for both $\delta^{18}\text{O}_{\text{BW}}$ and $\Delta^{17}\text{O}_{\text{BW}}$ using squared error, followed by a post hoc Conover-Iman test using a Holm-Bonferroni correction.

Results

Body Mass, Condition, and Heart Rate

In the Bear River Mountains, deer declined in body mass ($t = -3.37$, $P = 0.008$) and condition scores ($t = -5.68$, $P < 0.001$) between November 2021 and March 2022 (table 3) and then increased by December 2022 in mass ($t = 3.44$, $P = 0.011$) and condition ($t = 3.56$, $P = 0.006$). However, median heart rate during the week before capture did not differ between March and December 2022. In Pine Valley, body mass and condition scores, along with median heart rate, did not significantly differ between December 2021, March 2022, and December 2022. Between regions and across sampling periods, Bear River Mountains deer were 4 kg heavier and had body condition scores 1.2 points higher than those from Pine Valley.

Oxygen and Nitrogen Isotope Analysis

Analysis of $\delta^{13}\text{C}$ indicated that deer in both regions predominantly consumed C_3 plants across sampling periods (range of average $\delta^{13}\text{C}$ values, for Bear River Mountains deer: -24.2‰ to -23.5‰ ; for Pine Valley deer: -23.8‰ to -22.5‰ ; table 4), although Pine Valley deer had a higher $\delta^{13}\text{C}$ ($t = 2.49$, $P = 0.038$) than Bear River Mountains deer in December 2022, indicating incorporation of more C_4 plants. Analysis of $\delta^{15}\text{N}$ revealed minimal variation in $\delta^{15}\text{N}$ for deer in both regions across sampling, suggesting that deer did not differ in nutritional stress across time (range of average $\delta^{15}\text{N}$ values, for Bear River Mountains deer: 4.1‰ – 4.7‰ ; for Pine Valley deer: 4.5‰ – 5.2‰).

Oxygen and Hydrogen Isotope Analysis

Across all periods, Bear River Mountains deer had lower $\delta^{18}\text{O}_{\text{BW}}$ (November/December 2021: $W = 0$, $P < 0.001$; March 2022: $t = -10.89$, $P < 0.001$; December 2022: $W = 0$, $P = 0.010$), higher $\Delta^{17}\text{O}_{\text{BW}}$ (November/December 2021: $W = 63$, $P < 0.001$; March 2022: $t = 6.41$, $P < 0.001$; December 2022: $t = 3.35$,

Table 4: Variation in measured carbon and nitrogen isotopes (± 1 SD) across time frames at the two sampling locations

Variable	Bear River Mountains			Pine Valley		
	November 2021 (<i>n</i> = 7)	March 2022 (<i>n</i> = 3)	December 2022 (<i>n</i> = 4)	December 2021 (<i>n</i> = 5)	March 2022 (<i>n</i> = 6)	December 2022 (<i>n</i> = 6)
$\delta^{13}\text{C}$ (‰)	$-24.2 \pm .5$	$-23.5 \pm .5$	$-23.9 \pm .3^a$	-22.8 ± 1.2	-23.8 ± 1.1	-22.5 ± 1.1^a
$\delta^{15}\text{N}$ (‰)	$4.6 \pm .8$	$4.7 \pm .9$	$4.1 \pm .7$	4.6 ± 1.4	5.2 ± 1.3	4.5 ± 1.5

^aSignificant difference between measurements ($t = 2.49$, $P = 0.038$).

$P = 0.010$), and lower $\delta^2\text{H}_{\text{BW}}$ (November/December 2021: $W = 0$, $P < 0.001$; March 2022: $t = -16.58$, $P < 0.001$; December 2022: $t = -10.08$, $P < 0.001$) values than Pine Valley deer (figs. 1, 2; tables 3, S2). Those trends suggest that deer in the Bear River Mountains relied less on food water from diet items like leaves (i.e., fractionating plant tissue) and more on drinking water than Pine Valley deer because of the ample drinking water sources and lack of access to food due to snow cover.

In the Bear River Mountains, deer stable isotope values in November 2021 differed from other periods, with higher $\delta^2\text{H}_{\text{BW}}$ (November 2021–March 2022: $t = 3.58$, $P = 0.006$; November 2021–December 2022: $t = 3.89$, $P = 0.006$) and $\delta^{18}\text{O}_{\text{BW}}$ (November 2021–March 2022: $t = 4.46$, $P = 0.002$; November 2021–December 2022: $t = 8.91$, $P < 0.001$) and lower $\Delta^{17}\text{O}_{\text{BW}}$ (November 2021–March 2022: $t = -3.47$, $P = 0.007$; November 2021–December 2022: $t = -4.11$, $P = 0.004$). These differences suggest that deer had a greater reliance on food water

from diet items like leaves in November 2021 than in March and December 2022, which had higher snow cover.

In Pine Valley, deer stable isotope values in December 2022 differed from other periods, with higher $\Delta^{17}\text{O}_{\text{BW}}$ (December 2021–March 2022: $t = 3.27$, $P = 0.005$; December 2021–December 2022: $t = 5.37$, $P < 0.001$) and lower $\delta^2\text{H}_{\text{BW}}$ (December 2021–March 2022: $t = -3.36$, $P = 0.006$; December 2021–December 2022: $t = -3.29$, $P = 0.005$) and $\delta^{18}\text{O}_{\text{BW}}$ (December 2021–March 2022: $t = -4.19$, $P = 0.001$; December 2021–December 2022: $t = -4.69$, $P < 0.001$). These differences suggest that deer relied less on food water from items like leaves and more on drinking water in December 2022 than in other periods.

Estimating FMR based on heart rate rather than body mass alone changed how well the predicted $\Delta^{17}\text{O}_{\text{BW}}$ values agreed with the measured values (i.e., absolute value of predicted $\Delta^{17}\text{O}_{\text{BW}}$ compared to measured $\Delta^{17}\text{O}_{\text{BW}}$) and changed the resulting inferences

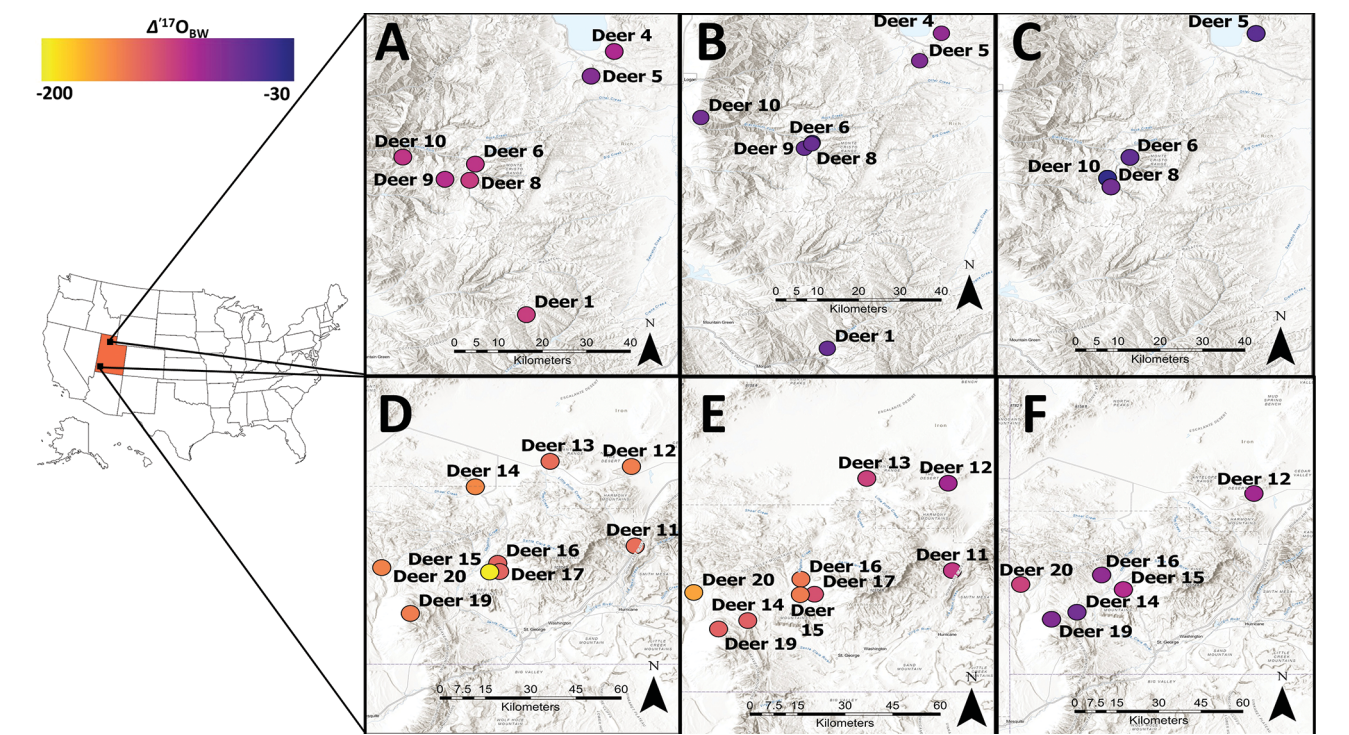


Figure 1. Maps of capture locations of mule deer in the Bear River Mountains and Pine Valley (Utah). Values of $\Delta^{17}\text{O}_{\text{BW}}$ (per meg) displayed for Bear River Mountains deer for November 2021 (A), March 2022 (B), and December 2022 (C) and for Pine Valley deer for December 2021 (D), March 2022 (E), and December 2022 (F). BW = body water sample.

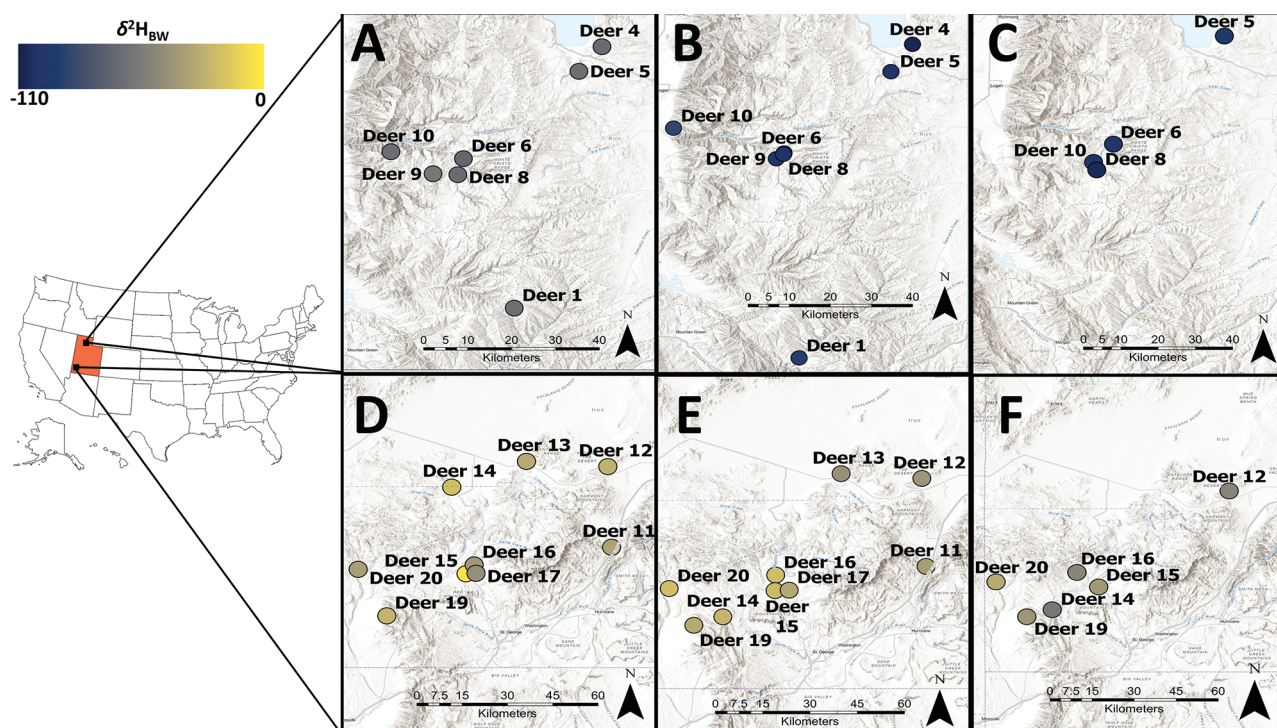


Figure 2. Maps of capture locations of mule deer in the Bear River Mountains and Pine Valley (Utah). Values of $\delta^2\text{H}_{\text{BW}}$ (‰) displayed for Bear River Mountains deer for November 2021 (A), March 2022 (B), and December 2022 (C) and for Pine Valley deer for December 2021 (D), March 2022 (E), and December 2022 (F). BW = body water sample.

regarding oxygen and water fluxes. The body mass modeling approach performed the best, as after pooling all periods from both regions, the mean absolute differences between predicted and measured values were 14 per meg (± 13 per meg) for $\Delta^{17}\text{O}_{\text{BW}}$ and 1.5‰ ($\pm 1.1\text{‰}$) for $\delta^{18}\text{O}_{\text{BW}}$ (fig. 3; table S7). RMSE between predicted and measured values for the body mass model were 19 per meg for $\Delta^{17}\text{O}_{\text{BW}}$ and 1.9‰ for $\delta^{18}\text{O}_{\text{BW}}$. When evaluating individual periods for each region for the body mass model, the mean absolute differences were 12–18 per meg for $\Delta^{17}\text{O}_{\text{BW}}$ and 0.5‰ – 2.1‰ for $\delta^{18}\text{O}_{\text{BW}}$. The calculated oxygen flux values for the body mass model indicated that for Bear River Mountains deer, the contribution from drinking water more than doubled from November 2021 to March and December 2022, while the contribution from food water from items like leaves decreased as a result (fig. 4; table S8). For Pine Valley deer, the calculated fluxes for the body mass model indicated that the contribution from food water from items like leaves was highest in December 2021 and then fell in later periods, while the contribution from drinking water peaked in December 2022. For deer in both regions, the largest efflux across all periods was calculated as urinary water loss using the body mass model (fig. 5).

The heart rate model performed well but exhibited less agreement between measured and predicted values, with mean absolute differences of 22 per meg (± 16 per meg) for $\Delta^{17}\text{O}_{\text{BW}}$ (fig. 6) and 2.0‰ ($\pm 1.2\text{‰}$) for $\delta^{18}\text{O}_{\text{BW}}$, when pooling all data from both regions. RMSE was 27 per meg for $\Delta^{17}\text{O}_{\text{BW}}$ and 2.3‰ for $\delta^{18}\text{O}_{\text{BW}}$. When evaluating individual periods for each region,

the mean absolute differences were 12–30 per meg for $\Delta^{17}\text{O}_{\text{BW}}$ and 1.0‰ – 2.5‰ for $\delta^{18}\text{O}_{\text{BW}}$. The predicted oxygen inputs using the heart rate model were fairly consistent with the body mass model, but the heart rate model typically predicted a lower fractional contribution of drinking water and, as a result, a slightly higher fractional contribution of other inputs (e.g., food water and oxidase water). The models aligned closely regarding their predictions of the oxygen outputs, except—consistent with the differences in predicted drinking water—the body mass model predicted a higher fractional contribution of urinary water loss.

Discussion

Our findings support our prediction that during winter, mule deer relied more heavily on drinking water in the Bear River Mountains than in Pine Valley, and we also observed seasonal variation in reliance on different water sources. We draw these conclusions because the close agreement between predicted and measured $\Delta^{17}\text{O}_{\text{BW}}$ indicates accuracy in the estimated oxygen and water fluxes. Surprisingly, this agreement was slightly better when estimating FMR based on body mass alone (mean absolute difference = 14 per meg) rather than heart rate data from biologgers (22 per meg). Furthermore, the accuracy of predicted $\Delta^{17}\text{O}_{\text{BW}}$ was similar to a previous controlled study of captive deer mice (Steele et al. 2025). Collectively, our results support mule deer as seasonally facultative drinkers whose reliance on drinking water emerges when forage access is restricted (e.g., deep snow

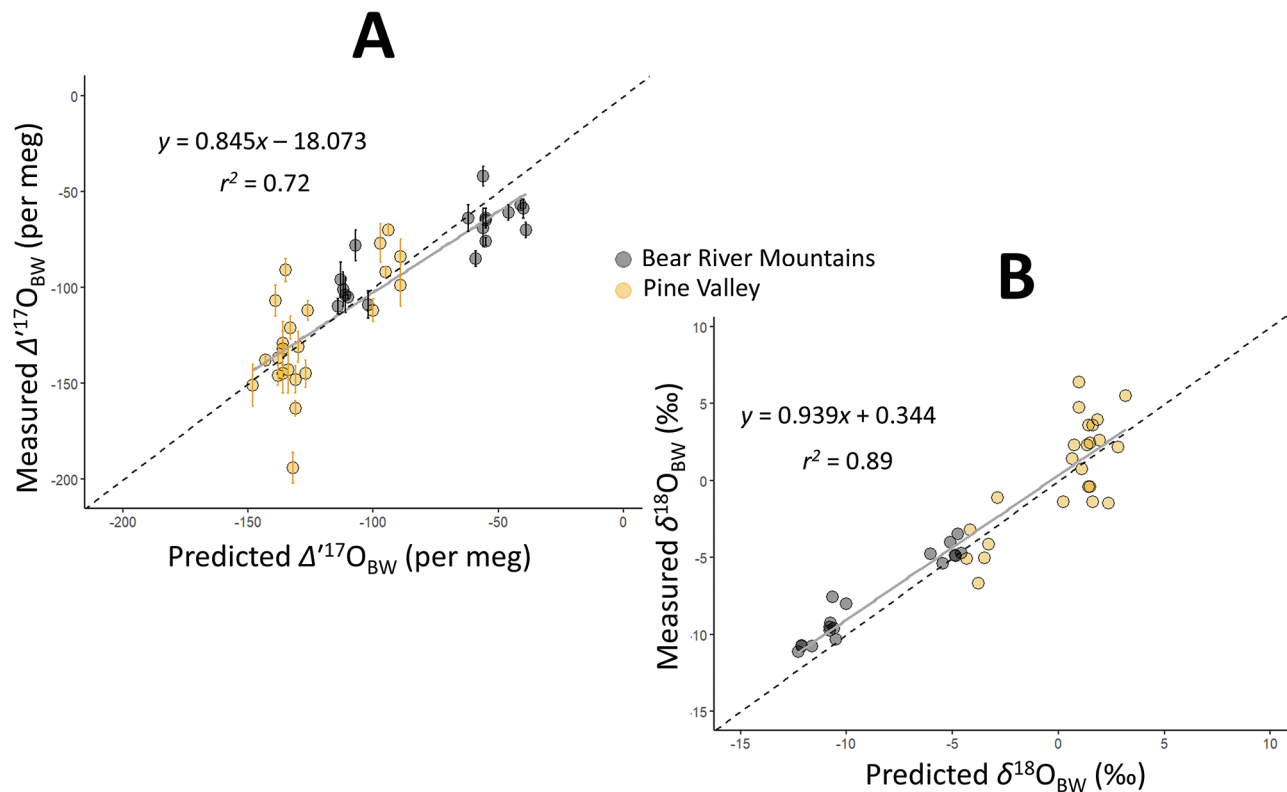


Figure 3. Predicted versus measured $\Delta^{17}\text{O}_{\text{BW}}$ (A) and $\delta^{18}\text{O}_{\text{BW}}$ (B) for free-ranging mule deer in two study regions in Utah. The gray lines are linear regressions, and the dashed lines are the 1:1 relationships (i.e., if predictions were perfect). Predicted values are from the body mass modeling approach (for full details, see apps. S2, S3). Data include repeated sampling of individuals in the Bear River Mountains ($n = 7$ deer) and Pine Valley ($n = 9$ deer). In A, vertical errors bars indicate ± 1 SD of replicate measurements of samples. In B, replicates of $\delta^{18}\text{O}_{\text{BW}}$ measurements all had SDs $< 0.3\text{‰}$, and no error bars are shown. BW = body water sample.

limiting foraging in the Bear River Mountains) or when forage water content is low, whereas semisucculent forage can meet much of their winter water demand under milder conditions (e.g., Pine Valley). Our findings for wild mule deer demonstrate, for the first time, the use of triple oxygen isotopes to understand the seasonal metabolism and water use of a free-ranging species, an application that could be particularly useful for North American ungulates and other species of management concern in the face of increasingly long and severe droughts (Cain et al. 2006; Krausman et al. 2006; van den Bosch et al. 2024). Importantly, this approach requires a minimal sample volume (30–45 μL of serum) that can be obtained during routine sampling, and although our study utilized a longitudinal approach, inferences can be generated from single samples.

Our findings indicate that use of water sources varied over space and time. In the Bear River Mountains, food water was the largest input to body water early in winter when snow cover was thin (November 2021). Thereafter, samples collected during March and December 2022 when deeper snow limited access to vegetation indicated reduced contribution of food water to body water. In this mountainous region, deer likely experienced reduced food intake and food quality during winter, which presumably contributed to the observed 10% seasonal decline in body mass. In

contrast, food water was the biggest input to body water for Pine Valley mule deer during all periods, likely because a lack of snow cover and milder climate year-round allowed consistent access to vegetation. Accordingly, Pine Valley mule deer maintained a consistent body mass over the three sampling periods. Like previous studies (Staudenmaier et al. 2022), our findings indicate that mule deer can meet their nutritional and water needs on low-quality forage in conditions similar to those observed in Pine Valley, even with minimal access to drinking water. Overall, these patterns in water intake and body mass suggest that deer in the Bear River Mountains likely maximize food intake in the summer and fall before vegetation is scarcer in winter, increasing reliance on drinking water (DeCesare et al. 2021; Knight 2022), while Pine Valley deer may not rely on drinking water because of the benefit of mild winters and consistent access to vegetation.

Our results indicate plasticity in the water balance strategies of individual deer. When forage is available, energy and water balance can be linked via the simultaneous incorporation of these resources from diet. Accordingly, Bear River Mountains deer did not heavily use abundant freshwater sources in November 2021 when snow cover was thin and forage was more available. When forage is restricted by deep snow cover, maintenance of water and energy balance appear to decouple, leading to greater reliance on

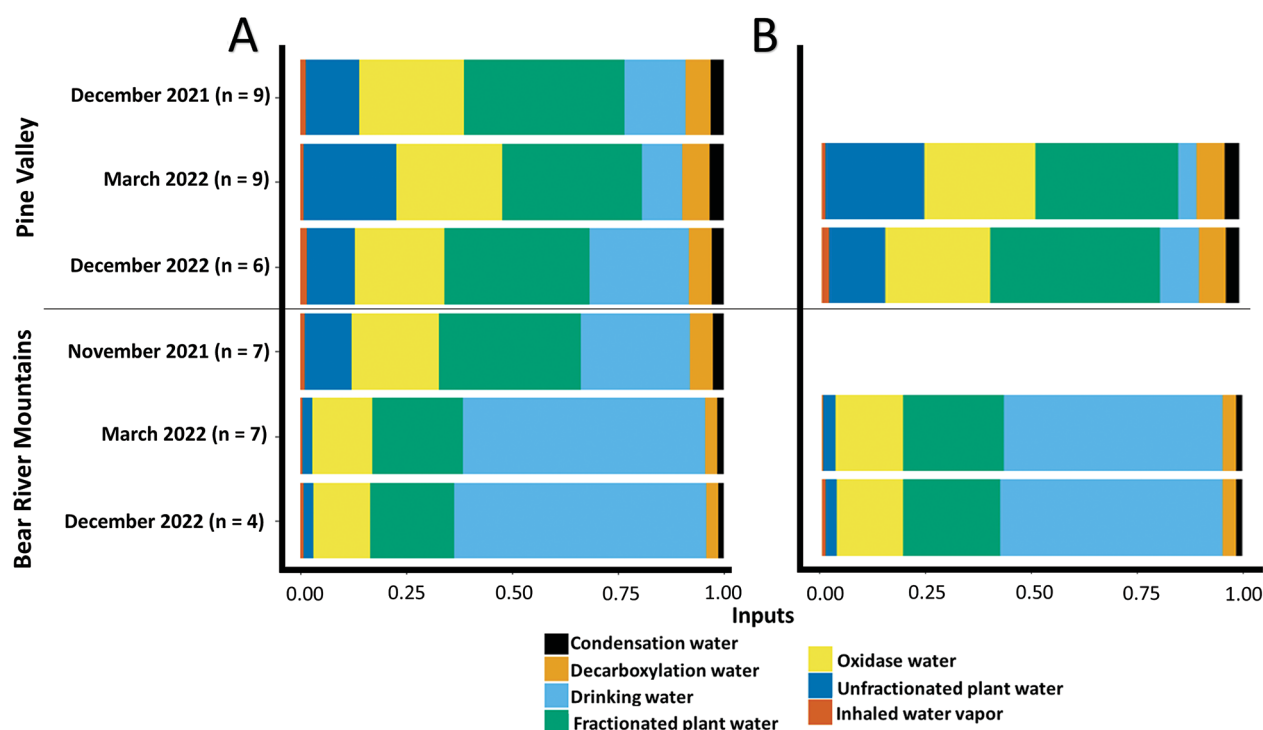


Figure 4. Mean fractional contributions of different oxygen influxes for free-ranging mule deer in two study regions in Utah. Predictions generated via two different modeling approaches: the body mass model (A) and the heart rate model (B; for full descriptions of both modeling approaches, see apps. S2, S3). Standard deviations for each influx ranged from <0.01 to 0.14 (for full details, see table S8).

drinking water. While deer in the Bear River Mountains had ample freshwater sources nearby, this decoupling may result in other deer with fewer water sources but similar or greater snow depth facing energetically taxing travel to find water sources (Parker et al. 1984; Hobbs 1989) and the potential of increased predation risk (Crosmary et al. 2012; Harris et al. 2015).

The lack of snow cover and depth in Pine Valley, and apparent continual reliance on food water, contrasts with the clear dependence of mule deer on drinking water documented in previous studies during summer in arid regions (Hervert and Krausman 1986; Hazam 1987). In summer, female deer generate considerable heat and lose substantial water not only for thermoregulation but also for lactation (Moen 1978). In contrast, thermoregulatory water losses are minimized, and lactation is typically absent during winter. The energetic demand for gestation has also not yet peaked, which usually occurs in spring during the third trimester (dependent on latitude; Pekins et al. 1998). As such, in regions with similar climates to Pine Valley, winter vegetation may be sufficient to meet both the energy and water needs of deer until the demands of reproduction and thermoregulation increase.

Our findings highlight the utility of modeling $\Delta^{17}\text{O}_{\text{BW}}$ for understanding the dependence on different water sources for free-ranging animals and how this dependence varies seasonally and by regional differences. By modeling $\Delta^{17}\text{O}_{\text{BW}}$, we concluded that Pine Valley deer in our study had little reliance on drinking water during winter. The results of the model estimating FMR based on body mass suggest that ~40% (7/18) of the deer from Pine

Valley in December 2021 and March 2022 obtained $\leq 10\%$ of their oxygen influx from drinking water. The results of the model estimating FMR based on heart rate suggest that two-thirds (12/18) of the Pine Valley deer in December 2021 and March 2022 obtained $\leq 10\%$ of their oxygen influx from drinking water, with ~20% (4/18) of the deer not drinking water at all. In contrast, both modeling approaches indicated that all deer from the Bear River Mountains obtained $\geq 15\%$ of their oxygen influx from drinking water. Mule deer appear to be obligate drinkers in summer (e.g., Hervert and Krausman 1986), but our results indicate that they may not be in winter.

Contrary to our expectations, estimating FMR using heart rate data did not improve model accuracy. Specifically, mule deer with high heart rates (high FMR) often had predicted $\Delta^{17}\text{O}_{\text{BW}}$ that differed from measured values by a mean of 30 per meg and resulted in estimated lower reliance on drinking water, especially during March 2022 in Pine Valley (fig. 4). Previous work on deer mice likewise found that elevated metabolic rates reduced the accuracy of predicted $\Delta^{17}\text{O}_{\text{BW}}$ (Steele et al. 2025), which may reflect physiological changes that occur when metabolism is elevated but lack an empirical basis for adjusting model parameters (for sensitivity analysis, see app. S4; tables S9, S10). It is also possible that the equations to convert heart rate to FMR may have provided inaccurate estimates because they were derived from a previous study with a small sample size ($n = 3$) of younger deer (Kautz et al. 1981). Despite the lack of model improvement by incorporating heart rate, we urge continued exploration of proxies

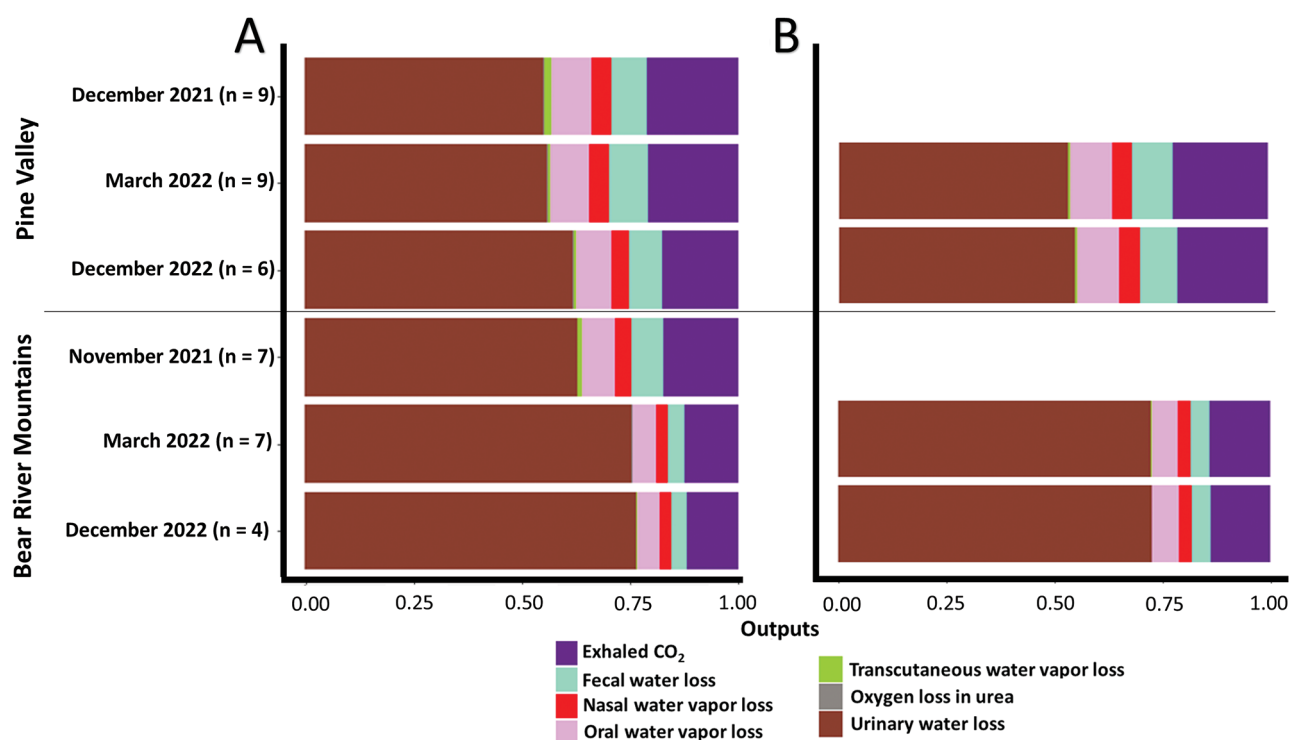


Figure 5. Mean fractional contributions of different oxygen effluxes for free-ranging mule deer in two study regions in Utah. Predictions generated via two different modeling approaches: the body mass model (A) and the heart rate model (B; for full descriptions of both modeling approaches, see apps. S2, S3). Standard deviations for each influx ranged from <0.01 to 0.08 (for full details, see table S8).

for metabolic rate and other means to constrain estimates of oxygen fluxes. Although parameters were informed based on limited data, we emphasize that the strong performance of the model using FMR based on body mass is highly encouraging for future use of triple oxygen isotopes in wildlife management and conservation. There is potential to further increase the accuracy of modeling predictions by modifying parameters at the individual level (e.g., ratio of fractionating plant material and percentage of body water turned over per day) that we adjusted at the site and sampling period level because of a lack of variation in $\Delta^{17}\text{O}_{\text{BW}}$ and $\delta^2\text{H}_{\text{BW}}$ among deer from each site during different sampling periods. However, individual-based modifications to models should be justified by large variation among individuals in both isotope values and location-specific environmental parameters (e.g., NDVI).

Similar to prior studies (Kohn 1996; Hu et al. 2023; Feng et al. 2024), we assumed that water from plant tissues, such as stems, was not fractionated (Yakir 1992; Landais et al. 2006; Sanchez-Bragado et al. 2019). However, while studies in temperate climates support this assumption (e.g., Landais et al. 2006), studies in arid and tropical climates, where transpiration can be more intense, indicate that plant water in stems can be strongly fractionated (De Wispelaere et al. 2016; Knutson 2025; Sharp et al. 2025), and uncertainty remains regarding the θ value for fractionation between leaf water and meteoric water (Landais et al. 2006; Sharp et al. 2025). In our study, it is plausible that unexpectedly isotopically enriched plant water may have occurred in the semiarid

Pine Valley region. This could potentially explain the decreased prediction accuracy for $\Delta^{17}\text{O}_{\text{BW}}$ and $\delta^{18}\text{O}_{\text{BW}}$ values of deer from Pine Valley using both models. Future research should continue to explore the dynamics of stem water fractionation and fractionation factors related to leaf water.

The variation in reliance on plant water and drinking water that we inferred among deer populations in the Rocky Mountains provides critical information for wildlife management and provides needed evidence of different ungulate water balance strategies (Cain et al. 2006), especially given increasing occurrence of more severe and longer droughts (Yuan et al. 2023). In North America, the most profound changes are expected for mammals in the American Southwest (van den Bosch et al. 2024). Prolonged droughts create challenges for the management of populations that are obligate drinkers because surface water sources are becoming less predictable, scarcer, or more ephemeral in many regions (McCluney et al. 2012; Veldhuis et al. 2019). At the same time, drought can desiccate highly used habitats and reduce the water and energy available from natural forage, potentially shifting deer toward irrigated or otherwise subsidized vegetation where plant water status remains buffered (Leclerc et al. 2025). Populations that rely on food water will also face aridification that senesces plants earlier in the season, potentially creating phenological mismatches between the availability of food and water and the onset of winter conditions.

Measurements of $\Delta^{17}\text{O}_{\text{BW}}$ could help interpret behavioral and geographic shifts that can occur as the climate changes (Cain

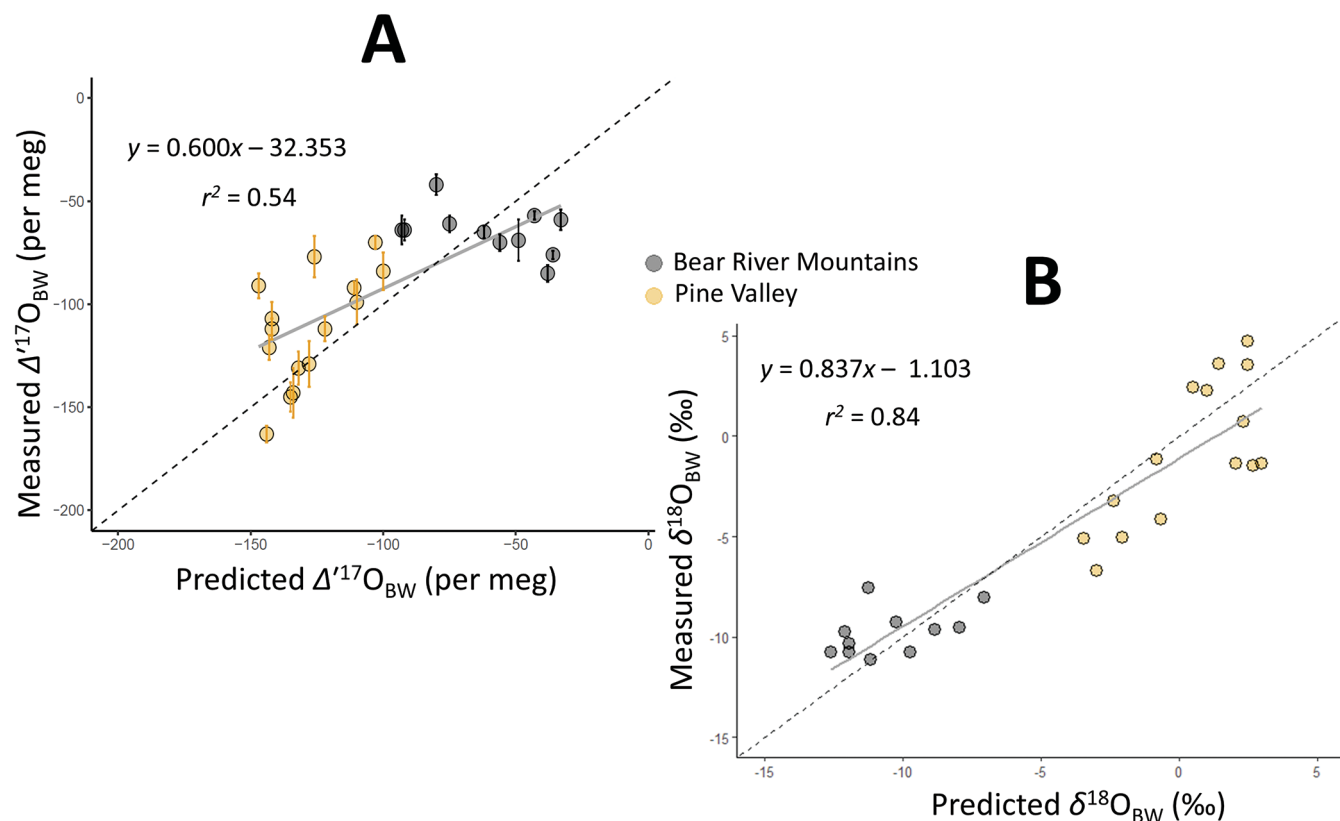


Figure 6. Predicted versus measured $\Delta^{17}\text{O}_{\text{BW}}$ (A) and $\delta^{18}\text{O}_{\text{BW}}$ (B) for free-ranging mule deer in two study regions in Utah. The gray lines are linear regressions, and the dashed lines are the 1:1 relationships (i.e., if predictions were perfect). Predicted values are from the heart rate modeling approach (for full details, see apps. S2, S3). Data include repeated sampling of individuals in the Bear River Mountains ($n = 7$ deer) and Pine Valley ($n = 9$ deer). In A, vertical errors bars indicate ± 1 SD of replicate measurements of samples. In B, replicates of $\delta^{18}\text{O}_{\text{BW}}$ measurements all had SDs $< 0.3\text{‰}$, and no error bars are shown. BW = body water sample.

et al. 2006), including shifts toward surface water as conditions became drier and hotter (Harris et al. 2020). In drought-prone systems, the same integration of isotopic inference with landscape indicators of vegetation water status that explain drought-driven redistribution (e.g., toward irrigated agricultural areas; Leclerc et al. 2025) could help identify when and where deer are likely to transition from reliance predominantly on food water to greater dependence on drinking water sources. $\Delta^{17}\text{O}_{\text{BW}}$ analysis could also be useful where provisioning of surface water is used as a management strategy, by revealing variation among species and over time in the use of provisioned versus natural sources of water (Rosenstock et al. 1999; Krausman et al. 2006; Larsen et al. 2012).

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