COMPARING PREDICTED AND MEASURED TRIPLE OXYGEN ISOTOPE ($\Delta^{17}O$) VALUES OF BODY WATER SAMPLES OF CAPTIVE DEER MICE (*PEROMYSCUS MANICULATUS*) AND NON-NATIVE GEMSBOK (*ORYX GAZELLA*)

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Abstract

Maintaining water balance is critical to all animals. Animals obtain water from drinking and the food they consume (pre-formed water), and through endogenous synthesis by the metabolic pathways (metabolic water). Understanding the contributions of these water sources to an animals’ total body water is critical but is challenging to measure in free-ranging wild animals. A newly developed technique, the $\Delta^{17}O_{BW}$ method, only requires one sample from an animal and measures triple oxygen stable isotopes ($^{16}O$, $^{17}O$, and $^{18}O$; $\Delta^{17}O$). This method relies upon two main assumptions: 1) the $\Delta^{17}O$ value derived for metabolic water is relatively fixed at -441 per meg; and 2) the $\Delta^{17}O$ value derived for pre-formed water is ~41 per meg. To further validate this method, I conducted an experiment using captive deer mice (*Peromyscus maniculatus*) and sampled a free-ranging, invasive population of gemsbok (*Oryx gazella*) in New Mexico. I compared measured and predicted $\Delta^{17}O_{BW}$ values to refine modeling capabilities using a basic and complex model. Both models accurately predicted measured $\Delta^{17}O_{BW}$ values, but the complex model seems prone to overestimating the influence of metabolic water. This shortcoming of the complex model may prove challenging to the interpretation of $\Delta^{17}O_{BW}$ measurements of some desert and water-stressed animals.

Introduction

All animals need energy for basic life functions\(^1\). Even while at rest animals are constantly expending and generating energy via metabolic processes\(^1\). These metabolic processes are also constantly consuming and producing water\(^1\). Maintaining an appropriate amount of water within the body (‘water balance’) is equally critical to animal function and survival as meeting energy demands\(^1\). If an animal’s water output outweighs their input, over time this animal may struggle to conduct metabolic reactions, digest and absorb nutrients, and expel waste\(^2\). This highlights the critical, direct relationship between water balance and energy requirements\(^1\).

The ramifications of non-native species introductions are increasing the need to understand how animals maintain water and energy balance because many species must acclimate to increased competition for resources or face extirpation\(^3,4\). Animals in extreme environments such as deserts are particularly vulnerable to the impacts of species introductions. Desert species have unique physiological and behavioral adaptations to conserve water and energy to survive harsh desert climates\(^5\). The introduction of a non-native species that can potentially outcompete native species poses a significant threat to native desert species that already are sensitive to small environmental
fluctuations. Monitoring metabolism and water intake is particularly important in these settings for assessing the potential negative impacts of a species introduction.

Most animals are ~70-90% water and need to offset water loss that occurs through exhalation of moist breath and through evaporation from the skin, and excretion of liquid water in waste products. These losses are offset by inputs from pre-formed sources (drinking and food water) and internal metabolic processes. Critically, these internal processes include the de novo synthesis of water using oxygen molecules inhaled from the atmosphere. This production of water, termed “metabolic water”, is a byproduct of the chemical reactions of metabolism. As such, metabolic water production is directly linked to the rate of metabolism (metabolic rate). However, few methods are available to directly measure an animal’s metabolic rate and their reliance on different water sources in a natural setting. Instead, most studies are conducted in captivity using methods like respirometry and many captive studies cannot easily account for the multiple environmental variables encountered by animals in the wild.

Alternatively, methods currently available for studies of free-ranging animals are often hampered by prohibitive costs and logistics. These include methods such as the “doubly-labeled water” (DLW) technique which involves injecting a captured animal with stable isotopes of hydrogen and oxygen ($^2$H$_2^{18}$O), then releasing the animal. Days to weeks later the same animal is re-captured and a blood sample is collected, and the different rates of decline in $\delta^2$H and $\delta^{18}$O are used to infer water intake and metabolic rate (via CO$_2$ production). When studying a limited or threatened population, the necessity of multiple capture events for DLW greatly reduces the applicability of this method.

Recently, a potential solution to this dilemma was developed, requiring only a single blood sample to estimate metabolism and water intake. This method is based upon measuring $\Delta^{17}$O in body water ($\Delta^{17}$O$_{BW}$), which is a quantification of the relative amounts of the three stable oxygen isotopes (i.e., $^{17}$O and $^{18}$O are heavy isotopes of oxygen, compared to the common form of $^{16}$O, expressed as $\delta^{17}$O and $\delta^{18}$O respectively) that are naturally found in an animal’s body water. $\Delta^{17}$O is calculated from measurements of $\delta^{17}$O and $\delta^{18}$O which have a near constant relationship when plotted against each other (Figure 1A). This relationship occurs because the isotopic variation of $\delta^{17}$O and $\delta^{18}$O is typically based on mass (i.e., via mass-dependent fractionation) and means that a sample with a high $\delta^{18}$O value is expected to also have a high $\delta^{17}$O value. However, there are small positive and negative deviations from this expected relationship, representing mass-independent fractionation (e.g., supersaturation, Rayleigh distillation, stratospheric intrusions, etc.) which are quantified as $\Delta^{17}$O. Importantly, $\Delta^{17}$O acts as a natural tracer of water sources.

Both pre-formed and metabolic water have near constant $\Delta^{17}$O values, of 41 per meg (parts per million) and -441 per meg respectively. Therefore, the $\Delta^{17}$O value of an animal’s body water should indicate their reliance on metabolic water, which varies greatly among species. Some animals primarily rely on pre-formed water and have little input from metabolic water, resulting in a $\Delta^{17}$O$_{BW}$ value near 0 per meg like African elephants (Loxodonta africana; Figure 1B).
In contrast, desert-adapted animals like kangaroo rats (genus *Dipodomys*) may lack access to pre-formed water and instead primarily rely on metabolic water resulting in a \( \Delta^{17}O_{BW} \) value closer to -200 per meg\(^{7,13}\). However, this is a “basic” modeling approach to determining \( \Delta^{17}O_{BW} \). More “complex” models have been described that incorporate different aspects of an animals’ ecology and physiology while also integrating abiotic factors like relative humidity and ambient temperature\(^{14}\). While this more complex model potentially provides more accurate predictions of \( \Delta^{17}O_{BW} \), the complex model requires a higher degree of background knowledge regarding the focal animal\(^{14}\), whereas the basic model can be utilized with minimal information about environmental and dietary factors\(^{7}\).

![Figure 1](image)

**Figure 1.** A) \( \delta^{17}O \) and \( \delta^{18}O \) represent the abundance of \( ^{17}O \) and \( ^{18}O \) relative to the abundance of \( ^{16}O \). Deviations from this slope (i.e., residuals) are represented as \( \Delta^{17}O \) (From reference 7; pg. 659; Figure 1). B) The variance of \( \Delta^{17}O \) in an animal’s body water (\( \Delta^{17}O_{BW} \)) depending on the contribution from meteoric and metabolic water.

While initial captive studies using the \( \Delta^{17}O_{BW} \) method found support for predicted trends of a decrease in \( \Delta^{17}O_{BW} \) in response to increased metabolic rate\(^2,7\), predicted values demonstrated a substantial, consistent underprediction of measured \( \Delta^{17}O_{BW} \) values using the basic model\(^7\). However, these studies lacked the ability to measure different water inputs consistently and accurately and did not apply the more complex modeling approach when generating predictions. Measuring inputs more accurately and testing the complex model should allow for refinements that will improve interpretation of \( \Delta^{17}O_{BW} \) measurements of free-ranging animals. In particular, modifications are necessary for interpreting measurements from desert herbivores, that likely are obtaining most of their water from their diet and metabolic water.

To improve upon initial \( \Delta^{17}O_{BW} \) captive studies\(^2,7\), I housed deer mice (*Peromyscus maniculatus*) in a metabolic phenotyping system within a temperature control cabinet for continuous measurements of food, water, \( O_2 \) consumption, \( CO_2 \) production, and evaporative water loss. I provided deer mice with diets of differing NaCl concentration in an effort to manipulate water intake before obtaining \( \Delta^{17}O_{BW} \) measurements. I then collected \( \Delta^{17}O_{BW} \) measurements from an invasive population of gemsbok (*Oryx gazella*) in New Mexico, an antelope species regarded for their water-conservation adaptations for the harsh desert environment\(^5\). I compared measured \( \Delta^{17}O_{BW} \) values from the captive study and gemsbok samples with predicted \( \Delta^{17}O_{BW} \) values from both the basic and complex models to ascertain the accuracy of estimates and determine areas for improvement.
Methods

Captive Environment

In December 2021, eight deer mice were placed into 21x37x14cm cages as part of a metabolic phenotyping system (Promethion; Sable Systems International – NV, USA). Each cage contained three “hoppers” that were metal drop-down containers connected to mass monitors that continuously weighed each hopper (see Figure 2). The first hopper was a feeding hopper covered by a grate to provide small slits for feeding. The second hopper was a water hopper that contained a typical rodent drinker. The final hopper was a mass hopper and provided a covered walk-in platform for mice to enter. Once a mouse entered this platform for a prolonged period of time (≥5 seconds) a weight was recorded. Combined, these three hoppers allowed for continuous measurement of mass, food intake, and water intake. The metabolic phenotyping system also provided continuous measurement of O\textsubscript{2} consumption, CO\textsubscript{2} production, and evaporative water loss. The system was housed within a temperature control cabinet (Model 7000-25-1; Caron – OH, USA) which allowed for adjustment of temperatures to a fixed value. This research was approved under Old Dominion University Institutional Animal Care and Use Committee Protocol #20-001.

The experimental phase was initiated on 19-May-2022 and lasted 70 days, with blood samples being collected every 14 days from individual mice. Over the course of these 70 days, mice were exposed to different treatments consisting of different diets and temperatures over 14-day periods. The diets exposed mice to either a control diet containing 0.49% NaCl Teklad diet (TD.96208; Envigo – IN, USA) or a treatment diet of 4% NaCl Teklad diet (TD.92034). Temperatures within the cabinet were manipulated from either a control temperature of 25°C or a treatment temperature of 15°C. I analyzed samples from two different mice; one on the control diet and the other on the experimental diet. I predicted that increasing the NaCl content of diet would result in an increase in water intake, resulting in an increase in Δ\textsuperscript{17}O\textsubscript{bw}.

Invasive Gemsbok Study Area

Blood samples were obtained from gemsbok from public hunters at White Sands Missile Range (WSMR; New Mexico, US) at two locations: 1) Stallion Range; and 2) Rhodes Canyon (Figure 3). WSMR offers public hunts from

![Figure 2. Promethion cage layout with the feeding hopper (front right), water hopper (back right), and mass hopper with red-shaded frames (center). This is a stock photo provided by Sable Systems International which includes an exercise wheel (far left) that was not used in this experiment.](image)

![Figure 3. Map of White Sands Missile Range (WSMR) highlighting the Stallion Range and Rhodes Canyon sites where public hunts will occur.](image)
September to February each year to control the introduced gemsbok population. Blood samples were collected in September 2022 from culled, adult-male gemsbok in a 1.3mL microtube and then transferred to Old Dominion University (Norfolk, VA; ODU) where they were centrifuged to separate plasma for analysis. I compiled Δ\(^{17}\)O\(_{BW}\) measurements from 10 individual gemsbok to provide an average measured value to compare with predicted values. Since September is the rainy season for this region, I predicted that measured Δ\(^{17}\)O\(_{BW}\) would be highest during this period compared to values obtained during the cold and dry winter months of December and January.

**Sample Processing**

Plasma samples were distilled to obtain body water samples using previously described methodology\(^ {16}\). To briefly summarize, plasma samples were inserted into a 9” glass pipette (Kimble 883350-0009). The large opening of the pipette was then flame sealed via a torch\(^ {16}\). The narrow end of the pipette was then connected to a vacuum pump via a series of tubing, the larger end of the pipette was dipped in liquid nitrogen until frozen, and then the vacuum was applied before the narrow end was quickly flame sealed\(^ {16}\). After sealing, the larger end of the pipette was placed on a slide warmer, with the narrow end extending outwards; as the sample thawed and the water slowly became vapor, the water eventually condensed at the narrow end because of the cooler temperature\(^ {16}\). A final flame seal then separated the narrow end, leaving a makeshift microcapillary tube of distilled body water\(^ {16}\).

**Stable Isotope Analysis**

Distilled samples were measured via a cavity ring-down spectroscopy (CRDS) instrument (Picarro L2140-i; Picarro – CA, USA) at ODU. I measured samples 7–17 times (depending on final sample volume) and I removed initial measurements from the data to limit the memory effect of previous measurements. Using the remaining measurements, I calculated a mean value, which in turn, provides an estimate of metabolic water production. I compiled the mean values of multiple distillation samples for each individual sample to obtain an overall average to represent that specific sample. United States Geological Survey (USGS) water standards (USGS47, 48, and 50) and in-house standards (VA01, VA02) that were verified via internationally accepted water standards (Vienna Standard Mean Ocean Water [VSMOW] and Standard Antarctic Light Precipitation Water [SLAP]), were used to standardize the Picarro instrument during each analysis. This allowed for corrections to be made to raw data based on instrument error. An example “run” on the Picarro is provided in Table S1 to display the setup needed to obtain accurate and precise data, with many runs lasting 72+ hours.

**Data Analysis**

The Picarro provides measurements of \(^{17}\)O and \(^{18}\)O as ratios of isotopic abundancies (δ\(^{17}\)O and δ\(^{18}\)O, which are used to ultimately calculate Δ\(^{17}\)O) in reference to the “base” form of oxygen (\(^{16}\)O). These ratios are calculated in reference to internationally accepted standards: VSMOW and SLAP. Normalization to what is referred to as VSMOW-SLAP scale reduces the potential for instrumental bias and allows data to be more comparable with findings within the isotope literature. By measuring USGS and in-house standard waters in conjunction with VSMOW and SLAP, values on the VSMOW-
SLAP scale for USGS and in-house standard waters can thus be determined allowing for generation of a correction factor using linear regression for adjusting raw measurements of all samples to VSMOW-SLAP scale at the completion of each analysis run. I applied the correction factor scale using R (version 4.0.3). Once δ¹⁷O and δ¹⁸O values were obtained on VSMOW-SLAP scale, I then solved for Δ¹⁷O.

Results

Correction Factors

Separate correction factors were applied across the 13 sampling runs conducted on the Picarro. For full details of the corrections applied to raw measurements and the values obtained for waters used during analyses, please see Tables S2 and S3.

Manipulation of Deer Mice Water Intake and Metabolic Rate

Deer mice housed at 25°C and fed the 0.49%NaCl control diet drank an average of 2.77g of water per day, while mice housed at the same temperature and fed the 4%NaCl diet drank an average of 5.92g of water per day. Mice housed at 25°C and fed the 1%NaCl control diet averaged a metabolic rate of 27.25 kJ/d, while mice housed at 15°C and also fed the control diet averaged a metabolic rate of 41.13 kJ/d.

Predicted Versus Measured Δ¹⁷O Values

The complex model predicted Δ¹⁷O_BW on average 13.8 per meg lower than the measured values, while the basic model predicted Δ¹⁷O_BW on average 1.3 per meg lower than the measured values (Figure 4). Both models predicted the Δ¹⁷O_BW of the mouse on the 4%NaCl diet within 5 per meg of the measured value, and the averaged gemsbok Δ¹⁷O_BW within 12 per meg of the mean value.

Discussion

The initial findings of this research suggest that while both models appear to accurately predict measured Δ¹⁷O_BW values, adjustments may need to be made to the complex model to better anticipate Δ¹⁷O_BW values. The complex model accurately predicted the averaged gemsbok measured Δ¹⁷O_BW value and the measured Δ¹⁷O_BW value of the deer mouse on the 4%NaCl diet, but the model underpredicted the Δ¹⁷O_BW value of the mouse on the 0.49%NaCl diet by >30 per meg. This likely is due to the complex model’s overestimation of the influence of metabolic water on Δ¹⁷O_BW values.

The complex model suggested that the deer mouse consuming the 0.49%NaCl diet had a total body water that was >35% derived
from metabolic water. This value would be more comparable to that of desert rodents that are adapted to be nearly water independent. The complex predictive model is heavily reliant on the Water Economy Index (WEI). WEI is the ratio of the rate of total water intake to the metabolic rate; essentially water consumed a day (mL) divided by energy exerted a day (kJ). The complex model assumes that if an animal’s WEI falls below a certain threshold then this animal is essentially “water independent”. The mouse on the control diet generated a WEI value that fell into this category leading to a highly inaccurate predicted Δ17O_BW value. In contrast, the mouse on the experimental ‘salty’ diet consumed more water as predicted, leading to a WEI value that surpassed this threshold, resulting in an accurate predicted Δ17O_BW value.

While predicted Δ17O_BW using the basic model were accurate for both deer mouse scenarios and the averaged gemsbok value, the inability for this basic model to account for variation in dietary Δ17O_BW values that was not tested in these preliminary findings may lead to issues. For example, many desert reptiles that obtain most of their water from their diet feed on insects or small mammals that likely possess low Δ17O_BW values that differ greatly from pre-formed water values. In addition, many desert herbivores obtain most of their water from their diet. Many of these plants possess extremely low Δ17O values (Figure 5). While the basic model was able to accurately predict September gemsbok values, these values were obtained during the rainy season. The basic model may be unable to accurately predict gemsbok values in December and January when gemsbok are relying more on dietary water sources to meet their needs.

Figure 5. Water measurements that include both δ18O and Δ17O as of 2020. Plot has been divided into four quadrants based on the zero value for the x-axis and y-axis. Plant water values have both δ18O and Δ17O values that are significantly different from all other waters included due to unique fractionation (From reference 11; pg. 4; Figure 3B).

Future Directions

The next objective is to finalize analysis of the captive deer mice and free-ranging gemsbok data so that these datasets are complete. This will allow for further assessment of the predictions related to the diet manipulation for the captive experiment, along with the temperature manipulation. I will also explore the variation of the gemsbok Δ17O_BW values during the winter months to compare with the values obtained during the warmer, rainy season. Lastly, as more analyses are completed and data compiled, adjustments can be made to both models to predict and interpret Δ17O_BW values more accurately.

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**Literature Cited**


Table S1. Example of a “run” completed on the Picarro. Three in-house standards (VA01, VA02, VA03) verified via internationally-accepted water standards were used throughout the run to establish a correction curve to correct the raw values obtained. A conditioning vial refers to a water sample that was used to minimize the memory effect when maneuvering between samples with significant gaps in their $\delta^{18}$O values. A control vial refers to a water sample that is included to ensure the validity of the run after the correction curve is applied by verifying a known $\delta^{18}$O value. Measurement order refers to the number of measurements (injections) at that point of the process, while number of measurements refers to the number of measurements for that particular item. Autosampler job number refers to the order in which each item was listed for analysis. While a sample may have 30+ measurements, most of these measurements are removed due to the memory effect and only a select number of measurements remain for analysis.

<table>
<thead>
<tr>
<th>Description</th>
<th>Measurement Order</th>
<th>$\delta^{18}$O</th>
<th>Number of Measurements</th>
<th>Autosampler Job Number</th>
<th>Purpose</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conditioning Vial</td>
<td>1-70</td>
<td>~ 0</td>
<td>70</td>
<td>1</td>
<td>Warm-up instrument</td>
</tr>
<tr>
<td>Conditioning Vial</td>
<td>71-97</td>
<td>~ +4</td>
<td>27</td>
<td>2</td>
<td>Conditioning vial for positioning in-house standard</td>
</tr>
<tr>
<td>Heavy $\delta$ In-House Lab Standard (VA01)</td>
<td>98-157</td>
<td>~ +8</td>
<td>60</td>
<td>3</td>
<td>In-house standard for establishing correction curve</td>
</tr>
<tr>
<td>Control vial</td>
<td>158-184</td>
<td>~ +4</td>
<td>27</td>
<td>4</td>
<td>Control vial</td>
</tr>
<tr>
<td>Control vial</td>
<td>185-211</td>
<td>~ -2</td>
<td>27</td>
<td>5</td>
<td>Control vial &amp; positioning unknown samples</td>
</tr>
<tr>
<td>Distilled Deer Mice Samples</td>
<td>212-361</td>
<td>???</td>
<td>150</td>
<td>6-17</td>
<td>Unknown samples</td>
</tr>
<tr>
<td>Slightly negative $\delta$ In-House Lab Standard (VA 02)</td>
<td>362-394</td>
<td>~ -4</td>
<td>33</td>
<td>18</td>
<td>In-house standard for establishing correction curve</td>
</tr>
<tr>
<td>Control vial</td>
<td>395-437</td>
<td>~ -10</td>
<td>43</td>
<td>19</td>
<td>Control vial &amp; positioning in-house standard</td>
</tr>
<tr>
<td>Light $\delta$ In-House Lab Standard (VA03)</td>
<td>438-470</td>
<td>~ -9</td>
<td>33</td>
<td>20</td>
<td>In-house standard for establishing correction curve</td>
</tr>
<tr>
<td><strong>Total Measurements</strong></td>
<td></td>
<td></td>
<td><strong>470</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Estimated run time</strong></td>
<td></td>
<td></td>
<td><strong>72.43 hours</strong></td>
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</tbody>
</table>

Table S2. Number and dates of analysis runs (‘Sampling Day’), along with the $\delta^{17}$O and $\delta^{18}$O correction equations obtained for that analysis run. Both of these correction equations were used to correct raw $\delta^{17}$O and $\delta^{18}$O, which were then used to calculate a corrected $\Delta^{17}$O value.

<table>
<thead>
<tr>
<th>Sampling Day</th>
<th>$\delta^{17}$O Correction</th>
<th>$\delta^{18}$O Correction</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 (14-June-2022)</td>
<td>0.980015x + 0.265737</td>
<td>0.992541x + 0.885625</td>
</tr>
</tbody>
</table>
Table S3. Samples commonly run during analysis runs either for use as a standard to construct a correction equation, or as a control water to add validity to the run. Mean $\delta^{17}$O, $\delta^{18}$O, and $\Delta^{17}$O values are displayed for each water, along with the difference between this mean and the established value for this parameter that was determined over two years of sampling within the lab.

<table>
<thead>
<tr>
<th>Sample Name</th>
<th>Mean $\delta^{17}$O (‰)</th>
<th>Difference from established $\delta^{17}$O (‰)</th>
<th>Mean $\delta^{18}$O (‰)</th>
<th>Difference from established $\delta^{18}$O (‰)</th>
<th>Mean $\Delta^{17}$O (per meg)</th>
<th>Difference from established $\Delta^{17}$O (per meg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>STD 01</td>
<td>-10.487</td>
<td>0.002</td>
<td>-19.839</td>
<td>0.014</td>
<td>37.6</td>
<td>-4.1</td>
</tr>
<tr>
<td>STD 02</td>
<td>-1.120</td>
<td>-0.029</td>
<td>-2.174</td>
<td>-0.050</td>
<td>28.6</td>
<td>0.2</td>
</tr>
<tr>
<td>STD 03</td>
<td>2.594</td>
<td>-0.004</td>
<td>4.944</td>
<td>-0.014</td>
<td>-13.4</td>
<td>-4.5</td>
</tr>
<tr>
<td>STD 04</td>
<td>-4.513</td>
<td>0.030</td>
<td>-8.580</td>
<td>0.004</td>
<td>26.2</td>
<td>-3.5</td>
</tr>
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<td>STD 05</td>
<td>4.420</td>
<td>0.009</td>
<td>8.402</td>
<td>0.013</td>
<td>-7.5</td>
<td>1.9</td>
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<tr>
<td>Control 01</td>
<td>-3.335</td>
<td>-0.039</td>
<td>-6.340</td>
<td>-0.080</td>
<td>17.1</td>
<td>3.0</td>
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<tr>
<td>Control 02</td>
<td>-5.260</td>
<td>0.014</td>
<td>-9.996</td>
<td>-0.019</td>
<td>30.4</td>
<td>4.4</td>
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<tr>
<td>Control 03</td>
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<td>-0.024</td>
<td>0.357</td>
<td>-0.029</td>
<td>-3.5</td>
<td>-1.7</td>
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<tr>
<td>Control 04</td>
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<td>0.001</td>
<td>6.075</td>
<td>0.001</td>
<td>0.5</td>
<td>0.3</td>
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