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Research Article

Annual isotopic diet ($\delta^{13}C$) of *Eremotherium laurillardi* (Lund, 1842) and climate variation ($\delta^{18}O$) through the late Pleistocene in the Brazilian Intertropical Region

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Abstract

We inferred the annual isotopic diet ($\delta^{13}C$) of an individual of the giant ground sloth *Eremotherium laurillardi* found in Toca dos Ossos (Ourolândia, Bahia, Brazil) through the extension of its third inferior molar. This individual lived in the region at 40,779–39,617cal yr BP. One year of its life was recorded in a length of 67 mm in the tooth. Two years were recorded in this molariform, during which the diet and climate did not change much, and substantial precipitation occurred during the middle of the year, which is in opposition to the modern pattern. The mean carbon ($\mu\delta^{13}C = -13.9 \pm 1.8‰$) and oxygen ($\mu\delta^{18}O = 22.5 \pm 2.9‰$) isotopic values were similar to values for other individuals of the species found in the same cave but different from the values found in other localities of the Brazilian Intertropical Region, which allows us to suggest that this region had more precipitation and lower temperatures in comparison to today. The oxygen isotopic values found in dated fossils of *E. laurillardi* and from two other taxa found in the same cave (*Toxodon platensis*, and *Notiomastodon platensis*) could help in the understanding of the climatic variation that occurred in the region.

Keywords: Annual diet, Stable isotopes, Radiocarbon dating, Xenarthra, Late Quaternary

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INTRODUCTION

Eremotherium laurillardi (Lund, 1842) was a Megatheriinae giant ground sloth that lived in the late Pleistocene of a great part of America and was the only species of the genus that had a distribution from the southern United States to the south of Brazil (Cartelle and De Iuliis, 1995, 2006; Cartelle et al., 2015; Dantas et al., 2017). There are at least two other species, *Eremotherium eomigrans* De Iuliis & Cartelle, 1999 and *Eremotherium sefvei* De Iuliis & St-André, 1997, but these were geographically restricted to the United States and Bolivia, respectively (De Iuliis and St-André, 1997; De Iuliis and Cartelle, 1999).

Eremotherium laurillardi could reach 2360 kg (Dantas, 2022) and its diet is known mainly by data from Brazil through stable carbon isotopes (Oliveira et al., 2020; Asevedo et al., 2021; Lopes et al., 2021; Omena et al., 2021 and references therein), microwear analysis (Oliveira et al., 2020), and relative muzzle width (Dantas and Santos, 2022), but there are additional isotopic data from Mexico (Pérez-Crespo et al., 2015) and Belize (Larmon et al., 2019). All this information allows us to attribute a mixed-feeder diet to this species.

In general, studies of stable carbon isotopes represent the average diet of the individual's life; however, Larmon et al. (2019) showed that it is possible to examine the annual diet of this species through a serial analysis in the molariform's tissue, allowing better understanding of its diet and the environmental conditions in the area in which it lived.

Thus, using the same approach as Larmon et al. (2019), we examine the annual isotopic diet of an individual of *E. laurillardi* found in a cave in Bahia Brazil to evaluate whether the annual climate seasonality influenced its diet and habitat and the environmental conditions that prevailed through the late Pleistocene in the cave region where its fossil and other fossil taxa were found.

MATERIAL AND METHODS

Study area

The studied material was collected in Toca dos Ossos cave (6°40′24.56″S, 35°22′34.89″W), Ourolândia Municipality, Bahia State (BA; Fig. 1). This is an unmapped cave formed in (possibly) late Tertiary Caatinga limestone; it comprises a major stream passage with an adjacent floodwater maze of spongework patterns (Auler et al., 2006).

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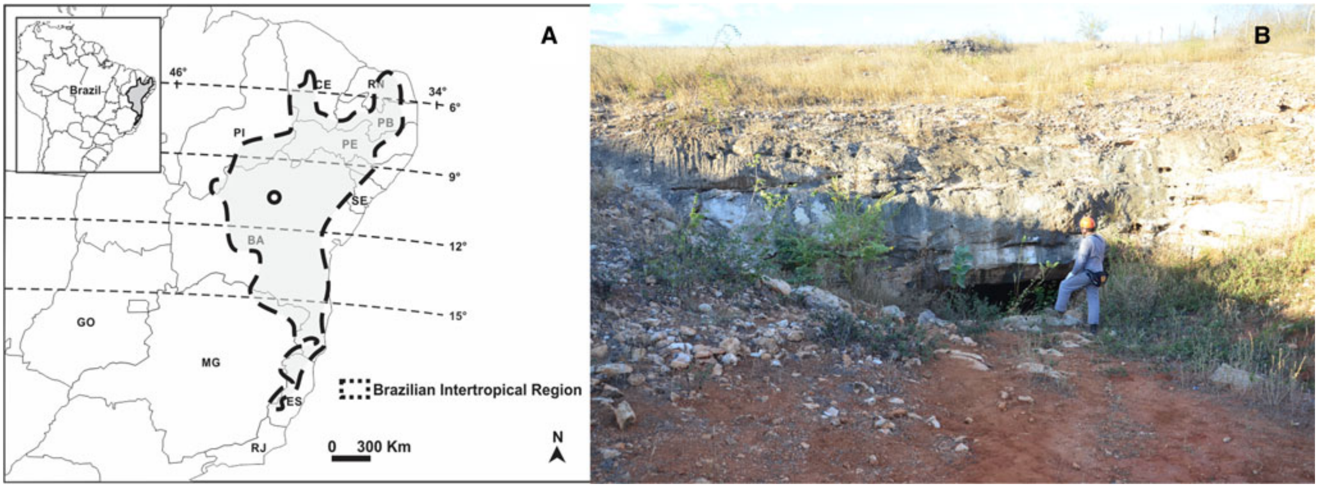

Figure 1. (A) Location map of the Brazilian Intertropical Region (BIR; sensu Dantas et al., 2022), highlighting the municipality of Ourolândia, Bahia, Brazil (white circle). BA, Bahia; CE, Ceará; ES, Espírito Santo; MG, Minas Gerais; PB, Paraíba; PE, Pernambuco; PI, Piauí; RN, Rio Grande do Norte; SE, Sergipe. (B) The entrance of Toca dos Ossos cave. (Image: Ricardo Fraga, 2015)

As Ourolândia, BA, does not have a meteorological station, we downloaded information relative to temperature and precipitation from the meteorological data bank (Banco de Dados Meteorológicos para Ensino e Pesquisa) from the Instituto Nacional de Meteorologia collected by the meteorological station no. 83186 in Jacobina, BA (~66 km from Ourolândia, BA), from 1964 to 2021. On average, this region exhibits an annual temperature of 24°C and annual precipitation of 831 mm.

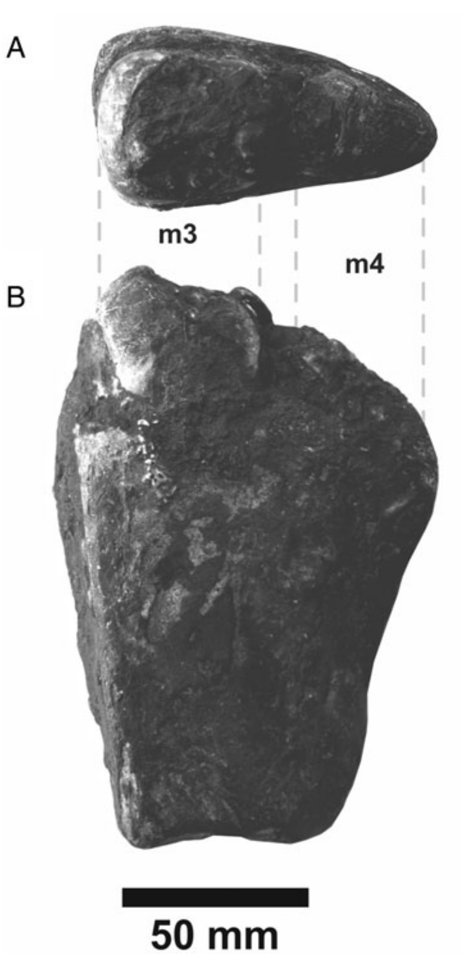

Figure 2. Dentary fragment of *Eremotherium laurillardi* (LEG 0742) in occlusal view (A) showing the third and fourth inferior molariforms (m3, m4); and in medial view (B).

Study material and serial analysis

The studied material is part of the scientific collection of the Laboratório de Ecologia e Geociências (LEG) of the Universidade Federal da Bahia, Instituto Multidisciplinar em Saúde, campus Anísio Teixeira (UFBA/IMS-CAT).

We analyzed the values of the isotopic ratios of carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) through the extension of the third inferior molariform, which was inserted in a dentary fragment of *Eremotherium laurillardi* (LEG 0742; Fig. 2). This type of tooth is hypselodontic and grows continuously throughout the life of the animal (Paula Couto, 1979). These analyses were performed on the inner orthodentin, because Larmon et al. (2019) suggest that this tissue suffers minimal diagenetic changes.

The serial analysis consists of sampling the tissue sequentially along the direction of tooth growth and inferring changes in feeding with seasonal variations and environmental and habit changes (e.g., Higgins, 2018; Larmon et al., 2019). Each sample was collected along the height of the tooth crown, starting at the occlusal area. A total of 12 samples were taken from the m3 (Table 1).

An annual cycle can be inferred in hypselodontic tooth based on maximum and minimum oxygen isotope values, the distance between two maximum or minimum peaks representing growth during 1 year. In proboscideans, an annual cycle is represented by every ~15 mm (e.g., Metcalfe and Longstaffe, 2012), in toxodonts, at 11–17 mm (Gomes et al., 2023), and in giant ground sloths (*E. laurillardi*), at ~70 mm (Larmon et al., 2019).

Isotopic analyses ($\delta^{13}C$, $\delta^{18}O$) were performed using the carbonate (CO_3^{2-}) present in the mineral fraction of hydroxyapatite. They were carried out at the Center for Applied Isotope Studies, University of Georgia, USA. Laboratory data are calibrated in delta (δ) notation, $[(R_{sample}/R_{standard} - 1)*1000]$ (Coplen, 1994), using the Vienna Pee Dee Belemnite (VPDB) scale for $\delta^{13}C$, and the Vienna Standard Mean Ocean Water (VSMOW), an

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Table 1. Distance of each serial sample to the occlusal face, carbon isotopic values ($\delta^{13}C_{VPDB}$), food resource proportions, standard niche breadth (B_A), oxygen isotopic values ($\delta^{18}O_{VSMOW}$), and radiocarbon dating for *Eremotherium laurillardi* (LEG 0742) from Ourolândia, BA.

			p_i				
Sample	Distance (mm)	$\delta^{13}C$ (‰)	C_3 (%)	C_4 (%)	B_A	$\delta^{18}O$ (‰)	Age (cal yr BP)
UGAMS 53717	2.90	−12.5	0.97	0.03	0.07	26.2	40,779–39,617
UGAMS 53718	3.30	−12.9	0.99	0.01	0.01	25.3	—
UGAMS 53719	3.80	−18.3	1.00	—	0.00	17.7	—
UGAMS 53720	4.30	−13.0	1.00	—	0.00	24.7	—
UGAMS 53722	5.70	−15.5	1.00	—	0.00	20.3	—
UGAMS 53723	6.60	−12.9	0.99	0.01	0.01	24.3	—
UGAMS 53724	7.50	−12.4	0.96	0.04	0.09	23.3	—
UGAMS 53725	8.30	−14.8	1.00	—	0.00	21.4	—
UGAMS 53726	9.50	−12.8	0.99	0.01	0.03	23.4	—
UGAMS 53727	10.50	−15.7	1.00	—	0.00	17.0	—
UGAMS 53728	11.30	−13.0	1.00	—	0.00	23.5	—
UGAMS 53730	13.50	−12.8	0.99	0.01	0.03	22.6	—

international isotopic standard distributed by the International Atomic Energy Agency, for $\delta^{18}O$ (Coplen, 1994; Higgins, 2018).

Radiocarbon dating (^{14}C AMS)

For radiocarbon dating, the quoted uncalibrated dates are given in radiocarbon years before 1950 (yr BP), using the ^{14}C half-life of 5568 years. The error is quoted as 1 standard deviation and reflects both statistical and experimental errors. The date has been corrected for isotope fractionation. The reliability of the applied technique for purification of hydroxyapatite was previously demonstrated (Cherkinsky, 2009); however, the radiocarbon dating in bioapatite provides younger ages than those made using collagen (Zazzo and Saliège, 2011; Zazzo, 2014).

Thus, we used here the correction of radiocarbon dating of bioapatite to a collagen pattern (Eq. 1) proposed by Dantas and Cherkinsky (2023), and later calibrated the radiocarbon dates as calendar ages before the present, using the CALIB 8.1 program (Reimer et al., 2020) and the same standard error found in the $^{14}C_{bioapatite}$ and the SHCal20 curve (Hogg et al., 2020); the 2σ measured ages are reported in Table 1. This regression presents a high correlation ($R^2 = 0.98$), a low percent predicted error (%PE = 0.01), and a moderate standard error of the estimate (%SEE = 25.00).

$$\log_{10}{}^{14}C_{collagen} = 1.09^{*}\log_{10}{}^{14}C_{bioapatite} - 0.31 \qquad \text{(Eq. 1)}$$

Enrichment and consumption of food resources ($\delta^{13}C$)

The interpretation of carbon isotopic values for mammals is generally based on the known average for C_3 plants ($\mu\delta^{13}C = -27 \pm 3‰$), C_4 plants ($\mu\delta^{13}C = -13 \pm 2‰$), and CAM plants (intermediate values between the $\delta^{13}C$ of C_3 and C_4 plants) (e.g., MacFadden, 2005).

Based on the regression presented by Tejada-Lara et al. (2018) and using 2014 kg as the mean weight of adult individuals of *E. laurillardi* (Dantas, 2022), we estimated the isotopic enrichment ($\varepsilon^{*}_{diet\text{-}bioapatite}$) of this taxon to be 14‰. Adding the enrichment value of 14‰, $\delta^{13}C$ values more negative than −13‰ indicate that this taxon lived in a habitat dominated by C_3 plants; in contrast, those higher than +1‰ indicate a habitat dominated by C_4 plants.

Such values will establish the end-member values to interpret the isotope abundances recorded in the material. The proportion of the food ingested can be established with the carbon isotopic ratios using Eqs. 2 and 3 of the mathematical model proposed by Phillips (2012). Thus, f represents the proportion of the two types of food (1, C_3 plants; 2, C_4 plants); $\delta^{13}C_{mix}$ represents the carbon isotopic abundance found in each dentin sample; and, the $\delta^{13}C$ values used for the interpretation were $\delta^{13}C_1 = -13‰$ and $\delta^{13}C_2 = 1‰$.

$$\delta^{13}C_{mix} = -13.0f_1 + \delta^{13}C_2 f_2 \qquad \text{(Eq. 2)}$$

$$1 = f_1 + f_2 \qquad \text{(Eq. 3)}$$

Width of isotopic ecological niche

According to Pianka (1973), ecological niche dimensions allow us to infer explored habitats, consumed resources, and so on, and the variation in these dimensions interferes with the structure and diversity of communities. Based on the values obtained for the resources, the isotopic niche width was calculated (Eq. 4), where B = isotopic niche width and p_i = proportion of resources consumed. The ecological niche width values found can be standardized using the Levins measure (Eq. 5; Levins, 1968), where the results must vary between 0 and 1, indicating whether the animal is a specialist (0) or a generalist (1). Where: B_A = standardized niche width; n = number of resources consumed.

$$B = 1/\sum p_i^2 \qquad \text{(Eq. 4)}$$

$$B_A = B - 1/\text{n} - 1 \qquad \text{(Eq. 5)}$$

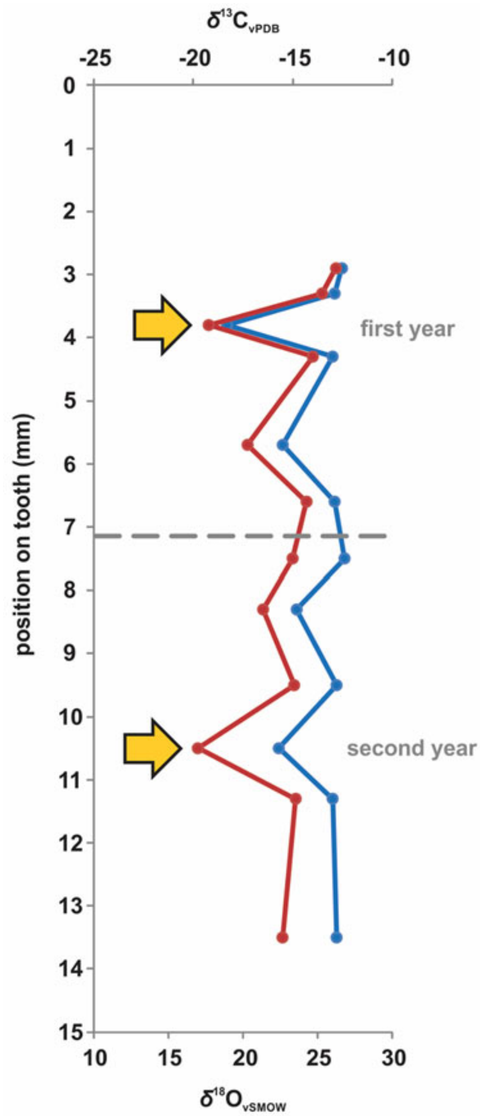

Figure 3. Carbon isotopic values ($\delta^{13}C$; blue line) and oxygen isotopic values ($\delta^{18}O$; red line) variation recorded in inferior third molariform inner orthodentin of *Eremotherium laurillardi* from Ourolândia, Bahia, Brazil (LEG 0742). The orange arrows show the most negative values of $\delta^{18}O$; an annual cycle occurs in a length of 67 mm in the tooth.

Oxygen 18 ($\delta^{18}O$) in tropical regions

Oxygen is absorbed mainly through water intake in obligatory drinkers and through food consumption in nonobligatory drinkers (Bocherens and Drucker, 2013). The $\delta^{18}O$ in these mammals could be comparable, because the oxygen isotopic values of plant tissues, in most cases, are similar to those from the local precipitation found in ponds, rivers, and lakes (Sponheimer and Lee-Thorp, 2001).

The $\delta^{18}O$ in mammal fossil tissues allows inference of variations in temperature and aridity, In temperate regions, the temperature is the main factor driving the variations of $\delta^{18}O$ values, while in tropical regions with temperatures above 20°C, the amount of precipitation is the main driving factor, with $\delta^{18}O$ values becoming lower with increasing amounts of precipitation (Dansgaard, 1964), allowing a marked seasonal variation of the $\delta^{18}O$ records in mammal fossil tissues. Thus, in tropical regions, higher $\delta^{18}O$ values indicate drier periods, while lower values indicate increased humidity due to high precipitation.

RESULTS AND DISCUSSION

Radiocarbon dating and isotopic diet ($\delta^{13}C$)

The specimen LEG 0742 lived in Ourolândia, BA, between40,779 and 39,617 cal yr BP ($^{14}C_{bioapatite} = 28,460 \pm 270$ yr; converted to $^{14}C_{collagen} = 35,085 \pm 270$ yr; Table 1). This is the second-oldest radiocarbon date found for this species in the Brazilian Intertropical Region (BIR) and is in agreement with previously available radiocarbon dates (40–10 cal kyr BP; Dantas and Cherkinsky, 2023).

The inner orthodentin band exhibited $\delta^{13}C$ values ranging from −18.3‰ to −12.4‰ ($\mu\delta^{13}C = -13.9 \pm 1.8$‰; Fig. 3, Table 1). This individual had a diet almost exclusively composed of C_3 plants ($p_i = 99\%$), being a specialist ($B_A = 0.02$). The diet of this giant ground sloth does not show variations over the analyzed cycles, maintaining the high consumption of C_3 plants, but presenting an exclusive consumption of C_3 plants in wet months. This is the first attempt to access the seasonal isotopic diet pattern through serial isotopic analyses of *E. laurillardi* in the BIR.

The mean $\delta^{13}C$ values of *E. laurillardi* (LEG 0742) are similar to two published samples from Ourolândia, BA ($\mu\delta^{13}C = -12.7 \pm 0.1$‰; ANOVA, $F_{obs} = 0.79$, $p = 0.39$; Pansani et al., 2019; Table 2), one of these being dated to 17,352–17,072 cal yr BP ($^{14}C_{bioapatite} = 12,400 \pm 30$ yr; converted to $^{14}C_{collagen} = 14,185 \pm 30$ yr). However, the carbon isotopic values of this sample are more negative than in other localities of the BIR ($\mu\delta^{13}C = -5.4 \pm 2.8$‰; ANOVA, $F_{obs} = 92.53$, $p < 0.05$; Omena et al., 2021 and references therein).

Oxygen isotopes ($\delta^{18}O$) and tooth growth

The $\delta^{18}O$ recorded in the inner orthodentin of *E. laurillardi* (LEG 0742) varied between 17.0‰ and 26.2‰ ($\mu\delta^{18}O = 22.5 \pm 2.9$‰;

Table 2. Carbon isotopic values ($\delta^{13}C_{VPDB}$), food resource proportions, standard niche breadth (B_A), oxygen isotopic values ($\delta^{18}O_{VSMOW}$), and radiocarbon dating for mammal taxa from Ourolândia, BA.

			p_i			
Taxa	Sample	$\delta^{13}C$ (‰)	C_3 (%)	C_4 (%)	$\delta^{18}O$ (‰)	Age (cal yr BP)
Eremotherium laurillardi	UGAMS 53717	−12.5	0.97	0.03	26.2	40,779–39,617
	UGAMS 42447	−12.8	0.99	0.01	23.8	17,352–17,072
Toxodon platensis	UGAMS 42449	−11.8	0.91	0.09	25.1	13,950–13,810
Notiomastodon platensis	UGAMS 42448	0.0	0.07	0.93	27.3	35,209–34,628

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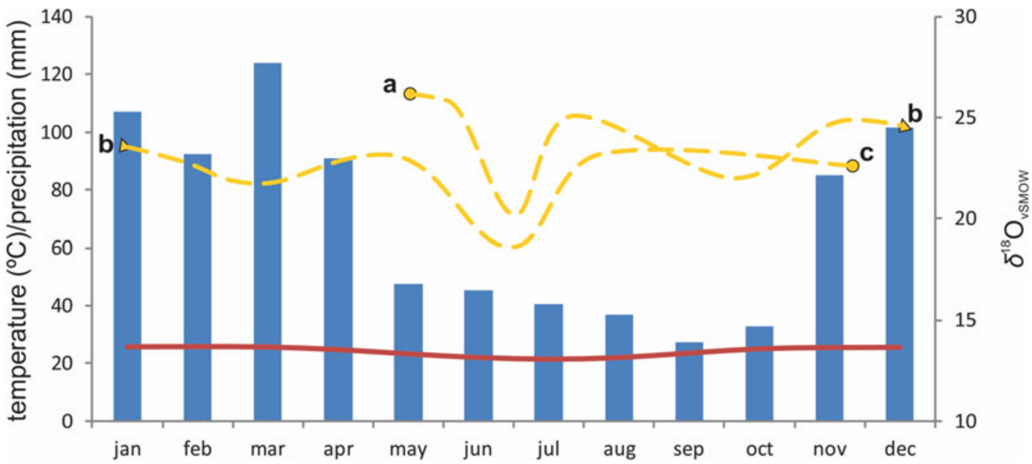

Figure 4. Average precipitation (blue bars) and temperature (red line) for the municipality of Jacobina, Bahia, Brazil (1964–2021), and the $\delta^{18}O$ values of *Eremotherium laurillardi* during the late Pleistocene of Ourolândia, BA, Brazil. In the orange dotted lines, a–b is the representation of 8 final months of the first year of LEG 0742, while b–c is the representation of 11½ months of the second year of LEG 0742.

Table 1) and is similar to the $\delta^{18}O$ recorded in other *E. laurillardi* fossils found in the same cave, one being from 15 cal ka BP ($\mu\delta^{18}O = 24.2 \pm 0.5‰$; ANOVA, $F_{obs} = 0.62$, $p = 0.44$; Pansani et al., 2019). However, in comparison with several localities of the BIR, Ourolândia looks like it had more precipitation and lower temperatures ($\mu\delta^{18}O = 30.0 \pm 1.7‰$; ANOVA, $F_{obs} = 129.70$, $p < 0.05$; Omena et al., 2021 and references therein).

A 1-year dry period cycle was recorded in the m3 (LEG 0742) in a length of 67 mm (growth rate of ∼5.6 mm/month; Fig. 3), similar to the 70 mm/yr found by Larmon et al. (2019) in an individual of *Eremotherium laurillardi* from Belize.

Climatic seasonality

Considering that the lower $\delta^{18}O$ values recorded in the tooth represent the wetter period in half of 1 year (June/July), plus the growth rate per month, we suggest that this sample could represent nearly 20 months between two different years (Fig. 4). The first year shows environmental conditions through 8 months (tentatively attributed to May–December; Fig. 4), while the second year represents 11½ months (January-November; Fig. 4).

The $\delta^{18}O$ values of the second half of the first and second years allow us to suggest a drier condition in comparison with the first half of each of these years, similar to the present pattern in Ourolândia, BA (Fig. 4). The precipitation maximum in Ourolândia, BA, presently occurs between November and April. During the late Pleistocene, it looks like this occurred in the middle of the year (May–August; Fig. 4). Another feature observed is that the second year was wetter than the first one recorded in this tooth (Fig. 4).

The carbon and oxygen isotopic values present a strong correlation ($R^2 = 0.77$, $p < 0.05$), suggesting that the oxygen was acquired mostly by the consumption of C_3 plant resources and that the wet climate in the region influenced *E. laurillardi*'s diet of C_3 plants.

Correlation between $\delta^{18}O$ from mammals to $\delta^{18}O$ from stalagmites

In Ourolândia, BA, there are radiocarbon dates associated with carbon and oxygen isotopic values for *E. laurillardi* (two samples, UGAMS 42447 and the mean values of UGAMS 53717; Table 2), plus *Notiomastodon platensis* and *Toxodon platensis* (one sample each, UGAMS 42448 and 42449, respectively; Table 2), revealing the occurrence of these taxa in Ourolândia, BA, between ∼14 cal ka BP and ∼40 cal ka BP, at least.

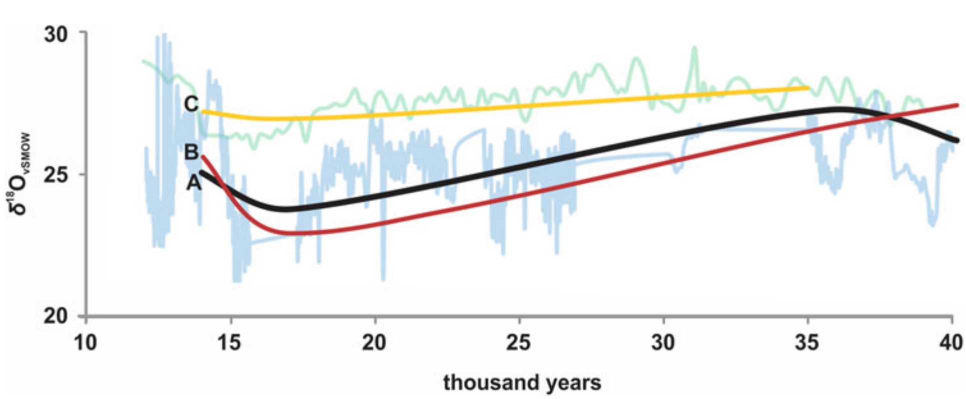

Figure 5. Comparison of the oxygen isotopic values through 40 ka in the late Pleistocene recorded in mammalian tissues (dark line; A) and in stalagmites from Lapa sem Fim cave, Luizlândia, Minas Gerais, Brazil (red line; B) and Botuvera cave, Botuvera, Santa Catarina, Brazil (orange line; C). Light blue represents the complete $\delta^{18}O_{stalagmites}$ distribution observed in Botuvera cave; light green represents the complete $\delta^{18}O_{stalagmites}$ distribution observed in Lapa sem Fim cave.

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Table 3. Dated mean oxygen isotopic values ($\delta^{18}O_{VSMOW}$) recorded in mammalian taxa fossils from Ourolândia, BA, and in stalagmites from two Brazilian caves.

	$\delta^{18}O_{VSMOW}$ (‰)		
Mammals (taxa)	Botuvera cave (n)	Lapa sem Fim (n)	Age (cal yr BP)
25.1 (*Toxodon platensis*)	27.2 ± 1.1 (2)	25.7 ± 0.0 (2)	13.9
23.8 (*Eremotherium laurillardi*)	27.0 (1)	22.9 (1)	17.2
27.3 (*Notiomastodon platensis*)	28.1 ± 0.1 (2)	26.6 (1)	34.9
26.2 (*Eremotherium laurillardi*)	—	27.5 ± 0.2 (2)	40.2

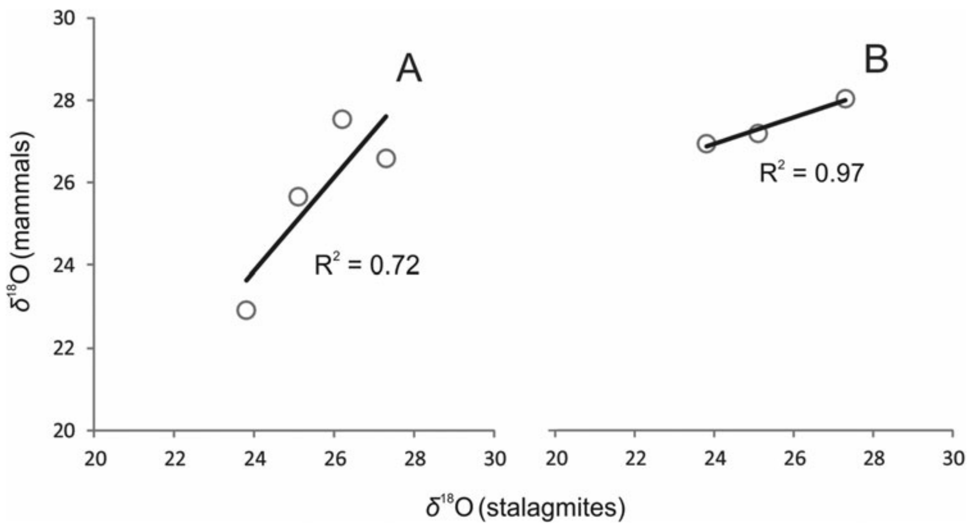

Figure 6. Correlation between oxygen isotopic values recorded in mammals ($\delta^{18}O_{mammals}$) and the oxygen isotopic values recorded in stalagmites ($\delta^{18}O_{stalagmites}$) in Lapa sem Fim cave (Luizlândia, Minas Gerais, Brazil; A) and Botuvera cave (Botuvera, Santa Catarina, Brazil; B).

The *E. laurillardi* and *T. platensis* individuals demonstrated a major consumption of C_3 plants ($p_i = 91–99\%$; Table 2) and acquired their main oxygen isotopic signature from the water present in C_3 plant tissues they fed on, while the *N. platensis* individual demonstrated a major consumption of C_4 plants ($p_i = 93\%$; Table 2) and acquired its oxygen isotopic signature mainly from the water available in the region, that is, ponds, lakes, and rivers.

The oxygen isotopic signatures of these mammals ($\delta^{18}O_{mammals}$), although limited and acquired from different sources, could be similar because the isotopic values found in plant tissues, in most cases, are similar to those of the local precipitation (Sponheimer and Lee-Thorp, 2001 and references therein; Marshall et al., 2007); thus, these values could represent the variation of the oxygen isotopic values found in meteoric water through time in Ourolândia, BA (Fig. 5A).

In fact, when we compare the distribution of $\delta^{18}O_{mammals}$ with the most complete oxygen isotopic variation recorded in stalagmites ($\delta^{18}O_{stalagmites}$) from two Brazilian caves—Lapa sem Fim, Minas Gerais State (Strikis et al., 2018), and Botuvera, Santa Catarina State (Cruz et al., 2005; Fig. 5B and C, Table 3)—during the same period, a clear similarity is noted (Lapa sem Fim cave, $R^2 = 0.72$, $p = 0.14$; Botuvera cave, $R^2 = 0.97$, $p = 0.10$; Fig. 6), although the number of samples do not allow the comparison to be statistically significant.

The $\delta^{18}O_{mammals}$ from Ourolândia, BA, has good correlation with the isotopic data from Lapa sem Fim cave (Luizlândia, MG) and Botuvera cave (Botuvera, SC), even though these localities were influenced by two different climatic conditions, the first by the Intertropical Convergence Zone (Strikis et al., 2018) and the second by the South American Summer Monsoon and South Atlantic Convergence Zone (Cruz et al., 2005).

CONCLUSIONS

Eremotherium laurillardi was the largest giant ground sloth in the late Pleistocene of the Brazilian Intertropical Region. Its diet has been investigated over the last decade, allowing us to know better its paleoecology, which the present paper amplifies through the investigation of the isotopic diet of one individual from ∼40 cal ka BP, recorded in an inferior third molariform found in Toca dos Ossos cave (Ourolândia, BA).

The m3 was examined through 13.5 mm of crown height, and 1 year of its life was recorded in a length of 67 mm, a similar value found for an *Eremotherium* in Belize (70 mm). Almost 2 years were recorded in this sample, and its isotopic diet does not vary much (−18.3‰ to −12.4‰; $\mu\delta^{13}C = -13.9 \pm 1.8‰$), being rich in C_3 plants. The oxygen isotopic values of this individual show lower values (17.0‰ to 26.2‰; $\mu\delta^{18}O = 22.5 \pm 2.9‰$), but are comparable with those of other taxa found in the same cave, which allows us to suggest that this region had more precipitation and lower temperatures than other localities in the BIR. During the late Pleistocene, the substantial precipitation occurred in the middle of the year, in contrast to the current pattern.

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The oxygen isotopic values found in dated fossils of *E. laurillardi*, *T. platensis*, and *N. platensis* had good correlation with the oxygen isotopic values found in stalagmites from the Lapa sem Fim cave, thus adding to our understanding of the climatic variation that occurred in the region.

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