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# Late Quaternary population expansion in gray brocket deer [*Subulo gouazoubira* (G. Fisher, 1814), Cervidae, Mammalia] in Brazil

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ABSTRACT: There is little information about the changes in the abundance of mammalian species in South America during the late Quaternary, which is a key parameter to understanding past ecological and evolutionary dynamics. Here, we describe a conspicuous increase in the abundance of the gray brocket deer (*Subulo gouazoubira* G. Fisher, 1814; Mammalia) during the late Quaternary in Brazil based on paleontological evidence. We studied the material retrieved from pitfall deposits in Cuvieri Cave (Brazil) representing three time intervals (Late Pleistocene, Pleistocene/Holocene transition, and Holocene). The deposits in this cave were previously characterized in terms of facies composition, chronology, and overall taxa and taphonomy. We combined previous data with taxonomic identification at the species level for deer (morphological and ancient DNA analyses), quantification of the number of individuals for large mammals (>10 kg), taphonomic analyses, and stratigraphic distribution of specimens. Our results show that while in the Late Pleistocene gray brocket deer corresponded to up to 18% of 38 individuals, in the Holocene they represented at least 82% of 78 individuals. We interpret this change in frequency as a considerable increase in abundance in the surroundings of the cave, after excluding major taphonomical biases. The causes for this phenomenon are uncertain but could have involved a surplus of food availability and predation release due to the late Quaternary extinction event.
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KEYWORDS: abundance change; artiodactyla; cave; Lagoa Santa; paleontology; South America

## Introduction

There is little molecular or paleontological evidence of how the abundance of mammalian species in South America varied during the last 30 000 years (Marín et al., 2007; Barnosky et al., 2016; Moscardi et al., 2020; Pires et al., 2020), despite this time interval being well-characterized by the extinction of several species from different trophic levels, the arrival of humans to the continent, and the transition from a glacial to an interglacial period (Barnosky and Lindsey, 2010; Hubbe et al., 2013; Villavicencio et al., 2016; Galetti et al., 2017), which are major drivers impacting species abundance (Laundré et al., 2014). The limited evidence available on past mammalian species abundance is skewed toward the southern and colder portion of the continent and comprises only a few taxa (Marín et al., 2007; Moscardi et al., 2020; Pires et al., 2020). This knowledge gap is unfortunate, given that species abundance is a basic parameter to understanding ecological and evolutionary dynamics across populations, species, and communities

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†Unfortunately, Luís B. Piló passed away in May, 2022. This work could not have been done without his generous contributions. This is our tribute to our dear friend.

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(Futuyma and Kirkpatrick, 2017; Begon and Townsend, 2020). At the population level, for instance, abundance is a key aspect of a species' ability to avoid extirpation, due to the role it plays in vulnerability to demographic and environmental stochasticity and accumulation of detrimental genetic variation (Caughley, 1994; Rogers and Slatkin, 2017). At the community level, abundance may also control the type and intensity of interspecific ecological interactions (Morris, 2003; Holdridge et al., 2016). Therefore, it is important to understand the changes in species abundance over time, in particular for understudied continents such as South America. Here, we aim to contribute to this knowledge gap by describing population size changes in the gray brocket deer [*Subulo gouazoubira* (G. Fisher, 1814); Mammalia; (Bernegossi et al., 2022)] in the Brazilian Cerrado domain (i.e., the Brazilian savanna; Fig. 1(A)).

The gray brocket deer weighs between 11 and 25 kg as an adult (Black-Décima et al., 2010; Gallina-Tessaro et al., 2019; Silva-Caballero and Ortega, 2022) and is a species occurring primarily in tropical, subtropical, and semiarid regions south and east of the Amazon forest (Fig. 1(A)). It inhabits moderately humid to dry regions in areas with some cover, avoiding dense forests and occasionally feeding on open habitats, if they are close to covered areas (Black-Décima and Vogliotti, 2016). Gray brocket deer eat a variety of vegetal parts (leaves, twigs, flowers, roots, bark, buds, seeds, and fruits) from several plant species (Black-Décima et al., 2010; Black-Décima and Vogliotti, 2016), complementing their diet with fungi, feces, invertebrates, bones, and soil (Richard and Juliá, 2001). The species is solitary but can occasionally be found in pairs or, rarely, in groups of up to four individuals (Black-Décima, 2000; Black-Décima et al., 2010). The gray brocket deer has an evident role in ecological interactions, as a herbivore, seed predator, and disperser, as well as a prey of small to large-sized carnivores (Juliá and Richard, 2000; Gallina-Tessaro et al., 2019). The species is relatively abundant across most of its geographic distribution (Black-Décima et al., 2010; Black-Décima and Vogliotti, 2016), including the Cerrado domain (Fig. 1(A); Leeuwenberg et al., 1999; Marinho-Filho et al., 2002).

The Cerrado is one of the largest domains in South America and occurs predominantly in a tropical, wet–dry climate (Klink and Machado, 2005). Although the Cerrado is mainly composed of savannas, the vegetation can vary from grasslands to forested areas (Ribeiro and Walter, 2008). It is home to around 220 mammalian species from 34 families (Carmignotto et al., 2012). Of those, 15 species, including the gray brocket deer, are large (mean adult weight >10 kg; six herbivores, three omnivores, three carnivores, two insectivores, and one piscivore). In addition to gray brocket deer, only capybara (*Hydrochoerus hydrochaeris*, Linnaeus, 1766) is considered abundant (Marinho-Filho et al., 2002).

Although the paucity of reliable chronological information precludes a better understanding of past communities at a local level (Auler et al., 2006; Barnosky and Lindsey, 2010; Hubbe et al., 2013), the number of extinct species, ranging from ground sloths (e.g., *Catonyx cuvieri*, *Valgipes bucklandi*) to the saber-toothed cat (*Smilodon populator*), recovered from Quaternary deposits attests to greater species-level richness in the past (e.g., Winge, 1888; Cartelle, 1999, 2020; Bergqvist and Almeida, 2013). However, this knowledge is not accompanied by a corresponding understanding of past population size.

Here, we studied thousands of faunal specimens (i.e., complete or fragmented bones and teeth; Lyman, 1994), from the Cuvieri Cave deposits (Fig. 1(A),(B),(C)) that spanned three consecutive time intervals: Late Pleistocene, Pleistocene/Holocene transition, and Holocene. This study aims to contribute to our understanding of species abundance in the Quaternary by quantifying the representation of gray brocket deer and other different large mammals in the fossil record over the periods represented by the deposits in Cuvieri Cave.

## Materials and methods

### Materials

We analyzed specimens excavated in Cuvieri Cave (Fig. 1(A)). The cave consists of a subhorizontal passage that ends in three vertical pits, of which two were excavated (Locus 2, and Locus 3; Fig. 1(B)). A detailed description of the cave, sedimentary facies, chronology, and excavation procedures can be found in Data S1, including a new Bayesian model for the ages at Locus 2 based on 17 $^{14}$C dates on collagen, as well as in Haddad-Martim et al. (2017) and Hubbe et al. (2011).

All registered specimens (i.e., those collected in situ) and sieved specimens (i.e., those found within sediments during sieving) from the two sedimentary facies of Locus 2 and from four facies of Locus 3 [Mottled diamicton (MD), Reddish brown diamicton (RBD), Brown diamicton (BD), and Mottled silt loam (MSL)] were studied (Fig. 1(C)). The specimens recovered from the facies Brown breccia (BB) of Locus 3 were considered if they were found in uncemented sediments.

A total of 22 730 registered specimens were studied (Fig. 1(C)): (i) 6439 specimens from the Late Pleistocene (>30 000 year; facies MD, RBD, BB, and MSL of Locus 3); (ii) 329 specimens from the Pleistocene/Holocene transition (14 790–12 775 cal BP to 10 755–8445 cal BP; facies RBD of Locus 2); and (iii) 15 962 specimens from the Holocene (<10 755–8445 cal BP; 15 857 from facies Fossiliferous brown diamicton (FBD) of Locus 2 and 105 from facies BD of Locus 3).

The specimens recovered from the sieved material were not counted individually, because the vast majority consists of small fragments that cannot be identified anatomically or taxonomically and because of their large numbers, totaling thousands per facies. In this material, we approximated their contribution to the abundance of species in the fossil record by estimating their volume.

### Taxonomic identification

#### Morphological identification

All specimens (22 730 registered and thousands sieved) were inspected and those belonging to large taxa (mean adult weight >10 kg) were identified taxonomically to at least the family level based on a comparative study of extant mammal collections (collections visited: Coleção Renato Kipnis, Laboratório de Estudos Evolutivos Humanos, Universidade de São Paulo, Brazil; Museu de Zoologia, Universidade de São Paulo, Brazil; Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Brazil; and Núcleo de Pesquisa e Conservação de Cervídeos, Universidade Estadual Paulista Júlio de Mesquita Filho, Brazil). Cervidae species were identified using astragalus, calcaneus, and naviculo-cuboid bones due to their abundance and intact condition. The nomenclature adopted here follows established references for both extant and extinct species (Wilson and Reeder, 2005; Presslee et al., 2019; Cartelle, 2020; Bernegossi et al., 2022), and some material had been previously identified in other studies (Mayer, 2011; Hubbe, 2008; Hubbe et al., 2011; Mayer et al., 2016; Chahud and Okumura, 2022).

#### Molecular identification

*Mazama* and *Subulo* have very similar astragalus, calcaneus, and naviculo-cuboid bones. Hence, to support the morphological

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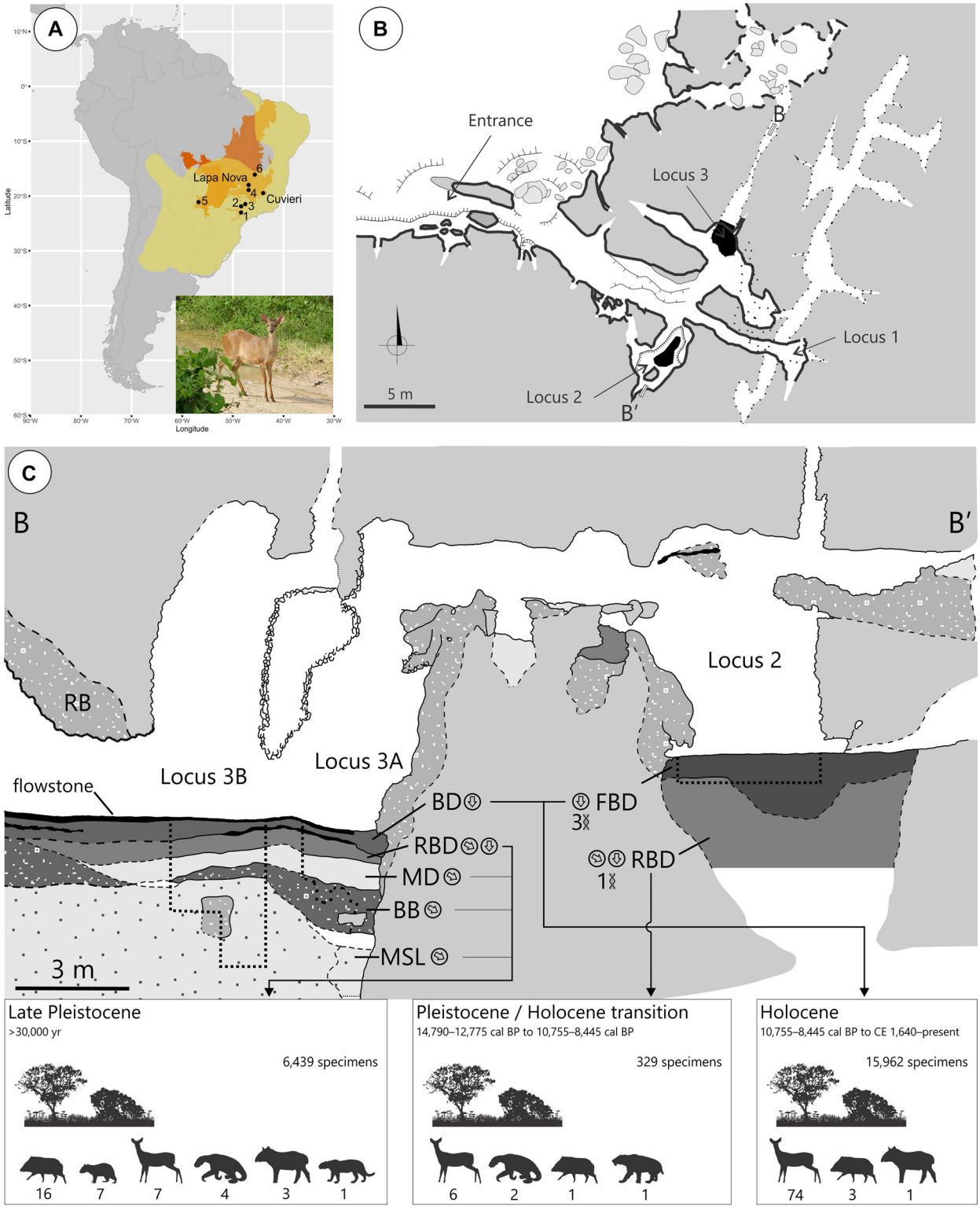



**Figure 1.** (A) The distribution range of the gray brocket deer (*Subulo gouazoubira*, yellow) and the Cerrado domain (orange). Black dots represent the localities discussed in Data S1. The inset depicts an adult male gray brocket deer. (B) Plan of Cuvieri Cave with the black areas representing the localities from which fossils for this study were retrieved. (C) Profile of the B–B′ section from Fig. 1(B) detailing the facies observed. Arrow symbols next to the facies acronyms represent the source of the terrigenous sediments (down arrow: epikarst sediment; diagonal arrow: doline sediment). The number near the DNA symbol next to the facies acronyms is the sample of DNA for the molecular identification of deer species. Dotted lines represent the excavation sites. Solid lines within excavation sites indicate observed contacts. Dashed lines outside excavation sites indicate inferred contacts. At the bottom, summary information relating facies and the time intervals, the number of registered specimens analyzed, likely vegetation cover, and the minimum number of individuals per taxa. BD: Brown diamicton; FBD: Fossiliferous brown diamicton; RBD: Reddish brown diamicton; MD: Mottled diamicton; BB: Brown breccia; MSL: Mottled silt loam; RB: Red breccia. See Haddad-Martim et al. (2017), Hubbe et al. (2011), and Data S1 for details regarding the sedimentary facies, chronology, and the geology of the cave. In A: species distribution based on Black-Décima and Vogliotti (2016) and Cerrado distribution based on IBGE (2015). Photo by: José Maurício Barbanti Duarte. In (B) and (C) Figure adapted from Haddad-Martim et al. (2017). Maps courtesy of Laboratório de Estudos Evolutivos Humanos and Grupo Bambuí de Pesquisas Espeleológicas. [Color figure can be viewed at wileyonlinelibrary.com]

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taxonomic identification of the gray brocket deer, which is the focal taxon of our study, we used ancient DNA analyses.

DNA was extracted from four petrous bones: one from the Pleistocene/Holocene transition, and three from the Holocene (Fig. 1(C)). The sample size is a compromise between available specimens ($n = 27$), and the fact is that the procedure is destructive. Petrous bone was chosen, as it yields a higher percentage of endogenous DNA due to its higher density, which increases DNA preservation (Gamba et al., 2014). We drilled 50–70 mg of bone powder from each sample.

Details of the lab procedures for DNA extraction, library builds, sequencing, and mapping are provided in Data S1.

### *Number of taxa and individuals and bone modifications*

For each of the time intervals, we computed the number of taxa and the minimum number of individuals (MNI) per taxon. MNI was calculated from the most abundant skeletal element part identified taxonomically, taking into consideration the symmetry of the mammalian body (e.g., left proximal humerus) and also considering conspicuous differences in ontogenetic stages. The use of the MNI metric in this context allows for the inference of the number of individuals contained in natural trap assemblages that represent the Cuvieri fossil record (see Badgley, 1986 for a similar application).

For each time interval, all specimens were analyzed for the presence of the following bone modifications: (i) bone abrasion; (ii) carnivore tooth marks; (iii) intense fragmentation of long bones (specimens composed of <50% the complete skeletal element were considered as intensely fragmented); and (iv) articulated skeletons. Within each time interval, the frequency of bone modifications was classified into four ordinal categories, representing their relative frequency: (i) very rare (≤1%); (ii) rare (>1%–≤10%); (iii) moderate (>10%–≤50%); and (iv) common (>50%). The breakdown of bone modifications in these common levels of occurrence permits contextualizing the frequency of bone modification within the most likely processes that generated the assemblages studied.

For Locus 3, bone modification classification was based on tabulated data available elsewhere (Hubbe, 2008; Mayer, 2011). For Locus 2, classification was based on previously unreported visual inspection of specimens.

### *Selected species stratigraphic distribution within each Locus*

To aid our interpretations, we constructed three-dimensional (3D) distribution plots for registered specimens from selected taxa based on the three-dimensional coordinates retrieved for each specimen during the excavation. For Locus 2, we considered astragalus, calcaneus, and naviculo-cuboid specimens from Cervidae. For Locus 3, we considered all specimens from Cervidae, Tayassuidae, and *Cuniculus rugiceps* Lund, 1837. Plots were produced using the package "plotly" (Sievert, 2020) in R (R Core Team, 2023).

## Results

### *Taxonomic identification*

#### *Morphological identification*

We identified nine large species (five extant and four extinct) belonging to six families (Table 1 and Fig. 1(C)). The morphological identification of the Cervidae specimens at the species level was not simple. We are confident that the specimens belong to either red brocket deer or gray brocket deer. However, despite these species belonging to different genera, they have very similar skeletons, including the astragalus, calcaneus, and naviculo-cuboid morphologies. Based on comparisons with the reference material, we tentatively assigned most of the specimens to gray brocket deer (74 from 87 deer individuals; Table 1). Supporting this interpretation are: (i) the molecular identification results (see the subsection "Molecular identification" below); (ii) the fact that during the formation of the fossiliferous deposits, the surrounding area of the cave was composed of relatively open vegetation cover (see Data S1); and (iii) analysis of 29 δ13C samples from deer teeth (four from Locus 3 and 25 from Locus 2) suggests that these specimens primarily fed in relatively open habitats (Hubbe et al., 2024). This environmental reconstruction is consistent with gray brocket deer habits, in contrast to red brocket deer, which is found in closed canopy environments (Black-Décima and Vogliotti, 2016).

#### *Molecular identification*

Our results indicate that the four DNA samples analyzed were identified as gray brocket deer (see Data S1 and Tables S1 and S2). Given that a total of 80 deer individuals were available from Locus 2, the odds of sampling four specimens from gray brocket deer without this species consisting of the majority of the sample are low (5.8%). Therefore, the anatomical, ecological, isotopic, and DNA evidence indicate that the most abundant Cervidae species found in Cuvieri Cave is gray brocket deer.

### *Number of taxa and individuals and bone modifications*

Not all species occur in all time intervals (Table 1 and Fig. 1(C)). Besides the fact that all extinct taxa are absent from the Holocene deposits, the saber-toothed cat occurs only in the Pleistocene/Holocene transition facies, the ground sloth *C. cuvieri* and the extinct paca *C. rugiceps* occur only in the Late Pleistocene facies, and the ground sloth *V. bucklandi* occurs both in the Pleistocene/Holocene transition and Late Pleistocene facies.

The gray brocket deer is disproportionately overrepresented in the Holocene deposits compared to the Pleistocene deposits (Table 1 and Fig. 1(C)). In the Late Pleistocene facies, gray brocket deer accounted for at least 10.52% of the total 38 individuals estimated from the MNI. In the Pleistocene/Holocene transition facies, this species comprised 60.00% of 10 individuals. In the Holocene facies, they represented 82.05% of 78 individuals. However, these values likely underestimate the species' frequency in these periods, as many bones were too fragmented or polished for proper identification at the species level. Given that all identifiable deer specimens were identified as gray brocket deer, it is probable that all unidentified specimens also belong to this species (see DNA analysis results above). Therefore, we estimate that the abundance of gray brocket deer in the Late Pleistocene could be as high as 18.42% (7/38). Even in this most conservative estimate for the frequency of gray brocket deer in the Late Pleistocene, there is still a marked increase in the species' frequency in the later periods.

All the Holocene deer individuals were found in Locus 2 FBD facies, with the exception of a single gray brocket deer individual recovered from Locus 3 BD facies (which is interpreted as being the equivalent of Locus 2 FBD facies;

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**Table 1.** Taxa, the minimum number of individuals (MNI), and summary information for each time interval from Cuvieri Cave deposits. In cases where more than one species is presented in a row, MNI was determined at the family level.

| Family | Species | Common name | Late Pleistocene | Pleistocene/Holocene transition | Holocene |
|---|---|---|---|---|---|
| Cervidae | *Subulo gouazoubira* | Gray brocket deer | 4 | 6 | 64 |
| Cervidae | sp indeterminate | Deer | 3 | 0 | 10 |
| Cuniculidae | *Cuniculus rugiceps** | Paca | 7[a] | 0 | 0 |
| Felidae | *Panthera onca* | Jaguar | 1 | 0 | 0 |
| Felidae | *Smilodon populator** | Saber-toothed cat | 0 | 1[b] | 0 |
| Scelidotheriidae | *Catonyx cuvieri** *and Valgipes bucklandi** | Ground sloth | 4 | 2[b] | 0 |
| Tapiridae | *Tapirus terrestris* | Tapir | 3 | 0 | 1[b] |
| Tayassuidae | *Pecari tajacu and Tayassu pecari* | Peccary | 16 | 1 | 3 |
| | Number of families | | 6 | 4 | 3 |
| | Sum of the minimum number of individuals | | 38 | 10 | 78 |
| | *S. gouazoubira* relative frequency (%) | | 10.52 | 60.00 | 82.05 |
| | Accumulation rate (individuals/century) | | —[c] | 0.18–0.49[d] | 0.66–0.94[d] |
| | Accumulation rate (individuals/m³) | | 4.9 | —[e] | 23.6 |
| | Area of fossiliferous deposits excavated (%) | | ~78 | 100 | ~75 |
| | Volume of fossiliferous sediment excavated (m³) | | ~7.8 | <0.3[a] | ~3.3[f] |
| | Number of registered specimens | | 6.439 | 329 | 15.962 |
| | Volume sieved specimens (cm³) | | ~174 | ~8 | ~116 |

*Extinct.
[a]Quantified in Mayer et al. (2016).
[b]Quantified in Hubbe et al. (2011), one individual was identified only at the family level.
[c]There is no reliable chronology to allow determining the rate for this time interval.
[d]A range is presented because the calculations are based on the minimum and maximum duration of deposit formations, as determined by the adopted chronological model (see Data S1).
[e]It is not possible to determine this value with accuracy because individuals from this time interval were found within the <0.3 m³ of the Reddish brown diamicton (RBD) facies, but also associated with fragments of RBD within Fossiliferous brown diamicton (FBD) facies.
[f]This value is considered only when the RBD in Locus 2 became a clearly distinguishable facies.

Fig. 1(C); Haddad-Martim et al., 2017). In fact, this deer was the only large-sized mammal found in BD facies.

Peccaries, the second most common mammal found, presents a different distribution: data suggests that it became less frequent over time, corresponding to 42.11%, 10.00%, and 3.85% for the Late Pleistocene, the Pleistocene/Holocene transition, and Holocene, respectively (Table 1 and Fig. 1(C)).

The MNI of large mammals, the total number of registered specimens, and the relative volume of sieved specimens (volume of sieved specimens/volume of excavated sediments) are higher for the Holocene deposits in comparison to the Late Pleistocene deposits. The MNI is around 2.5 times higher, the registered species is around two times higher, and the relative volume of sieved specimens is around 1.58 times higher (Table 1).

We lack robust information regarding the timing of Late Pleistocene deposits' formation to properly understand how the temporal duration of deposit formation impacts the observed results. However, if we extrapolate the rate of individual deposition observed in the well-contextualized Holocene deposit to account for the difference in specimen count and MNI solely based on the temporal duration of deposit formation, it would suggest that the Late Pleistocene deposits formed in less than 5.2 thousand years, which is highly unlikely (see Data S1). Additionally, little can be said with confidence about the Pleistocene/Holocene transition deposit since only a small volume of sediments was excavated.

Because there are no clear taphonomic differences between the three temporally distinct assemblages (Table 2), we conclude that there are no taphonomic processes differentially influencing the abundances of gray brocket deer in the three temporal periods.

**Table 2.** Frequency of bone modifications for each time interval from Cuvieri Cave deposits. very rare (≤1%), rare (>1%–≤10%), common (>50%).

| | Late Pleistocene | Pleistocene/Holocene transition | Holocene |
|---|---|---|---|
| Bone abrasion | Rare | Rare | Rare |
| Carnivore tooth marks | Very rare | Very rare | Very rare |
| Fragmented specimens[a] | Common | Common | Common |
| Articulated skeletons | Rare | Rare | Rare |

[a]Specimens composed of <50% of the total of the corresponding skeletal element.

### *Stratigraphic distribution*

The most abundant skeletal elements of deer in the Holocene facies from Locus 2 are relatively evenly distributed over the stratigraphy (Fig. 2, plotting was limited to right calcaneus specimens to aid visualization; see also Fig. S1 for the interactive 3D plot with all specimens). There are no discernible clusters in the Locus stratigraphy, supporting, together with the obtained chronology, that the inclusion of individuals in the Locus was relatively constant over time. In Locus 3, deer, peccaries, and extinct paca specimens occur in more than one of the Late Pleistocene facies (Fig. 3; see also Fig. S2 for the interactive 3D plot). As mentioned above, gray brocket deer were also found in the Holocene facies (BD; Figs. 3 and S2).

## Discussion

Climate and mammalian species richness changed during the late Quaternary in South America (Barnosky and Lindsey, 2010; Hubbe et al., 2013; Villavicencio et al., 2016;

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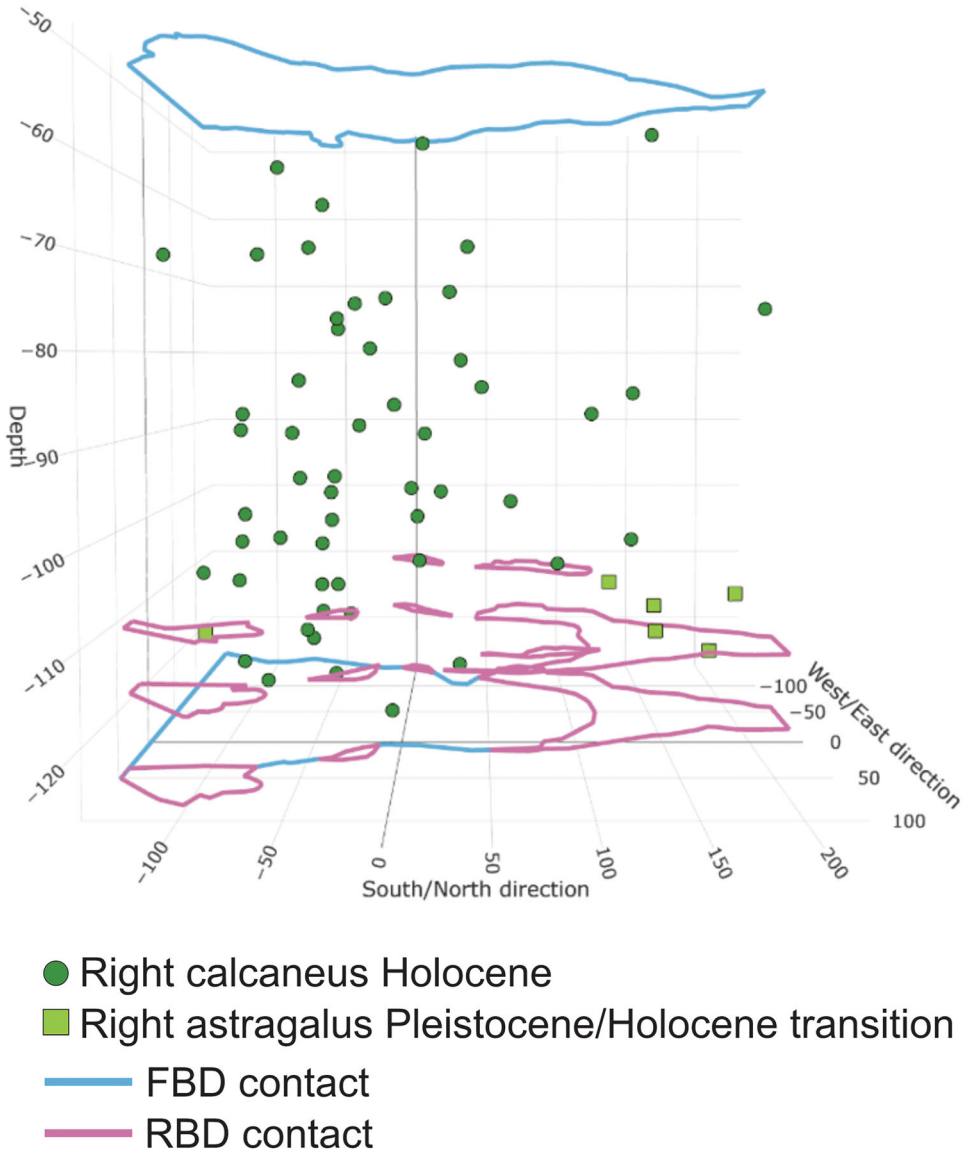



**Figure 2.** Distribution of right Holocene calcanei and right Pleistocene/Holocene transition astragali from *Subulo gouazoubira* in Locus 2. Colored lines represent the top, intermediate (for reddish brown diamicton; RBD), and bottom contours of the fossiliferous brown diamicton (FBD) and RBD facies. The depth axis is not on the same scale as the other axes. Units in all axes are in cm. [Color figure can be viewed at wileyonlinelibrary.com]

Galetti et al., 2017), which likely had important implications for the variation in living mammalian species abundance (Laundré et al., 2014). However, little is known about the changes in species abundance over this time period in South America (Marín et al., 2007; Barnosky et al., 2016; Moscardi et al., 2020; Pires et al., 2020). Our study of the fossil record in Cuvieri Cave provides new information in this regard.

Regarding the variation in species richness observed in Cuvieri Cave, the absence of extinct species in Holocene deposits (Table 1 and Fig. 1(C)) is in accordance with the timing of their extinction in the region (Hubbe et al., 2013; Raczka et al., 2017). Besides that, other changes in species richness in different time intervals (e.g., the presence of the jaguar (*Panthera onca*) in the Late Pleistocene and its absence in the other time intervals) are most likely explained by the probabilistic process responsible for the formation of fossiliferous deposits, combined with the undersampling of the Pleistocene/Holocene transition facies (<0.3 $m^3$ excavated; Table 1 and Fig. 1(C)).

In terms of species abundance, there is a marked change over time in the frequency of gray brocket deer (Table 1 and Fig. 1(C)). There is a noticeable increase in the frequency of individuals between the Late Pleistocene and the Pleistocene/Holocene transition (from up to 18% to 60%), although this may be biased by the low volume excavated from the Pleistocene/Holocene transition facies. There is a substantial increase in the frequency of this species between the Pleistocene/Holocene transition and the Holocene (from 60% to at least 82%) and a jump in the frequency if one compares the Late Pleistocene with the Holocene (from up to 18% to at least 82%), which are the better-sampled facies.

We propose that this change in frequency is better explained by a marked increase in the abundance of the species over time in the vicinity of Cuvieri Cave, rather than being generated by major taphonomical biases (Lyman, 2017). Among the many taphonomic agents that can bias species representation, the three most likely to affect the representation of gray brocket deer in Cuvieri Cave deposits would have been: (i) variation in the likelihood of a specimen being deposited and preserved inside the cave; (ii) a few events of catastrophic mortality (i.e., nonselective mortality of individuals) from gregarious species generated the fossil assemblage; and (iii) major changes in vegetation in the surrounding landscape could alter the likelihood of deer living in the vicinity of the cave. In what follows, we argue that these sources of bias are unlikely causes of the pattern found in Cuvieri Cave.

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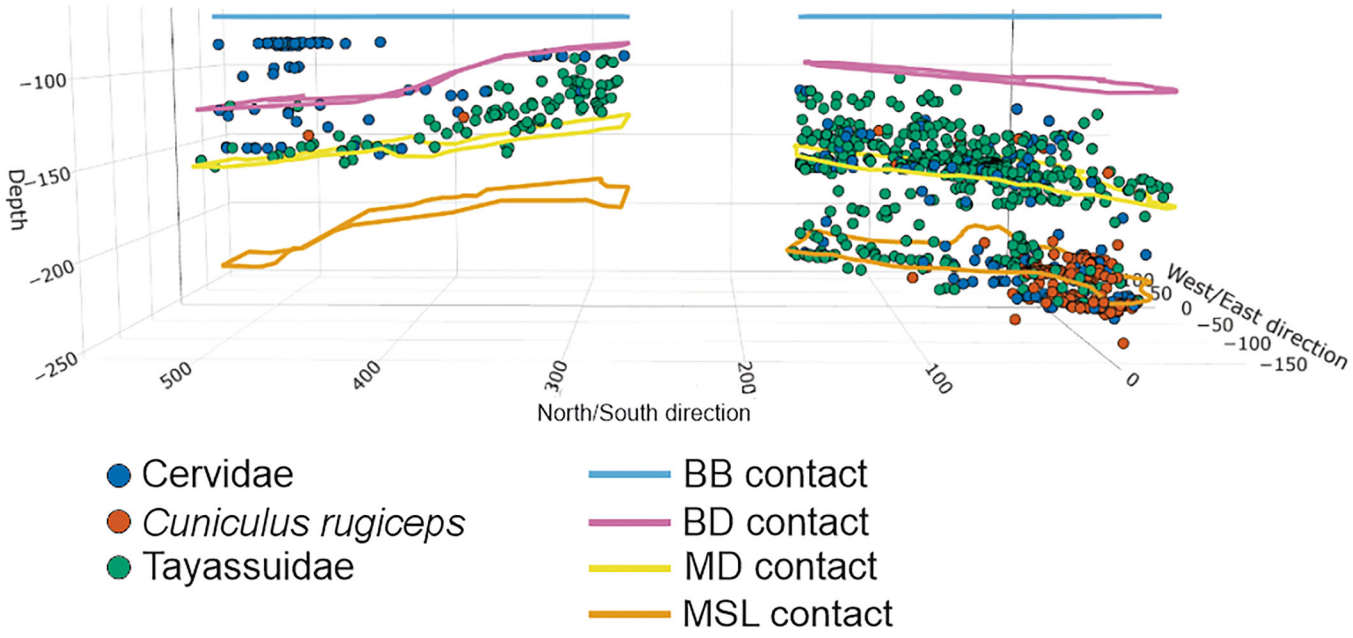



**Figure 3.** Distribution of Holocene (facies brown diamiction; BD) and Late Pleistocene (other facies) specimens from Cervidae, Late Pleistocene specimens from Tayassuidae, and *Cuniculus rugiceps* in Locus 3. Colored lines represent the top contours of the BD, reddish brown diamicton (RBD), mottled diamicton (MD), and brown breccia (BB) facies. The absence of specimens in deeper portions of the excavation area between ~300 and 500 cm in the South/North direction reflects the fact that we did not tabulate the coordinates of these specimens and does not indicate an absence of specimens. The South/North axis is not on the same scale as the other axes. Units in all axes are in cm. [Color figure can be viewed at wileyonlinelibrary.com]

### *Was there variation in the likelihood of a specimen being deposited and preserved inside the cave?*

First, the major mechanism for specimen accumulation in both Locus 2 and Locus 3 is the entrapment of individuals in pitfalls (Hubbe et al., 2011; Haddad-Martim et al., 2017). This is supported by: (i) the morphology of the cave; (ii) the discrepancies in the frequency of specimens, their bone modifications, and the taxonomy of specimens found in sediments at the bottom of the pitfalls and at the main conduct of the cave (Hubbe et al., 2011; Haddad-Martim et al., 2017); (iii) the origin and accumulation processes of the sediments (Hubbe et al., 2011; Haddad-Martim et al., 2017); and (iv) the rarity of abrasion and predator marks on specimens inside both loci.

As a consequence, all disarticulation and fragmentation occurred within the pitfalls, under the same processes (e.g., sedimentation, trampling, and water dripping; Hubbe et al., 2011; Haddad-Martim et al., 2017; Data S1). Moreover, paleoclimatic, sedimentologic, and isotopic data (refer to Data S1 and Discussion below) suggest that facies were deposited under roughly similar environmental conditions.

Second, the accessibility to Locus 2 and Locus 3 within the cave was similar over time, as peccaries, deer, tapirs, and large ground sloths were found in both Locus 2 and Locus 3 (Fig. 1(C); Hubbe et al., 2011; Haddad-Martim et al., 2017). Additionally, peccaries and deer were found across all time ranges (Fig. 1(C)) and in more than one facies from the Late Pleistocene (Figs. 3 and S2).

It is also worth noting that there is no observed trend of association between the volume of sediments excavated, the time span of deposits, the MNI, and the number of specimens recovered (Table 1). This argues against such taphonomical biases as an explanation for the observed pattern.

### *Could a few events of entrapment involving several individuals from gregarious species have generated the fossil assemblage?*

The difference in the frequency of taxon bones found in the accumulation deposit could potentially be explained by a few events involving several individuals from a particular taxon simultaneously getting trapped. If this had happened, the difference in observed frequencies among taxa would primarily reflect those few events of collective entrapment, rather than a difference in the abundance of taxa over time in the vicinity of the cave. However, it is unlikely that the assemblage found in Cuvieri Cave is the result of such few events.

First, the stratigraphic distribution of specimens shows that individuals are widely spread within and among facies (Figs. 2, 3, S1, and S2). Furthermore, there is evidence of minimal vertical displacement of specimens within and between the deposits. This is supported by: (i) relatively low-energy depositional processes and the mechanism of specimen incorporation into the facies (pitfall entrapment; Haddad-Martim et al., 2017; Hubbe et al., 2011) and (ii) mechanical refitting of specimens from Locus 3, as well as chronology for articulated skeletons and isolated specimens at similar depths in Locus 2 (Hubbe et al., 2011; Mayer et al., 2016).

Second, the time span for the formation of the facies supports the idea that specimen accumulation occurred over several millennia (Fig. 1(C); see Data S1).

Third, the behavior biology of gray brocket deer and tapirs also favors the interpretation of several independent entrapment events for these species, as they are usually solitary (Eisenberg and Redford, 1999; Black-Décima, 2000; Black-Décima et al., 2010). If we assume that the extinct paca was also solitary like its extant relatives (Eisenberg and Redford, 1999), the same reasoning applies. There is no evidence to date that the ground sloth species found in Cuvieri Cave exhibited gregarious behavior, although it has been suggested that other giant sloth genera may have had gregarious behavior (Lindsey et al., 2020; Tomassini et al., 2020). Peccaries, on the other hand, are typically found in groups (Eisenberg and Redford, 1999) and may get trapped collectively (personal observation). Thus, the relatively high number of individuals from this family in the Late Pleistocene (Table 1 and Fig. 1(C)) could result from a few entrapment events. However, the stratigraphic data do not support this interpretation.

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### Were there major vegetational changes in the surrounding landscape?

Given that vegetation changes over time and that gray brocket deer avoids dense forests and open areas distant from more closed areas (Black-Décima and Vogliotti, 2016), the frequency increase of this species over time could simply reflect changes in vegetation cover in the surroundings of the cave. A closed forest or open grassland environment during the Late Pleistocene and Pleistocene/Holocene transition would inhibit the species from reaching the cave's entrance more often, leading to a low frequency of animal entrapment. However, this is an unlikely scenario since palynological and sedimentological evidence does not suggest that the facies were formed in either one of those conditions (Fig. 1(C); see subsection "The paleontological site Cuvieri Cave" in the Supplementary Material for details).

The paleodietary proxy stable isotope $\delta^{13}C$ analysis on deer teeth from the Late Pleistocene and Holocene facies from Cuvieri Cave also supports the interpretation that there was no major vegetational change in the surrounding landscape over time (Hubbe et al., 2024). Individuals from the Late Pleistocene and Holocene had no significant difference in diet, which was predominantly composed of $C_3$ plants from open canopy environments through time (Hubbe et al., 2024). Although we cannot precisely determine the stratigraphic position of three out of four Pleistocene individuals (since they belong to sieved material), the four teeth were sampled from different depths, spanning ~100 cm, and three facies. The 25 teeth from the Holocene facies were sampled over most of this facies depth range.

### Biological versus taphonomical signal

Given the unlikelihood of taphonomic biases being responsible for the changes in abundance observed, we propose that the high frequency of gray brocket deer in Cuvieri Cave deposits during the Holocene is predominantly a biological phenomenon. Given the observed increase in the rate of individuals' entrapment over time (Table 1 and Fig. 1(C)), the observed pattern is better explained as a marked change in this species' abundance in the surroundings of the cave. This interpretation is also supported by the regional fossiliferous context. An analysis of specimens excavated in the 19th century by Peter W. Lund in 75 caves from the Lagoa Santa Karst shows that gray brocket deer, while frequent in cave deposits (Fig. 4), was not the most frequent species in the region, and it was found in similar frequencies as other extant taxa. Even if we consider all four Cervidae species identified in Lund's material, to account for species misidentification, they occur in 35 caves in comparison to the most abundant family in the fossil record, Scelidotheriidae (*C. cuvieri* and *V. bucklandi*), which occurs in 42 caves. Although this regional collection derives from excavations without rigid chronological, taphonomical, and stratigraphic control, it represents a diverse sampling of Quaternary cave deposits in the region, especially since Lund focused his attention on caves with extinct species. In this context, we expect that if gray brocket deer had been as abundant during most of the Pleistocene as it was during the Holocene, this species would prevail considerably in the material collected by Lund, which is not the case.

The findings from the Lapa Nova Cave (Fig. 1(A); Hubbe and Auler, 2012) are also consistent with the abundance change suggested by the findings from Cuvieri Cave. Lapa Nova Cave, located approximately 350 km from Cuvieri Cave, is currently within the Cerrado domain as well and contains a Holocene accumulation of at least 121 Mazama/Subulo individuals, along with a few individuals from other genera that were trapped in a pitfall.

At present, we lack the data to narrow down the timing of this population expansion of gray brocket deer. The stratigraphic distribution of this species in the Holocene facies of Locus 2 does not show a clear pattern of change in the number of individuals over different depths (Figs. 2 and S1), suggesting that after 10 755–8445 cal BP this species was already abundant. However, there is not enough information prior to that to allow determining when this pattern was established. This issue stems from: (i) the fact that the excavations in Cuvieri Cave stopped before the facies in Locus 2 were fully excavated, which precluded a better sampling and understanding of older Holocene and Pleistocene/Holocene transition facies; and (ii) the absence of Pleistocene facies younger than 30 000 years in Locus 3.

We also currently have no data to discuss the geographic distribution of this population event. In principle, there is no reason to believe this event was a restricted local process since past and present ecological/environmental conditions found in the vicinity of Cuvieri Cave were most likely found elsewhere too. If the interpretation that most individuals at Lapa Nova Cave belong to Holocene gray brocket deer proves correct over time, then the geographic distribution of the gray brocket deer population increase event described here would be at least a regional phenomenon. More sites excavated in a manner that allows for the recovery of robust evidence on relative abundance over the time interval of interest, and the geographic distribution of the species will contribute to solving the temporal and spatial scale of the population increase episode described here. Genetic markers could also be used to gain insights into these aspects (Lessa et al., 2003; Marín et al., 2007).

### Potential causes of this population increase event

The reasons why gray brocket deer, in particular, experienced this population increase are unclear. While deer species tend to become abundant when the carrying capacity of the ecosystem increases (Côté et al., 2004), *Pecari tajacu* shares several characteristics with gray brocket deer that would make it a suitable candidate for population expansion, such as reproducing most of the year, reaching sexual maturity within the first year of life, living in diverse habitats, and consuming a variety of food items (Mayor et al., 2007; Black-Décima et al., 2010; Gongora et al., 2011; Guimarães et al., 2013). However, the record in Cuvieri Cave suggests that peccaries decreased in abundance over time, underscoring the complexity of ecological factors that influence abundance variation (Terborgh et al., 2001; Ruscoe et al., 2011; Lyman, 2017).

Although the causes of this deer population increase remain speculative, one possibility is that climate change affected vegetation richness and, indirectly, animal species abundance (Blois and Hadly, 2009). The similarity in diet preferences of gray brocket deer between the Pleistocene and Holocene periods (Hubbe et al., 2024) argues against significant changes in food type availability. Nevertheless, climate change can alter both the abundance and nutritional quality of various taxa (Blois and Hadly, 2009; Raczka et al., 2017), potentially benefiting the gray brocket deer's diet. In North America, cervid body shows a strong correlation with both forage quality and quantity, as well as intraspecific competition (Wolverton et al., 2007, 2009), which suggests that a similar pattern could be observed in the gray brocket deer. If that is the case, future analysis of variation in body size based on skeletal estimates could contribute to elucidating the potential causes of the change in gray brocket deer abundance. Additional, nonexclusive possibilities include: (i) the extinction of large or

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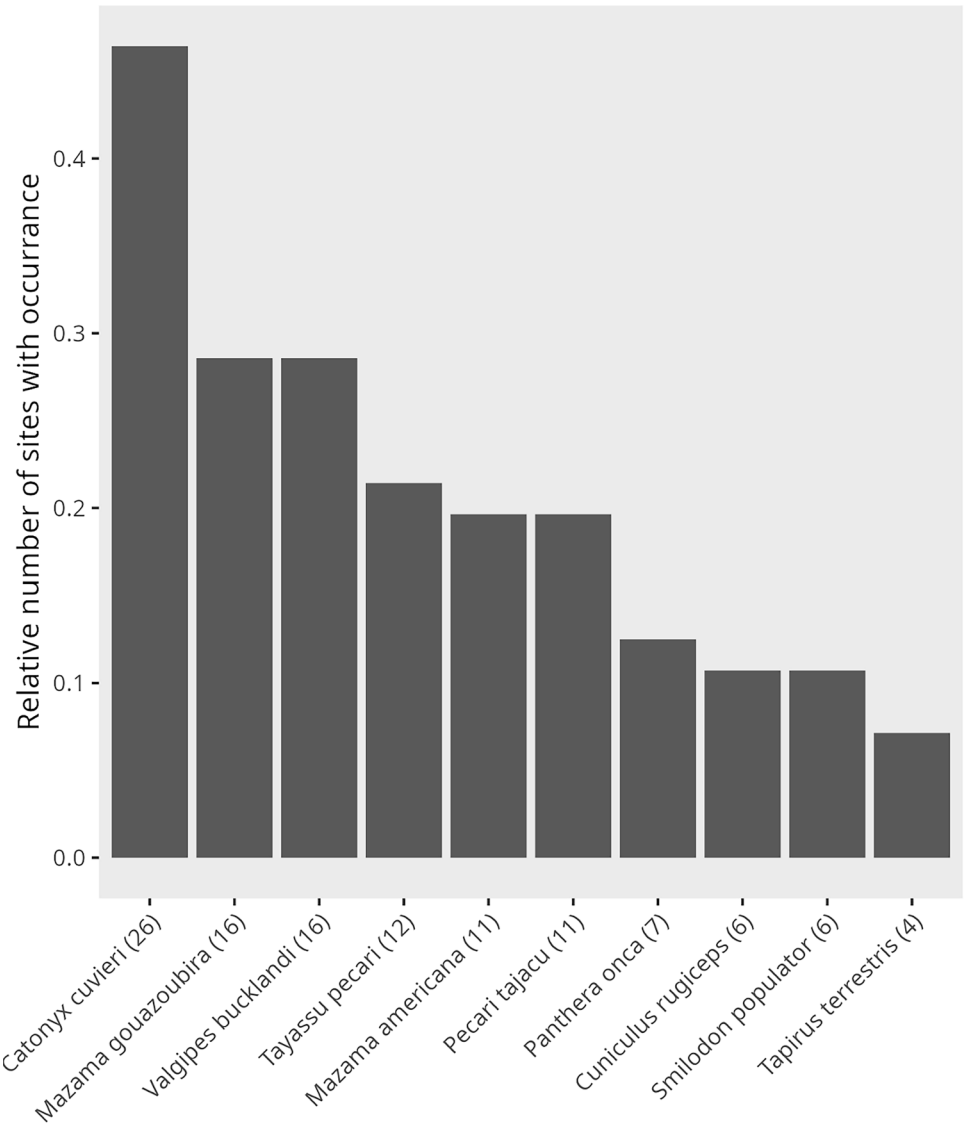



**Figure 4.** The relative number of sites excavated by Peter W. Lund in the Lagoa Santa Karst region that contain fossils from the taxa found in Cuvieri Cave. The relative number of sites was determined by dividing the number of sites excavated by Peter W. Lund where each species was found by the total number of caves (56) that contained fossils of large species. Values in parentheses represent the absolute number of sites with occurrences. Data were retrieved from Lund's Katalog (Lund, 1845).

mega herbivores, which could have generated a surplus of food that was converted into gray brocket deer biomass, as at least two species of ground sloths and one extinct horse survived in the region until the end of the Pleistocene (Hubbe et al., 2013); (ii) release from predation, as at least two hypercarnivores (the saber-toothed cat and the canid *Protocyon troglodytes* Lund, 1838) that might have preyed on gray brocket deer (Prevosti and Schubert, 2013; Bocherens et al., 2016) went extinct, with the saber-toothed cat surviving until the very end of the Pleistocene (Hubbe et al., 2013); and (iii) the possibility that climate directly influenced species abundance by affecting individual physiological constraints to ecological factors (see Berteaux et al., 2006).

## Conclusions

The pitfall deposits at Cuvieri Cave show a significant increase in gray brocket deer frequency between the Late Pleistocene and the Holocene. Due to the nature of the cave deposits and the methods employed to excavate these deposits, we are able to rule out potential taphonomic processes capable of generating a conspicuous change in a species' frequency over time. Thus, we argue that the pattern observed is better explained by an increase in gray brocket deer abundance between the Pleistocene and the Holocene in the surroundings of the cave. Our study adds new evidence about the changes in the abundance of mammalian species in South America during the late Quaternary, which has implications for the understanding of past ecological and evolutionary dynamics in tropical South America. Although we are unable to refine the timing and geographic distribution of this population increase event, nor the causes of such a phenomenon, we anticipate that our contribution can generate more interest in studying changes in species abundance over time and their overall consequences for understanding the ecological dynamics that shaped the composition of extant biomes in South America.

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### *Data Availability Statement*

The data that support the findings of this study are available from the corresponding author upon reasonable request.

## Supporting information

Additional supporting information can be found in the online version of this article.

**Figure S1.** Distribution of the astragalus, calcaneus, and naviculo-cuboid specimens from deer in Locus 2 for the Holocene (circles) and Pleistocene/Holocene transition (squares). For Cervidae sp. indeterminate there is no anatomical distinction, while for S. goazoubira each anatomical element is represented independently by side. Colored lines represent the top, intermediate (for reddish brown diamicton; RBD), and bottom contours of the fossiliferous brown diamicton (FBD) and RBD facies. The depth axis is not on the same scale as the other axes. Units in all axes are in cm. Note that you can select in the upper right corner which variables will appear in the figure.

**Figure S2.** Distribution of Holocene (facies brown diamiction; BD) and Late Pleistocene (other facies) specimens from Cervidae, and Late Pleistocene specimens from Tayassuidae, and Cuniculus rugiceps in Locus 3. Colored lines represent the top contours of the BD, reddish brown diamicton (RBD), mottled diamicton (MD), and brown breccia (BB) facies. The absence of specimens in deeper portions of the excavation area between ~300 and 500 cm in the South/North direction reflects the fact that we did not tabulate the coordinates of these specimens and does not indicate an absence of specimens. The South/North axis is not on the same scale as the other axes. Units in all axes are in cm. Note that you can select in the upper right corner which variables will appear in the figure.

**Figure S3.** Difference in the staining observed in specimens recovered from the Pleistocene/Holocene transition (facies reddish brown diamicton; RBD; upper row) and Holocene (facies fossiliferous brown diamicton; FBD; lower row).

**Figure S4.** Bayesian model for Locus 2, Cuvieri Cave. Outlier analysis output is noted as 'O:posterior probability/prior probability'.

**Table S1.** Statistics of the shotgun sequencing for the four deer samples from Locus 2, Cuvieri Cave, Brazil.

**Table S2.** Length and nucleotide sequences for each region for the four deer samples From Locus 2, Cuvieri cave, Brazil.

## References

Auler, A.S., Piló, L.B., Smart, P.L., Wang, X., Hoffmann, D., Richards, D.A. et al. (2006) U-series dating and taphonomy of Quaternary vertebrates from Brazilian caves. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 240, 508–522. Available from: https://doi.org/10.1016/j.palaeo.2006.03.002

Badgley, C. (1986) Taphonomy of mammalian fossil remains from Siwalik rocks of Pakistan. *Paleobiology*, 12, 119–142. Available from: https://doi.org/10.1017/S0094837300013610

Barnosky, A.D. & Lindsey, E.L. (2010) Timing of Quaternary megafaunal extinction in South America in relation to human arrival and climate change. *Quaternary International*, 217, 10–29. Available from: https://doi.org/10.1016/j.quaint.2009.11.017

Barnosky, A.D., Lindsey, E.L., Villavicencio, N.A., Bostelmann, E., Hadly, E.A., Wanket, J. et al. (2016) Variable impact of late-Quaternary megafaunal extinction in causing ecological state shifts in North and South America. *Proceedings of the National Academy of Sciences*, 113, 856–861. Available from: https://doi.org/10.1073/pnas.1505295112

Begon, M. & Townsend, C.R. (2020) *Ecology: from individuals to ecosystems*. New Jersey: John Wiley & Sons.

Bergqvist, L.P. & Almeida, E.B. (2013) Diversidade de mamíferos fósseis brasileiros. *Revista Geociências—UNG-Ser*, 9, 54–68.

Bernegossi, A.M., Borges, C.H.S., Sandoval, E.D.P., Cartes, J.L., Cernohorska, H., Kubickova, S. et al. (2022) Resurrection of the genus *Subulo* for the gray brocket deer, with designation of a neotype. *Journal of Mammalogy*, 104, 619–633. Available from: https://doi.org/10.1093/jmammal/gyac068

Berteaux, D., Humphries, M., Krebs, C., Lima, M., McAdam, A., Pettorelli, N. et al. (2006) Constraints to projecting the effects of climate change on mammals. *Climate Research*, 32, 151–158. Available from: https://doi.org/10.3354/cr032151

Black-Décima, P. (2000) Home range, social structure, and scent marking behavior in brown brocket deer (Mazama gouazoubira) in a large enclosure. *Mastozoología Neotropical*, 7, 5–14.

Black-Décima, P. & Vogliotti, A. (2016) Mazama gouazoubira. The IUCN Red List of Threatened Species, e.T29620A22154584. Accessed October 22, 2021. Available from: https://doi.org/10.2305/IUCN.UK.2016-2.RLTS.T29620A22154584.en

Black-Décima, P., Rossi, R.V., Vogliotti, A., Cartes, J.L., Maffei, L. & Duarte, J.M.B. et al. (2010) Brown brocket deer Mazama gouazoubira (Fischer 1814). In: Duarte, J.M.B. & Gonzalez, S. (Eds.) *Neotropical cervidology: Biology and medicine of Latin American deer*. Jaboticabal: Funep/IUCN, pp. 190–201.

Blois, J.L. & Hadly, E.A. (2009) Mammalian response to Cenozoic climatic change. *Annual Review of Earth and Planetary Sciences*, 37, 181–208. Available from: https://doi.org/10.1146/annurev.earth.031208.100055

Bocherens, H., Cotte, M., Bonini, R., Scian, D., Straccia, P., Soibelzon, L. et al. (2016) Paleobiology of sabretooth cat Smilodon populator in the Pampean Region (Buenos Aires Province, Argentina) around the Last Glacial Maximum: insights from carbon and nitrogen stable isotopes in bone collagen. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 449, 463–474. Available from: https://doi.org/10.1016/j.palaeo.2016.02.017

Carmignotto, A.P., de Vivo, M. & Langguth, A. (2012) Mammals of the Cerrado and Caatinga: distribution patterns of the tropical open biomes of Central South AmericaIn: Patterson, B.D. & Costa, L.P. (Eds.) *Bones, clones and biomes. The history and geography of recent neotropical mammals*. Chicago, Illinois: University of Chicago Press, pp. 307–350.

Cartelle, C. (1999) Pleistocene mammals of the Cerrado and caatinga of Brazil. In: Eisenberg, J.F. & Redford, K.H. (Eds.) *Mammals of the Neotropics—The Central Neotropics*. Chicago: University of Chicago Press, pp. 27–46.

Cartelle, C. (2020) Cave Paleontology in the Lagoa Santa Karst. In: S. Auler, A. & Pessoa, P., (Eds.) *Lagoa Santa Karst: Brazil's Iconic Karst Region, Cave and Karst Systems of the World*. Cham: Springer International Publishing. pp. 209–225. Available from https://doi.org/10.1007/978-3-030-35940-9_11

Caughley, G. (1994) Directions in conservation biology. *The Journal of Animal Ecology*, 63, 215–244. Available from: https://doi.org/10.2307/5542

Chahud, A. & Okumura, M. (2022) Cervidae and Tayassuidae from the Holocene deposits of the Cuvieri Cave, State of Minas Gerais, eastern Brazil; taxonomic and paleoenvironmental considerations.

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*Historical Biology*, 35, 74–83. Available from: https://doi.org/10.1080/08912963.2021.2022134

Côté, S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C. & Waller, D.M. (2004) Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics*, 35, 113–147. Available from: https://doi.org/10.1146/annurev.ecolsys.35.021103.105725

Eisenberg, J.F. & Redford, K.H. (1999) *Mammals of the neotropics, volume 3: The Central Neotropics: Ecuador, Peru, Bolivia, Brazil*. Chicago: The University of Chicago Press.

Futuyma, D.J. & Kirkpatrick, M. (2017) *Evolution*. Sunderland: Sinauer Associates, Inc.

Galetti, M., Moleón, M., Jordano, P., Pires, M.M., Guimarães, P.R., Pape, T. et al. (2017) Ecological and evolutionary legacy of megafauna extinctions. *Biological Reviews*, 93, 845–862. Available from: https://doi.org/10.1111/brv.12374

Gallina-Tessaro, S., Pérez-Solano, L.A., Reyna-Hurtado, R. & Escobedo-Morales, L.A. (2019) Brocket deer. In: Gallina-Tessaro, S. (Ed.) *Ecology and conservation of tropical ungulates in Latin America*. Springer, pp. 395–414.

Gamba, C., Jones, E.R., Teasdale, M.D., McLaughlin, R.L., Gonzalez-Fortes, G., Mattiangeli, V. et al. (2014) Genome flux and stasis in a five millennium transect of European prehistory. *Nature Communications*, 5, 5257. Available from: https://doi.org/10.1038/ncomms6257

Gongora, J., Reyna-Hurtado, R., Beck, H., Taber, A. & Altrichter, M. (2011) Pecari tajacu. The IUCN Red List of Threatened Species, e.T41777A10562361. Accessed July 26, 2022. Available at: https://doi.org/10.2305/IUCN.UK.2011-2.RLTS.T41777A10562361.en

Guimarães, D.A., Cardoso, D.L., Ferreira, M.A.P. & Albuquerque, N.I. (2013) Puberty in male collared peccary (Pecari tajacu) determined by quantitative analysis of spermatogenic cells. *Acta Amazonica*, 43, 99–103. Available from: https://doi.org/10.1590/S0044-59672013000100012

Haddad-Martim, P.M., Hubbe, A., Giannini, P.C.F., Auler, A.S., Piló, L.B., Hubbe, M. et al. (2017) Quaternary depositional facies in cave entrances and their relation to landscape evolution: the example of Cuvieri Cave, eastern Brazil. *Catena*, 157, 372–387. Available from: https://doi.org/10.1016/j.catena.2017.05.029

Holdridge, E.M., Cuellar-Gempeler, C. & terHorst, C.P. (2016) A shift from exploitation to interference competition with increasing density affects population and community dynamics. *Ecology and Evolution*, 6, 5333–5341. Available from: https://doi.org/10.1002/ece3.2284

Hubbe, A. (2008) Contextualização taxonômica, tafonômica e morfométrica dos remanescentes ósseos da megamastofauna da Gruta Cuvieri (MG), um sítio paleontológico do Pleistoceno tardio (Dissertation). São Paulo: Universidade de São Paulo.

Hubbe, A. & Auler, A. (2012) A large Cervidae Holocene accumulation in Eastern Brazil: an example of extreme taphonomical control in a cave environment. *International Journal of Speleology*, 41, 297–305. Available from: https://doi.org/10.5038/1827-806X.41.2.15

Hubbe, A., Haddad-Martim, P.M., Hubbe, M., Mayer, E.L., Strauss, A., Auler, A.S. et al. (2011) Identification and importance of critical depositional gaps in pitfall cave environments: the fossiliferous deposit of Cuvieri Cave, eastern Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 312, 66–78. Available from: https://doi.org/10.1016/j.palaeo.2011.09.010

Hubbe, A., Hubbe, M. & Neves, W.A. (2013) The Brazilian megamastofauna of the Pleistocene/Holocene transition and its relationship with the early human settlement of the continent. *Earth-Science Reviews*, 118, 1–10. Available from: https://doi.org/10.1016/j.earscirev.2013.01.003

Hubbe, A., Pestle, W.J., Hubbe, M., Amirali, A., Chim, E.N., Oliveira, R.E. et al. (2024) Late Quaternary millennial-scale stability of the feeding strategy of the gray brocket deer [Subulo gouazoubira (G. Fisher, 1814); Mammalia] in Southeastern Brazil. *bioRxiv*. [Preprint] Available from: https://doi.org/10.1101/2024.11.08.621301

IBGE. (2015) *Mapa de Vegetação do Brasil*. Map 1:250,000. Rio de Janeiro: IBGE.

Juliá, J.P. & Richard, E. (2000) Predators of brown brocket deer (Mazama gouazoubira) in a secondary rainforest of Premontane Forest in the Norwest of Argentina. *IUCN Deer Specialist Group, Newsletter*, 16, 11.

Klink, C.A. & Machado, R.B. (2005) Conservation of the Brazilian cerrado. *Conservation Biology*, 19, 707–713. Available from: https://doi.org/10.1111/j.1523-1739.2005.00702.x

Laundré, J.W., Hernández, L., Medina, P.L., Campanella, A., López-Portillo, J., González-Romero, A. et al. (2014) The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? *Ecology*, 95, 1141–1152. Available from: https://doi.org/10.1890/13-1083.1

Leeuwenberg, F., Oliveira-Cabral, I. & Lara-Resende, S. (1999) Gray brocket deer (Mazama gouazoubira) in the Brazilian savanne. *Deer Specialist Group News*, 15, 14.

Lessa, E.P., Cook, J.A. & Patton, J.L. (2003) Genetic footprints of demographic expansion in North America, but not Amazonia, during the Late Quaternary. *Proceedings of the National Academy of Sciences*, 100, 10331–10334. Available from: https://doi.org/10.1073/pnas.1730921100

Lindsey, E.L., Lopez Reyes, E.X., Matzke, G.E., Rice, K.A. & McDonald, H.G. (2020) A monodominant late-Pleistocene megafauna locality from Santa Elena, Ecuador: insight on the biology and behavior of giant ground sloths. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 544, 109599. Available from: https://doi.org/10.1016/j.palaeo.2020.109599

Lund, P.W. (1845) *Katalog over Professor Dr. PW Lund palaeontologiske samling. 2. Afdeling Breccier*. Kopenhaguen: Zoologiske Museum.

Lyman, R.L. (1994) *Vertebrate taphonomy. Cambridge manuals in archaeology*. Cambridge: Cambridge University Press.

Lyman, R.L. (2017) Paleoenvironmental reconstruction from faunal remains: ecological basics and analytical assumptions. *Journal of Archaeological Research*, 25, 315–371. Available from: https://doi.org/10.1007/s10814-017-9102-6

Marín, J.C., Casey, C.S., Kadwell, M., Yaya, K., Hoces, D., Olazabal, J. et al. (2007) Mitochondrial phylogeography and demographic history of the Vicuña: implications for conservation. *Heredity*, 99, 70–80. Available from: https://doi.org/10.1038/sj.hdy.6800966

Marinho-Filho, J., Rodrigues, F.H.G. & Juarez, K.M. (2002) The Cerrado mammals: diversity, ecology, and natural history. In: Oliveira, P.S. & Marquis, R.J. (Eds.) *The Cerrados of Brazil: ecology and natural history of a neotropical savanna*. New York: Columbia University Press, pp. 266–284.

Mayer, E.L. (2011) Processos de formação de um depósito fossilífero em abismo na Gruta Cuvieri (MG): taxonomia, tafonomia e distribuição espacial de fósseis de mamíferos do Pleistoceno (Dissertation). São Paulo: Universidade de São Paulo.

Mayer, E.L., Hubbe, A., Kerber, L. & Haddad-Martim, P.M. (2016) Reassessment of a large extinct species of Cuniculus Brisson, 1762 (Rodentia: Caviomorpha) from the Quaternary of Brazil: taxonomic, biogeographic and taphonomic remarks. *Acta Palaeontologica Polonica*, 61, 743–758. Available from: https://doi.org/10.4202/app.00236.2016

Mayor, P., Guimarães, D.A., Le Pendu, Y., Da Silva, J.V., Jori, F. & López-Béjar, M. (2007) Reproductive performance of captive collared peccaries (Tayassu tajacu) in the eastern Amazon. *Animal Reproduction Science*, 102, 88–97. Available from: https://doi.org/10.1016/j.anireprosci.2006.10.015

Morris, D.W. (2003) Toward an ecological synthesis: a case for habitat selection. *Oecologia*, 136, 1–13. Available from: https://doi.org/10.1007/s00442-003-1241-4

Moscardi, B., Rindel, D.D. & Perez, S.I. (2020) Human diet evolution in Patagonia was driven by the expansion of Lama guanicoe after megafaunal extinctions. *Journal of Archaeological Science*, 115, 105098. Available from: https://doi.org/10.1016/j.jas.2020.105098

Pires, M.M., Rindel, D., Moscardi, B., Cruz, L.R., Guimarães, P.R., dos Reis, S.F. et al. (2020) Before, during and after megafaunal extinctions: human impact on Pleistocene-Holocene trophic networks in South Patagonia. *Quaternary Science Reviews*, 250, 106696. Available from: https://doi.org/10.1016/j.quascirev.2020.106696

Presslee, S., Slater, G.J., Pujos, F., Forasiepi, A.M., Fischer, R., Molloy, K. et al. (2019) Palaeoproteomics resolves sloth relationships. *Nature Ecology & Evolution*, 3, 1121–1130. Available from: https://doi.org/10.1038/s41559-019-0909-z

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Prevosti, F.J. & Schubert, B.W. (2013) First taxon date and stable isotopes ($\delta^{13}C$, $\delta^{15}N$) for the large hypercarnivorous South American canid *Protocyon troglodytes* (Canidae, Carnivora). *Quaternary International*, 305, 67–73. Available from: https://doi.org/10.1016/j.quaint.2012.07.003

Raczka, M.F., Bush, M.B. & De Oliveira, P.E. (2017) The collapse of megafaunal populations in southeastern Brazil. *Quaternary Research*, 89, 1–16. Available from: https://doi.org/10.1017/qua.2017.60

R Core Team. (2023) A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ribeiro, J.F. & Walter, B.M.T. (2008) As Principais Fitofisionomias do Bioma Cerrado. In: Sano, S.M., de Almeida, S. & Ribeiro, J.F. (Eds.) *Cerrado: Ecologia e Flora*. Brasília: Embrapa Informação Tecnológica.

Richard, E. & Juliá, J.P. (2001) Dieta de Mazama gouazoubira (Mammalia, Cervidae) en un ambiente secundario de Yungas, Argentina. *Iheringia. Série Zoologia*, 90, 147–156.

Rogers, R.L. & Slatkin, M. (2017) Excess of genomic defects in a woolly mammoth on Wrangel island. *PLoS Genetics*, 13, e1006601. Available from: https://doi.org/10.1371/journal.pgen.1006601

Ruscoe, W.A., Ramsey, D.S.L., Pech, R.P., Sweetapple, P.J., Yockney, I., Barron, M.C. et al. (2011) Unexpected consequences of control: competitive vs. predator release in a four-species assemblage of invasive mammals. *Ecology Letters*, 14, 1035–1042. Available from: https://doi.org/10.1111/j.1461-0248.2011.01673.x

Sievert, C. (2020) *Interactive web-based data visualization with R, plotly, and shiny*. Boca Raton, FL: CRC Press.

Silva-Caballero, A. & Ortega, J. (2022) Mazama gouazoubira (Cetartiodactyla: Cervidae). *Mammalian Species*, 54, seac008. Available from: https://doi.org/10.1093/mspecies/seac008

Terborgh, J., Lopez, L., Nuñez, P., Rao, M., Shahabuddin, G., Orihuela, G. et al. (2001) Ecological meltdown in predator-free forest fragments. *Science*, 294, 1923–1926. Available from: https://doi.org/10.1126/science.1064397

Tomassini, R.L., Montalvo, C.I., Garrone, M.C., Domingo, L., Ferigolo, J. & Cruz, L.E. et al. (2020) Gregariousness in the giant sloth Lestodon (Xenarthra): multi-proxy approach of a bonebed from the Last Maximum Glacial of Argentine Pampas. *Scientific Reports*, 10, 1–16. Available from: https://doi.org/10.1038/s41598-020-67822-9

Villavicencio, N.A., Lindsey, E.L., Martin, F.M., Borrero, L.A., Moreno, P.I., Marshall, C.R. et al. (2016) Combination of humans, climate, and vegetation change triggered Late Quaternary megafauna extinction in the Última Esperanza region, southern Patagonia, Chile. *Ecography*, 39, 125–140. Available from: https://doi.org/10.1111/ecog.01606

Wilson, D.E. & Reeder, D.M. (2005) *Mammal species of the world: a taxonomic and geographic reference*, 3rd ed. Baltimore, MD: Johns Hopkins University Press.

Winge, H. (1888) Jordfundne og nulevende Gnavere (Rodentia) fra Lagoa Santa, Minas Geraes, Brasilien: Med Udsigt over Gnavernes indbyrdes Slægtskab. *E. Museo Lunddii*, 3, 1–178.

Wolverton, S., Huston, M.A., Kennedy, J.H., Cagle, K. & Cornelius, J.D. (2009) Conformation to Bergmann's rule in white-tailed deer can be explained by food availability. *The American Midland Naturalist*, 162, 403–417. Available from: https://doi.org/10.1674/0003-0031-162.2.403

Wolverton, S., Kennedy, J.H. & Cornelius, J.D. (2007) A paleozoological perspective on white-tailed deer (Odocoileus virginianus texana) population density and body size in Central Texas. *Environmental Management*, 39, 545–552. Available from: https://doi.org/10.1007/s00267-005-0280-6

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