

VANISHED LAGOA SANTA: RODENT SPECIES LOSS IN THE LAST TWO CENTURIES

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ABSTRACT. The extensive work developed by Peter Lund and other naturalists in the nineteenth century in Lagoa Santa Karst has generated a large volume of data on the extinct and extant local fauna. Despite these classic pioneer works, little work has been done about the fauna currently present in the region. Therefore, this study analyzes the richness and diversity of the modern fauna of small rodents of the Lagoa Santa region and compares the results with the historical data of Lund and Winge. We collected owl pellets from calcareous caves in Lagoa Santa, Cordisburgo and Sete Lagoas. These pellets were divided in two categories for comparison: 'superficial' (collected on the surface of the cave floor) and 'stratified' (collected in small excavations in the cave floor). We identified a total of 18 rodent species: 13 Cricetidae, 3 Echimyidae and 2 Muridae. Richness considering the minimum number of individuals (MNI) was greater in 'stratified' samples than in 'superficial' samples, but the two sets of samples did not differ when considering rarefaction. According to the Shannon-Wiener and Pielou indices, the 'stratified' samples were more diverse and with less species dominance. Nine species mentioned or described by Lund and Winge in the nineteenth century as inhabiting this region were absent in our samples. The proportion of small mammals in owl pellets in the modern samples was different from historical data, with predominance of *Calomys* spp. instead of *Necromys lasiurus*, as recorded by Lund using similar methods. It is likely that human activities in the region over these 180 years have influenced the fauna of Lagoa Santa, triggering local or regional extinctions.

RESUMO. Lagoa Santa devastada: perda das espécies de roedores nos últimos dois séculos. O extenso trabalho desenvolvido por Peter Lund e outros naturalistas no século XIX no Carste de Lagoa Santa gerou um enorme volume de dados sobre a fauna local extinta e existente. Apesar destes trabalhos pioneiros clássicos, pouco se sabe sobre a fauna atual na região. Portanto, este estudo analisa a riqueza e diversidade da fauna moderna de pequenos roedores da região de Lagoa Santa e compara os resultados com os dados históricos obtidos por Lund e Winge (1836). Para isso, foram coletadas pelotas de coruja em cavernas calcáreas em Lagoa Santa, Cordisburgo e Sete Lagoas. As amostras foram divididas em duas categorias: 'superficial' (coletadas na superfície do chão das cavernas) e 'estratificada' (coletadas em pequenas escavações do chão das cavernas). Um total de 18 espécies de roedores foram identificados: 13 Cricetidae, 3 Echimyidae e 2 Muridae. A riqueza foi maior nas amostras 'estratificadas' quando comparadas no mesmo MNI com amostras 'superficiais', mas não diferiram na análise de rarefação. De acordo com os índices Shannon-Wiener e Pielou, a 'estratificada' foi considerada mais diversificada e com menor predominância de espécies. Nove espécies mencionadas ou descritas por Lund e Winge no século XIX como habitando a região foram ausentes em nossas amostras. A proporção de pequenos mamíferos nas amostras modernas foi diferente dos dados históricos, com predominância de *Calomys* spp. em vez de *Necromys lasiurus*, conforme registrado por Lund por métodos similares. É provável

que as atividades humanas na região ao longo desses 180 anos tenham influenciado a fauna de Lagoa Santa, provocando extinções locais ou regionais.

Key words: Cerrado. Environmental degradation. Herluf Winge. Owl pellets. Peter Lund.

Palavras-chave: Cerrado. Degradação ambiental. Herluf Winge. Pelotas de coruja. Peter Lund.

INTRODUCTION

The karst region of Lagoa Santa in Minas Gerais has a great historical and scientific importance to paleontology and mammalogy in South America. This is mainly due to the work of Peter Wilhelm Lund in the nineteenth century, who collected and described a considerable diversity of fossil and living animals, including megafauna and human remains (Paula-Couto 1950; Voss & Myers 1991; Cartelle 2002). Lund's work is one of the first scientific mammal surveys conducted in Brazil and represents an accurate picture of the local fauna almost two hundred years ago (Cartelle 2002).

In his incursions, Lund found a large quantity of recent and fossil owl pellets in limestone caves, which allowed the description of many species of small mammals, particularly rodents (Paula-Couto 1950). This was the first small mammal survey using this methodology in South America; in fact, Lund carefully recorded materials from recent or fresh samples of pellets as well as those obtained from sediments. Later, all material collected by Lund was sent to Denmark and studied in European scientific circles (Ávila-Pires 1960), resulting in several papers on the Lagoa Santa fauna, not only by Lund, but by other naturalists as well, particularly Herluf Winge (Winge 1887). With this material, Winge described a considerable number of small mammals from cave sediments and recent deposits in the Lagoa Santa area (Voss & Myers 1991).

Much of the current knowledge regarding small mammals in South America is due to the study of barn owl pellets (see Pardiñas & Cirignoli 2002). The barn owl (*Tyto furcata*) is one of the main predatory birds of small mammals around the world (Taylor 1994). The

barn owl regurgitates all undigested material in a rounded mass of fur and bones, which are known as pellets or egagropiles (Andrews 1990; Taylor 1994). These birds have high affinity for their shelters (e.g. caves), occupying them for long periods and documenting species assemblages in the pellets (Terry 2010a). Due to climatic conditions and environmental stability, these environments have a high preservation potential, which leads to the conservation of these deposits and eventual fossilization of bone material in the shelters (e.g. Hadly 1996; Grayson 2000). The barn owl is characterized as a generalist predator and can be considered a good sampler of the small mammal community at local and regional scales (Andrews 1990; Heisler et al. 2016). From assemblages derived from owl pellets it is possible to study the small mammal community, environmental changes (from present to ancient times), and anthropogenic impacts, like deforestation, on local diversity (Terry 2010a; Pardiñas et al. 2012).

The karst area from central Minas Gerais is one of the regions in Brazil with the most information regarding the living and extinct fauna, and the type locality of several species, especially small mammals. Despite considerable data secured by Lund about small mammals derived from owl pellets, no posterior studies were carried out in Lagoa Santa region using this approach. The present paper aims to compare, for the first time, the nineteenth century historical record rodent assemblage in the Lagoa Santa region with the modern assemblage, as defined by recent samples of owl pellets collected on the surface and in excavations. Special attention was directed to detect qualitative and quantitative changes in the two assemblages and potential correlations

with environmental transformations in the region during the last 180 years.

MATERIALS AND METHODS

Study area

This study was conducted in the karst region of central Minas Gerais, by manually collecting egagropiles in four caves in three different localities (Fig. 1): Salitre Cave (19° 07' 17" S and 44° 28' 24" W; SC, thereafter), Toca do Lixo (19° 33' 30" S, 43° 57' 03" W; TL, thereafter), Mariposas Cave (19° 33' 38" S, 43° 57' 39" W; MC, thereafter), and Mata Grande (19° 30' 02" S, 44° 15' 59" W; MG, thereafter). SC is very near the famous Maquiné Cave, one of the first caves studied by Lund (1836) in the Peter Lund Natural Monument, located in Cordisburgo, where sixteen caves have been explored (Travassos 2010) (Fig. S1). TL and MC are two small caves in Sumidouro State Park, which protects 100 registered caves and 170 historic and prehistoric archaeological sites (IEF 2008). Finally, MG, in the city of Sete

Lagoas is near Rei do Mato Cave, another famous cave and important archaeological site, with cave paintings and ceramic artifacts.

The climate in the region is Aw tropical humid, according to the Köppen classification (IEF 2008; Travassos 2010). The annual average temperature in the region is 21.7 °C with an annual rainfall of 1291 mm (IEF 2008, Travassos 2010).

The vegetation is typical of the Cerrado biome, but with the occurrence of some enclaves similar to Caatinga in the limestone outcrops, known as the Deciduous Seasonal Forest or “Mata Seca” (Piló 1998). At present, natural vegetation is restricted to only a few patches—most of them disturbed (Berbert-Born 2002); the landscape matrix is dominated by pastures, crops and *Eucalyptus* plantations (Travassos 2010).

Data from owl pellets

Modern rodent community

Modern samples were collected from fresh and disaggregated owl pellets from SC (collected in

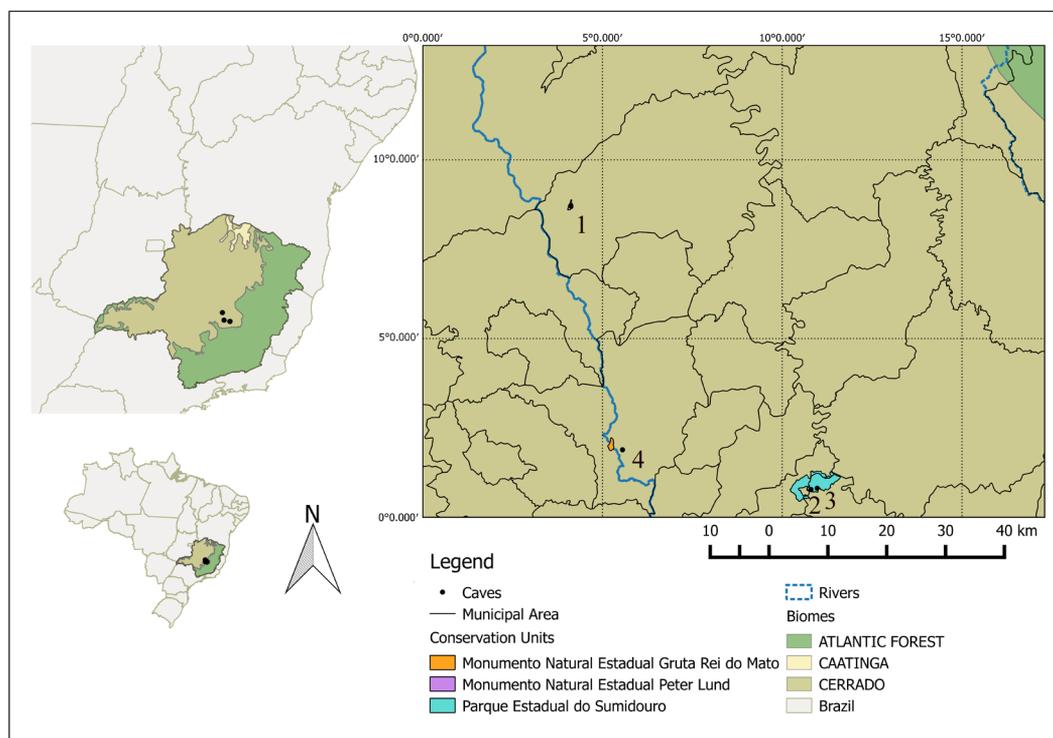


Fig. 1. Collecting localities of owl pellets samples: (1) Salitre cave, Peter Lund Natural Monument, Cordisburgo; (2) Mariposa cave and (3) Toca do Lixo, Sumidouro State Park, Pedro Leopoldo / Lagoa Santa; (4) Mata Grande cave, Sete Lagoas. Source: IBGE.

2009), TL (collected in 2010), MC (collected in 2010) and MG (collected in 2011). These samples vary in quantity, with hundreds to thousands of rodent specimens. Modern samples are divided in two categories: superficial and stratified.

'Modern superficial' samples were swept from cave floors and cavities. Most of the material was already fragmented, with few whole pellets. These samples are accumulations over several months to years. 'Modern stratified' samples were collected from a small excavation made in the floors of two caves. In the Salitre Cave, one excavation was performed at three different depths (layers) at the same point, each layer about 10 cm deep and 20 cm in diameter. In Toca do Lixo only one excavation was made (approx. 10 x 20 cm), because the soil was shallow over solid rock. MG and MC lacked any soil layer and excavation was not possible. Unfortunately, it was not possible to date these stratified samples, but we think it is reasonable to assume they represent several decades, since one fragment of modern ceramic was found together with the specimens in the second stratum excavation in Salitre Cave. Although the data were collected in different layers of stratified samples in Salitre Cave and they are not dated, they were analyzed as a single layer.

Fresh pellets typical of the barn owl (*Tyto furcata*) were identified at the collection sites, in addition to feathers and direct observations in some caves, indicating that the modern samples had originated from *T. furcata* pellets. Analysis of the stratified material also suggests the source to be *T. furcata*, because the bone material was well-preserved. Among the Strigiform birds, *T. furcata* is the species that causes the least damage to bones in the digestion process (Andrews 1990). Usually the bones in the *T. furcata* pellets are in good condition, with a relatively complete skeleton and longer non-fragmented bones (Andrews 1990). Barn owls generally eat small mammals weighing less than 200 g (Motta-Junior 2006), and in the samples small rodents less than 200 g predominated, corroborating the origin proposed for the material.

All samples were placed in the sun for dehydration, and then sieved to remove the sediment. Skulls, maxillas, molars and mandibles of rodents were manually separated. The identification of the rodent fragments was based on craniomandibular material by analyzing the cranial structures and morphology of the teeth using a stereomicroscope. For identification at the lowest possible taxonomic level, reference collections and specialized bibliography were used, although some fragments did not allow reliable identification to the species level, when they were

very fragmented or did not preserve diagnostic features. In addition, some genera did not have all specimens identified to the species level due to their many morphological similarities. Nomenclature of the species was based on Wilson & Reeder (2005) and Patton et al. (2015). For Cricetidae rodent teeth, the nomenclature follows Reig (1977), while for Echimyidae it follows Emmons & Vucetich (1998). All the material collected was deposited in the Mammalogy collection of the João Moojen Museum of Zoology (Universidade Federal de Viçosa, Brazil) (**Appendix 1**). The material was deposited in batches by species and stratum per cave, so all material for each species of each stratum of each cave has one voucher number.

Historical rodent community

Lagoa Santa has a long history of research on living and fossil small rodents during the nineteenth century (Winge 1887; Paula-Couto 1950). These records were collected, for the most part, from 1835 to 1849 by Lund, and were divided in two categories in this study: Historical and Fossil. 'Historical' data represent the community that was present almost two hundred years ago as observed in fresh and superficial pellets, in addition to live animals. 'Fossil' data are the records found exclusively in the sediments of the caves and not described as living species in the Lagoa Santa region by Lund or Winge.

A bibliographic survey was conducted to obtain the actual synonymy of the names proposed by Lund and Winge (e.g. Paula-Couto 1950; Ávila-Pires 1960; Voss & Myers 1991; Wilson & Reeder 2005; Pardiñas et al. 2008, 2016; Pardiñas & Teta 2013, 2011a; b, Patton et al. 2105). These 'Historical' and 'Fossil' data were used to compare the rodent fauna observed in the 'Modern' samples. Since the exact number of specimens collected and the sampling effort employed by Lund are not known, it is not possible to carry out statistical analyses comparing modern and historical samples. The comparisons in this paper are theoretical based on some abundance data of small mammals in pellets described by Lund in his memoirs (see Paula-Couto 1950). These comparisons are in the **Discussion** section below.

Data analysis

For each taxon the number of identified specimens (NISP) was determined as the sum of all the fragments of a taxon, and the minimum number of individuals (MNI) considered only the most frequent element of either the right or left side (Grayson 1973). In this study we only counted skulls, man-

dibles and maxillae; no part of the post-skull was considered in the calculation. The percentage of occurrence of each rodent species was estimated by dividing the number of items collected from each species by the total number of collected items. Species richness was defined as the number of species collected in each cave and the abundance of each species was determined by MNI.

For the analysis of a diversity, the Shannon-Wiener (H'), Simpson (D) and Pielou evenness (J') indexes were calculated (Magurran 2004). A Student's t test was performed to assess the differences between the Shannon-Wiener and Simpson values obtained for Salitre Cave and Toca do Lixo samples, in pairs, following the methodology of Magurran (2004). To compare species abundance in the 'Modern superficial' and 'Modern stratified' samples, a chi-square test was performed (χ^2) for samples from the Salitre Cave and Toca do Lixo. These analyses were performed in the Past program (Hammer et al. 2001).

Rarefaction analyses were performed to compare the richness between the 'Modern superficial' and 'Modern stratified' samples, employing the Estimate program, version 9.1 (Colwell 2013). The statistical significance of these comparisons was evaluated using 95% confidence limits for the rarefaction curve. The sampling unit was considered to be the number of samples collected by cave and stratum. The sampling effort was considered to be the sum total of MNI by cave and stratum.

In these statistical treatments (rarefaction and a diversity), *Calomys* spp. and *Oligoryzomys* spp. were considered only at the generic level. As most specimens of these genera were identified to the generic level, if we used only the specimens identified to the species level, we could underestimate the abundance of these species.

RESULTS

Six modern samples originating from the pellets of *T. furcata* were analyzed from four different caves: four from the cave floor surfaces ('Superficial') and the other two from excavations ('Stratified'). These samples included a total of 8658 identifiable items (NISP) of small rodents, comprising skulls, maxilla and mandible fragments. The minimum number of individuals (MNI) was 2871, corresponding to 15 genera and 18 species of rodents (Table 1, Figs. S2, S3).

Calomys tener, *C. expulsus*, *Necromys lasiurus* and *Oligoryzomys nigripes* were common in all the samples. In the 'Modern superficial' sample

from Salitre Cave (MNI=920), 13 rodent species were identified, of which *Cerradomys scotti* and *Pseudoryzomys simplex* stand out as exclusive to this sample. In the 'Modern stratified' sample from the same cave (MNI=231), 11 species were recorded, of particular note being two species of spiny rats, *Carterodon sulcidens* and *Trinomys setosus*. In the Toca do Lixo 'Modern superficial' (MNI=743) and 'Modern stratified' (MNI=48) samples, 12 and 7 species were observed, respectively. *Nectomys squamipes* and *Holochilus brasiliensis* were found only in Toca do Lixo and Mata Grande Cave. In Mariposa Cave (MNI=61), only four species were recorded. In Mata Grande Cave (MNI=868), 11 species were identified; this was the only sample that registered the murine rodent, *Mus musculus*.

Comparisons between the 'Modern superficial' and 'Modern stratified'

Richness and abundance varied among the samples, being greater in the 'Modern superficial' samples (considering *C. tener* and *C. expulsus* as *Calomys* sp., and *O. nigripes* and *O. mottogrossae* as *Oligoryzomys* sp.). In the superficial samples of SC and TL, higher species richness was observed (11 and 10 species, respectively) than in the stratified samples (9 and 5 species, respectively), although the sample size was much higher in the superficial sample (MNI SC=920 and TL=743) than stratified (MNI SC=231 and TL=48). *Cerradomys scotti*, *P. simplex*, *N. squamipes* and *H. brasiliensis* have only been recorded in the superficial samples. *Trinomys setosus* and *C. sulcidens* were exclusive to the stratified samples of SC. However, rarefaction curves showed no significant differences in species richness among the samples (Figs. S4). When comparing MNI across samples, greater diversity is seen in the 'Modern stratified' than in the 'Modern superficial' samples (Figs. S5, S6). But the confidence intervals (95% CI) were high and overlapped; thus, these samples were not distinct from each other in terms of species richness. The rarefaction curves also do not reach an asymptote, therefore, the sampling cannot be considered exhaustive, especially in the case of the stratified samples.

Table 1

Rodentia found in owl pellets in Salitre Cave (SC), Peter Lund Natural Monument, Cordisburgo; Toca do Lixo (TL) and Mariposa Cave (MC), Sumidouro State Park, Pedro Leopoldo / Lagoa Santa; Mata Grande Cave (MG), Sete Lagoas. MNI=minimum number of individuals. NISP=sum of all the fragments of the taxon. Modern superficial: SC-A, TL-A, MG, MC. Modern stratified: SC-S, TL-S. (%) Percentage of occurrence.

Species	SC-A	SC-S	TL-A	TL-S	MG	MC
	MNI (%)	MNI (%)	MNI (%)	MNI (%)	MNI (%)	MNI (%)
CRICETIDAE						
1. <i>Calomys expulsus</i>	55 (5.97)	98 (42.4)	35 (4.71)	2 (4.16)	82 (9.44)	3 (4.91)
2. <i>Calomys tener</i>	76 (8.26)	7 (3.3)	50 (6.72)	5 (10.41)	24 (2.76)	7 (11.47)
<i>Calomys sp.</i>	459 (49.89)	10 (4.3)	524 (70.52)	20 (41.66)	309 (35.59)	38 (62.29)
3. <i>Necomys lasiurus</i>	263 (28.58)	75 (32.4)	93 (12.51)	14 (29.16)	297 (34.21)	7 (11.47)
4. <i>Oligoryzomys nigripes</i>	25 (2.71)	6 (2.6)	20 (2.69)	1 (2.08)	77 (8.87)	6 (9.83)
5. <i>Oligoryzomys mattogrossae</i>	6 (0.65)	3 (1.2)	2 (0.26)	—	19 (2.18)	—
<i>Oligoryzomys sp.</i>	10 (1.08)	14 (6)	3 (0.40)	4 (8.33)	39 (4.49)	—
6. <i>Cerradomys scotti</i>	1 (0.1)	—	—	—	—	—
7. <i>Cerradomys subflavus</i>	10 (1.08)	5 (2.1)	8 (1.07)	1 (2.08)	3 (0.34)	—
8. <i>Rhipidomys mastacalis</i>	1 (0.1)	1 (0.4)	1 (0.13)	—	1(0.11)	—
9. <i>Thalpomys lasiotis</i>	7 (0.76)	8 (3.4)	1 (0.13)	—	—	—
10. <i>Akodon sp.</i>	2 (0.21)	2 (0.8)	—	—	—	—
11. <i>Pseudoryzomys simplex</i>	1 (0.1)	—	—	—	—	—
12. <i>Nectomys squamipes</i>	—	—	1 (0.13)	—	2 (0.23)	—
13. <i>Holochilus brasiliensis</i>	—	—	1 (0.13)	—	1 (0.11)	—
ECHIMYIDAE						
14. <i>Thrichomys apereoides</i>	2 (0.21)	—	2 (0.26)	1 (2.08)	—	—
15. <i>Trinomys setosus</i>	—	1 (0.4)	—	—	—	—
16. <i>Carterodon sulcidens</i>	—	1 (0.4)	—	—	—	—
MURIDAE						
17. <i>Mus musculus</i>	—	—	—	—	12 (1.38)	—
18. <i>Rattus sp.</i>	2 (0.21)	—	2 (0.26)	—	2 (0.23)	—
Total MNI	920	231	743	48	868	61
Total NISP	2898	572	2249	137	2628	174
Species identified	13	11	12	7	11	4

According to the Shannon-Wiener index (H'), the 'Modern superficial' samples from SC and TL were less diverse than 'Modern stratified' samples ($p < 0.006$ and $p = 0.001$, respectively) (Table 2). In relation to species abundance, the Pielou evenness index (J') shows that the 'Modern stratified' data are more uniform in abundance across the species. 'Modern strati-

fed' data also demonstrate greater diversity and lower species dominance, with Simpson index (D') values closest to one ($p < 0.0032$ for SC and $p < 0.0001$ for TL cave).

The fauna from the 'Superficial' and 'Stratified' modern samples are significantly different (χ^2 SC = 57.589, χ^2 TL = 23.561, $p < 0.05$). For the TL cave, the abundance of *Necomys* ($p = 0.002$)

Table 2

Diversity indices for modern owl pellets samples in Salitre Cave (SC), Peter Lund Natural Monument, Cordisburgo; Toca do Lixo (TL) and Mariposa Cave (MC), Sumidouro State Park, Pedro Leopoldo / Lagoa Santa; Mata Grande Cave (MG), Sete Lagoas. Modern superficial: SC-A, TL-A, MG, MC. Modern stratified: SC-S, TL-S. N = Sample size (MNI); S = Total species; H' = Shannon-Weaver; J = Equitability of Pielou; D' = Simpson's dominance.

Samples	N	S	H'	J	D' (1-D)
SC-A	920	11	0.93	0.387	0.504
SC-S	231	9	1.253	0.570	0.635
TL-A	743	10	0.653	0.238	0.311
TL-S	48	5	1.08	0.671	0.586
MG	868	9	1.132	0.515	0.629
MA	61	3	0.665	0.605	0.358

and *Oligoryzomys* ($p=0.016$) contribute towards the difference in the samples (Table 3). Several genera like *Calomys* ($p=0.013$), *Oligoryzomys* ($p=0.001$), *Thalpomys* ($p=0.001$) and *Trinomys* ($p=0.046$) differ significantly in abundance between 'Superficial' and 'Stratified' modern samples from SC.

DISCUSSION

This survey found a high species richness ($S=18$), greater than other short- and long-term studies using fresh owl pellets in the Cerrado, Pantanal and Atlantic Forest (Motta-Junior & Talamoni 1996; Motta-Junior & Alho 2000; Bonvicino & Bezerra 2003; Escarlante-Taveres & Pessoa 2005; Roda 2006; Scheibler & Christoff 2007; Bueno & Motta-Junior 2008; Magrini & Facure 2008; Souza et al. 2010; Rocha et al. 2011; Lemos et al. 2015). The results from this study indicate the most diverse sampling of pellets ever recorded for these biomes (Table S1), except for Peter Lund's survey.

The majority of the species found are common in the Cerrado Biome—inhabiting open areas such as grasslands, gallery forests, and woodland savanna—for example *C. expulsus*, *C. tener*, *N. lasiurus*, *T. lasiotis* (Patton et al. 2015). Despite reports of sympatry among

Calomys tener, *C. expulsus* and *C. cerqueirai* in the Lagoa Santa region (Bonvicino et al. 2010), in this study only *C. expulsus* and *C. tener* were identified. Although *C. tener* is slightly smaller than *C. expulsus* in some cranial features, the two species are difficult to separate, especially when the skull is fragmented, because the molars do not differ in discrete characters. *Calomys cerqueirai* exhibits many morphological similarities with *C. expulsus*, showing differences mainly in the external characteristics and some descriptive skull measurements, but with great overlap (see Bonvicino et al. 2010). Therefore, it was not possible to differentiate between the two species in this work. Some specimens collected may in fact be *Calomys cerqueirai*, which was described in the Lagoa Santa region (Bonvicino et al. 2010). A similar situation occurred with *Akodon* sp. specimens. *Akodon cursor* and *A. montensis* are sympatric in the Lagoa Santa region (see Geise et al. 2001), but the specimens from the pellets were too fragmented to differentiate the species (see Geise et al. 2005; Gonçalves et al. 2007). More complete specimens would need to be collected for a more accurate taxonomic identification.

Among the less frequent species in the sample are rodents with semi-aquatic habitat (*H. brasiliensis*, *P. simplex* and *N. squamipes*), the arboreal *Rhipidomys mastacalis*, and the spiny rat *Thrichomys apereoides*. Probably they are not well represented in the pellet samples because of their habitat preferences and medium to large body size. According to Taylor (1994), barn owls usually hunt smaller prey. Studies in Brazil have shown that they prefer rodents weighing an average of 10 to 40 g (Bonvicino & Bezerra 2003; Scheibler & Christoff 2007; Bueno & Motta-Junior 2008). In other studies, especially in flooded areas, an increase in the mass of prey is observed, represented by larger specimens such as *Holochilus* sp. (Roda 2006; Rocha et al. 2011).

Comparison of the richness and diversity in the Modern community: 'Superficial' and 'Stratified' data

The proportions of the faunistic elements differ between the 'Superficial' and 'Stratified' samples. In the deeper layer, there is a

Table 3

Comparison of rodent species abundance between superficial and stratified modern owl pellet samples in Salitre Cave (SC), Peter Lund Natural Monument, Cordisburgo; Toca do Lixo (TL), Sumidouro State Park, Pedro Leopoldo / Lagoa Santa. Modern superficial: SC-A, TL-A. Modern stratified: SC-S, TL-S. *Significant values ($p < 0.05$).

Species	Samples					
	SC-A x SC-S			TL-A x TL-S		
	χ^2	D.F.	p-value	χ^2	D.F.	p-value
<i>Calomys</i> sp.	6.205	1.000	0.013*	17.446	1.000	0.00002*
<i>Necomys lasiurus</i>	0.947	1.000	0.331	9.848	1.000	0.002*
<i>Oligoryzomys</i> sp.	10.044	1.000	0.001*	5.782	1.000	0.016*
<i>Cerradomys scotti</i>	0.252	1.000	0.615	–	–	–
<i>Cerradomys subflavus</i>	1.627	1.000	0.202	0.369	1.000	0.543
<i>Rhipidomys mastacalis</i>	1.060	1.000	0.303	0.066	1.000	0.796
<i>Thalpomys lasiotis</i>	10.347	1.000	0.001*	3.776	1.000	0.052
<i>Akodon</i> sp.	2.100	1.000	0.147	–	–	–
<i>Pseudoryzomys simplex</i>	0.252	1.000	0.615	–	–	–
<i>Nectomys squamipes</i>	–	–	–	0.066	1.000	0.796
<i>Holochilus brasiliensis</i>	–	–	–	0.066	1.000	0.796
<i>Thrichomys apereoides</i>	0.502	1.000	0.478	3.776	1.000	0.052
<i>Trinomys setosus</i>	3.982	1.000	0.046*	–	–	–
<i>Carterodon sulcidens</i>	3.982	1.000	0.046*	–	–	–
<i>Mus musculus</i>		1.000		–	–	–
<i>Rattus</i> sp.	0.502	1.000	0.478	0.133	1.000	0.715

decrease in the proportion of *Calomys* and an increase in *N. lasiurus* and other species like *Oligoryzomys* sp., *T. lasiotis* and *T. setosus* (see **Table 3**). Habitat specialist rodents (such as *T. lasiotis* and *T. setosus*) are more abundant in the stratified samples, whereas the superficial samples have greater representation of the more generalist and open habitat species (*C. tener* and *C. expulsus*). In other studies, when comparing the subfossil and modern samples, changes in the diversity of small mammals can be observed, with the most recent samples showing an impoverishment of owl prey species richness, and an increase in the presence of certain opportunistic taxa (Pardiñas et al. 2000; Terry 2010b).

Faunal composition changes in owl pellets could reflect the variation in prey availability or different foraging seasons (Lyman et al. 2003).

However, as we lack data on the present abundance of the local rodents, we cannot directly assess whether prey availability has changed. Moreover, these samples are aggregations of pellets over several years, and we could not analyze annual or seasonal variations in prey. Samples incorporated in the stratigraphic record should be understood as samples accumulated over time and, therefore, representing the general trend over several years and no single moments in time (Fürsich & Aberhan 1990).

Another explanation for the change in the proportion of rodents could be the differences in sample sizes. Considering the superficial sample of the Salitre Cave (MNI 920) and the stratified sample (MNI 231) at the same site, 11 and 9 species are represented respectively, but they did not differ in richness according to the rarefaction analysis (**Fig. S5**). Nonetheless,

according to the Shannon diversity index, the stratified sample is more diverse and abundant ($H' = 1.217$) than the superficial sample ($H' = 0.93$) in the Salitre Cave. This is contrary to the trend observed through many surveys, that diversity increases with increasing sample size (Grayson 1984).

Barn owls specialize in catching small mammals, but they are also opportunistic in the sense that they hunt a wide variety of species, especially those that are more abundant (Marti 1988). The decrease of *Calomys* sp. and the increase of *N. lasiurus* in the 'Stratified' sample may be attributable to the greater availability of *N. lasiurus* in the past. Habitat changes in the region have probably caused population declines of some habitat specialist species, like *T. lasiotis* and *C. sulcidens*, since it is known that some species are more vulnerable to habitat loss and fragmentation than others (Bright 1993). Habitat changes and habitat loss, along with other factors, may be related to a decrease in the diversity of small mammal species in the barn owl's diet during the twentieth century (Love et al. 2000).

Unfortunately, it was not possible to maintain better stratigraphic control and date the samples to establish the age of the deposits. We know that the stratified samples are not very old; and probably represent no more than the last century. Nevertheless, we found that the older samples tend to have a rodent fauna (abundance) more similar to that described by Lund in the nineteenth century.

Comparison of Modern and Historical community

The small mammals in the pellet samples reflect local wildlife in the landscape (Hadly 1999; Terry 2010a). Several species listed by Lund (1836, 1837, 1838, 1839) and Winge (1887) as living in Lagoa Santa were not found in the modern owl pellets collected in the region (**Table 4**). Winge and Lund recognized 25 species of Cricetidae rodents in the region, nine species of Echimyidae and two Muridae between the 'Historical' materials and 'Fossil' found on the floor in the caves (Winge 1887; Voss & Myers 1991). Of the 36 total species, 13

were found only in the sediments of caves, not being reported as living by Winge and Lund, and 23 were described as living forms. In this study, we only found 16 species in owl pellets (not considering *C. scotti* and *O. mattogrossae*, species not recognized at the time of Winge's publication [1887]), and two of these were recorded only in the 'Stratified' samples. 'Modern' species richness is lower than the 'Historical' assemblage described by Lund and Winge, with few or no arboreal and fossorial species, and relative abundances differ as well between the two periods.

In 1838, five species of spiny rats were described by Lund in this area (Lund 1838, p. 249). *Carterodon sulcidens* was known to Lund only by the remains found in caves (Lund 1837, p. 167). Today, *C. sulcidens* is Endangered (EN) in Minas Gerais (COPAM 2010). Meanwhile, *Clyomys laticeps* was rarely found in the region, while *T. setosus* and *T. apereoides* were more common (Lund 1837, p. 167; Lund 1838, p. 231, 262). The genus *Phyllomys* was later described from a few skeletal fragments, found in some caves located north of Lagoa Santa (Lund 1838b, p. 227). Today, the genus has two Endangered (EN) species in Minas Gerais (*P. brasiliensis* and *P. lundii*) and four in Brazil (*P. thomasi*, *P. unicolor*, *P. brasiliensis* and *P. lundii*) (COPAM 2010, MMA 2014).

Callistomys sp. and *Kannabateomys amblyonyx* were only found in the 'Fossil' material (Winge 1887), not occurring presently in the Lagoa Santa region, which may indicate a recent reduction in the geographic distribution of both genera (Voss & Myers 1991; Emmons & Vucetich 1998), or the difficulty of capturing these animals whose behavior makes them less accessible (Voss & Myers 1991). A recent study recorded *K. amblyonyx* about 72 km southeast of Sumidouro State Park, in a transition area of Atlantic Forest and Cerrado (Unidade Ambiental Peti, São Gonçalo do Rio Abaixo) (Da Silva et al. 2012). *Euryzygomatomys mordax* and *Dicolpomys fossor*, rodents with fossorial habits, were found only in fossil material and date from the late Pleistocene / Holocene (Hadler et al. 2008).

Among the Echimyidae listed by Lund, only *T. apereoides* was frequent in the 'Modern'

Table 4

Comparison of Historical community (specimens of rodents collected in the Lagoa Santa region in the XIX century) and Modern community. P=specimens found in the owl pellets in the caves; S=specimens with skin collected.

Species		Lund (1836)/Winge (1887)		Present study (2009-2011)
Name by Winge/Lund	Actual name	Fossil ¹	Historical ²	Modern ³
CRICETIDAE				
<i>Hesperomys simplex</i>	<i>Pseudoryzomys simplex</i>	X	P	P
<i>Hesperomys molitor</i>	<i>Lundomys molitor</i>	X		
<i>Hesperomys tener</i>	<i>Calomys tener</i>	X	P, S	P
<i>Hesperomys expulsus</i>	<i>Calomys expulsus</i>	X	P, S	P
<i>Sigmodon vulpinus</i>	<i>Holochilus brasiliensis</i>	x	P, S	P
<i>Habrothrix cursor</i>	<i>Akodon cursor</i>	x	P, S	P
<i>Habrothrix clivigenis</i>	[†] <i>Akodon clivigenis</i> ⁴	x		
<i>Habrothrix orycter</i>	<i>Thaptomys nigrita</i>	x	P	
<i>Habrothrix lasiotis</i>	<i>Thalpomys lasiotis</i>		P, S	P
<i>Habrothrix angustidens</i>	<i>Castoria angustidens</i>	x		
<i>Habrothrix lasiurus</i>	<i>Necomys lasiurus</i>	x	P, S	P
<i>Oxymycterus breviceps</i>	<i>Blarinomys breviceps</i>	x		
<i>Oxymycterus talpinus</i>	<i>Brucepattersonius talpinus</i>	x		
<i>Oxymycterus rufus</i>	<i>Oxymycterus dasytrichus</i>	x	P, S	
<i>Oxymycterus cosmodus</i>	[†] <i>Oxymycterus cosmodus</i>	x		
<i>Scapteromys labiosus</i>	<i>Bibimys labiosus</i>	x	P, S	
<i>Scapteromys principalis</i>	<i>Kunsia tomentosus</i>	x	P	
<i>Scapteromys fronto</i>	[†] <i>Gyldenstolpia fronto fronto</i>	x		
<i>Calomys anoblepas</i>	[†] <i>Juliomys anoblepas</i>	x		
<i>Calomys longicaudatus</i>	<i>Oligoryzomys nigripes</i>	x	P, S	P
<i>Calomys plebejus</i>	<i>Delomys plebejus</i>	x		
<i>Calomys rex</i>	<i>Sooretamys angouya</i>	x		
<i>Calomys coronatus</i>	<i>Euryoryzomys russatus</i>	x		
<i>Calomys saltator</i>	<i>Hylaeamys laticeps</i>		P, S	
<i>Calomys laticeps</i>	<i>Cerradomys subflavus</i>	x	P, S	P
<i>Rhipidomys mastacalis</i>	<i>Rhipidomys mastacalis</i>	x	P, S	P
<i>Nectomys squamipes</i>	<i>Nectomys squamipes</i>	x	P, S	P
ECHIMYIDAE				
<i>Dactylomys amblyonyx</i>	<i>Kannabateomys amblyonyx</i>	x		
<i>Lasiuromys villosus</i>	<i>Callistomys</i> sp.	x		
<i>Loncheres armatus</i>	<i>Phyllomys brasiliensis</i>	x	P	
<i>Echimys cayennensis</i>	<i>Trinomys setosus</i>	x	P, S	P
<i>Nelomys antricola</i>	<i>Thrichomys apereoides</i>	x	P, S	P
<i>Mesomys spinosus</i>	<i>Clyomys laticeps</i>	x	P, S	

(Table 4 cont.)

Species		Lund (1836)/Winge (1887)		Present study (2009-2011)
Name by Winge/Lund	Actual name	Fossil ¹	Historical ²	Modern ³
<i>Mesomys mordax</i>	[†] <i>Euryzygomatomys mordax</i>	x		
<i>Carterodon sulcidens</i>	<i>Carterodon sulcidens</i>	x	P, S	P
<i>Dicolpomys fossor</i>	[†] <i>Dicolpomys fossor</i>	x		
MURIDAE				
<i>Mus rattus</i>	<i>Rattus rattus</i>		P, S	P
<i>Mus musculus</i>	<i>Mus musculus</i> ⁵		P, S	P
TOTAL		34	23	16 ⁶

¹ Species found in the sediments of the caves.

² Species from fresh pellets and cave floors and collected alive.

³ 'Superficial' and 'stratified' modern samples.

⁴ According to an unpublished study, *Habrothrix clivigenis* appears to be similar to *Akodon paranaensis* (Pardiñas et al. 2015).

⁵ *M. musculus* was not registered in the samples of Salitre Cave and Toca do Lixo, but was collected in the Mata Grande sample.

[†] Extinct species.

* Not including *Oligoryzomys mattogrossae* and *Cerradomys scotti*.

fauna. *Carterodon sulcidens*, a rodent very common and abundant in pellets in the nineteenth century (Lund 1836, p. 126), presented one mandible in 'Stratified' samples of the SC. There are hardly any recent records for this species (Bezerra et al. 2011).

Several Cricetidae—*Thaptomys nigrita*, *Bibimys labiosus*, *Kunsia tomentosus*, *Hyaleamys laticeps* and *Oxymycterus dasytrichus*—described by Lund (1839b, p.291) and Winge (1887) as living fauna, were not found in our sample, although *T. nigrita* and *O. dasytrichus* (identified as *O. roberti*) have been collected near the study area (Ávila-Pires 1960; Leal et al. 2008). The lack of recent records of *K. tomentosus* in the Lagoa Santa region may be related to the intense landscape modification by human activities (Pardiñas et al. 2008).

Several species cited by Lund and Winge as living in the Lagoa Santa region (Lund 1839b, p. 291; Winge 1887) were found in this study and in nearby regions: *Oligoryzomys* sp., *C. tener*,

R. mastacalis, *N. squamipes*, and *H. brasiliensis* (Ávila-Pires 1960; Leal et al. 2008).

Winge (1887) reported that *P. simplex*, *C. subflavus* and *A. cursor* were common in fresh owl pellets and in fossil deposits in the caves. However, in our studies *P. simplex* was extremely rare, with only a single skull fragment found in the 'Modern' data, and *Akodon* represented just 0.21% of the modern rodents of the SC.

In 'Modern' samples, *Calomys* sp. represents 64% of the SC fauna and 80% of the sample of TL, and *N. lasiurus* was the second most abundant species, whereas in 1836, Lund reported that *N. lasiurus* was the most abundant rodent species in owl pellets, representing about 80% of individuals (Table 5).

In 'Modern' samples, *N. lasiurus* abundance increased in the stratified samples with depth, but the difference in the proportion was only significant in TL 'Superficial' vs. 'Stratified' ($p=0.003$). The same pattern was observed for

Table 5

Proportion of specimens in owl pellets described by Lund (1836), collected in Salitre cave (SC, 2009) and Toca do Lixo (TL, 2011). Modern superficial: SC-A, TL-A. Modern stratified: SC-S, TL-S.

Species	Historical (Lund 1836)	SC-A 2009	TL-A 2011	SC- S	TL-S
<i>Necomys lasiurus</i>	80	29	13	32	29
<i>Calomys</i> sp.		64	82	50	56
<i>Carterodon sulcidens</i>	5	0	0	0.4	0
<i>Thrichomys apereoides</i> , <i>Clyomys laticeps</i> and <i>Trinomys setosus</i>	1	0.2	0.3	0.4	2
Other rodents (<i>Thalpomys lasiotis</i>)	1	0.8	0.1	3	0
Other rodents (<i>Oligoryzomys</i> , <i>Cerradomys</i> , <i>Nectomys</i> , <i>Rhipidomys</i> , <i>Akodon</i> , <i>Pseudoryzomys</i> , <i>Holochilus</i>)		6	5	13	12
<i>Rattus</i>		0.2	0.3		
Other small animals	13				
Total	100	100	100	100	100

T. lasiotis, being more abundant in the stratified samples. This species has also been collected in nearby locations such as Serra do Cipó and Serra das Sempre Vivas (Leal et al. 2008), and this species is considered Vulnerable (VU) in Brazil (MMA 2014).

Some Cricetidae found exclusively as ‘Fossils’ from the caves (Lund 1839, p. 291; Winge 1887)—for example *Sooretamys angouya*, *Blarinomys breviceps* and *Delomys plebejus*—were not found in our samples. The last record for these species close to Sumidouro State Park was from Conceição do Mato Dentro, 50 km away from Lagoa Santa (Ávila-Pires 1960). The *B. breviceps* collected by Lund was fossil dated from the Pleistocene. It is probably extinct in the locality, and its existence in the region in the past could have been related to the more mesic environment (Silva et al. 2003). Meanwhile, *D. plebejus* should be considered a nomen dubium, as its equivalence to any of the living species is indeterminate (Voss 1993).

Environmental degradation

The differences in richness and abundance are important and may not be explained only by sample size or taphonomic bias. These changes in the small mammal proportions and pos-

sible local population declines can probably be related to environmental changes over the past 180 years. The fragmentation of the natural vegetation was undoubtedly the main factor contributing to the decline of medium and large mammals in the region (Trolle et al. 2007). During the last century, the Lagoa Santa region has also suffered bird population declines and the disappearance of many species recorded by Lund, Reinhardt and Burmeister. Over the years, the bird community, originally so diverse, has been replaced by a few generalist species, none of which were common in the last century (Christiansen & Pitter 1997).

Lund (1838b, p. 209, 210) already reported impacts caused by farming and exploitation of saltpeter, including possible extinctions of flora. Today, the Cerrado remnants are restricted to the dolines and rock outcrops, surrounded by pastures (Berbert-Born 2002; Travassos 2010). Studies on modern, historical and fossil rodents using owl pellets in a degraded area in North America showed variation in the richness and abundance in comparison with a preserved area, suggesting quick changes in the ecological baseline in the region. Thus, it is likely that anthropogenic processes there have led to a change in the vegetation and in the rodent

fauna (Terry 2010b), and our study found similar patterns in the Lagoa Santa region. Such landscape modifications over the last 180 years are likely to have resulted in homogenization of habitats and these changes were reflected in *T. fuscata* diets, with a marked increase of *Calomys* (*C. expulsus* and *C. tener*). *Calomys* species have been described as opportunistic and dominant in the anthropogenic environments (e.g. Bellocq 1990; Mills et al. 1991; Pardiñas et al. 2000). Pardiñas et al. (2000) have observed a similar pattern, with the dispersion and increased abundance of *Calomys* (*C. laucha* and *C. musculinus*) to the detriment of other small mammals, in human-modified landscapes.

These changes in rodent abundance and geographic ranges over the past 180 years could also be explained by climate change, although little is known about how rodent communities respond to climate change through time (Hadly 1996; Grayson 2000; Blois & Hadly 2009; Blois et al. 2010). For small rodents, a warmer climate may cause a local increase in abundance of species tolerant to higher temperatures (Terry et al. 2011). Unfortunately, no analysis has been done with meteorological data for this region and period to infer any changes.

CONCLUSIONS

In this paper, a great richness of the rodents in the central karst region of Minas Gerais was revealed by owl pellets, with *Calomys tener* and *C. expulsus* prevalent in the modern samples. The 'Modern' rodent community is less rich than the 'Historical' community described by Lund and Winge. This lower diversity of rodents currently observed in the Lagoa Santa region may result from environmental degradation in the last century. Despite the increase in studies about the rodent fauna, Brazil still presents gaps in information about historical and fossil communities. Studies should also emphasize digging sequences ('Stratified' samples) to understand the changes in the small mammal communities over the centuries. Such studies would generate more complete conclusions about how anthropogenic degradation affects

extinction processes, population declines and species invasion.

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APPENDIX 1

Voucher numbers

Table 1

Voucher numbers of specimens used in this study deposited in João Moojen Museum of Zoology (MZUFV).

Species	1	2	3	4	5	6	7	8
<i>Calomys expulsus</i>	3861	3867	3881	–	3811	3830	3845	3835
<i>Calomys tener</i>	3862	3868	3882	–	3812	3831	3846	3836
<i>Calomys</i> sp.	3863	3866	3880	3884	3810	3829	3847	3834
<i>Necromys lasiurus</i>	3860	3874	3883	3885	3813	3826	3838	3840
<i>Oligoryzomys nigripes</i>	3855	3872	3876	3888	3815	3827	3844	3833
<i>Oligoryzomys mattogrossae</i>	3856	3873	3875	–	3814	–	3843	–
<i>Oligoryzomys</i> sp.	3854	3871	3877	3887	3816	3828	3842	–
<i>Cerradomys scotti</i>	–	–	–	–	–	–	–	–
<i>Cerradomys subflavus</i>	3852	–	3879	3889	3820	3832	3841	–
<i>Rhipidomys mastacalis</i>	3851	–	–	–	3817	–	3849	–
<i>Thalpomys lasiotis</i>	3858	3869	3878	3886	3819	–	–	–
<i>Akodon</i> sp.	3853	3870	–	–	–	–	–	–
<i>Pseudoryzomys simplex</i>	3857	–	–	–	–	–	–	–
<i>Nectomys squamipes</i>	–	–	–	–	3818	–	3840	–
<i>Holochilus brasiliensis</i>	–	–	–	–	3821	–	3839	–
<i>Thrichomys apereoides</i>	3864	–	–	–	3825	–	–	–
<i>Trinomys setosus</i>	–	–	–	–	–	–	–	–
<i>Carterodon sulcidens</i>	–	–	–	–	–	–	–	–
<i>Mus musculus</i>	–	–	–	–	–	–	3850	–
<i>Rattus</i> sp.	3859	–	–	–	3822	–	3848	–

1. Salitre Cave, Cordisburgo, Minas Gerais, Brazil.
2. Salitre Cave, first layer, Cordisburgo, Minas Gerais, Brazil
3. Salitre Cave, second layer, Cordisburgo, Minas Gerais, Brazil
4. Salitre Cave, third layer, Cordisburgo, Minas Gerais, Brazil
5. Toca do Lixo Cave, Lagoa Santa, Minas Gerais, Brazil
6. Toca do Lixo Cave, first layer, Lagoa Santa, Minas Gerais, Brazil
7. Mata Grande Cave, Sete Lagoas, Minas Gerais, Brazil
8. Mariposa Cave, Lagoa Santa, Minas Gerais, Brazil

SUPPLEMENTARY ONLINE MATERIAL**Supplement 1**

https://www.sarem.org.ar/wp-content/uploads/2018/06/SAREM_MastNeotrop_25-1_Boroni-sup1.docx

Fig. S1. Sumidouro State Park: A) Lagoon Sumidouro in the dry season; B) Vegetation; C) Limestone outcrop. Peter Lund Natural Monument: D) Salitre Cave, collection point indicated by the arrow.

Fig. S2. Mandibles (md) and skull in ventral view (vv) and dorsal (dv) of rodents in owl pellets in central karst region of Minas Gerais. (A) *Calomys expulsus* (dv, vv, md); (B) *C. tener* (dv, vv, md); (C) *Necomys lasiurus* (dv, vv, md); (D) *Akodon* sp. (md); (E) *Thalpomys lasiotis* (md); (F) *Oligoryzomys nigripes* (dv, vv, md); (G) *O. mattogrossae* (dv, vv, md); (H) *Cerradomys subflavus* (dv, vv, md); (I) *C. scotti* (md).

Fig. S3. Mandibles (md) and skull in ventral view (vv) and dorsal (dv) of rodents in owl pellets in central karst region of Minas Gerais. (A) *Pseudoryzomys simplex* (vv); (B) *Holochilus brasiliensis* (vv, md); (C) *Nectomys squamipes* (vv, md); (D) *Rhipidomys matacalis* (dv, vv, md); (E) *Thrichomys apereoides* (dv, vv, md); (F) *Trinomys setosus* (md); (G) *Carterodon sulcidens* (md).

Fig. S4. Rarefaction analysis graph of all ‘Superficial’ samples. Blue = Salitre Cave; Green = Toca do Lixo; Yellow = Mata Grande Cave; Red = Mariposas Cave. Y axis = Estimated richness. X axis = sample number (MNI). CI = 95%.

Fig. S5. Rarefaction analysis graph of the Salitre Cave samples, Peter Lund Natural Monument, Cordisburgo. Red = ‘Superficial’; Blue = ‘Stratified’. Y axis = Estimated richness. X axis = sample number (MNI). CI = 95%.

Fig. S6. Rarefaction analysis graph of the Toca do Lixo samples, Sumidouro State Park, Pedro Leopoldo / Lagoa Santa. Blue = ‘Superficial’; Red = ‘Stratified’. Y axis = Estimated richness. X axis = sample number (MNI). CI = 95%.

Table S1. Rodents collected in owl pellets in the Cerrado and Atlantic Forest biomes. (A) Motta-Junior & Talamoni (1996); (B) Motta-Junior & Alho (2000); (C) Bonvicino & Bezerra (2003); (D) Bueno & Motta-Junior (2008); (E) Magrini & Facure (2008); (F) Rocha et al. (2011); (G) Roda (2006); (H) Souza et al. (2010); (I) Lemos et al. 2015; (J) Scheibler & Christoff (2007); (K) Escarlate-Tavares & Pessoa (2005); (L) Present study.