Palaeogeography, Palaeoclimatology, Palaeoecology 505 (2018) 73–85

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

The dominance of an extant gregarious taxon in an attritional accumulation: Taphonomy and palaeoecological implications

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ARTICLE INFO

Keywords:
Mammals
Cave environment
Temporal resolution
Quaternary
Caviomorpha
Kerodon rupestris

ABSTRACT

A recurrent aspect of the fossil record is the observation of a disproportionate number of specimens or individuals of a single taxon in some deposits, which is stated as dominance. Commonly, the dominance is explained as the result of catastrophic or short-term mass death events or are proxies for palaeoecological inferences regarding gregariousness. However, taphonomic, stratigraphic and chronologic analyses of fossiliferous deposits have shown that this is not always true. To contribute to the study of dominance in fossil assemblages, we describe a probable Quaternary skeletal accumulation dominated by the extant gregarious rock-dwelling rodent *Kerodon rupestris* recovered from Sumidouro do Sansão, a 65 m deep pitfall cave in northeast Brazil, and discuss the palaeoecological implications of our findings. We provide taxonomic identification, taphonomic analyses, and chronological assessment. Besides *K. rupestris* (minimum number of individuals, MNI = 35), we recorded three taxonomic groups, that are the ground sloth *Catonyx cuvieri* (MNI = 1), the anteater *Tamandua tetradactyla* (MNI = 1), and the cougar *Puma concolor* (MNI = 1). The taphonomic analysis of the *K. rupestris* remains supports the idea that entrapment of individuals was the main process of bone accumulation and that the death of cave inhabitants followed by short transport to the main hall possibly occurred. *Kerodon rupestris* remains persisted on the surface of the cave deposit for different time spans and were exposed to fragmentation, weathering, invertebrate boring and encrustation inside the cave environment. Direct dating suggests differences in the ages obtained and intermittent deposition of the individuals inside the cave. It highlights the influence of taphonomic controls on gregarious taxa, such as *K. rupestris*, towards dominating attritional time-averaged assemblages. Furthermore, it demonstrates that such assemblages do not necessarily support inferences about single event mortality and gregariousness of the dominant taxon.

1. Introduction

The formation of bone assemblages is a complex phenomenon influenced by biotic and abiotic factors. Depending on the influence of these factors (e.g. geologic setting or particular predators; Rogers and Kidwell, 2007) on the type of mortality (e.g. catastrophic or short-term mass death events and multiple death events [=attrition]; Eberth et al., 2007) and the relative degree of time-averaging (Kidwell and Flessa, 1996), assemblages can be overrepresented by a single taxon or some taxa. They can be either monotaxic assemblages, which are formed by only a single species or genus, or multitaxic assemblages, which include more than one species or genus (Eberth et al., 2007). Regarding the relative taxonomic abundance, assemblages can be classified as monodominant and multidominant (Eberth et al., 2007). Monodominant assemblages have 50% or more of the specimens or individuals represented by a single taxon. Multidominant assemblages, on the other hand, have 50% or more of the specimens or individuals represented by two or more taxa.

Monotaxic and monodominant assemblages may be very relevant to understanding the ecology of extinct species, such as gregarious behaviour (e.g. rhynchosaurs, Mukherjee and Ray, 2012; dinosaurs, Ibiricu et al., 2013; Zhao et al., 2014; cynodonts, Jasinoski and Abdala, 2017; mammals, Ladevèze et al., 2011). However, since such assemblages may not always be a consequence of a species' ecology (Hubbe and Auler, 2012; Müller et al., 2015; Roach and Brinkman, 2007), one must at least characterize its attritional or catastrophic type of mortality

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https://doi.org/10.1016/j.palaeo.2018.05.028
Received 2 January 2018; Received in revised form 18 April 2018; Accepted 18 May 2018
Available online 23 May 2018
0031-0182/

(Eberth et al., 2007) before attempting any kind of palaeoecological study. The understanding of the relative degree of time-averaging (Kidwell and Flessa,1996) and the processes of assemblage formation are critical aspects to this aim, and approaches integrating biotic characteristics (e.g. anatomy and palaeobiology) with contextual data (taphonomy, geomorphology, stratigraphy, and chronology) can provide coherent explanations.

Fossiliferous deposits of different geologic ages have preserved monodominant assemblages in diverse contexts, including fluvial settings (Triassic, Mukherjee and Ray, 2012; Cretaceous, Ibiricu et al., 2013; Quaternary, Price, 1944), marshy settings (Pleistocene, Lindsey and Lopez, 2015), caves (Quaternary, Cartelle and Bohorquez, 1982; Holocene, Hubbe and Auler, 2012), hillslopes (Holocene, Backwell et al., in press) and tanks (Quaternary, Araújo-Júnior et al., 2013). However, only in a few instances were the genesis and/or evolution of the monodominant assemblages investigated, which hampers reliable depositional and palaeoecological inferences. To contribute to the understanding of relative taxonomic abundance in fossil assemblages, we describe an assemblage of medium- and large-sized mammals dominated by the extant gregarious rock-dwelling rodent, *Kerodon rupestris* Wied, 1820 (Fig. 1A). In addition, we present a taphonomic interpretation and chronological assessment for this assemblage and discuss the palaeoecological implications of our findings using examples of the literature with interpretations of mass mortality and gregariousness in extinct taxa. The assemblage was recovered from Sumidouro do Sansão, a limestone pit cave in Serra da Capivara, northeast Brazil (Fig. 1B–D).

1.1. The genus Kerodon F. Cuvier, 1823

Kerodon is a habitat specialist rodent that inhabits rocky outcrops and has adaptations associated with climbing skills, such as clawless fingers (Dunnum, 2015). There are two extant species within the genus, *Kerodon rupestris* (Fig. 1A) and *Kerodon acrobata* Moojen, Locks and Langguth, 1997 (Dunnum, 2015). *Kerodon rupestris* is polygynous and highly social (Mares and Lacher Jr, 1987) and its current distribution is restricted to the dry Brazilian Biomes, the Caatinga and part of the Cerrado. The fossil record of *K. rupestris* is restricted to the Quaternary of Brazil (Ferreira et al., 2012; Guérin et al., 1993; Kerber et al., 2016; Lessa et al., 2008; Oliveira et al., 2013) and the fossils assigned to this rodent have been found within the modern range of the species (Kerber et al., 2016).

2. Material and methods

2.1. Location and study site

The Serra da Capivara region (Fig. 1B, D) is located in the State of Piauí, northeast Brazil, and preserves archaeological and palaeontological records (e.g. Guérin and Faure, 2008; Guidon et al., 1994). In the northwest part of the study area, there are sandstone rock cliffs of the Serra da Capivara National Park. To the southeast, there are flat domains with limestone rock cliffs where caves developed and were filled with Quaternary deposits (Rodet, 1997) (Fig. 1B).

Sumidouro do Sansão (lat. 8.857944 S, long. 42.544306 W; FUMDHAM archives) consists of a cave with a 65 m deep vertical shaft (Rodet, 1997; Fig. 1C). The cave entrance is located on the top of the hillside and is about 10 × 5 m wide (Figs. 1C, 2A; FUMDHAM archives). After the entrance, there is an expansion in the diameter of the vertical shaft (area A in Fig. 1C) followed by a reduction in the diameter and a final expansion forming a large main hall at the bottom of the pit (area B in Fig. 1C, Fig. 2B). The irregularity of the shaft results in areas with negative sloping cave walls (Fig. 1C; areas A and B). The main hall contains a sediment cone with its apex just below the cave entrance. Its surface is formed by poorly sorted lithoclasts presenting a wide range of particle sizes and in the deepest eastern area of this hall, there is a pond (Figs. 1C, 2B).

Sumidouro do Sansão was discovered in 1984, and explored between 1986 and 1988 by the team of the Fundação Museu do Homem Americano (FUMDHAM archives; Guérin et al., 1996). Later, Guérin (1991) reported remains of *Catonyx* Ameghino, 1891 (medium-sized extinct ground sloth) from the site. Guérin et al. (1996) mentioned one specimen was collected, and other specimens, supposedly from the same individual, are still lying on the bottom of the pit (Figs. 1C, 2C). Afterwards, Mayer (2013) reported *Kerodon rupestris*, indeterminate species of *Galea* Meyen, 1833, *Thrichomys* Trouessart, 1880 and Myrmecophagidae from this site. Although we did not visit the cave due to technical difficulties, a recent survey conducted in 2018 found a cluster of disarticulated and fragmentary remains of small vertebrates near the area where the *Catonyx cuvieri* McDonald, 1839 specimens (see Section 3.1 Taxonomic identification) are still lying (Figs. 1C, 2C) and few remains of medium-sized mammals scattered in other areas of the cave (Shirlene Matos and Estevan Eltink, pers. comm.).

2.2. Specimens recovery and taxonomic identification

The specimens here analysed are housed in the palaeontological collection of Fundação Museu do Homem Americano (FUMDHAM), Piauí, Brazil. We inspected all the material recovered in 1987 and 1988, which we estimate to comprise between 3000 and 4000 remains of extinct and extant vertebrate taxa of diverse body sizes. In some cases in which more than one specimen were stored under the same collection number, we relabelled each specimen with the original collection number plus a new number to allow future assessment of our analysis. We focused on 1161 specimens of medium- and large-sized mammals (body weight above 500 g) recorded under 14 original collecting numbers, each one containing from 1 to 275 specimens. According to the information on the labels placed with the sets of specimens, they were collected from the surface of the sediments in the main hall of the cave, in the area where the *C. cuvieri* remains are still lying and its surroundings (Figs. 1C, 2C). There are only two sets of specimens for which proximity to the *C. cuvieri* remains was not specified on the labels (total of 327 specimens) and for three sets information about sieving is present (total of 49 specimens). In consequence, it is important to note that, we have information of where the specimens were collected in the main hall of the cave but not about the exact location of each specimen. In addition, due to the lack of a systematic protocol of recovery of the material and the fact that the deposit has not been excavated, our analyses of specimens and taxa are most likely affected by collecting bias. Consequently, the numbers of specimens and individuals and the taxonomic composition reported here for medium- and large-sized mammals from the Sumidouro do Sansão are probably underestimated.

We carried out the taxonomic identification by comparing the material with fossil and modern skeletons deposited at FUMDHAM as well as published data.

2.3. Taphonomy

We used the term “specimen” to refer to a complete or fragmented bone, and “element” to refer to a single anatomical part of the skeletal system represented by a specimen (Lyman, 1994). To investigate the genesis and evolution of the assemblage, we examined: 1) encrustation; 2) fragmentation; 3) weathering stages; 4) tooth marks; 5) abrasion marks; 6) invertebrate traces; 7) calculated the number of identifiable skeletal parts (NISP), the minimum number of individuals (MNI) and the minimum number of skeletal elements (MNE); and 8) ascertained the bone accumulation processes.

The aspect of calcite encrustation was noted to describe its absence or its extension through little, medium or large areas of the bone surface, respectively considered as less than 30% covered, above 30% and less than 70% covered and above 70% covered. Regarding fragmentation, specimens comprising at least 90% of the respective skeletal element were noted as complete; specimens encompassing less than 50%