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Paleontology and paleoecology of guano deposits in Mammoth Cave, Kentucky, USA

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ABSTRACT

Bat guano deposits are common in the Mammoth Cave system (Kentucky, USA). Paleontological remains associated with these deposits are important records of local landscape changes. Recent excavations in the cave suggest that vertebrate remains in most of these deposits are dominated by Chiroptera. Although no extinct fauna were identified, the presence of a large roost of *Tadarida brasiliensis* in the Chief City section is beyond the northern extent of its current range suggesting that this deposit dates to an undetermined interglacial period. Stable isotope analyses of *Tadarida*-associated guano indicate a C3 prey signature characteristic of forested habitat. This was unexpected since this species is typically associated with open environments. Further ecomorphological analysis of wing shape trends in interglacial, Holocene, and historic-aged assemblages indicate that interglacial faunas are dominated by fast-flying, open-space taxa (*T. brasiliensis*) while late Holocene and Historic assemblages contain more taxa that utilized closed forest or forest gaps.

Introduction

Bat guano is an important component of the Mammoth Cave paleontological record. Guano derived from roosting bats provides a nutrient-rich substrate for life in deep cave environments. In addition to the remains of bats that created the guano, arthropod, microbe, and non-aerial vertebrate communities rely on guano nutrients (Fletcher, 1982; Fenolio et al., 2006). In Mammoth Cave, all of these guano communities have the potential to be recovered from guano deposits.

The guano of insectivorous bats is a valuable archive of paleoenvironmental information. Osteological remains of guano-producers and associated fauna are often preserved in cave guano deposits (Frank and Benson, 1998; McFarlane et al., 2002; Gaudin et al., 2011) providing specific clues to the ecological context of guano communities. Recent work has explored the use of stable isotopes and pollen in bat guano as climate proxies (Maher, 2006; Wurster et al., 2007, 2008, 2010a,b; Batina and Reese, 2011). The balance of research on cave guano deposits in the last few decades has demonstrated the importance of these contexts for preserving materials that are useful for reconstructing local climate and ecological conditions.

Paleontological remains within Mammoth Cave have been recognized since the 1950s. Although extensively mined in the early 19th century for the production of salt-peter, significant deposits of guano remain, most notably in the Chief City section. Jegla and Hall (1962) reported on the fossil *Tadarida* from this area, indicating an age for the guano deposits >38,000 ^{14}C yr BP. Investigations carried out nearly 40 yr later found guano in this area to be >54,000 ^{14}C yr BP (Colburn, 2005).

Mammoth Cave National Park was formally established in 1941. Located in the central Kentucky counties of Barren, Edmonson, and Hart, the principal feature of the Park is Mammoth Cave, the world's longest mapped cave system (~644 km, mapped length). The portion of the Park south of the Green River lies within the Central Kentucky Karst portion of the Pennyroyal Plateau, while the northern portion lies within the Chester Upland of the Western Coal Field (Palmer, 1981). The cave lies entirely within the Interior Low Plateaus of the Interior Plains physiographic province.

The primary cave strata are Mississippian limestones including the St. Louis, Ste. Genevieve, and Girkin formations. In the uplands near the Green River, these strata are capped by the Big Clifty Formation, a sandstone layer roughly 15 m thick (Palmer, 1981:48).

This study focuses on the identification of materials recovered during the Mammoth Cave Trail Rehabilitation Project (2007–2008). After a discussion of the geochronological context of paleontological samples, we shift to our main analytical focus, the identification of vertebrate remains (MC) and the geochemical analysis of guano-bearing sediments (CW).

Materials and methods

Field sampling and excavation

Coordinated excavations with the University of Kentucky, Program for Archaeological Research were undertaken in three field sessions between

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Table 1
Size categories in identified bat remains.

Small bat
Myotis leibii
Perimyotis subflavus
Medium bat
Corynorhinus rafinesquii
Corynorhinus townsendii
Lasionycteris noctivagans
Myotis lucifugus
Myotis septentrionalis
Myotis austroriparius
Myotis sodalis
Lasiurus borealis
Myotis grisescens
Nycticeius humeralis
Tadarida brasiliensis
Large bat
Eptesicus fuscus
Lasiurus cinereus

December 2007 and July 2008 (Ahler, 2012). Areas of archaeological and paleontological importance were examined via test excavations and spot sediment sampling (Table S1; Fig. S1). A total of 43 m^2 was excavated throughout the Historic Section, Historic Lantern Tour, Gothic Avenue, Cleveland Avenue, and Frozen Niagara. Additional spot collecting for paleontological remains was undertaken in Great Onyx Cave. This total encompasses all of the excavation undertaken for this project, including areas of both archaeological and paleontological importance. Test units targeting archaeological contexts were dry-screened through 6.5 mm mesh in the cave. Intact paleontological deposits were typically removed from the cave as bulk samples. In addition to a small number of bones that were removed directly from excavation units, ~1233 L (~280 gal) of sediment and guano samples were transported to the Illinois State Museum to be processed and analyzed for paleontological remains. To our knowledge, these are the first stratigraphically controlled paleontological excavations to take place within the cave.

Paleontological remains and trace organic materials

Bulk sediment samples were set aside for off-site processing and paleontological analyses based on their potential to preserve small bones or organic materials (i.e., hair, insect remains). Large bulk samples (>1 gal) were wet screened through nested 6.4 mm, 2.0 mm, and 0.8 mm screens. Small samples (<4.3 L or <1 gal) were dry screened through the same mesh sizes and the residue retained in case it was needed for further analyses. All samples were subsequently sorted by hand and a 1× hand-lens. Identifiable bones were removed from all screened samples, however, some unidentifiable, fragmentary remains were left in the smallest sized matrix (<2.0 mm) because we could not justify the labor of sorting very small materials that were undiagnostic below family level. All extracted bones were subsequently examined, and the number of identified specimens (NISP) calculated. Portions of the remaining bulk samples were examined for trace organic materials (e.g., hair, insect cuticle) and processed for biogeochemical analyses (^{14}C and stable isotopes). We identified osteological remains to the finest taxonomic category possible, which in many cases meant only identification to higher taxonomic levels encompassing multiple species or even genera. Sometimes remains could not be identified any more precisely than simply “Bat” with reference to relative size (Table 1). Taxonomic identification of specimens is tabulated by excavation unit and cave section (Tables S1, S2).

Stable isotope and ^{14}C analyses

Wet chemistry pretreatment of bulk guano samples followed protocols modified from Mizutani et al. (1992). Bulk samples were dry-sieved and the 1 mm to 220 um fraction retained for analyses. These samples were de-carbonated with 2M HCl, for 3–4 h, until the reaction was complete. The resulting slurry was screened through 10 um Nitex mesh to remove clay-sized particles, rinsed to neutrality with DI water and lyophilized. The remaining sample consists of highly comminuted organic material and silicate minerals. Examination under low- and high-power microscopy indicate the organic fraction of these samples is predominantly insect fragments, with varying amounts of detrital charcoal and trace amounts of degraded chiropterid hair. Although these protocols are similar to previous work on bat guano deposits from the West Indies (McFarlane et al., 2002), they are not as aggressive as the guano pretreatment technique of Wurster et al. (2010b) in their study of *Tadarida* guano deposits in Arizona. Trials on MACA guano samples utilizing these methods yielded very low sample weights, primarily due to the chemical removal of the highly comminuted insect fragments.

Stable carbon isotope analyses of biological tissues have the potential to quantitatively measure contributions of C3 and C4 vegetation to herbivore diets (DeNiro and Epstein, 1978; Schimmelmann and DeNiro, 1985). The source of guano deposits in Mammoth Cave is insectivorous bats. The guano produced by these animals contains abundant, albeit fragmentary, remains of their insect prey. In eastern North America, bats are relatively flexible feeders, optimally utilizing seasonal “booms” in the populations of certain insect taxa (Lacki et al., 1995; Lee and McCracken, 2005).

Stable isotope analyses were performed on 27 bulk guano samples. After de-carbonation, organic preservation was evaluated through C:N (Carbon:Nitrogen ratio) and loss-on-ignition analyses. C:N and stable isotope ($\delta^{13}C$, $\delta^{15}N$) analyses took place on a ThermoFinnigan MAT 253 continuous flow system with an attached thermal combustion/elemental analyzer device at the Keck Paleoenvironmental and Environmental Stable Isotope Laboratory at the University of Kansas, Lawrence. Montana soil (NIST Ref Mat. 2711) and a peach leaves standard (NIST Ref Mat. 1547) were used to determine quality control. Results compiled over 2 yr show the $\delta^{15}N$ to be measured better than $\pm$ 0.42‰, and the $\delta^{13}C$ to be better than $\pm$ 0.22‰. Loss-on-ignition (LOI) analyses follow internal lab protocols used in sediment analyses (following Dean, 1974). Small (~0.5 mL) samples were dried overnight at 100 °C, weighed and ignited at 500 °C for 1 h, then weighed. They were ignited again at 900 °C for 1 h, and weighed a second time. Prior to weighing, samples were cooled in a desiccator. Complete combustion of organic matter was expected to occur at 500 °C, and the disassociation of $CaCO_3$ at 900 °C.

Decarbonated bulk guano samples were submitted to the W. M. Keck Carbon Cycle AMS facility at the University of California, Irvine and Aeon Laboratories in Tucson, AZ for ^{14}C dating. All finite ^{14}C dates were calibrated using Calib 7.0 (Stuiver and Reimer, 1993) using the intCal13 dataset (Reimer et al., 2013). All reported calibrated age ranges are 2-sigma (Table 2). It is important to note that all ^{14}C dates are on bulk guano, therefore they provide only minimum constraints on the age of cave deposits in this study (Wurster et al., 2009).

Results

Chronology of paleontological localities

Four chronological periods are recognized in the Mammoth Cave paleontological record based on stratigraphic context, geochronological data, and biogeographic information. The earliest contexts are those associated with abundant *T. brasiliensis* remains dating to an undetermined interglacial period. A second group of assemblages from Gothic Avenue dates to the late Wisconsinan Farmdalian interstadial. Finally,