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## Neotaphonomic study of two *Tyto alba* assemblages from Botswana: Palaeoecological implications

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### Abstract

By producing pellets rich in micromammal remains, owls are important contributors to small vertebrate accumulations in archaeological sites. Neotaphonomic studies are necessary to evaluate predation and fossilization biases before using pellet-derived assemblages to assess palaeoenvironmental reconstructions and micromammal community changes in plio-quadernary deposits. In this study, barn owl (*Tyto alba*) pellets were collected from two localities of Botswana with markedly different environments: the northern Kalahari (arid) and the Okavango Delta (humid). The taxonomic and taphonomic analyses of the two samples were compared with data from the literature on other *T. alba* pellet assemblages from Sub-Saharan Africa. This study provides additional data for the wildlife inventory at a local scale and further information about the diet and hunting habits of *Tyto alba* in this area, as well as its taphonomic impact on local rodent species. It confirms that barn owl assemblages are reliably good indicators of local environmental conditions. An application of palaeoecological methods was also made in order to evaluate the accuracy and performance of palaeoenvironmental reconstructions based on micromammal assemblages produced by owls in an archaeological context. Here, we discuss some methodological issues facing micromammal studies in southern Africa.

**Keywords:** Micromammals, Botswana, Owl pellets, Taphonomy, Palaeoecology,

### 1. Introduction

Over the past few decades, extensive work has been done on the general biogeographical distribution of rodents, as well as clarification of the relationships within and between genera. Current knowledge on the taxonomy and distribution of rodents in the southern African subregion was comprehensively summarized by Monadjem et al. in 2015 in their book *Rodents of Sub-Saharan Africa*. Similarly, a more up-to-date syntheses were also published for other small taxa such as southern African bats (Monadjem et al., 2010), as well as a recent taxonomic update of bats and shrews in *Mammals of the World* (Wilson et al., 2018, 2019). Such accurate data provides useful tools not only for taxonomists and biologists, but also for palaeontologists and archaeologists working on fossil sites and palaeoenvironmental reconstructions, with new fossil data on African rodents continuing apace. Previous studies on Pleistocene micromammalian fauna, undertaken before the recent development of molecular techniques, have already highlighted the limitations of traditional taxonomic methods and the need for future reanalysis of the faunal lists (see, for instance Avery, 1998). Moreover, it is now well known that characterizing the origin of fossil accumulations is crucial to avoid any bias in the interpretations, and that most of the small mammal accumulations in palaeontological and archaeological contexts were made by predation (e.g., Denys, 1985; Andrews, 1990; Denys et al., 1997; Stoetzel et al., 2011; Fernandez-Jalvo and Avery, 2015; Fernandez-Jalvo et al., 2016). It is therefore necessary to establish modern taphonomic referentials on a wide range of predators to better characterize the impact of their diet, hunting strategies and digestive processes on particular species, and the anatomical representation of preys in an assemblage. Furthermore, these referentials have to be compiled using contrasting geographic regions, where predator and prey species are different and may present divergent taphonomic patterns (Denys et al., 2011). However, neotaphonomic works remain scarce in some areas, notably in tropical Africa, as well as in Botswana. To our knowledge, only one

piece of work, by Denys (1985), on barn owl (*Tyto alba*) pellets from the Okavango Delta has been performed in this region; unfortunately, the taphonomic study was not complete and did not look at digestion marks.

Studies based on the content of owl pellets rely on the presupposition that owls hunt prey randomly, without any preference for one or several species. Abundant literature has been produced on this topic, most of it assessing the effectiveness of owls as good estimators of species richness and prey abundance (Avenant, 2005; Terry, 2010; Andrade et al., 2016). This is especially the case with the barn owl, which has been widely used to estimate biodiversity in African ecological studies (Avery et al., 2002, 2005; Hanney, 1962; Reed, 2005; Thiam et al., 2008; Appendix A). Being constant to their roosting site, barn owls generally accumulate large amounts of small mammal bones at the foot of the nesting tree. Over time, these bones accumulate and gradually mix with sediments, resulting in variable size accumulations of micromammalian remains in archaeological and palaeontological sites (see e.g. Andrews, 1990; Avery, 2001; Fernandez-Jalvo and Avery, 2015).

In this paper, we provide new data on pellets from the barn owl (*Tyto alba*) collected from two localities in Botswana with markedly different environments, i.e. the Okavango Delta and the Kalahari Desert. Our objective is to contribute to the development of neotaphonomic referentials for the southern half of Africa, which would be applicable to the fossil context. We also use traditional ecological indices employed for palaeoenvironmental reconstructions in order to discuss the accuracy of these methods for predation assemblages.

## 2. Material and methods

### 2.1. Sampling of the pellets

Fresh barn owl (*Tyto alba*) pellets were collected from two localities in Botswana (Fig. 1) and stored at the National Museum of Natural History, Paris (zoology, mammals) under the collection numbers MNHN- ZM 2020-574 (Maun pellets Okavango) and MNHN-ZM 2020-575 (Kalahari).

The first assemblage comes from the Ghanzi District. More than a hundred pellets were collected in July 2001 by Jean-François Noblet from the Dqae Qare San Lodge in the Kalahari Desert, located approximately 24 kms from Ghanzi, Botswana. During storage, the pellets were infested with mites that fed on the undigested fur and hair of rodents. Many empty pupae and larvae feces were observed. Bones were not affected by moth action, but the digestion of hair by moths resulted in the crumbling of most of the pellets, so it was not possible to count them individually. Dqae Qare San Lodge is located in the western part of the Republic of Botswana, in the middle of the Kalahari Desert, a vast semiarid sandy savanna extending for 930,000 km<sup>2</sup> and covering much of Botswana and parts of Namibia and South Africa. The landscape around the collecting area is typical of the central Kalahari thornveld, a gently undulating sandveld with open vegetation consisting of bushes (e.g. *Rhigozum trichotomum*) and camel thorn trees (*Vachellia erioloba*) (Mares, 1999). The climate is semi-arid, with mean maximum daily temperatures exceeding 35° (January) and mean minimum temperatures of around 2.5 °C (July). The long-term mean annual rainfall is around 375 mm although this can vary by up to 50% year on year (Mares, 1999).

The second assemblage comes from the rural Ngamiland District. Eighty-five pellets were collected in the early 1980s by Dr R Seitre (associate researcher at the National Museum of Natural History of Paris) from a swamp island in the Okavango Delta wetlands (Ngamiland Delta), 50 km north of Maun. Taphonomic studies on this assemblage were previously led by Denys (1985), who attributed the pellets to *Tyto alba*. However, although a species list was compiled, no study was made on either the digestion or relative proportion of micromammals. The Okavango Delta in Botswana is the second world's largest inland delta, formed where the Okavango River reaches a tectonic trough in the central part of the endorheic basin of the Kalahari. The Okavango Delta is unique in that it consists of a wetland located in a desert – a delta that does not flow into the sea. The area includes permanent swamps and seasonally flooded grassland. Papyrus (*Cyperus papyrus*) and reed rafts constitute a large part of the swampy Okavango's Delta vegetation, along with mokolwane palms (*Hyphaene petersiana*), acacia and some riparian trees (Mitsch and Gosselink, 2015). The seasonal flooding of the floodplains is crucial for maintaining specific habitats for several small mammal species. This region constitutes a major transition zone between wooded (moist) savannas to the north and dry savannas (grasslands) with low trees and *Acacia* spp. to the south (Cole, 1986).

## 2.2. Methods

### 2.2.1. Taxonomic identifications

Most specimens from the two assemblages were identified to a species level. However, identification beyond the genus level has not been possible for a few specimens for which we lack clear diagnostic criteria. Those specimens which could not be identified at genus level are noted as “indeterminate murid”, “indeterminate nesomyid”, etc., and numbers were estimated by counting the mandibular and maxillary fragments. The three lower molars of the murids were referred to as the m1, m2, m3 and the three upper molars as the M1, M2, M3. We used the m1 and M1 teeth (*in situ* and isolated) to quantify the minimal number of individuals (MNI) of the various micromammal species present in both assemblages. Mandibles, maxillae and portions thereof which did not contain identifiable dental or alveolar characters were classified as “indeterminate rodent”. The length of the upper and lower dental rows were taken using a Mitutoyo caliber (precision 0.01 mm). Observations and identifications were made under a Nikon SMZ800N stereomicroscope, and photographs of specimens were taken using a Dino-Lite AM7915MZTL digital microscope (digital zoom max. 220x – 5 MP).

Systematic and taxonomic investigation relies on both osteological and dental observations, referring to Monadjem et al. (2015) for rodents and Wilson et al. (2016), Wilson et al. (2017), Wilson et al. (2018) for the Afrosoricida, Macroscelidea and Eulipotyphla orders. Data concerning the geographical distribution and ecology of the identified species came from Kingdon et al. (2013), Monadjem et al. (2015), Wilson et al. (2016), Wilson et al. (2017), Wilson et al. (2018) and the IUCN (*International Union for Conservation of Nature*) red list database.

### 2.2.2. Diversity indices

We compared the diet diversity of the barn owls responsible for both assemblages using diversity indices commonly used in (palaeo)ecology: Shannon–Wiener index ( $H'$ ), Simpson’s diversity index ( $E$ ) and the Equitability index ( $J$ ). A community composed of many species but with a dominant species is not intuitively perceived as more diverse than a community with fewer species but whose numbers are close. Two components of diversity must therefore be taken into account, the richness and the equitability (Hammer and Harper, 2006; Lyman, 2008; Marcon, 2015).

The **Shannon–Wiener index**, sometimes referred to as the Shannon–Weaver index, assesses both species abundance (number of taxa) and species evenness (number of individuals belonging to each taxa); it is equally sensitive to rare and abundant species (Harper, 1999; Hammer and Harper, 2006). It can be obtained with the formula:  $H' = -\sum p_i \ln p_i$ , with  $p_i = n_i/n$  (the proportion of species  $i$ ).

The **Simpson index of diversity** can be obtained with the formula:  $E = 1 - \sum p_s^2$ , with  $p_s$  corresponding to the probability for a random individual to belong to the species  $s$ . This index can be interpreted as the probability that two individuals selected at random belong to different species. It takes into account the relative abundance of each species, as well as the number of species present: as species richness and evenness rise, so diversity increases. The index ranges within the interval [0; 1]. Its value decreases with the evenness of the distribution:  $E = 0$  if a single species has a probability of 1,  $E = 1 - 1/S$  if the  $S$  species have the same probability  $p_s = 1/S$ . The value 1 is reached for an infinite number of species, with null probabilities.

Finally, the (Pielou’s) **Equitability index** ( $J$ ) corresponds to  $H'$  divided by the logarithm of the number of taxa:  $J = H'/H_{\max}$  with  $H'$  = calculated Shannon index,  $H_{\max}$  = theoretical maximum diversity =  $\ln S$  ( $S$  = total species richness). It measures the evenness with which individuals are distributed among the taxa present, with an index value normalized between 0 and 1.

Some non-mammalian preys were found in the pellet assemblage from the Kalahari Desert (one bird, one large beetle and three lizards). We chose not to take them into consideration for the calculation of indices, along with the indeterminate rodents, in order to focus on the diversity of small mammals. This type of indicator only makes sense in a well-defined complex of taxa; for instance, summing a number of insect and squamate species to a number of mammal species is of little interest.

### 2.2.3. Taphonomic analyses

The taphonomic investigation followed standard methodology based on the quantitative and qualitative analysis of alterations observed on cranial and postcranial elements (e.g., Andrews, 1990; Denys et al., 1997; Fernandez-Jalvo et al., 2016). This included identification of skeletal element representation, fragmentation patterns and analysis of bone surface modifications (digestion, beak marks, post-depositional alterations etc.).

Percentage of representation (PR) of skeletal elements allows one to evaluate the proportion of bones absent from an assemblage, whether because they were not ingested, were lost during ingestion or because they were dissolved during the digestion process. The determination of PR also enables the tooth loss to be assessed and comparisons to be made between preys with dissimilar skeletons. The PR formula was defined by Dodson and Wexlar (1979) and refined by several scientists for the counting of elements from pellets:  $PR = OF / (TF * MNI)$ , where OF is the frequency of every skeletal element observed in the pellet assemblage and TF is the theoretical frequency of skeletal elements from a fully preserved skeleton. For a typical mouse-like murid, the theoretical frequencies of an individual are: 1x crania, 2x mandible, 2x maxilla, 2x scapula, 2x humerus, 2x radius, 2x pelvis, 2x femur, 2x tibia, 54x vertebra, 4x incisor, 12x molar, 20x phalange, 20x metapodium, 24x rib. The MNI was calculated on the basis of the most commonly occurring skeletal element in the assemblage.

We analyzed the fragmentation of tibiae, femora and humeri to quantify the crushing of preys by the raptor and to evaluate the preservation state of the material. Pellets of nocturnal raptors are characterized by the high percentage of unfragmented and/or well-conserved bones in comparison with diurnal birds of prey (Andrews, 1990).

The study of digestion patterns on teeth and bone surfaces remains one of the best criteria to identify the predator category at the origin of a micromammal assemblage (Fernandez-Jalvo et al., 2016). It is based on the percentage of digested elements as well as the degree of digestion. The study of digestion relies on the notion that each type of predator causes specific digestive alterations, enabling several categories of predators to be established based on the intensity of the digestive processes (Andrews, 1990; Denys, 2014; Fernandez-Jalvo et al., 2016). For instance, *Tyto alba* is considered as a predator with low digestive alterations on ingested elements (category 1 predation). Digestion traces were observed on isolated and *in situ* incisors and on the proximal part of the femora. Photographs of taphonomic modifications were taken using a Scanning Electron Microscope (SEM) Hitachi SU 3500 from the *Service Commun de Microscopie Electronique du Museum national d'Histoire naturelle* (MNHN-Paris).

#### 2.2.4. Ecological study and application to fossil assemblages

Palaeoenvironmental and palaeoecological reconstructions rely on the principle of actualism and use the taxonomic affinities of fossil taxa alongside living species. These methods often target particular taxa, but a set of taxon-free (or taxon-independent) methods have been developed in recent years for evaluating fossil communities (see Reed, 2013; Andrews and Hixson, 2014). In this paper, we present some methods conducted either at a specific, generic or subfamily scale and thus dependent on taxonomy to a certain degree. Two types of models were used for these reconstructions: presence/absence of taxa and relative frequencies. Variations in the frequencies of small mammals can yield important information on changes in faunal communities and past environments (Andrews, 1990). On the other hand, in some cases where the taphonomic and predation bias may be difficult to estimate, one may find the use of a presence/absence method, in order to avoid the ecological signatures of one or a few abundant taxa masking the actual environmental signature to be more useful (Reed, 2003). In order to test and discuss the effectiveness of these methods, we applied several indices commonly used for palaeoenvironmental reconstructions in Africa to our modern assemblages. The ratio Gerbillinae/Murinae (Jaeger, 1976) is a method that relies on the absence/presence of taxa; methods based on the relative frequencies are the Taxonomic Habitat Index (Evans et al., 1981) and the Micromammal Niche Model (Reed, 2007).

The **Gerbillinae/Murinae ratio** (G/M ratio) was established by Jaeger (1976) and resumed by Fernandez-Jalvo et al. (1998) and Denys (1998), Denys (1999). Species from the Gerbillinae subfamily (gerbils and jirds) are adapted to semi-desertic and desertic habitats and are therefore consistent with arid, open environments (with some exceptions, though never in forested habitats), whereas Murinae (mice) tend to be more abundant in moist and closed environments. Calculation of the G/M ratio has been used as an indicator of present environments for different biogeographic zones in Africa (Denys, 1998, 1999; Fernandez-Jalvo et al., 1998). It is calculated by dividing the MNI of Gerbillinae by the MNI of Murinae, and sometimes by dividing

the number of species. It is worth mentioning that in some cases, the calculation of the ratio has been found to be inappropriate for specific areas, such as some North African regions (Stoetzel et al., 2011).

The **Taxonomic Habitat Index (THI)** (Evans et al., 1981; Andrews, 2006) is an ordination method of palaeoecological reconstruction using weighted averages. It offers the advantage of considering the habitat diversity in which a community of mammals occurs without including relative proportions, thus avoiding artificial biases of the over- or underrepresentation of some species. Habitat preferences of extant species are based on data available from the literature, averaged for generic and subfamily groupings. For each taxon, a weighted value is assigned to the different types of habitat in which they occur, the sum of these values being equal to 1. A global index cumulating the values obtained for every species is then calculated for each habitat type and divided by the number of species to produce a single score for the (palaeo)assemblage. For the southern subregion of Africa, Fernandez-Jalvo et al. (1998) and Andrews (2006) suggest five primary habitat types into which species can be sorted, including forest, woodland, bushland, grassland and semidesert. These habitats are detailed by Andrews (2006) as follows:

<i>Forest</i>	closed multiple canopy, tall tree, evergreen to semi-deciduous, herbaceous ground vegetation
<i>Woodland</i>	open to closed single canopy, tall tree, deciduous, herbaceous and grass ground vegetation
<i>Bushland</i>	open to closed single canopy, low to tall shrubs, deciduous, mainly grass ground vegetation
<i>Grassland</i>	trees and shrubs less than 20% canopy cover or absent
<i>Semi-desert</i>	widely spaced shrub canopy, low, deciduous, mainly annual grass and herb ground vegetation

**Taxonomic Biome Index (TBI):** in addition to the habitat category, we used an additional ecological unit corresponding to seven extant African biomes, such as delineated by Olson et al. (2001) who placed emphasis on the vegetation and floristic diversity to the exclusion of faunal components (Table 1). The biomes considered, therefore, are: mediterranean forests, woodlands, and scrub; deserts and xeric shrublands; mangroves; montane grasslands and shrublands; flooded grasslands and savannas; tropical and subtropical grasslands, savannas and shrublands; tropical and subtropical moist broadleaf forests. The temperate coniferous forests and the tropical and subtropical dry broadleaf forests biomes that are also represented in Africa were not taken into consideration due to their marginal distribution and their significant distance from the study zone.

In the case of uncertain specific identifications, for both THI and TBI, we calculated the mean values for each possible species (for instance, the value for *Gerbilliscus* sp. from the two study assemblages was obtained by dividing the summed scores of *G. brantsii* and *G. leucogaster* by two, as it was not possible to decide in favour of one species or the other). It is readily apparent that genus scores provide less detailed information than species scores; however, most of the rodent species within a same genus tend to share similar habitat preferences. A compilation of THI values for African rodents based on habitat preferences was provided by Fernandez-Jalvo in 1998, but recent insights on the ecological preferences of rodent species, as well as integration and/or exclusion of species within several genera, made it necessary to (re)calculate the vast majority of the specific and generic scores. The newly calculated habitat and biome scores are given in Appendices B and C.

The **Micromammal Niche Model** (Reed, 2007) was developed as a component of the THI. Niche index values are derived from the THI scores for each taxon following the formula: Niche index ( $t_i$ ) =  $\sum_{j=1}^5 (R_j \times S_j)$ , where  $R_j$  is the habitat rank (1 for semi-desert, 2 for grassland, 3 for bushland, 4 for woodland and 5 for forests) and  $S_j$  is the THI score for the taxon in the habitat. For example, *Desmodillus* has a score of  $1.75 = (5 \times 0) + (4 \times 1) + (3 \times 0.25) + (2 \times 0.25) + (1 \times 0.5)$ . Calculation of the niche index gives a ranking of habitat preferences, with low values indicating an open/dry habitat and higher values indicating a more moist/closed habitat.

### 3. Results & discussion

#### 3.1. Micromammal diversity

##### 3.1.1. Faunal list and general observations

In total, 12,295 identifiable skeletal elements were recovered from the studied pellets: 9632 remains from the Kalahari, belonging to at least 135 individuals (MNI) and 14 small mammal taxa, and 2663 remains

from the Okavango, belonging to 98 individuals and 10 small mammal taxa. The list of preys from the two pellet assemblages from Botswana show differences in terms of diversity and species composition (Table 2, Fig. 2).

The Kalahari assemblage shows the largest diversity of micromammals, including 11 genera of rodents and at least 14 species. It also showed two species of shrews (genus *Crocidura*) and one species of elephant shrew (*Elephantulus intufi*). Among the rodents, the Muridae family was the most diversified with at least nine species belonging to eight genera including Gerbillinae (*Desmodillus*, *Gerbilliscus*) and Murinae (*Aethomys*, *Mastomys*, *Micaelamys*, *Mus*, *Rhabdomys*). Nesomyidae were represented by three genera from the Cricetomyinae (*Saccostomus*) and the Dendromurinae (*Dendromus*, *Steatomys*) sub-families, and Bathyergidae with a single genus (*Fukomys*). The micromammal composition of this assemblage shows slightly higher diversity than previous studies on rodent communities in the southern Kalahari using trapping stations (Nel and Rautenbach, 1975). The presence of *Aethomys chrysophilus* suggests a slightly wider distribution of this taxon than presented in Monadjem et al. (2015). In addition, one bird (Passeriformes indet.), three lizards (Lacertilia indet.) and one large-sized insect (Coleoptera indet.) were found in the pellet assemblage.

The Okavango assemblage displays the lowest diversity of micromammals, with six genera of rodents and one genus of shrew (*Crocidura*) for a total of nine rodent species and two shrews. Muridae are represented by at least five species belonging to five genera (*Gerbilliscus*, *Mastomys*, *Otomys*, *Thallomys*), and Nesomyidae by two genera (*Dendromus*, *Steatomys*) and at least four species. Currently, only a few studies on small mammals have been conducted in the Okavango Delta region in Botswana. The limited live trapping of rodents was carried out by Graham (1964) as part of a tsetse fly control survey, as part of field ecological studies of the southern Okavango Integrated Water Development Project (SMEC, 1987) and the Okavango Delta ecological zoning exercise (CSIR/WTC, 1997), but the data supplied were fragmentary. Ferguson et al. (2010) surveyed the Koanaka Hills (Nqcumtsa Hills) in western Ngamiland and provided a list of mammals likely to occur in this region using both the data and information from published literature, including on rodents. More recently, Taylor et al. (2018) published an updated mammal checklist of small mammals from the upper Okavango catchment in Angola. Even though the 11 species of micromammals from the pellet assemblage are under sampled compared to the number of species expected based on literature and GBIF records, our results indicate that barn owl proved to be more efficient samplers of the rodents than traditional live trapping methods for the Okavango region.

### 3.1.2. Diversity indices

Indices like Shannon Diversity ( $H'$ ), Simpson ( $D$ ) and Equitability ( $J$ ) have proved to provide useful general information of prey habitats (Avery, 2003, 2007) but they are sensitive to sample size. For this reason, it is relevant to calculate the rarefaction curves in advance, with the slope of the curve showing the expectation of the number of taxa ( $S$ ) as a function of the MNI. Fig. 3 shows that the Kalahari and the Okavango assemblage curves approach a horizontal plateau (a theoretical asymptote means that the inventory effort is optimal); hence, it can be assumed that the estimation of diversity indices may be little affected by sampling bias. Values of the diversity indices are shown in table 3. The Kalahari assemblage exhibits the highest values for the Shannon Diversity index ( $H'$ ) and the Simpson index ( $E$ ). Contrastingly, the Equitability index values are rather similar.

### 3.1.3. Systematic notes

Assessment of the micromammalian fauna from the two study assemblages required a careful examination of the many taxa whose cranial or dental morphology lacked clear diagnostic traits. Morphologically there can be a great overlap in appearance and measurements for relative species. Furthermore, within various genera (like *Rhabdomys*, for instance), some species can only be distinguished by molecular characteristics. In such cases, we relied on the known extant distribution of the taxa to assess the species. In the following section, we present some of the criteria used for various specific identifications, as well as a morphological description of the taxa for which we were unable to provide specific identification (specimens marked as “sp.”).

Dendromurinae remains are difficult to identify due to their high fragmentation rate in owl pellet assemblages and the lack of evident specific dental, cranial or biometrical characters for southern forms. However, we identified three forms of *Dendromus* by considering the dental morphology and molar dimensions. *D. melanotis* showed the most bunodont pattern, with the absence of the longitudinal link between t6 and t9 as

seen on *D. mesomelas*. According to Denys (1994), *D. mystacalis* has smaller teeth than the other two species and a less bunodont dental pattern. Specimens from the Kalahari fall within the morphological and size variations attributed to the three species, but it is possible that the longitudinal crests may appear reduced by wear; therefore, specimens from the Kalahari assemblage were attributed to *D. cf. melanotis*, *D. cf. mesomelas* and *D. mystacalis*.

Three *Steatomys* species are known in Botswana: *S. krebsii*, *S. parvus*, and *S. pratensis*, with an extant overlapping geographical distribution (Monadjem et al., 2015). All of the specimens from the Kalahari assemblage are similar in size and molar conformation and were attributed to *S. pratensis*, which tends to be larger than the two other species (mean global length skull (GLS) = 24,5 mm) (Monadjem et al., 2015). We observed that the height of the mandible at the position of the foramen is also higher in *S. pratensis* than in *S. parvus*, and that these two species show less alternated cusps on their lower first molars than *S. krebsii*, the latter having a more posterior protoconid compared to the paraconid. The cusps of the upper molars of *S. krebsii* also seem better separated and less fused into transverse laminae. On the basis of these criteria, we separated three morphological forms of *Steatomys* from the Okavango Delta assemblage and identified them as *S. cf. krebsii*, *S. pratensis* and *S. parvus*.

*Gerbilliscus* species (excluding the sub-genus *Gerbillurus* species) are difficult to reliably distinguish using dental and cranial characteristics. Besides *G. paeba*, two other species can be found in Botswana: *G. leucogaster* and *G. brantsii*. The horseshoe-shaped anteroconid on the m1 is highly variable depending on the age of the specimen and the wear of the teeth, and does not constitute a reliable diagnostic criterion for distinguishing between the two species. Subtle differences in the shape of the cranium (De Graaff, 1981) may help to separate them, but in the absence of a better diagnostic key, material from the two pellet assemblages were allocated to *Gerbilliscus* sp.

Three *Mastomys* species occur in Botswana: *M. coucha*, *M. natalensis* and *M. shortridgei* (Monadjem et al., 2015). The *Mastomys* from the Kalahari assemblage have been attributed to *M. natalensis* due to the extant distribution of this species, but *M. natalensis*, *M. coucha* and *M. shortridgei* may co-occur in the swampy habitats of northern Botswana. According to Eiseb et al. (2021), the specimens can be distinguished through skull shape, with a longer length and width of the nasal bone for *M. natalensis*, an increased width of the braincase and size of bullae for *M. coucha* and an increased length of the longest palatal foramen for *M. shortridgei*. The Okavango *Mastomys* only evidenced a preserved anterior skull and the available measurements lie within the range of variation of the three species; therefore, the specimens were attributed to *Mastomys* sp. It is possible, however, that *M. shortridgei*, *M. natalensis* and *M. coucha* are present together in the assemblage from the Okavango swamps.

In addition to *M. musculus*, three species of *Mus* (sub-genus *Nannomys*), endemic to southern Africa, can be found in Botswana: *M. indutus*, *M. minutoides* and *M. setzeri*. Based on dental morphology, *M. indutus* displays a highly reduced anterolabial cusp, inducing an acute shape of the m1 anterior extremity, while *M. setzeri* and *M. minutoides* share a more similar m1 shape, with the two anterior cusps being more symmetrical. On the other hand, *M. musculus* can be easily distinguished from the three previous species by its larger teeth and a diagnostic notch on the inner face of the upper incisors. Based on the mandibular dental morphology, all specimens from the Kalahari sample were attributed to *M. indutus*. Identification of the specimens from the Okavango assemblage was not so evident, with specimens displaying a similar size but different upper and lower molar shapes. The upper M1 prelobe of the Okavango *Mus* is relatively well elongated and aligned with the central row of cusps, with the t1 positioned far posterior of the anterior lobe, as well as a slightly reduced upper M3; they show absent or small t3 on the M2. The specific attribution of these specimens remains uncertain; therefore, we chose to keep Denys' (1985) attribution to *M. cf. minutoides* in the absence of a larger sample of *Mus* from this region.

### 3.2. Taphonomic analyses

#### 3.2.1. Anatomical representation

The relative abundance of skeletal parts shows no significant variation between assemblages from the Kalahari and Okavango, the former showing slightly higher mean frequencies of anatomical elements than the latter. We observed a high frequency of “robust” bones like mandibles, humeri, femora and tibiae and a lack of



small bones such as metapodials and phalangias (Table 4, Fig. 4). The anatomical representation profiles were compared with data from several recent works on modern barn owl pellets from South Africa (caves of Makapansgat and Boomplaas: Andrews, 1990; Lamberts Bay, Western Cape: Matthews, 2002) and other countries (Chott Boul, Mauritania: Bruderer and Denys, 1999; Namib-Naukluft Park, Namibia; Morogoro and Lake Natron, Tanzania: Cacciani, 2004). The different representation profiles have a similar general appearance, with high representation being constant for long bones (femora, tibiae, pelvises and mandibles). The distinctly low values obtained from the Boomplaas assemblage could result from a sorting bias, predator misidentification or due to the younger age of the barn owl responsible for the pellet accumulation (See Table 4 and Fig. 4).

### 3.2.2. Fragmentation of bones

Characterization of predator species based on bone fragmentation from pellets was initially developed by Dodson and Wexlar (1979) then Korth (1979), who observed the preferential location of breakages and frequencies for all the long bones. *Tyto alba* has been shown to present a high preservation rate of intact bones. In both assemblages from Botswana, the fragmentation of long bones is low, with an average fragmentation of 4.5% for the pellets from the Kalahari and 3.2% for the Okavango (Table 5). Both assemblages show a very high proportion of intact femora and humeri. Epiphyseal detachments from the proximal and distal parts are frequent, with epiphysis being isolated from the body of the bone. Fragile elements such as ribs are frequently fragmented.

### 3.2.3. Surface alterations of bones and teeth

The digestion pattern observed on femoral heads and incisors (*in situ* and isolated) was similar between the two pellet assemblages, with the majority of remains showing light or no digestion (Table 6). Some incisors or femora showed moderate digestion (Fig. 5), but none of the remains showed heavy digestion. Percentages and grades of digestion in the study assemblages were compared with other *Tyto alba* assemblages from Northern Cape (Matthews, 2002) and other African localities (Bruderer and Denys, 1999; Cacciani, 2004).

### 3.2.4. Synthesis of the taphonomic impact on prey bones and diversity

The results of the taphonomic study show that the two bone assemblages from the Kalahari Desert and the Okavango Delta correspond well to category 1 predation. Despite some differences in the digestion pattern that fits into the variability observed for *Tyto alba* assemblages, we observed similar trends in the anatomical representation and pattern of fragmentation. This provides further evidence that the barn owl has a similar pattern of bone modification throughout the world (e.g., Andrews, 1990; Cacciani, 2004; Denys et al., 2018; Fernandez et al., 2017; Rey-Rodríguez et al., 2019).

The composition of the faunal community reflects the habitat preferences of the barn owl for open countryside landscapes, such as pastureland, grassland, cultivated, etc. (König and Weick, 2010). As this raptor is an active hunter, especially at night, most of the species identified within the two assemblages were crepuscular and/or nocturnal. The faunal lists created using the pellet analysis show significant variations in terms of species composition between the assemblages from the Kalahari and the Okavango (Table 7). This highlights the wide diversity of the barn owl's diet, reflecting environmental differences in the study regions and demonstrates its importance as a taphonomic agent suitable for precise palaeoenvironmental reconstructions.

The barn owl is usually considered to be an opportunistic predator (Andrews, 1990; Andrade et al., 2016); however, the absence of some genera among the Okavango pellets may reflect environmental conditions rather than a hunting trait. Indeed, the swamps and marshes here display a lesser diversity of habitats than the *Acacia* savanna (Denys, 1999).

It is, however, interesting to note the existence of three probable *Steatomys* species in the same pellet assemblage from Okavango and even within the same pellet. The absence of *D. mystacalis* in the assemblage from Okavango, which is found outside the swamps, may indicate that the owl responsible for the assemblage only hunts on the nearby islands and inside the swamps. This can also be deduced from the presence of *C. mariquensis* in the pellets. In contrast, the faunal list from the Kalahari pellets shows a greater diversity, with 11 rodent genera out of the 17 generally found in barn owl pellets (assuming that the upper limit of the prey weight that can be transported by *T. alba* was estimated at 200–250 g; see Andrews, 1990; Dodson and Wexlar, 1979;

Yom-Tov and Wool, 1997). *M. namaquensis*, *M. natalensis* and *R. bechuanae* are commensal species (Monadjem et al., 2015) whose presence in the assemblage may have been due to domestic settlements near the collecting site.

Barn owls often tend to hunt a greater diversity of prey in harsh climates such as deserts and high latitudes and in seasonal conditions when prey are scarce (Taylor, 1994, 2004). Conversely, they are usually more specialist feeders in productive areas with an abundance of available prey. In an archaeological context, variations in species proportions in fossil assemblages accumulated by barn owls thus may serve as an indicator of the ecological structure of the surrounding habitats.

### 3.3. Ecological indices

At least two species of the subfamily Gerbillinae have been identified within the assemblages from the Kalahari and one has been found in the assemblage from the Okavango Delta. The presence of *Gerbilliscus* is important in both assemblages in terms of number of individuals, although in different amounts. In contrast, Murinae is the most abundant subfamily in both assemblages, with the highest proportion in the Okavango assemblage, despite a lower diversity than in the Kalahari. Values from the Gerbillinae/Murinae ratio are shown in Fig. 6, where they are compared with values from a more arid place located in the south of the Kalahari Desert (low sand dunes forming the west bank of the Nossob River in the Kalahari Gemsbok National Park) through trapping stations (Nel and Rautenbach, 1975). The values of the G/M ratio are consistent with the fact that the Kalahari is more arid and open than the Okavango.

A review of published *T. alba* pellet analysis for Sub-Saharan Africa was undertaken to calculate the G/M ratios from different localities, in order to check the reliability of the ratio as an environmental indicator. The compilation of the G/M ratio values is provided in Appendix A.

Considering the results, we were unable to find significant association between the G/M ratio values and landscape openness. For instance, the faunal list of preys published by Vernon (1972) showed ratio variation between 0.25 and 41.2 for the same locality (Cape Province). A similarly contradictory result is seen in Reed (2005), with assemblages from Serengeti, Tanzania, collected in close localities (roosts 7, 24 and 29) for which G/M ratio values vary between 0.9 and 25.33 for a similar grassland environment.

Comparison of the THI (Fig. 7) and the TBI (Fig. 8) shows several variations between the two assemblages, in accordance with the G/M ratio result showing drier conditions for the assemblage from the Kalahari compared to the Okavango. Moreover, the Micromammal Niche index of the rodent taxa from the Kalahari and Okavango (Table 8) ranges from 1.75 (*D. auricularis* associated with dry savanna) to 3.5 (*Thallomys* associated with closer environments). The average niche index is lower for the Kalahari (2.6) than for the Okavango (2.9), giving a consistent picture of the arid Kalahari *versus* the moister Okavango.

In the biome-category analysis (TBI), the two assemblages are dominated by species with tropical and subtropical grasslands biome affinities. The Kalahari pellet assemblage also shows an important score for species with deserts and xeric shrublands biome affinities, while the Okavango assemblage shows a greater score for species with flooded grasslands and savannas biome affinities.

On the other hand, small differences can be observed between the two study assemblages in the habitat-category analysis (THI). Both are almost equally dominated by species with bushland and grassland savanna affinities. The semi-desert habitat tends to be more represented in the Kalahari assemblage, whereas the woodland habitat is more strongly represented in the Okavango Delta.

## 4. Implications for Plio-Pleistocene palaeoenvironmental reconstructions

As the calculation of the G/M ratio is relatively straightforward to estimate and is not restrained by the difficulties of identifying fossil specimens to species, it has been considered a valuable indicator of open or closed habitats for palaeoenvironmental reconstructions (Jaeger, 1976; Dauphin et al., 1994; Fernandez-Jalvo et al., 1998; Reed, 2007; Meunier et al., 2020). In southern Africa, species of Gerbillinae are really abundant in sandy habitats and dry regions (Monadjem et al., 2015). However, ratio values can be affected by numerous and hardly quantifiable factors (for instance, predation habits, seasonality, precipitations, sample size) which make comparisons with other assemblages rarely relevant. The abundance in Sub-Saharan Africa of the many Nesomyidae species that occupy niches similar to those of Muridae is also an important feature that should be

further considered when using this ratio. Moreover, in recent analysis on the modern distribution of the South African *Gerbilliscus*, Campbell et al. (2011) it was noted that *Gerbilliscus* is found in a variety of habitats and is not exclusive to savanna or grassland environments, as is frequently alleged in palaeoenvironmental reconstructions, highlighting the necessity of an accurate assessment of the species modern environmental tolerance limits. In Tanzania, Reed (2003) also questioned the relevance of this method, and found a somewhat surprisingly better correlation in open environments, using a Soricidae/Murinae rather than a Gerbillinae/Murinae ratio, but encountered some difficulties explaining it.

The THI analysis of the Kalahari and Okavango assemblages has yielded results that are consistent with the environmental conditions around barn owl nests. The Kalahari and Okavango faunas are both dominated by species with grassland and bushland habitat affinities and, to a lesser extent, with woodland affinities (Fig. 7). In contrast, the TBI analysis produced using biome affinities returned a more accurate environmental distinction between the two assemblages, with an important wetland component for the Okavango fauna and a marked arid condition for the Kalahari fauna (Fig. 8). As they are heavily reliant upon accurate niche models, taxonomic habitat and biome analyses are expected to improve once new information from modern ecological studies are provided for southern African rodents. In the meantime, explicitly defined habitat categories and standardized methodology provide a common framework for comparison of environmental data between fossil localities and actual landscapes. Numerous archaeological and palaeontological Plio-Pleistocene sites located in southern and south-central Africa may benefit from these new results and reflections enabling a more accurate reconstruction of the hominins palaeoenvironmental context. In South Africa, for instance, micromammal remains are frequently found in abundance in the numerous archaeological caves, making them productive proxies for inferring information about past environmental conditions. Most of the localities that have yielded hominin remains consist of cave sites or rock shelters which provided favourable roosting conditions for owls, often explaining the dense concentrations of fossilized small mammal remains. Avery has contributed substantially to the study of microfauna from many archaeological sites, including the renowned hominin-bearing localities of the Cradle of Humankind in the Sterkfontein Valley (Avery, 1995, 1998, 2001; Avery et al., 2010). Additionally, Matthews's works on the microfauna from several fossil bearing palaeontological and archaeological west coast sites dating from the Mio-Pliocene (Matthews, 1999; Matthews et al., 2007) and from Late Pleistocene to Holocene sites located in the south coast region of the Palaeo-Agulhas Plain (Matthews et al., 2005, 2009, 2011, 2019) have provided important insights on the evolution of environments and small mammal communities of South Africa. The taphonomic analysis carried out on these fossil cave and rock shelter assemblages tend to incriminate a category 1 predator, such as *T. alba* or *T. capensis*, showing the appeal of an exhaustive taphonomic referential for these predators. Yet, there are still a significant number of fossil assemblages from notorious hominin-bearing sites waiting for detailed microfaunal analysis.

In contrast to South Africa, which yielded good small mammal records, only a few micromammalian fossil assemblages have been provided for Plio-Pleistocene periods in Botswana. This could be partly due to the limited number of field surveys in Botswana compared to South Africa, raising hope that more sites remain to be found. The few sites that have yielded micromammalian fossil material are from the northwest part of the country: we can cite the archaeological sites of Drotsky's Cave (Robbins and Murphy, 1996) and Tsodilo Hills (Robbins and Murphy, 2000), although the micromammalian material is too scarce to elicit detailed palaeoenvironmental information. Pickford et al. (1988) compiled a diverse provisory list of micromammal species from a series of five Plio-Pleistocene cave fillings in Ngamiland. As it stands, the published faunal list requires reanalysis using current taxonomic methods; however, according to the authors, these fillings contain rich accumulations of micromammals which probably represent owl-accumulated coprocoenoses, suggesting the area has a high potential for tracking environmental changes and species dispersal from small mammals.

## 5. Conclusion and perspectives

This study presents the first combined taxonomic and taphonomic analysis of *Tyto alba* pellets in Botswana. It increases the modern referential for this predator in southern Africa, and brings additional data for the wildlife inventory at a local scale for the central Kalahari Desert and the Okavango Delta. Additionally, this study enhances the reference samples for estimating the current biodiversity of micromammal communities in the swamps of the Okavango Delta, an area which has received particularly scant attention.

The assemblage from central Kalahari thornveld is dominated by gerbils (*Gerbilliscus*), desert pigmy mice (*Mus indutus*) and the dendromurine *Steatomys*, and displays a high species diversity. The floodplains of the Okavango Delta are characterized by multimammate mice (*Mastomys*), pigmy mice (*Mus cf. minutoides*) and gerbils (*Gerbilliscus*). Predator bias linked to the hunting preferences and feeding processes of *Tyto alba* appeared to have little impact on the environmental reconstructions; therefore, the taphonomic analysis provides further evidence that *T. alba* assemblages are fairly representative of the environmental conditions in which the owl lives.

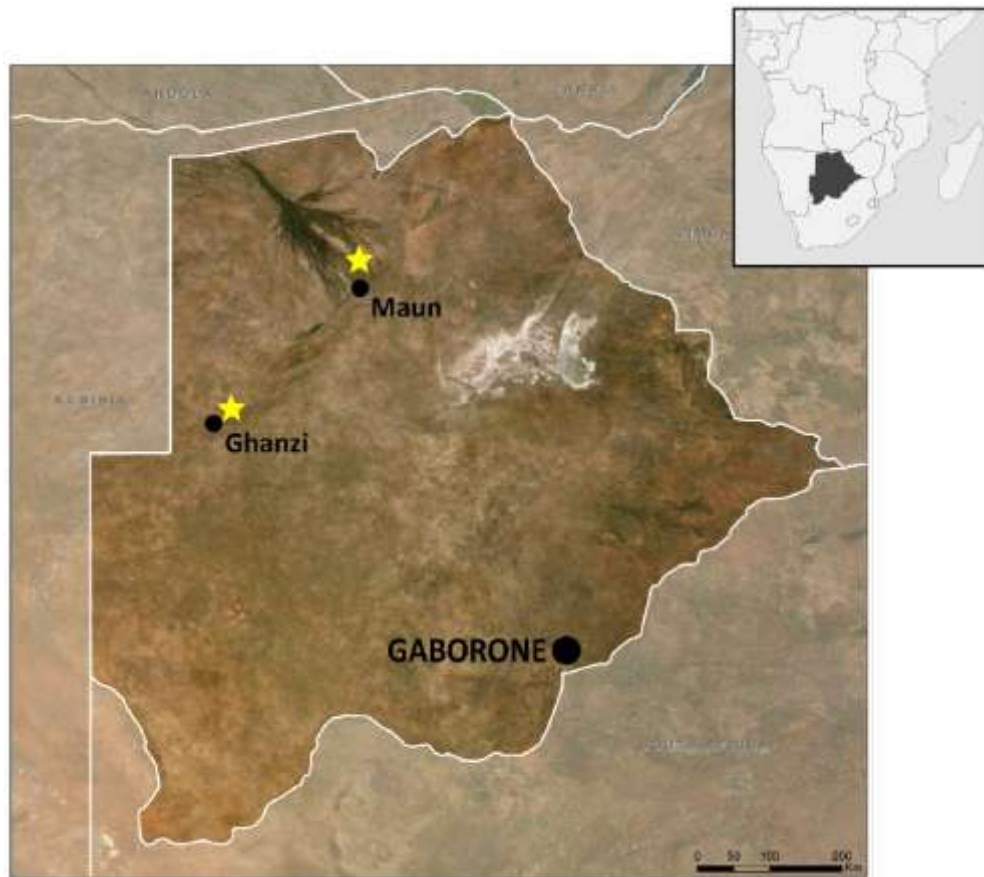
As owls are major accumulators of small vertebrates in palaeontological and archaeological sites, such works provide an essential prerequisite for studying past environments based on micromammal remains. One objective of the study was to examine the accuracy of palaeoenvironmental analyses based on micromammals for this region. Ecological indices based on the presence/absence and relative frequencies of small mammals were calculated for the two assemblages, providing results that were consistent with the observed habitats. As a taxonomic ratio, the Gerbillinae/Murinae ratio failed to deliver a strong correlation between the high scores and open habitats. In some cases, it illustrates certain trends in environmental shift at a small geographic or temporal scale, but it does not constitute a reliable or accurate method for describing actual environments and, therefore, past landscapes. The Taxonomic Habitat and Biome Indices clearly reflect the ecological flexibility of small mammals in their habitats. Analyses of the two study assemblages yielded distinct environmental signals for assemblages with similar taphonomic agency, yet the results obtained were highly dependent on the habitat classes and the niche models that were employed.

By the end of the 20th century, micromammals had been abundantly used to deduce environmental conditions during the Pliocene and the Pleistocene in southern Africa. Since then, however, progress in various fields such as ecology, systematics or taphonomy have challenged some of these earlier results. Micromammal studies therefore require new methodologies and integrative approaches inspired by other fields of studies for a greater accuracy. Amongst others, there are many ways statistical, computer-aided analysis could help improve reconstructions of palaeoenvironments around archaeological and palaeontological sites and at a more global scale.

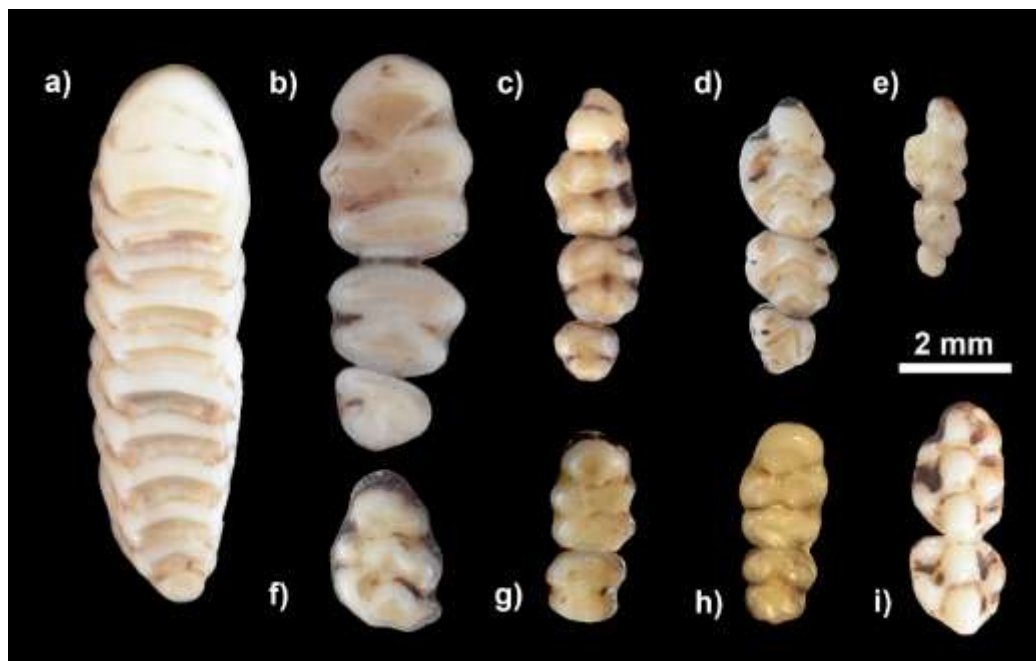
## **Acknowledgments**

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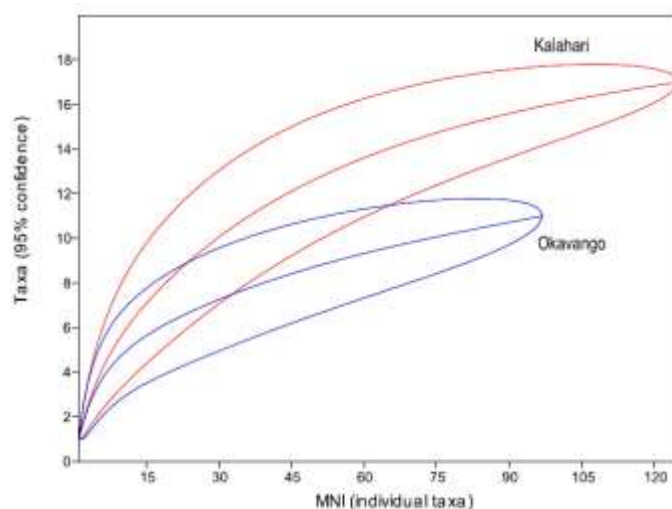
## Figures



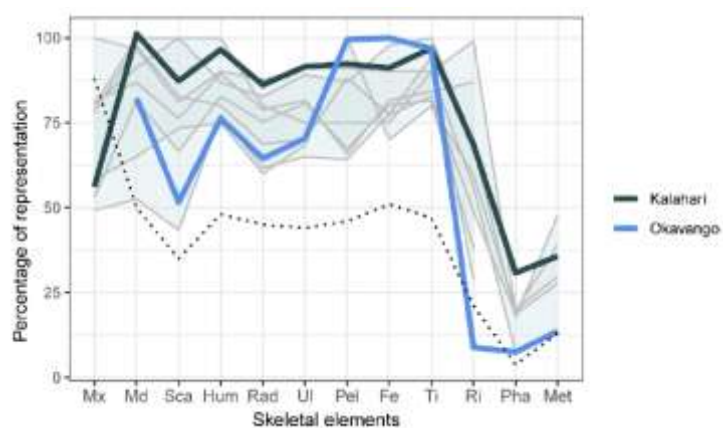
**Fig. 1.** Geographic location of the pellet collecting sites (yellow stars). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



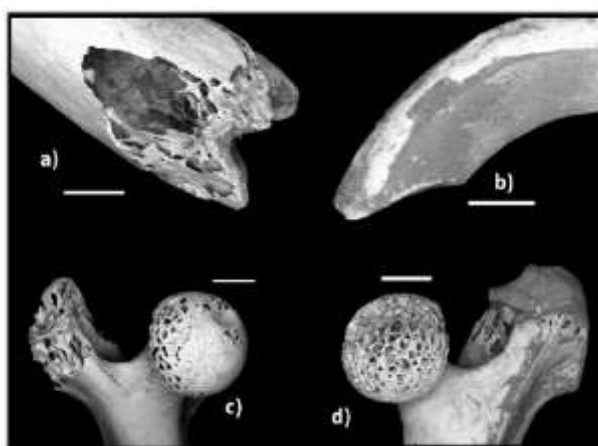
**Fig. 2.** Size comparison of some rodent upper left molars from the two study pellet assemblages. Specimens came from the Okavango Delta (a, d, i) and the Kalahari Desert (b, c, e, f, g, h). a) M1M2M3 *Otomys angoniensis*; b) M1M2M3 *Gerbilliscus brantsii/leucogaster*; c) M1M2M3 *Saccostomus campestris*; d) M1M2M3 *Mastomys* sp.; e) *Mus indutus*; f) M1 *Aethomys chrysophilus*; g) M1M2 *Desmodillus auricularis*; h) M1M2 *Gerbilliscus paeba*; i) M1M2 *Gerbilliscus paeba*. Scale: 2 mm.



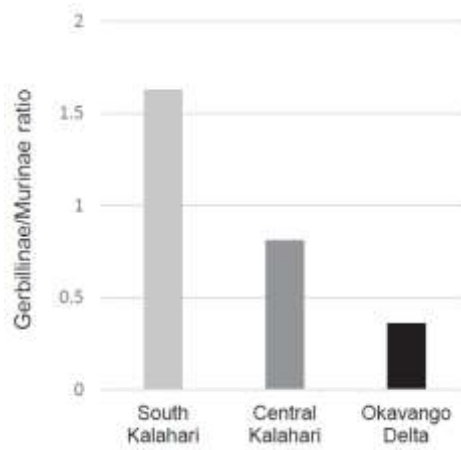
**Fig. 3.** Point by point individual rarefaction curves for the Okavango and Kalahari micromammal assemblages, with estimated species richness and 95% confidence interval.



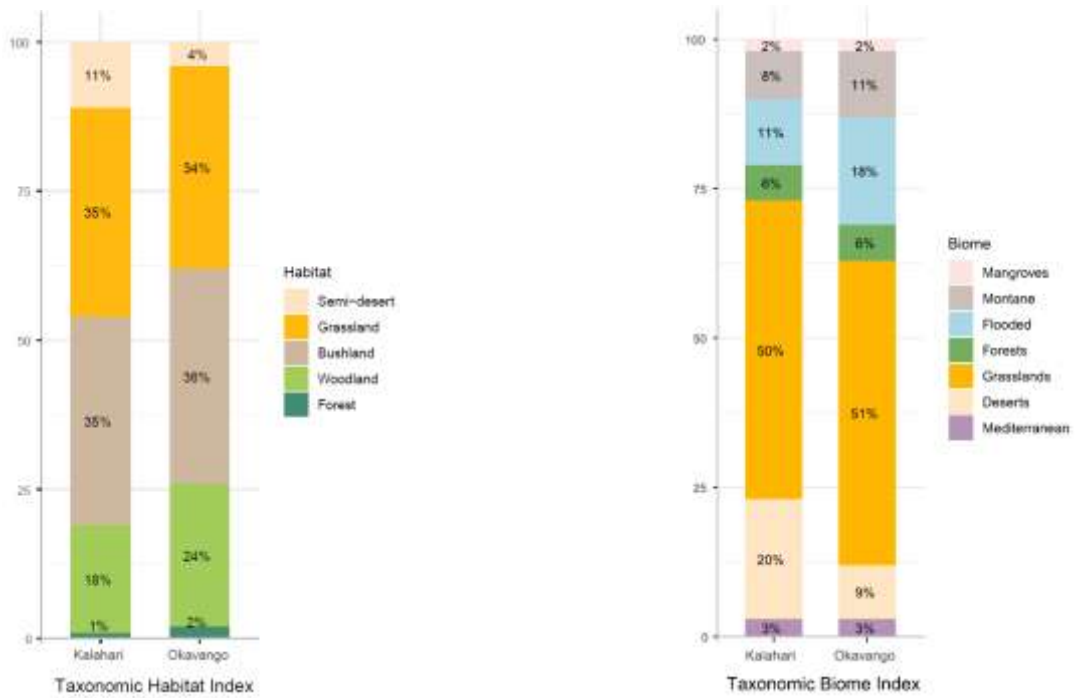
**Fig. 4.** Anatomical representation of the rodent remains from the Kalahari and Okavango pellet assemblages (this work). Shaded area with grey lines in the background represent values for other *T. alba* assemblages from Africa (Andrews, 1990; Matthews, 2002; Cacciani, 2004). The dotted line represents distinctly low values for *T. alba* assemblage from Boomplaas, South Africa (Andrews, 1990). Detailed values are shown in Table 4.



**Fig. 5.** Example of rodent remains from Kalahari pellet assemblage with taphonomic alterations: a) puncture mark resulting from beak or claw perforation; b) rodent upper incisor displaying light to moderate digestion, with partially dissolved enamel all along the body of the tooth and modified dentine; c) rodent femur with light to moderate digestion; d) rodent femur with moderate digestion. Pictures were taken using a Scanning Electron Microscope. Scale = 1 mm.



**Fig. 6.** Gerbillinae/Murinae ratio calculated using the pellet assemblages from Kalahari and Okavango (this work). Data for low dune in the Kalahari Gemsbok National Park came from Rautenbach et al. (1975).



**Fig. 7.** Taxonomic Habitat Index (THI) based on the presence/absence and ecological preferences of the micromammal taxa of the two study assemblages. Column numbers correspond to the habitat score percentage.

**Fig. 8.** Taxonomic Biome Index (TBI) based on the presence/absence and ecological preferences of the micromammal taxa of the two study assemblages. Column numbers correspond to the biome score percentage.

## Tables

**Table 1.** Characteristics of the vegetation components associated with the current distinct ecoregions and biomes of Botswana. Data for the vegetation description and sources for ecoregions came from the website [www.worldwildlife.org/science](http://www.worldwildlife.org/science).

Biome	Ecoregion	Vegetation description
Tropical and subtropical grasslands, savannas, and shrublands	Kalahari Acacia-Baikiaea woodlands	Deciduous trees and bush savanna cover most of the ecoregion, with shrub savanna on plains between the sand ridges
	Southern Africa bushveld	Mixed or mopane savanna that varies from a dense, short bushveld to an open tree savannah
	Zambeian Baikiaea woodlands	Mosaic of dry deciduous <i>Baikiaea plurijuga</i> (Zambian teak) dominated forest, thicket and secondary grassland
	Zambeian and mopane woodlands	Dominance of the tree <i>Colophospermum mopane</i> that often forms pure stands to the exclusion of other species, with varying herbaceous component according to soil conditions
Flooded grasslands and savannas	Zambeian flooded grasslands	Patches of wetlands seasonally or permanently flooded characterized by a mosaic of edaphic grassland and semi-aquatic vegetation
	Zambeian halophytics	Saline desert almost devoid of macrophytic vegetation; the dominant plant form in the pans is a thin layer of algae, which covers the surface during the rainy season
Deserts and xeric shrublands	Kalahari xeric savanna	Open savanna with grasses, bushes and small trees in less arid areas; in drier areas, the dunes are sparsely populated by broom bushes and dune reeds

**Table 2.** Faunal list of the microvertebrates identified in pellet assemblages from the Kalahari and Okavango Delta, expressed in minimal number of individuals (MNI).

Species				Kalahari	Okavango
RODENTIA	Bathyergidae	Bathyerginae	<i>Fukomys damarensis</i>	1	
	Muridae	Gerbillinae	<i>Desmodillus auricularis</i>	1	
			<i>Gerbilliscus braneti/leucogaster</i>	32	20
			<i>Gerbilliscus (Gerbillurus) parha</i>	6	
		Murinae	<i>Aethomyz chrysophilus</i>	2	
			<i>Mastomys natalensis</i>	4	
			<i>Mastomys</i> sp.		33
			<i>Micaelomys namaquensis</i>	2	
			<i>Mus indutus</i>	32	
			<i>Mus cf. minutoides</i>		20
			<i>Otomys angolensis</i>		1
			<i>Rhabdomys bechuanae</i>	1	
			<i>Thalpomys</i> sp.		1
			Indeterminate murid	5	
	Nesomyidae	Cricetomyinae	<i>Saccostomus campestris</i>	3	
		Dendromurinae	<i>Dendromus cf. melanotis</i>	3	11
			<i>Dendromus cf. mesomelas</i>	4	
			<i>Dendromus myzocelis</i>	1	
			<i>Stenomys cf. kiribai</i>		1
			<i>Stenomys parvus</i>		3
			<i>Stenomys pratensis</i>	20	3
			<i>Stenomys</i> sp.		1
Total rodents				117	94
MACROSCELIDEA	Macroscelididae		<i>Elephantulus intayi</i>	7	
EULIPOTYPHLA	Soricidae	Crocidurinae	<i>Crocidura fuscanserina</i>	2	1
			<i>Crocidura hirta</i>	4	
			<i>Crocidura mariquensis</i>		3
Total micromammals				130	98
PASSERIFORMES			Passeriformes, indet.	1	
SQUAMATA			Lacertilis indet.	3	
COLEOPTERA			Coleoptera indet.	1	
Total preys				135	98



**Table 3.** Shannon Diversity index ( $H'$ ), Simpson index ( $E$ ) and Equitability index ( $J$ ) applied to the study pellet samples from the Kalahari and Okavango Delta.

Index	Kalahari	Okavango
$H'$	2.16	1.78
$E$	0.93	0.78
$J$	0.76	0.74

**Table 4.** Percentage of representation (PR) of rodent long bones from the pellet assemblages of the Kalahari and Okavango (this work). Additional data on PR for *Tyto alba* comes from Matthews (2002) for Western Cape 1, 2, 3; Andrews (1990) for Makapansgat and Boomplaas; Bruderer & Denys (1999) for Mauritania; Cacciani (2004) for Namibia and Tanzania 1, 2.

Site	Mj	Mx	Scn	Hum	Rad	Ul	Pel	Fe	Ti	Ri	Plu	Met
Kalahari	101.2	56.1	87.3	96.5	86.1	91.6	92.3	91.2	96.9	68.5	30.8	35.7
Okavango	82.2		51.6	76.3	64.5	70.4	99.5	100	96.8	8.9	7.5	13.6
Western Cape 1	91.3	80.4	100	86.9	82.6	89.1	86.9	97.0	100	66.6	17.8	47.8
Western Cape 2	65	58.3	73.3	75	60	68.3	100	70	90	59.8	20.1	29.7
Western Cape 3	100	80	100	100	80	75	75	75	90	99.1	19.7	39
Makapansgat	97.7	70.1	82.8	80.1	68.8	70	88.3	77.3	82.8	48.9	18.6	27.7
Boomplaas	50	88	35	48	45	44	46	51	47	21.2	3.8	13.0
Mauritania	96.7	100	81.1	90.2	87.7	91	91	98.2	90.2	56.2	7.5	13.6
Namibia	81.5	53	66.6	82.7	75.3	80.0	67.3	80.2	81.5	38.1	N/A	N/A
Tanzania 1	86.8	81.6	76.3	89.5	78.9	81.6	65.8	81.6	84.2	86.9	N/A	N/A
Tanzania 2	52.5	49.2	43.4	77.5	61.7	65	64.2	77.5	94.2	28.8	N/A	N/A

**Table 5.** Percentage of fragmentation (PF) of rodent long bones from the pellet assemblages of the Kalahari and Okavango (this work). NR: number of remains, PF: percentage of fragmentation (NR fragmented/NR total x100). Additional data on PF for *Tyto alba* comes from Dodson and Wexlar (1979) and Andrews (1990).

Fragmentation	Kalahari (This work)	Okavango (This work)	Dodson & Wexlar (1979)	Andrews (1990)
<b>Humerus</b>				
Complete (NR)	236	90	25	
Fragmented (NR)	9	6	3	
PF	3.8%	5.0%	10.7%	1%
<b>Femur</b>				
Complete (NR)	220	157	24	
Fragmented (NR)	9	9	-	
PF	3.9%	5.4%	0%	3%
<b>Tibia</b>				
Complete (NR)	131	169	17	
Fragmented (NR)	10	2	6	
PF	7.6%	1.2%	26.1%	3%
<b>Average PF</b>	<b>4.5%</b>	<b>3.2%</b>	<b>12%</b>	<b>2.3%</b>

**Table 6.** Grades and percentages of digestion (PD) of rodent femoral heads and incisors (*in situ* and isolated). NR: number of remains, PD: percentage of digestion. Additional data on PD for *Tyto alba* come from Andrews (1990), Matthews (2002) for the Northern Cape, Bruderer and Denys (1999) and Cacciani (2004) for the other localities.

	Kalahari (This work)	Okavango (This work)	Mauritania (Bruderer & Denys, 1999)	Namibia (Cacciani, 2004)	Tanzania (Cacciani, 2004)	Northern Cape (Matthews, 2002)	<i>Tyto alba</i> (Andrews, 1990)
<b>Femoral heads</b>							
No digestion	92	75	53.6	83.8	93.5	N/A	89
Light digestion	5.6	23.2	30	12.3	6.5		
Moderate digestion	2.2	1.9	10.4	3.0			
Heavy digestion		1.9	6				
<b>PD</b>	<b>7.8</b>	<b>27</b>	<b>26.4</b>	<b>16.2</b>	<b>6.5</b>	<b>N/A</b>	<b>11</b>
<b>Incisors</b>							
No digestion	83.5	72	72.4	90.7	86.9	90	95
Light digestion	10.3	26.9	24.4	9.3	13.1	7.5	
Moderate digestion	6.2	1.1	3.2			2.1	
Heavy digestion						0.3	
<b>PD</b>	<b>16.5</b>	<b>28</b>	<b>27.6</b>	<b>9.3</b>	<b>13.1</b>	<b>10</b>	<b>5</b>

**Table 7.** Faunal composition of the two pellet assemblages from Botswana. Comparison is made with the faunal list created by Monadjem et al. (2015) that includes rodent species occurring in the central Kalahari and the Okavango Delta susceptible of being hunted by *Tyto alba*.

Central Kalahari		Okavango Delta	
Modern inventory (Monadjem et al. 2015)	Study assemblage (this work)	Modern inventory (Monadjem et al. 2015)	Study assemblage (this work)
<i>Fukomys</i>	<i>Fukomys</i>	<i>Fukomys</i>	
<i>Graphiurus</i>		<i>Graphiurus</i>	
<i>Desmodillus</i>	<i>Desmodillus</i>	<i>Desmodillus</i>	
<i>Gerbilliscus</i>	<i>Gerbilliscus</i>	<i>Gerbilliscus</i>	<i>Gerbilliscus</i>
<i>Aethomya</i>	<i>Aethomya</i>	<i>Aethomya</i>	
		<i>Dasyomys</i>	
<i>Lemnicomya</i>		<i>Lemnicomya</i>	
<i>Malacothrix</i>			
<i>Mastomys</i>	<i>Mastomys</i>	<i>Mastomys</i>	<i>Mastomys</i>
<i>Micaelanys</i>	<i>Micaelanys</i>	<i>Micaelanys</i>	
<i>Mus</i>	<i>Mus</i>	<i>Mus</i>	<i>Mus</i>
		<i>Pelomys</i>	
<i>Rhabdomys</i>	<i>Rhabdomys</i>	<i>Rhabdomys</i>	
<i>Thalassomys</i>		<i>Thalassomys</i>	<i>Thalassomys</i>
<i>Zelotomys</i>		<i>Zelotomys</i>	
		<i>Otomys</i>	<i>Otomys</i>
<i>Saccostomus</i>	<i>Saccostomus</i>	<i>Saccostomus</i>	
<i>Dendromus</i>	<i>Dendromus</i>	<i>Dendromus</i>	<i>Dendromus</i>
<i>Stenomys</i>	<i>Stenomys</i>	<i>Stenomys</i>	<i>Stenomys</i>

**Table 8.** Taxonomic Habitat Index (THI) scores, niche index values and habitat summaries for the micromammals present in the study assemblages. THI data are derived from Monadjem et al. (2015) and Wilson et al. (2016, 2017).

	Forest 5	Woodland 4	Bushland 3	Grassland 2	Semi-desert 1	Niche	Habitat
<i>A. chrysophilus</i>		0.3	0.32	0.33	0.05	2.87	Dry-moist savanna
<i>C. fuscoviridis</i>		0.3	0.3	0.3	0.1	2.8	Dry-moist savanna
<i>C. hirtus</i>		0.2	0.4	0.4		2.8	Grassl./Dry savanna
<i>C. marquetensis</i>		0.3	0.4	0.3		3	Wetlands
<i>D. melanotis</i>	0.05	0.3	0.3	0.25	0.1	2.95	Grassl./Dry-moist sav.
<i>D. mesomelas</i>	0.05	0.3	0.35	0.3		3.1	Grassl./Dry-moist sav.
<i>D. mystacalis</i>	0.05	0.25	0.35	0.35	0	3	Grassl./Dry-moist sav.
<i>D. auricularis</i>			0.25	0.25	0.5	1.75	Dry savanna
<i>E. inaffi</i>			0.3	0.3	0.4	1.9	Dry sav./Semi-desert
<i>F. damarensis</i>			0.33	0.33	0.33	1.98	Grassl./Dry savanna
<i>G. brunsi/leucogaster</i>			0.45	0.45	0.1	2.35	Grassl./Dry savanna
<i>G. poebei</i>			0.4	0.4	0.2	2.2	Sandy ground
<i>M. infusus</i>		0.2	0.4	0.4		2.8	Dry savanna
<i>M. minutoides</i>	0.15	0.275	0.3	0.275		3.3	Ubiquitous
<i>M. namaquensis</i>	0.1	0.3	0.3	0.3		3.2	Dry savanna
<i>M. natalensis</i>		0.33	0.33	0.33		2.97	Dry-moist savanna
<i>O. angolensis</i>			0.25	0.75		2.25	Moist grasslands
<i>R. bochumae</i>		0.2	0.4	0.3	0.1	2.7	Dry savanna
<i>S. campestris</i>		0.33	0.33	0.33		2.97	Dry savanna
<i>S. krebsii</i>		0.3	0.4	0.3		3	Shrubl./Grasslands
<i>S. parvus</i>	0.05	0.3	0.3	0.35		3.05	Grassl./Dry savanna
<i>S. pratensis</i>		0.2	0.3	0.5		2.7	Grassl./Dry savanna
<i>Thalassomys</i>		0.5	0.5			3.5	Dry-moist savanna

**Appendix A.** Total small mammals and rodent diversity for modern predation assemblages of *Tyto alba* from Sub-Saharan Africa, with values of the Gerbillinae/Murinae ratio. N gerb: number of Gerbillinae species. N mur: Number of Murinae species.

Study	Country	Region	Site	Vegetation	Total MNI	MNI rodents	N gerb	N mur	MNI gerb	MNI mur	G/M ratio
Wimberborn 1996	Nazibia	Kenese	Etoha	Savanna woodland	95		3	3			
Laurie 1971	Tanzania	Serengeti	Olonekan	Acacia woodland	346	151	0	8	0	92	0
		Serengeti	Masai	Open plains and woodlands	512	320	0	8	0	228	0
		Serengeti	Sierba	Open plains	100	49	1	1	3	34	0.09
Vernon 1972	South Africa	Transvaal	Natal 1	Bushveld	235	136	0	3	0	109	0
		Transvaal	Natal 2	Cultivated farms in the bushveld	451	453	0	5	0	427	0
		Transvaal	Natal 3	Farm lands in the bushveld	130	36	0	3	0	76	0
		Transvaal	Natal 4	Bushveld	68	59	0	3	0	38	0
		Transvaal	Natal 5	Thornveld	146	127	0	2	0	53	0
		Western Cape	Cape Province 6	Deciduous shrubland	340	314	2	3	141	3	47
		Western Cape	Cape Province 7	Semi-desert vegetation	219	211	2	2	206	6	41.2
		Eastern Cape	Cape Province 8	Karoo thicket vegetation	36	24	1	3	4	16	0.25
		Northern Cape	Cape Province 9	Deciduous shrubland	152	148	1	3	40	25	1.8
		Northern Cape	Cape Province 10	Molopo riverbank	67	59	2	2	52	6	10.4
		Western Cape	Cape Province 11	Residual and scrub vegetation	119	85	1	3	16	8	2
		Transvaal	Transvaal 22	Sweet thornveld	427	382	1	4	51	223	0.23
		Transvaal	Transvaal 23	Rocky savanna	644	573	1	5	33	357	0.09
		Transvaal	Transvaal 24	Savanna	278	229	1	4	23	147	0.16
		Transvaal	Transvaal 25	Grassland	891	728	2	5	181	273	0.59
		Transvaal	Transvaal 26	Grassland	162	142	1	8	20	111	0.18
		Transvaal	Transvaal 27	Grassland	120	106	1	2	32	41	0.7
		Transvaal	Transvaal 28	Acacia woodland	220	221	1	1	4	191	0.02
Dean 1973	South Africa	Transvaal	Transvaal	Grassland	656	505	1	4	35	519	0.07
Nel & Raotesbach 1978	Nazibia	South	Kalahari	Arki shrub savanna	209	209	3	4			1.63
Demeter 1978	Nigeria	Kalbari	Lower Juma		54		1	4			
Brails 1981	South Africa	Transvaal	Swarthkranz	Grassland	130	122	1	3	4	98	0.04
Arvey 1982	South Africa	Western Cape	ABKA	Dense evergreen shrubland. Old field with short grass	74	64	1	2	46	3	15.33
		Western Cape	ABKE	Dense evergreen shrubland. Old field with short grass	460	367	1	2	49	26	1.02
		Western Cape	BTY	Old fields with short grass and scattered shrubs	529	337	1	2	11	13	0.05
		Western Cape	GBKA	Deciduous shrubland. Mainly old fields with short grass	709	533	1	2	82	82	1.32
		Western Cape	GREB	Dense evergreen mixed shrubland. Mainly old fields with short grass and scattered shrubs	2770	2053	1	2	177	126	1.42
Cox 1984	Zimbabwe	Mtshabele	Belavaya		277		1	5			
Larsson 1985	South Africa	Limpopo	Makapungut				1	6			
Brooker & Denny 1999	Mozambique	Sabai region	Choto Road	Hedophytic vegetation	61	58	8	3	40	19	
Be et al 2000	Senegal	Saint-Louis region	Crocodile	Herbaceous wetland	199	180	2	3	3	172	0.02
		Saint-Louis region	PC	Herbaceous wetland	140	135	2	2	4	123	0.03
		Saint-Louis region	Gaouie	Herbaceous wetland	77	70	2	2	2	60	0.02
		Saint-Louis region	Debarcades	Herbaceous wetland	55	56	1	2	13	41	0.32
		Saint-Louis region	Djoudi 1	Herbaceous wetland	55	52	1	2	2	51	0.04
		Saint-Louis region	Djoudi 2	Herbaceous wetland	38	35	1	2	1	33	0.03
Lekone et al 2001	Nigeria	Kaduna State	Kagoro Hill A	Southern Guinea Savanna	60	46	1	2	2	44	0.06
		Kaduna State	Kagoro Hill B	Southern Guinea Savanna	54	54	1	2	11	42	0.26
		Zaria	Sankuru C	Northern Guinea Savanna	140	133	1	3	90	43	2.09
		Zaria	Sankuru D	Northern Guinea Savanna	120	121	1	3	85	46	1.86
		Yobe State	Nigru E	Domin savanna	167	67	1	3	18	49	0.37
		Lake Chad	Nigru F	Sabai savanna	179	160	0	3	0	189	0
Cervino 2004	Nazibia	Bunga	Nasubi Naasibi Park						64		
Reid 2005	Tanzania	Arusha	Lake Natron		42	42		11	23	0.39	
	Tanzania	Serengeti	Serengeti 4	Grassland	275	186		9	94	0.08	
		Serengeti	Serengeti 13	Wooded grassland (savanna)	223	158		19	44	0.45	
		Serengeti	Serengeti 3	Wooded grassland	253	127		4	71	0.08	
		Serengeti	Serengeti 7	Grassland	277	201		54	60	0.9	
		Serengeti	Serengeti 24	Grassland	294	221		95	18	5.94	
		Serengeti	Serengeti 29	Grassland		164		182	5	25.33	
		Serengeti	Serengeti 44	Woodland/forest	82	55		3	41	0.07	
Thiam et al 2013	Senegal	Fatic region	Senegal River 1999	Semi-arid grassland	34			17	17	1	
		Fatic region	Senegal River 1991	Semi-arid grassland	747			741	6	133.5	
		Fatic region	Senegal River 1992	Semi-arid grassland	846			777	171	4.24	
		Fatic region	Senegal River 1993	Semi-arid grassland	140			18	124	0.12	
		Fatic region	Senegal River 1999	Semi-arid grassland	975			800	90	9.07	
		Fatic region	Senegal River 1999	Semi-arid grassland	228			181	65	2.81	
		Fatic region	Senegal River 2002	Semi-arid grassland	708			660	113	8.86	
Nshupungu & Lubabwa 2017	Nazibia	Zambezi region	Katima Mulilo - Dry season				2	136	151	0.99	
		Zambezi region	Katima Mulilo - Wet season				2	110	48	2.99	
Present study	Botswana	Ghanzi	Kliskat	Kalahari thornveld	126	112		39	48	0.81	
		Nyemanzhe	Orange	Wetland	98	94		20	68	0.28	

**Appendix B.** Taxonomic Habitat Index (THI) scores for the micromammals present in the study assemblages.

<b>Kalahari</b>	<b>Forest</b>	<b>Woodland</b>	<b>Bushland</b>	<b>Grassland</b>	<b>Semi-desert</b>
<i>A. chrysophilus</i>		0.3	0.32	0.33	0.05
<i>C. fuscomurina</i>		0.3	0.3	0.3	0.1
<i>C. hirta</i>		0.2	0.4	0.4	
<i>D. melanotis</i>	0.05	0.3	0.3	0.25	0.1
<i>D. mesomelas</i>	0.05	0.3	0.35	0.3	
<i>D. mystacalis</i>	0.05	0.25	0.35	0.35	
<i>D. auricularis</i>			0.25	0.25	0.5
<i>E. intuft</i>			0.3	0.3	0.4
<i>F. damarensis</i>			0.33	0.33	0.33
<i>G. brantsii</i>			0.45	0.45	0.1
<i>G. leucogaster</i>			0.45	0.45	0.1
<i>G. paeba</i>			0.4	0.4	0.2
<i>M. indutus</i>		0.2	0.4	0.4	
<i>M. namaquensis</i>	0.1	0.3	0.3	0.3	
<i>M. natalensis</i>		0.33	0.33	0.33	
<i>R. bechuanae</i>		0.2	0.4	0.3	0.1
<i>S. campestris</i>		0.33	0.33	0.33	
<i>S. pratensis</i>		0.2	0.3	0.5	

<b>Okavango</b>	<b>Forest</b>	<b>Woodland</b>	<b>Bushland</b>	<b>Grassland</b>	<b>Semi-desert</b>
<i>C. fuscomurina</i>		0.3	0.3	0.3	0.1
<i>C. mariquensis</i>		0.3	0.4	0.3	
<i>D. melanotis</i>	0.05	0.3	0.3	0.25	0.1
<i>G. brantsii</i>			0.45	0.45	0.1
<i>G. leucogaster</i>			0.45	0.45	0.1
<i>M. minutoides</i>	0.15	0.275	0.3	0.275	
<i>M. natalensis/shortridgei</i>		0.33	0.33	0.33	
<i>O. angoniensis</i>			0.25	0.75	
<i>S. krebsii</i>		0.3	0.4	0.3	
<i>S. parvus</i>	0.05	0.3	0.3	0.35	
<i>S. pratensis</i>		0.2	0.3	0.5	
<i>Thallomys sp.</i>		0.5	0.5		

**Appendix C.** Taxonomic Biome Index (TBI) scores for the micromammals present in the study assemblages.

<b>Kalahari</b>	<b>Mediterranean</b>	<b>Deserts</b>	<b>Grasslands</b>	<b>Forests</b>	<b>Flooded</b>	<b>Montane</b>	<b>Mangroves</b>
<i>A. chrysophilus</i>		0.2	0.4	0.1	0.2	0.1	
<i>C. fuscumurina</i>		0.1	0.6		0.1	0.1	0.1
<i>C. hirta</i>		0.1	0.6	0.1	0.1		0.1
<i>D. melanotis</i>	0.1	0.1	0.3	0.15	0.2	0.1	0.05
<i>D. mesomelas</i>	0.1		0.4	0.1	0.2	0.2	
<i>D. mystacalis</i>			0.5	0.1	0.2	0.2	
<i>D. auricularis</i>		0.55	0.45				
<i>E. intufi</i>		0.35	0.65				
<i>F. damarensis</i>		0.2	0.6		0.2		
<i>G. brantsii</i>		0.2	0.5		0.1	0.2	
<i>G. leucogaster</i>		0.2	0.6	0.05		0.1	0.05
<i>G. paeba</i>	0.2	0.4	0.4				
<i>M. indutus</i>		0.2	0.45		0.2	0.15	
<i>M. namaquensis</i>	0.15	0.25	0.4		0.05	0.15	
<i>M. natalensis</i>		0.05	0.4	0.4	0.1		0.05
<i>R. bechuanae</i>		0.55	0.45				
<i>S. campestris</i>		0.2	0.5	0.15	0.15		
<i>S. pratensis</i>			0.75		0.15	0.1	

<b>Okavango</b>	<b>Mediterranean</b>	<b>Deserts</b>	<b>Grasslands</b>	<b>Forests</b>	<b>Flooded</b>	<b>Montane</b>	<b>Mangroves</b>
<i>C. fuscumurina</i>		0.1	0.6		0.1	0.1	0.1
<i>C. mariquensis</i>			0.4	0.1	0.4	0.1	
<i>D. melanotis</i>	0.1	0.1	0.3	0.15	0.2	0.1	0.05
<i>G. brantsii</i>		0.2	0.5		0.1	0.2	
<i>G. leucogaster</i>		0.2	0.6	0.05		0.1	0.05
<i>M. minutoides</i>	0.1		0.4	0.2	0.1	0.15	0.05
<i>M. natalensis/shortridgei</i>		0.025	0.4	0.2	0.35		0.025
<i>O. angoniensis</i>			0.45		0.35	0.2	
<i>S. krebsii</i>	0.1	0.1	0.4		0.2	0.2	
<i>S. parvus</i>		0.1	0.75		0.15		
<i>S. pratensis</i>			0.75		0.15	0.1	
<i>Thallomys sp.</i>		0.3	0.55	0.025	0.05	0.05	0.025

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