Taphonomic implications of roosting behavior and trophic habits in two species of African owl

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Abstract

As some of the most common predators of micromammals, owls are implicated in the formation of many fossil assemblages. Actualistic research on owl-accumulated assemblages has tended to focus on owls roosting in caves. Comparatively few data are available on the roosting behavior, and prey preference of owls in open habitats. This paper presents observations on the roosting and prey habits of two sympatric species of owl in the Serengeti region of northern Tanzania, the Barn Owl, *Tyto alba affinis*, and the Spotted Eagle Owl, *Bubo africanus*. The Barn Owl and Spotted Eagle Owl are found to segregate by roosting habit, with Barn Owls occupying cavity roosts and Eagle Owls appearing on the ground or in tree crowns. Previous studies comparing these two species suggested a close similarity in trophic habits. A comparison of large samples (MNI = 1012) at cavity and exposed roosts shows identical taxonomic representation, though differences are found in the relative abundance of some taxa and significant differences in prey body mass.
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1. Introduction

Micromammals (< 500 g) are widely used as paleo-environmental indicators at archeological and paleontological sites [15,37,36,55,63,20,4,24,67]. Their occurrence at these sites is often mediated by predators that can have a strong taphonomic influence on an assemblage [44,7]. Taphonomic stability is a vital assumption when exploring environmental change – is faunal change a function of climate or a shift in taphonomic mode, such as the accumulating agent? It is this question that has made predator diagnosis a standard part of taphonomic research in zooarcheology [3,33,1,42,25,43].

Owls are common predators of small mammals and are widely recognized as accumulating agents [13,28,19,1,25].

Their significant contribution to the zooarcheological record stems in part from a digestive physiology that, in many species, results in the regurgitation of pellets containing well preserved prey remains [51,32,30,50,18]. This paper presents observations on the roosting and trophic habits of two sympatric species of owl in the Serengeti region of northern Tanzania, the Barn Owl, *Tyto alba affinis*, and the Spotted Eagle Owl, *Bubo africanus*. Since nearly all the Serengeti roosts were located outside large caves and rockshelters, these data provide examples of how dense bone concentrations may be found in open-air archeological contexts. Additionally, the faunal data from the roosting sites is used to test whether in fact Spotted Eagle Owls and Barn Owls have strong and unique preferences in the prey that they catch or whether these two common owls may be treated as taphonomically equivalent for the purpose of

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paleoenvironmental analysis. Actualistic data on African owls are sparse. While the Barn Owl has been studied extensively in other parts of its range, few observations are available for the African subspecies. Even less is known about the Spotted Eagle Owl, and only rarely are side by side comparisons attempted (e.g. [7]).

The results demonstrate a strong segregation in roosting habit between African Spotted Eagle Owls and Barn Owls. Additionally, a strong similarity is found in the taxonomic composition of the prey species leading to the conclusion that, within certain limits of precision, these two species produce very similar taphonomic overprints (i.e. may be considered isotaphonomic) with regard to trophic habits, while very distinct with regard to roosting preference.

2. Study area and methods

The data stem from 18 months of continuous field work (1998−2000) in the region of Serengeti National Park, Tanzania (Fig. 1A) including Lake Manyara and Tarangire National Parks. Owl roosts were located and identified as such either by direct observation of an owl, or by the presence of pellets and bone detritus from

deteriorated pellets. Many of the roosts had owls in residence. Owl species are reported only for those observations in which a clear visual identification could be made. Barn Owls were identified by their white face disk; dark eyes; orange-buff colored uppers (dorsal surface) with dark speckles or patches; and white, or lightly spotted breasts. Eagle Owls have uppers of buff-grey with irregular dark grey or beige patches; yellow eyes; grey breast with bars and 'ear' tufts [68]. These two species as they appear in northern Tanzania are similar in size, with the Spotted Eagle Owls perhaps just slightly larger.

Collections of fresh pellets, and bone detritus were made from 61 roosting sites in and around the Serengeti National Park (Fig. 1B). The geographic coordinates of the roosts were recorded on a Garmin 12XL GPS receiver. Six closely positioned roosts − three cavity roosts and three exposed roosts − were selected for faunal analysis (Fig. 1C). The six roosts are clustered in roughly a cross pattern. Roost 23 to the north is firmly established in the shrubbed woodlands. Opposite this is Roost 3 located to the south, in the grasslands, but just at the border between the transition from grasslands to woodlands. Cavity Roost 13 and Exposed Roost 18 are
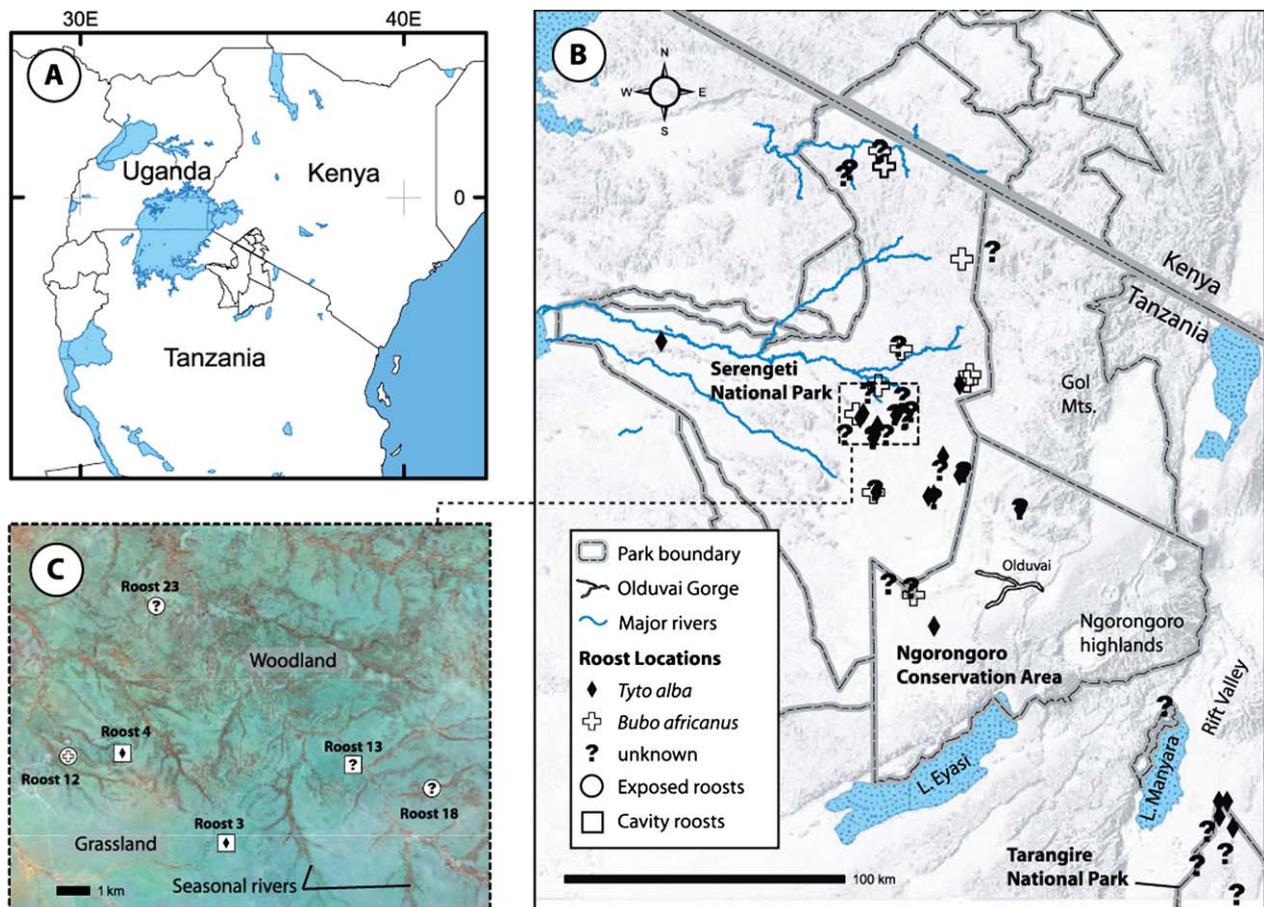

Fig. 1. Study area with the geographic distribution of owl roosts. Hillshading courtesy of the SRTM project Farr and Kobrick [23].

to the east in the catchment of the Ngare Nanyuki River, an area of dry, treed grasslands and open woodlands. The remaining two roosts, Cavity Roost 4 and Exposed Roost 12, are in the vicinity of the research institute and park headquarters. This area is a woodland grassland mosaic. Bulk samples of the bone detritus below each roost were made from surface scrapes and stored in sealed plastic bags.

Specimens were iteratively sorted with the aid of printed and digital identification keys [9,14,26,54,16]. Final taxonomic assignments were made by comparison with collections at the American Museum of Natural History (AMNH); Field Museum, Chicago (FMNH); National Museum of Natural History, Smithsonian Institution (NMNH) and the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK). Identification relied primarily on discrete dental characteristics of the molars in order to maintain a consistent pattern of taxonomic assignment across specimens with different preservation. Comparisons were made against all taxa known to occur in the subregion as reported in Davies and Berghe [12] and Wilson and Reeder [65]. The taxonomic classification used here follows that of Wilson and Reeder [65]. The analysis is conducted at the generic level as this is the lowest common ranking at which all specimens can be identified accurately and efficiently from discrete diagnostic criteria. An exception is made for bats, which are identified to Suborder only. Statistical analyses were conducted using the *R* statistical package [35,41].

3. Results

3.1. Preferred roosting sites

Of the 61 roosts located during this study, 29 had one or more owls in residence: Spotted Eagle Owls were roosting in 10 locations and Barn Owls in the other 19 (Table 1). Roosts were always monotypic and the two species almost always exploit different roosting types. Spotted Eagle Owls were observed exclusively in exposed roosts such as tree crowns and in the open among rocky outcrops. Barn Owls occupied cavity roosts: for example, in the Serengeti region Barn Owls were observed roosting in the twilight regions of rock fissures, the hollow interior of dead trees that are still standing, and the hollowed interior of living trees, especially baobabs (*Adansonia digitata*). In only three cases were Barn Owls observed at exposed roosts. A test of independence between owl species and roost type is significant (Yate's corrected log-likelihood test of independence, $G_{adj} = 17.768$, $p < 0.01$) [57], indicating that Barn Owls and Eagle Owls segregate by roosting habit. A by-product of the difference in roosting habit is the density of bones on the ground. Generally a higher density of bones exist on the ground beneath cavity roosts than beneath exposed roosts because cavity roosts occur in confined spaces that concentrate pellets in one place. In contrast, at exposed roosts such as in trees, the owls may from time to time shift to another branch causing the cast pellets to be distributed over a larger area.

3.2. Prey preference

Despite the evidence for segregated use of roost types, both cavity roosts and exposed roosts had the same 17 mammalian taxa, as listed in Table 2. The faunal composition of cavity roosts and exposed roosts is

Table 1
Roost preference by species

Species	Cavity	Exposed	Totals
Bubo africanus	0	10	10
Tyto alba affinis	16	3	19
Totals	16	13	29

Table 2
Taxonomic relative abundance tabulated as minimum number of individuals (MNI) for six roosts

	Cavity roosts			Exposed roosts			Totals
	3	13	4	18	12	23	
Insectivora							
Crocidura	104	63	89	40	9	5	310
Suncus	8	4	0	1	0	0	13
Macroscelidea							
Elephantulus	0	1	0	1	0	2	4
Chiroptera							
Microchiroptera gen. indet.	4	0	0	3	0	1	8
Rodentia							
Murinae							
Acomys	1	2	0	1	1	0	5
Arvicanthis	5	3	21	4	0	14	47
Lemniscomys	4	2	3	5	1	6	21
Mastomys	9	4	35	2	1	21	72
Mus	41	24	27	30	2	10	134
Praomys	1	0	0	2	0	0	3
Thallomys	7	4	2	3	5	26	47
Zelotomys	3	5	6	1	0	1	16
Cricetomyinae							
Saccostomus	6	2	7	7	1	11	34
Dendromurinae							
Dendromus	24	26	33	9	2	4	98
Steatomys	32	64	44	14	4	2	160
Gerbillinae							
Gerbillus	3	15	1	3	0	0	22
Tatera	1	4	7	3	0	3	18
Totals	253	223	275	129	26	106	1012

identical. Relative abundances of the fauna are also very similar. Results from single classification analysis of variance (ANOVA) conducted on the arcsine transformed MNI abundance values for each taxon (with MNI > 15) show most taxa do not differ significantly in abundance between cavity and exposed roosts. The arcsine transformation, where, $MNI_t = \sin^{-1}(\sqrt{MNI})$, is used to normalize the distribution of proportions and percentages [57]. *Lemniscomys* is the only taxon to show a significant difference, being more abundant at exposed roosts ($F = 37.498$, $p = 0.004$). A nearly significant result is also noted for *Dendromus* in the opposite direction ($F = 9.451$, $p = 0.037$ note: a conservative value of alpha is used to adjust for 12 unplanned tests, $\alpha = 0.05/12 = 4.17 \times 10^{-3}$).

3.3. Prey mass

Cavity roosts and exposed roosts also exhibit different distributions of prey body mass. The histograms in Fig. 2 show the distribution of specimen body mass, using average estimates for each taxon taken from published sources [39,48]. The range of mass values is the same since the two roost types have identical faunas, but the exposed roosts show a significant increase in the frequency of individuals from taxa weighing more than 60 g (Wilcoxon two-sample test, $W = 78,376$, $p \ll 0.01$) [57].

4. Discussion

4.1. Roosting habits

The Barn Owl roosting data acquired in this study corroborate results from other studies on Barn Owls that show they are capable of exploiting a wide variety of places as roosts, including: barns and sheds, tree cavities, chimneys, hay bales, wells, Hamerkop nests,

church towers, agricultural silos and cliff cavities [8,59,68,40,66]. Barn Owls are reported also to roost on the ground and in dense tree canopies [8,10], but the common quality to these roosting sites is the need for a dark, and enclosed space. Even when ground roosting or roosting in trees they will seek out circumstances that mimic a cavity. Of the three instances during the current study in which a Barn Owl was observed roosting in the open, one was in the branches of a short *Acacia* growing on a hill slope in which the tree crown stretched to the ground, creating a dark pseudo-cavity. Similarly, another tree crown roost was in a stand of very dense-canopy *Acacia* along a river bank. Only once, was a Barn Owl observed in a fairly open tree canopy.

In open areas devoid of artificial structures or caves a variety of roosting sites are still available to host Barn Owls. The two primary roosting sites observed during this study were small vertical fissures in granitic rock outcroppings and the hollowed interiors of living and dead trees. The study area is dotted with outcroppings of Cambrian basement rocks such as inselbergs and kopjes [29,38]. These outcroppings often develop vertical fissures that are preferred roosting places for Barn Owls. The areas beneath these perches accumulate concentrations of microvertebrate remains and the perches themselves were heavily covered in droppings – both indications of extended use. Barn Owls are noted to be animals of habit, using roosts, and even the same parts of a roost repeatedly ([8], personal observation).

The hollowed interiors of trees are another source of Barn Owl roosting sites. The trunks of dead trees may remain upright on the landscape after the crowns of the tree have toppled. These tall columns become catchments for the ejected pellets of owls either roosting inside the hollowed trunk, or using the top rim as a perch. Alternatively, living trees may form hollow cores as they age. The baobab tree, *A. digitata*, is particularly amenable to this phenomenon. Baobabs are soft wooded members of the *Bombacaceae*, the family
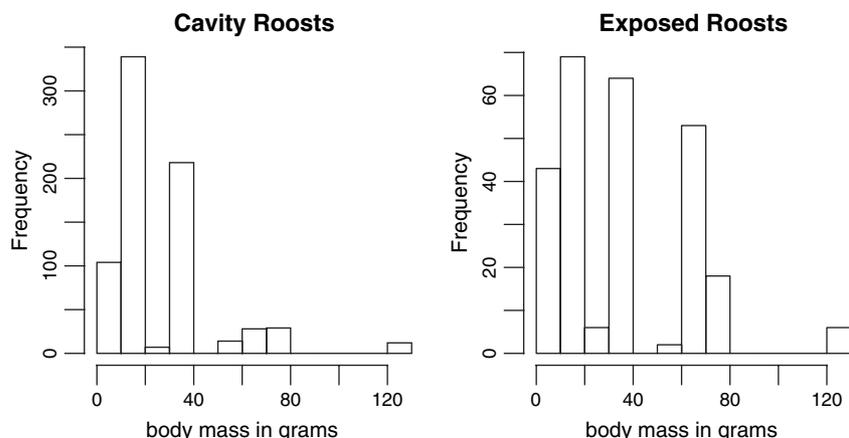

Fig. 2. Prey body mass histograms at cavity roosts and exposed roosts.

including the kapok and balsa wood trees. Baobabs are very long lived [58] and stout, with trunks up to 10 m in diameter [64]. As these trees mature the cores often become hollow, providing an opportunity for owls to roost and nest inside. Seven baobab roosting sites were observed in Tarangire National Park during the current survey. Pellets aggregate at the base of the hollowed interior where they remain protected from the elements for the life of the tree.

Spotted Eagle Owls are reported to prefer rocky areas and to roost either in trees or on the ground [27]. Brain [7] describes a Spotted Eagle Owl roosting in a dolomitic cave, the roost occurring at the base of a 9-m deep shaft. Similarly, [17] reports a Spotted Eagle Owl roost along the edge of a lava bubble. In the Serengeti, Spotted Eagle Owls were observed roosting in open settings such as the sparse canopy of *Acacia* trees, or out on kopjes and inselbergs. Both Barn Owls and Spotted Eagle Owls will use rock outcroppings as roosts. The difference being that Barn Owls will roost deep inside a fissure while Spotted Eagle Owls roost on the rocks, in trees sprouting from the rocks or on the ground near the base of the rocks.

4.2. Trophic comparison

A fundamental and important result of this study is that both cavity roosts and exposed roosts have the same taxonomic representation. Thus any of the standard faunal similarity indices that rely on presence/absence data such as the Dice, Jaccard, Simpson or Raup-Crick indices [22] should not be affected strongly by sampling from cavity versus exposed roosts.

Subtle differences exist in the rank abundance of taxa. In general there is a good rank correlation between open roosts and cavity roosts (Kendall rank correlation $\tau = 0.556$, $p = 0.001826$) as illustrated in Fig. 3. Two taxa are conspicuous in the results, *Thallomys*, and *Lemniscomys*. *Thallomys* shows the greatest shift in rank abundance between cavity roosts and exposed roosts, and a low (but non-significant) probability in the ANOVA results. *Thallomys*, commonly known as the Acacia Tree Rat, is an arboreal rodent that nests, and feeds in *Acacia* trees [62,34,39,56]. The differential representation of *Thallomys* is important because it is an indicator of woodland habitats. The prevalence of this taxon in the prey of tree roosting owls, such as the Spotted Eagle Owl, is easily explained by opportunistic predation. Barn Owls exhibit several anatomical specializations for hunting terrestrial prey in open habitats. These include wings designed for slow, buoyant flight, feathers specialized for silent flight, long legs for catching prey in tall vegetation, and an exceptional acoustical sensory and positioning system for finding prey [49]. Importantly, these adaptations are not optimal for pursuit predation of volant prey, or for
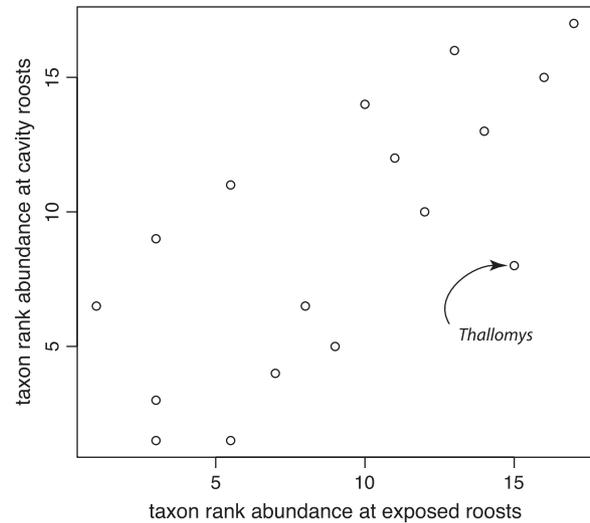

Fig. 3. Taxon rank abundance scatterplot.

hunting in densely wooded vegetation where a more agile form of flight and better visual perception are required [46]. Long term visual sighting and radio telemetry confirm their preferential use of open grasslands, and margin habitats between grasslands and more closed vegetation [8,10,30,31,59]. In contrast the available data indicate Eagle Owls are more prone to roosting in trees and thus may be more common in woodland habitats. Eagle owls are also described as a "perch and pounce" predator in contrast with Barn Owls, which hunt more from the wing over open areas [27,59]. Hence, the prevalence *Thallomys* in tree roosts may result from opportunistic predation by a "perch mode" predator like the Eagle Owl that spends most of its time in tree canopies.

The significant results shown for *Lemniscomys* are more enigmatic. *Lemniscomys* spp. are semi-diurnal, terrestrial rodents, that feed on grass leaves and stems [62,34,39]. Why this taxon should be more prevalent at exposed roosts is unclear. The prey body mass is well within the limits for both species, and if anything it is the Barn Owl that would be expected to favor a terrestrial, grassland taxon. The difference in percent abundance is not very strong (1.2% in cavity roosts versus 4.6% in exposed roosts) yet the variation within each group is small enough to yield a significant result in the ANOVA. The shift in rank abundance for this taxon, however, is not very strong between cavity roosts and exposed roosts.

Mean prey mass also appears to differ between cavity and exposed roosts. All prey taxa have masses within the range of both owl species, but one of the smallest prey taxa, *Dendromus*, has a nearly significant result in the ANOVA (second lowest probability, $p = 0.037$) indicating a preference at cavity roosts, while the histograms of prey body mass indicate a greater abundance of larger taxa in the range of 60–80 g at exposed roosts.

While the larger Eagle Owl is expected to take larger prey items at greater frequency, differences in hunting habit may also be a contributing factor. The Barn Owl spends more time hunting on the wing and may suffer greater energetic costs for transporting larger prey items than a perch predator such as the Spotted Eagle Owl.

4.3. Taphonomic and zooarcheological implications

Zooarcheologists have adopted two approaches to the taphonomic treatment of micromammals. Tchernov [60] has proposed that owl-accumulated coprocoenoses represent the activities of multiple species of owls, i.e. a guild, though probably dominated by the Barn Owl. Tchernov [60] views guilds as beneficial, since the diversity of owl species helps assure that the full diversity of potential prey taxa are represented. However, the effect of multiple predators becomes problematic when analyzing changes across different assemblages, especially when comparing relative abundances as opposed to presence/absence of taxa. This concern sponsored a more detailed taphonomic approach, summarized by Andrews [1], in which an effort is made to identify different predators and compensate for their effects. The current study is relevant to both perspectives.

The guild view may be appropriate for caves and rockshelters since these landscape features attract many owls species including both Barn Owls and Spotted Eagle Owls. The Serengeti data show that dense bone concentrations can form under protected conditions favorable to fossilization in areas outside large caves and rockshelters. Both fissures and tree stumps have been proposed previously as taphonomic modes for various fossil accumulations [6,21], and the results of the current survey support the idea that this taphonomic mode is perhaps more common than previously thought. Furthermore, the Serengeti survey suggests that owl roosts are more segregated in areas outside caves and rockshelters and thus the guild model is not a suitable assumption when analyzing faunas from open-air sites. Cavity roosts occurring in open-air settings may further differ from cave roosts in the duration of the sampling interval. Baobabs, though long lived, sample a relatively short interval compared to inselbergs and caves.

When making detailed comparisons, relative abundance data have been shown to contain significant ecological information Reed [52], and predator bias becomes a more prominent issue. For example, in their analysis of the FLK locality at Olduvai Gorge, an open-air archaeological site, Fernandez-Jalvo et al. [25] implement a detailed taphonomic analysis in order to identify accumulating agents at different levels. As a result of their taphonomic analysis they attribute changes in faunal composition between some of the levels to a shift from a Barn Owl to an Eagle Owl. The faunal shift, they argue, arises because Eagle Owls may prefer gerbils to a greater degree than Barn Owls, and thus observed changes in *Gerbillus* between levels at FLK reflect this bias rather than shifting environment. The results presented here, and elsewhere Reed [52] show a strong similarity in the composition and relative abundance of prey taken by Barn Owls and Spotted Eagle Owls, indicating that a gerbil bias does not exist for all Eagle Owls. The relative influence of different predators needs to be tested in a similar manner for a wider range of predators.

5. Conclusions

As a result of field surveys in the Serengeti region of northern Tanzania, this study found strong segregation in the roosting habits of the two most common, large-bodied owl species. Barn Owls were restricted mostly to small cavities inside rock outcroppings, dead trees, or the hollowed interiors of living trees such as the baobab. Spotted Eagle Owls were never found in cavities and instead were noted to roost either in tree crowns, or on the ground near or on large rocks such as kopjes or inselbergs. From this fact it is argued that large concentrations of micromammal bones may appear in open-air context, but most likely in spatially discrete patches stemming from the size of the cavity occupied by a Barn Owl, or the size of the tree or preferred rock perch used by other owls.

The general lack of a strong difference between exposed roosts and cavity roosts suggests that Barn Owls and Spotted Eagle Owls may be considered isotaphonomic with regards to prey composition unless very sensitive measures of relative abundance are required. This result is similar to the conclusions reached by Brain [7] from a smaller comparison of Barn Owl pellets deposited at Swartkrans Cave versus those of a Spotted Eagle Owl roosting 300 m away. Comparing the major microvertebrate groups, Brain concludes that, "accumulations built up in any particular cave by Spotted Eagle and by Barn Owls would probably not differ much in species composition. In fact, in these terms it would not be possible to separate one set of food remains from the other." (p. 122). Similar findings are also reported by Mendelsohn [45] in the analysis of modern pellets from Barn Owls and Spotted Eagle Owls in South Africa.

Even where taxonomic differences in prey composition do occur, one may still wonder how great is the impact on the analysis of these assemblages. There is a potential impact on diversity studies, taxonomic habitat indices (THI), and ecological structure analysis (ESA) [2,5,11,47,53,61]. Species richness is identical between the two roost types, but sample sizes are quite different and thus the actual richness may be greater at

the exposed roosts. The effect of taphonomic agency on THI and ESA are less clear as these methods are designed to emphasize ecological community structure more than taxonomic community structure [1,53]. The robustness of these analyses should be tested using random sampling experiments in order to better understand their response to taphonomic variability.

Acknowledgements

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