

## 9. Serengeti micromammals and their implications for Olduvai paleoenvironments

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### Abstract

Fossil micromammals are widely used as paleoenvironmental indicators in Pliocene hominin fossil localities, and many assemblages are believed to be accumulated by predators such as owls. This chapter examines modern owl-accumulated micromammal assemblages from Serengeti, Tanzania. These modern roost data are used to examine the fidelity of the taxonomic signal and its sensitivity to change across habitats within an ecosystem. The modern data show that the relative abundance of prey taxa in owl-accumulated assemblages varies across habitats in a predictable fashion. This provides a basis for applying the analysis of fossil micromammal assemblages to intra-basin scales using relative abundance as well as biome or regional scales using presence/absence of taxa. Using the modern micromammal assemblages as analogues, the latter part of the chapter explores taphonomic and paleoenvironmental change through Bed I times at Olduvai Gorge.

### Introduction

Olduvai Gorge is significant for preserving fauna at a transitional period in Earth's climatic history between the warmer, more stable Pliocene and the oscillating extremes of the glacial Pleistocene and also for yielding early discoveries of *Australopithecus boisei*/*Paranthropus boisei* and *Homo habilis*. Synchronic studies of hominin behavioral ecology at Olduvai and elsewhere using a landscape approach require detailed paleoenvironmental reconstructions to effectively test land use models (Blumenschine and Masao, 1991; Peters and Blumenschine, 1995; Blumenschine and Peters, 1998), as do

diachronic studies of hominin adaptation in response to climate change.

Detailed paleoenvironmental and paleoecological analyses are bolstered by multiple lines of evidence of which the mammalian fauna is a crucial component (Vrba, 1992). Among mammals, the smallest are well suited for paleoenvironmental analysis and for testing evolutionary models (Avery, 1982). Micromammals are speciose and embody a rich array of adaptations ranging from dedicated faunivory to hyper-grazing. They have the potential to provide paleoenvironmental signals at a finer scale than other lines of evidence (e.g., macromammals and palynology)

and they are more likely to be accumulated independently from the activities of hominins (but see Fernandez-Jalvo et al., 1999). Owls are one of the primary predators of small mammals, and understanding this predator–prey system is vital to micromammal taphonomy and paleoecology.

This chapter re-examines Plio-Pleistocene Olduvai fossil micromammals in light of new data on modern, owl-accumulated assemblages, or coprocoenoses, taken from different parts of the Serengeti ecosystem. With the actualistic data I pursue two fundamental questions. First, does the fauna found in a coprocoenosis match what one would expect for the surrounding habitat? On one hand predators sampling the biocoenosis are constrained to the prey that inhabit that environment. However, predators exert preferences for certain habitats. Barn owls, for example, exhibit numerous morphological and behavioral adaptations for hunting terrestrial prey in open habitats such as grasslands, raising the question of whether woodland or forest fauna will appear at all in a barn owl assemblage (Andrews, 1983; Tchernov, 1992). This question falls under the rubric of accuracy; it asks, “How accurately does a coprocoenosis represent the surrounding habitat?” A second set of questions focuses on precision. In going from one habitat to another at what point are changes in habitat reflected in the fauna? Or phrased another way, how sensitive is the coprocoenosis to changing habitat, both in terms of taxonomic composition (presence or absence) and the relative abundance of taxa?

These questions are fundamental to the analysis of fossil micromammal assemblages, yet they remain, for the most part, unanswered. Before delving into these issues, a general overview of the predator–prey system formed between owls and small mammals is provided. Following this review, I summarize data collection methods and present results from the analysis of modern assemblages. The latter part of the chapter then turns to

applying the results to micromammal faunas at Olduvai Gorge.

## Background

For many years, mammalogists and ornithologists have benefited from the hunting and digestive processes of owls (Glue, 1970; Denbow, 2000). Owls routinely regurgitate the remains of consumed prey in a compact bolus of bone wrapped in fur called a pellet. Pellets provide neontologists with a non-invasive way to study the diet of owls and aid paleontologists by concentrating bones at a single spot (Davis, 1959). Owls sample the surrounding faunal community (or biocoenosis) and return to selected roosting spots where they deposit dense concentrations of pellets. At some fossil localities bone densities are so great that the most reasonable explanation is that owls accumulated them. The phenomenon is common to many cave sites and rock shelters (de Graaff, 1960, 1961; Levinson, 1982; Avery, 1987, 1992; Andrews, 1990), but similar dense concentrations are also known from open-air sites (e.g., Fernandez-Jalvo et al., 1998). Further support that owls were accumulating fossil faunas comes from the discovery of fossilized impressions of pellets (Denys, 1987b; Gawne, 1975), and from detailed taphonomic analysis of micromammal bones (Andrews, 1990; Fernandez-Jalvo and Andrews, 1992; Dauphin et al., 1994, 1997; Denys et al., 1997; Fernandez-Jalvo et al., 1998).

Numerous studies have investigated modern owl pellet assemblages, but the current effort is unique in focusing on the aggregate assemblages resulting from the decay of many pellets (coprocoenosis). Generally, such assemblages are deprecated by neontologists focusing on the ecology of owls or micromammals (e.g., see Lyman and Power, 2003). However, for paleobiologists and zooarchaeologists, the coprocoenosis is the appropriate unit of analysis. Time averaging

buffers many short-term fluctuations resulting in an assemblage more like the fossil record. There are two approaches to the taphonomic analysis of coprocoenoses. By one route, one can attempt to reverse taphonomic biases; but this route is difficult because so many interacting factors are in play, and at present we know very little about these processes. A more direct route is to study correlations between the coprocoenosis and the ecological parameters of interest. This approach uses modern taphonomic assemblages as analogues or reference assemblages to be compared with fossil assemblages. Similarities between fossil and taphonomic assemblages are assumed to result from similar ecological processes, though the processes themselves are treated as a “black box.” Of course these two approaches are not mutually exclusive. One can start by forming analogues, and exploring correlations, while prying open the box to understand the causal mechanisms responsible for the associations between coprocoenoses and the environments from which they were derived. This is the general approach that I adopted, and either route is preferable to simply ignoring taphonomic biases on micromammal assemblages altogether.

### **Modern Micromammal Assemblages**

This section covers the analysis of nine modern, owl-accumulated micromammal assemblages from the Serengeti region of northern Tanzania. A brief introduction to the study area is presented first, followed by a summary of the collection methodology, including a description of the ecological trends within the ecosystem that produce habitat differences between roosting sites. The basic faunal composition is tabulated, and this is followed by a description of the habitat proclivities of the species as enumerated in niche models developed from the literature on small mammal ecology. The subsequent sections

examine the patterns of faunal composition and abundance between roosting sites and address potential artifacts such as sample size and predator bias.

### **SERENGETI ECOSYSTEM STUDY AREA**

Field data were gathered between November 1998 and April 2000. The Serengeti ecosystem straddles the Tanzania–Kenya border in East Africa between 34 and 36° E longitude and 1–2° S latitude. Serengeti National Park in Tanzania encompasses an area of 14,763 km<sup>2</sup> but the larger ecosystem—defined as the area covered by the wildebeest migration—extends into neighboring Masai Mara National Reserve (1,510 km<sup>2</sup>) to the north in Kenya, Ngorongoro Conservation Area (8,094 km<sup>2</sup>) to the southeast, the Loliondo Game Controlled Area (4,000 km<sup>2</sup>) to the east, Maswa Game Reserve (2,200 km<sup>2</sup>) to the southwest, and the Ikoronogo and Grumeti Game Controlled Areas (5,000 km<sup>2</sup>) to the northwest (Sinclair, 1995b). In total, the ecosystem covers an expanse of roughly 24,000 km<sup>2</sup> as shown in Figure 1.

### **COLLECTION OF MICROMAMMAL SAMPLES**

The category, “small mammals” refers to animals weighing less than 5 kg (after Andrews, 1990), and the term “micromammal” refers to a subset weighing less than a few hundred grams. In Africa, rodents (Order Rodentia) and shrews (Order Insectivora) are the most abundant micromammal prey of owls, but elephant shrews (Order Macroscelidea), bats (Order Chiroptera), rabbits and hares (Order Lagomorpha), and small primates (Order Primates) must also be considered as well as juvenile members of some of the larger mammals.

A total of 61 roosting sites were found in and around the Serengeti National Park, of which nine have been analyzed and the

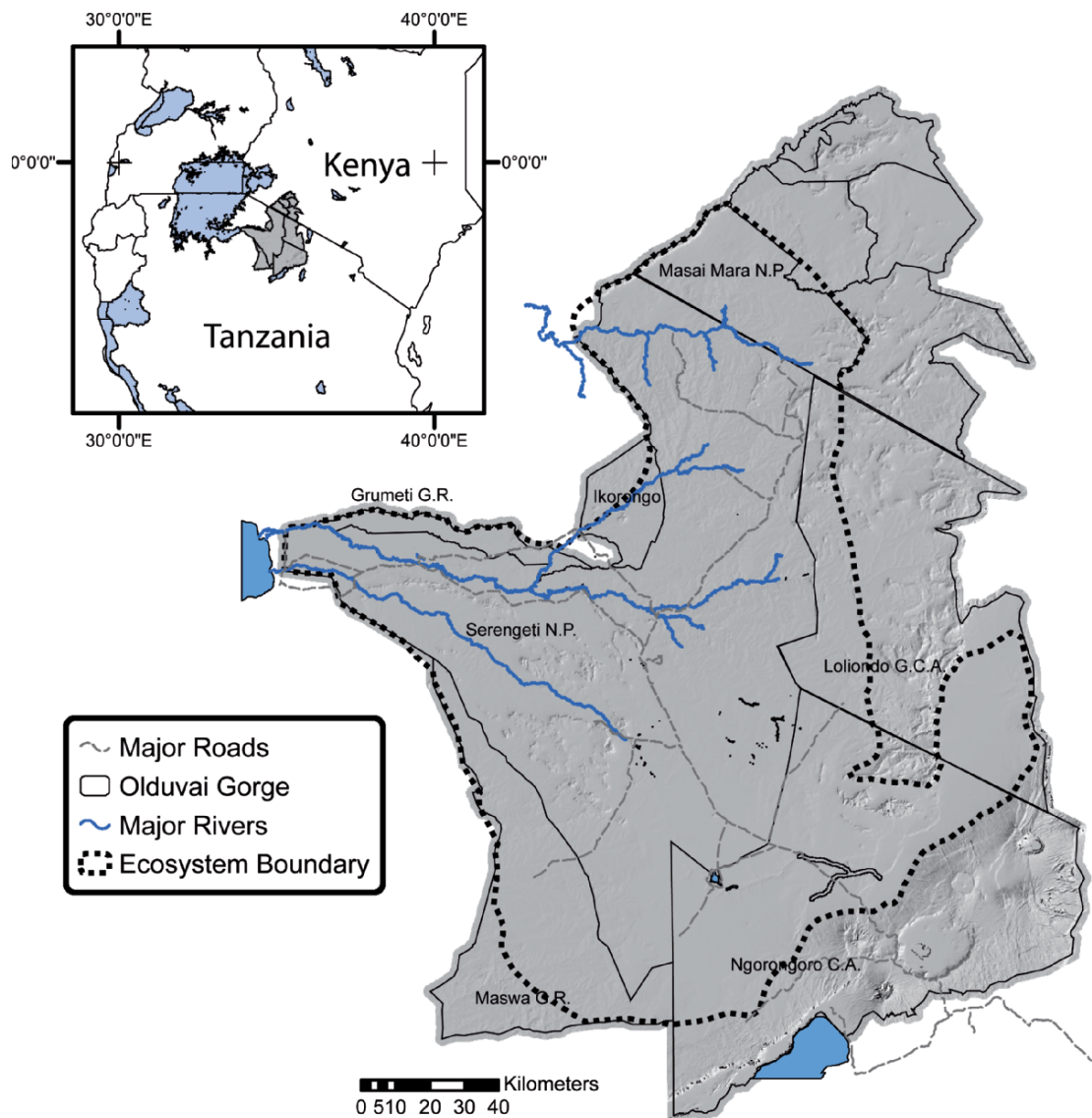


Figure 1. Map of the Serengeti National Park and adjacent protected areas, overlying a shaded area depicting the extent of the Serengeti Ecosystem. The ecosystem is defined as the area covered by the wildebeest (*Connochaetes taurinus*) during their annual migrations. Map inset shows the location of the study area within the East African subregion.

results presented here. Roost locations were recorded on a Garmin XL12 GPS receiver. Table 1 provides summary information on the analyzed roosts. Modern roosting sites 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. Roosts were located with the help of other researchers and by targeted investigation of rock outcroppings such as escarpments,

inselbergs, and kopjes as well as hollowed trees and woodland thickets.

Many of the roosts had owls in residence. Barn Owls, *Tyto alba*, were identified by their white face disk, dark eyes, orange-buff-colored upper body (dorsal surface) with dark speckles or patches, and white or lightly spotted breasts. Eagle Owls, *Bubo africanus*, have uppers of buff-grey with irregular dark grey or beige patches, yellow eyes, grey breast

Table 1. Summary of the roosts selected for analysis arranged by latitude. Geographical coordinates are given in decimal degrees. An asterisk ( \* ) indicates a roost where an owl's identity was confirmed by visual sighting. Identities at other roosts were inferred from pellet morphology, feathers, and the roost type, e.g., cavity or tree crown

Roost no.	Collection date	Owl species	Latitude	Longitude
44	September 18, 1999	<i>Tyto alba</i>	-1.64596	34.80920
23	January 6, 1999	<i>Bubo africanus</i>	-2.36593	34.86813
4	November 1, 1998	<i>Tyto alba</i> *	-2.43132	34.85326
12	December 2, 1998	<i>Bubo africanus</i> *	-2.43268	34.82940
13	December 19, 1998	<i>Tyto alba</i>	-2.43625	34.95496
18	December 30, 1998	<i>Bubo africanus</i>	-2.44666	34.98977
3	October 26, 1998	<i>Tyto alba</i> *	-2.47109	34.89905
7	October 3, 1998	<i>Tyto alba</i> *	-2.68508	34.89518
24	January 9, 1999	<i>Tyto alba</i> *	-2.69849	35.06356

with bars and “ear” tufts (Zimmerman et al., 1996). In northern Tanzania, these two species are similar in size, with the spotted eagle owls being slightly larger. At roosts where the owls were not present, indirect evidence from feathers, pellet morphology, and the physical structure of the roost, provide a reliable indicator of roost occupation. Barn owls are restricted to roosting in cavities such as the hollowed interiors of trees, or vertical fissures in rock outcroppings. Eagle owls, on the other hand roost in exposed settings such as tree crowns, or on the ground near rocks. These differences and their potential impact on faunal composition are discussed below.

Barn owls and eagle owls were the only birds observed in direct association with collected pellets and coprocoenoses; however, other owls large enough to prey on small mammals are known to occur in the study area, including: Verreaux's Eagle Owl, *Bubo lacteus*; the African Wood Owl, *Strix woodfordii nigricantior*; and the Grass Owl, *Tyto capensis*. The first two are reported to roost in tree crowns, while grass owls prefer to ground roost in wet grasslands (Vernon, 1972; Fry et al., 1988). It is possible that all of these species may have contributed fauna to roosts that have been attributed to *Bubo africanus*, though it is considered unlikely for various reasons. First, *Bubo africanus* is the most abundant, exposed-roosting owl in the

study area based on the observations made during this study. Second, the prey items are all in the size range expected for *Tyto alba affinis* and *Bubo africanus* with no evidence of larger species, such as hedgehogs (*Erinaceus albiventris*) that are preferred prey of *Bubo lacteus* (Fry et al., 1988). For these reasons it is reasonable to presume that cavity roosts contain prey primarily accumulated by barn owls, and that exposed roosts are primarily the work of spotted eagle owls.

Micromammal specimens were iteratively sorted with the aid of printed and digital identification keys (Davis, 1965; Foster and Duff-Mackay, 1966; Coetzee, 1972; Delany, 1975; Rogers and Stanley, 2003). Final taxonomic assignments were made by comparison with collections at the American Museum of Natural History, New York NY (AMNH); Field Museum of Natural History, Chicago IL (FMNH); National Museum of Natural History, Washington DC (NMNH); and the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany (ZFMK). The assemblages include many complete or partially complete skulls, but most taxa are also represented by isolated teeth. 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 (1994) and Wilson and Reeder (1993). The taxonomic classification used here follows that of Wilson and Reeder (1993). Shrews were identified only by maxillary specimens because the mandibles and lower dentition of some genera cannot be distinguished readily. 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, and *Mus* for which two subgenera, *Mus* and *Nannomys*, are readily diagnosed. Statistical analyses were conducted using the R statistical package (Ihaka and Gentleman, 1996; Maindonald and Braun, 2003).

#### SERENGETI VEGETATION AND ROOST HABITATS

Roost specific habitat analysis included the area within a 1.5-km radius surrounding each roost. The 1.5-km analysis radius covers approximately 707 ha and is based on ranging behavior of *Tyto alba* in North American and European telemetry studies (Colvin, 1984; Taylor, 1994). No studies have been conducted yet on the ranging behavior of either *Tyto* or *Bubo* species in Africa. Land cover data were compiled from multiple sources as part of a combined project on Serengeti vegetation mapping (Reed, 2003). The principal land cover data are derived from over 800 spot surveys of vegetation throughout the ecosystem. These data were combined with Landsat 7 ETM + satellite imagery to produce a detailed land cover map of the entire Serengeti-Mara ecosystem. Additional vegetation and land cover data derive from published maps and unpublished databases. From these data, details of vegetation cover, precipitation, and topographic heterogeneity could be quantified for the areas surrounding each roosting site.

Generally, the distributions of woody and herbaceous plant cover across the ecosystem

follow a pattern resulting from three levels of influence: climate, topography, and disturbances (Pratt and Gwynne, 1977). These factors are largely interdependent and in concert produce ecological gradients and repeated patterns of land form. The most important gradients relevant to land cover include a north-by-northwest rainfall gradient (Figure 2) with the lowest mean annual precipitation (ca. 400 mm) and a more unimodal pattern of annual rainfall found at the heart of the rain shadow just northwest of the Ngorongoro highlands and trending toward higher precipitation (ca. 1200 mm) with a more bimodal pattern in the north (Norton-Griffiths et al., 1975). Much of the southern Serengeti ecosystem is blanketed by natrocarbonatitic ash from Pleistocene and Holocene eruptions of nearby volcanoes (Dawson, 1963; Hay, 1976). The pattern of ashfall from the eruptions followed the prevailing winds, the same factor inducing the rainfall gradient. Thus, there is a compound gradient in precipitation, topographic heterogeneity, soil mineral composition, and soil depth. Local variation in edaphic conditions due to topography, i.e., soil catenas (Milne, 1935; Jager, 1982), augment the compound gradient and influence soil texture, mineral composition, and soil moisture availability over short distances (ca. 10–100 m).

Disturbance factors, such as fire, grazing, browsing, and burrowing, have important local influence on plant species composition and community structure (Bell, 1969, 1982; McNaughton, 1983; Dublin and Douglas-Hamilton, 1987; Dublin et al., 1990; McNaughton and Banyikwa, 1995; Sinclair, 1995a), but seem to be secondary determinants of woody/grass ratios compared with more pervasive climatic factors (e.g., precipitation, temperature, winds) or edaphic factors (including soil moisture availability, mineral composition, texture) (Belsky, 1990, 1995; Coughenour and Ellis, 1993).

The analyzed collections are distributed along the gradient in different land cover zones as shown in Figure 2. Roosts 24 and 7 are located to the south, in the short- to mid-grass

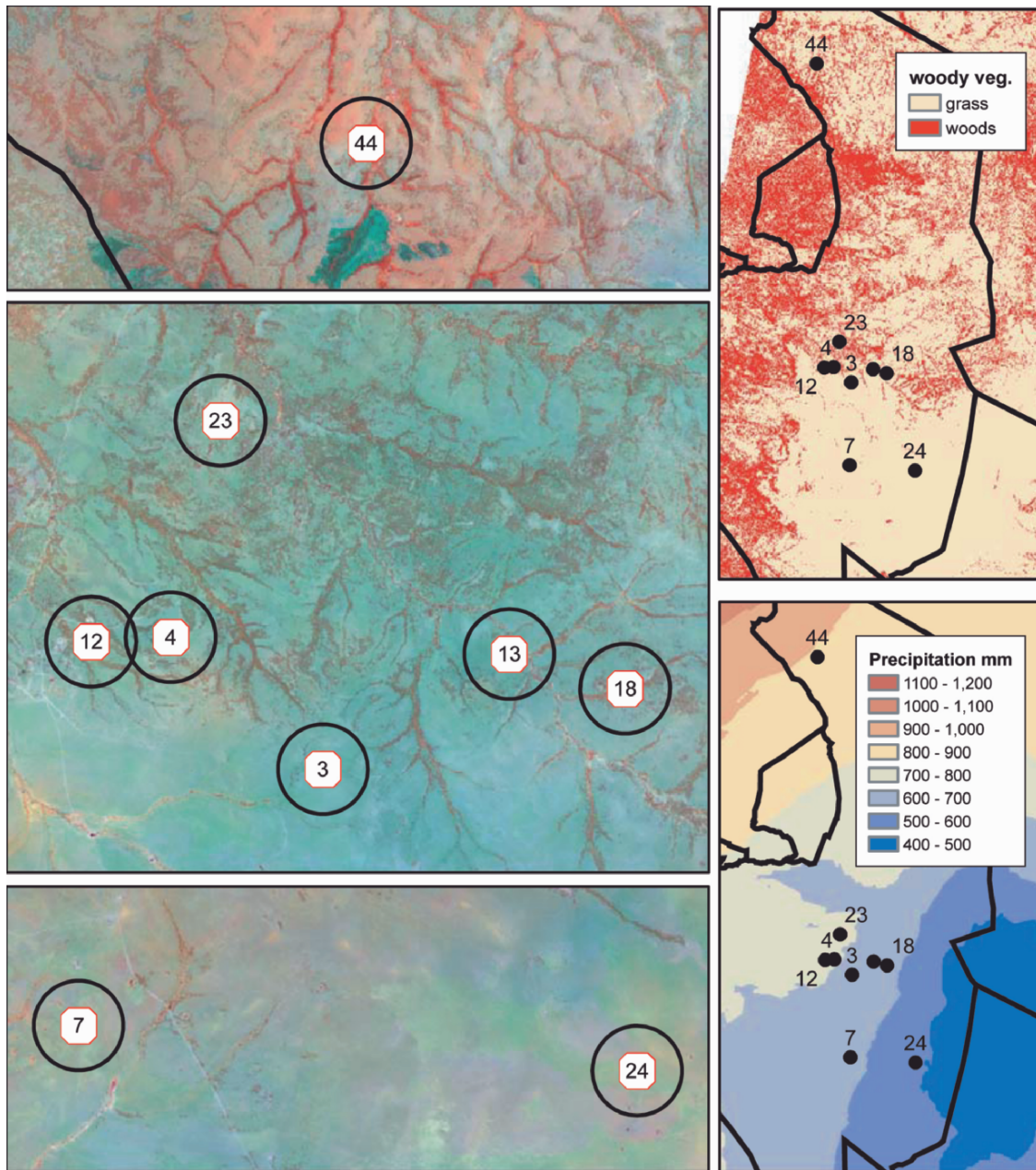


Figure 2. Distribution of analyzed roost sites. The upper right pane shows the roosts against a background map of woody vegetation, and against precipitation in the lower right. Remaining panes show close-ups of roosts outlined by 1.5-km buffer against a Landsat background. The background includes a semi-transparent overlay of the vegetation classification to highlight woody vegetation.

plains. Roost 3 is located in shrubbed grasslands, at the transition from grasslands to woodlands. Roosts 13 and 18 are to the east in the catchment of the Ngare Nanyuki River where deeper soils support woody vegetation, but under relatively low rainfall due to adjacent hills. Two roosts, 4 and 12, are in the vicinity

of the Serengeti Wildlife Research Center and Seronera. This area is a mosaic of grasslands and stands of dense woodland. Further north, roost 23 is firmly established in the shrubbed woodlands. Far to the north, roost 44 lies along the tributaries of the Mara River system in tall, moist grasslands adjacent to dense-canopy,





Table 3. Taxonomic representation presented as the number of identified specimens (NISP). Taxa are grouped by order and the Rodentia are further subdivided into subfamilies

Taxa	Roost no.									Total NISP
	3	4	7	12	13	18	23	24	44	
<b>Order Insectivora</b>										
<i>Crocidura</i>	114	91	76	9	66	47	5	75	27	510
<i>Suncus</i>	8	0	0	0	4	1	0	0	0	13
<b>Order Macroscelidea</b>										
<i>Elephantulus</i>	0	0	0	0	1	1	4	0	0	6
<b>Order Chiroptera</b>										
<i>Microchiroptera</i> gen. Indet.	5	0	0	0	0	4	2	0	0	11
<b>Order Rodentia</b>										
Subfamily Murinae										
<i>Acomys</i>	1	0	0	1	3	2	0	0	2	9
<i>Aethomys</i>	0	0	0	0	0	0	0	1	16	17
<i>Arvicanthis</i>	15	79	23	0	4	11	48	2	68	250
<i>Dasymys</i>	0	0	0	0	0	0	0	0	12	12
<i>Lemniscomys</i>	8	8	14	1	4	11	14	5	1	66
<i>Mastomys</i>	27	140	8	1	9	6	56	8	34	289
<i>Mus (Mus)</i>	69	37	94	3	29	33	15	11	0	291
<i>Mus (Nannomys)</i>	47	39	9	0	46	61	8	2	4	216
<i>Praomys</i>	1	0	0	0	0	4	0	0	1	6
<i>Thallomys</i>	18	9	0	10	11	10	85	0	0	143
<i>Zelotomys</i>	13	22	11	0	17	1	1	0	1	66
Subfamily Cricetomyinae										
<i>Saccostomus</i>	18	24	10	1	8	17	36	0	0	114
Subfamily Dendromurinae										
<i>Dendromus</i>	67	104	60	3	79	23	7	52	10	405
<i>Steatomys</i>	97	137	182	8	216	44	3	309	22	1018
Subfamily Gerbillinae										
<i>Gerbillus</i>	8	2	142	0	48	3	0	107	0	310
<i>Tatera</i>	2	15	33	0	13	8	7	223	10	311
<b>Total</b>	<b>518</b>	<b>707</b>	<b>662</b>	<b>37</b>	<b>558</b>	<b>287</b>	<b>291</b>	<b>795</b>	<b>208</b>	<b>3401</b>
Subtotal Insectivora	122	91	76	9	70	48	5	75	27	523
Subtotal Rodentia	391	616	586	28	487	234	280	720	181	2937
Subtotal Murinae	199	334	159	16	123	139	227	29	139	1365
Subtotal Dendromurinae	164	241	242	11	295	67	10	361	32	1423
Subtotal Gerbillinae	10	17	175	0	61	11	7	330	10	621

in rodents the diversity is partitioned among genera. At the ordinal level, rodents make up 69% of the assemblage.

Overall, the fauna recovered from the modern assemblages is consistent with a tropical mosaic of grassland and woodland, albeit one in which the larger, more diurnal taxa are under-represented. A bias toward nocturnal species is expected for an owl-accumulated assemblage. Looking more closely, Tables 3 and 4 indicate differences between roosts. For example, the genus *Thallomys* represents 18 and 28% of

the fauna at roosts 12 and 23 respectively but less than 3% elsewhere. Gerbils make up 21 and 35% of the fauna at roosts 7 and 24 but are rare at the other roosts. Before exploring the cause for these differences it is useful to review the habitat proclivities of the different taxa involved. For this purpose, habitat preferences are enumerated into niche models as described below. Following the discussion of niche models comes a more thorough look at the abundance patterns between roosting sites in different habitats using correspondence

Table 4. Taxonomic representation presented as the minimum number of individuals (MNI). Taxa are grouped by order and the Rodentia are further subdivided into subfamilies

Taxa	Roost no.									Total MNI
	3	4	7	12	13	18	23	24	44	
<b>Order Insectivora</b>										
<i>Crocidura</i>	104	89	76	9	63	40	5	73	27	486
<i>Suncus</i>	8	0	0	0	4	1	0	0	0	13
<b>Order Macroscelidea</b>										
<i>Elephantulus</i>	0	0	0	0	1	1	2	0	0	4
<b>Order Chiroptera</b>										
<i>Microchiroptera</i> gen. Indet.	4	0	0	0	0	3	1	0	0	8
<b>Order Rodentia</b>										
Subfamily Murinae										
<i>Acomys</i>	1	0	0	1	2	1	0	0	1	6
<i>Aethomys</i>	0	0	0	0	0	0	0	1	5	6
<i>Arvicanthis</i>	5	21	7	0	3	4	14	1	17	72
<i>Dasymys</i>	0	0	0	0	0	0	0	0	4	4
<i>Lemniscomys</i>	4	3	7	1	2	5	6	4	1	33
<i>Mastomys</i>	9	35	3	1	4	2	21	4	10	89
<i>Mus (Mus)</i>	21	14	37	2	11	9	7	5	0	106
<i>Mus (Nannomys)</i>	20	13	4	0	13	21	3	1	1	76
<i>Praomys</i>	1	0	0	0	0	2	0	0	1	4
<i>Thallomys</i>	7	2	0	5	4	3	26	0	0	47
<i>Zelotomys</i>	3	6	2	0	5	1	1	0	1	19
Subfamily Cricetomyinae										
<i>Saccostomus</i>	6	7	5	1	2	7	11	0	0	39
Subfamily Dendromurinae										
<i>Dendromus</i>	24	33	21	2	26	9	4	17	4	140
<i>Steatomys</i>	32	44	61	4	64	14	2	93	7	321
Subfamily Gerbillinae										
<i>Gerbillus</i>	3	1	44	0	15	3	0	29	0	95
<i>Tatera</i>	1	7	10	0	4	3	3	66	3	97
<b>Total</b>	<b>253</b>	<b>275</b>	<b>277</b>	<b>26</b>	<b>223</b>	<b>129</b>	<b>106</b>	<b>294</b>	<b>82</b>	<b>1665</b>
Subtotal Insectivora	112	89	76	9	67	41	5	73	27	499
Subtotal Rodentia	137	186	201	17	155	84	98	221	55	1154
Subtotal Murinae	71	94	60	10	44	48	78	16	41	462
Subtotal Dendromurinae	56	77	82	6	90	23	6	110	11	461
Subtotal Gerbillinae	4	8	54	0	19	6	3	95	3	192

analysis. Sampling issues are also considered, with attention given to both sample size effects and the influence of different owl species that accumulate the assemblages. These steps lay the groundwork for the testing and calibration of two common analytical methods, taxonomic ratios, and taxonomic habitat indices (THI). The modern data are examined with each of these techniques and the results compared against the actual habitats surrounding each roost.

## MICROMAMMAL NICHE MODELS

Rather than provide lengthy written description of the taxa, condensed numerical summaries of habitat preference are given in the form of niche models. Niche models, though not termed as such, were developed as a component of the taxonomic habitat index (THI) by Nesbit-Evans et al. (1981), who described an animal's habitat preference using five major tropical habitat types: forest, woodland-bushland,

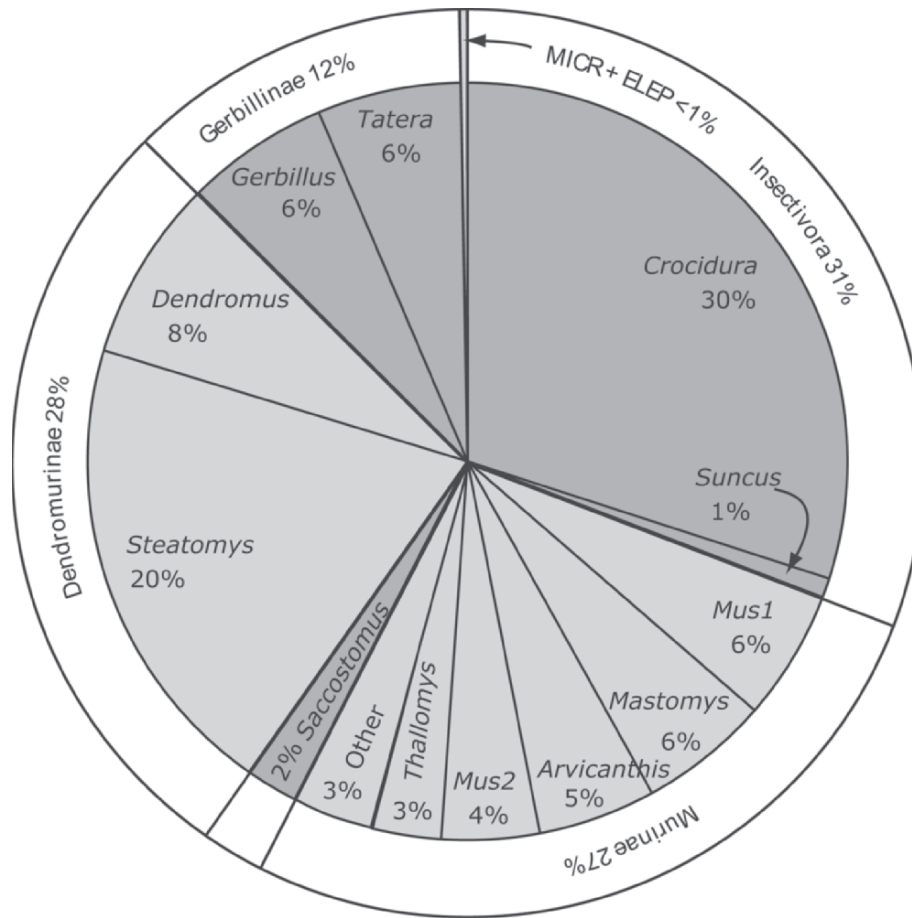


Figure 3. Pie chart of relative abundances (% NISPn) of all mammalian taxa from all roosts combined.

grassland, desert and semi-desert, and wet or swamp habitats. An animal's total habitat use was partitioned into these classes based on published descriptions of the taxon by Meester and Setzer (1971) and Kingdon (1974a, b). For example, Nesbit-Evans et al. (1981, p. 102) score the African elephant, "0.33 forest, 0.33 woodland-bushland, 0.23 grassland, and 0.11 semi-desert." This set of closed-sum numerical weights for a given taxon is what I call a niche model. Averaging the niche model values for all taxa appearing in a habitat gives the THI. A variant of THI uses averages weighted by the taxon abundance (Andrews, 1990).

A shortfall of this method is that the inventors provide no clear guidelines on how to distribute the values in the niche model across the habitat classes. Theoretically a niche model

should be based on probability of a particular habitat (say, Habitat 1) for a given taxon (Taxon A);  $p(H_1|T_A)$ . This probability could be ascertained by systematic survey of museum collection records, a task that will only become practical as records and field collection notes are digitized. Quantitative assessments of habitat use are often available in the literature, though care should be taken not to confuse habitat indication with habitat association. The former is given by the probability above and is the appropriate niche estimator for paleoenvironmental interpretation. Habitat association asks what is the probability of finding Taxon A, given a particular habitat,  $p(T_A|H_1)$ . The two are clearly different. A rare and endemic species may be unique to a single habitat, thus  $p(H_1|T_A) = 1.00$ , but because it occurs

Table 5. Niche models for Serengeti rodents based on data from Fernandez-Jalvo et al. (1998) except those taxa indicated by an asterisk (\*)

	Land cover and ranks				
	Forest	Woodland	Bushland	Grassland	Semi-Arid
<b>Taxa</b>	5	4	3	2	1
<i>Arvicanthis</i>	0	0	0.25	0.75	0
<i>Aethomys</i>	0.18	0.25	0.4	0.18	0
<i>Mastomys</i>	0	0.33	0.33	0.33	0
<i>Mus</i>	0.35	0.19	0.26	0.2	0
<i>Oenomys</i>	0.5	0.5	0	0	0
<i>Pelomys</i>	0	0	0.5	0.5	0
<i>Thallomys</i>	0	0.5	0.5	0	0
<i>Grammomys</i>	0.4	0.35	0.2	0	0.05
<i>Zelotomys</i>	0	0	0.2	0.7	0.1
<i>Gerbillus</i>	0	0	0.2	0.2	0.6
<i>Tatera</i>	0	0	0.4	0.6	0
<i>Steatomys</i>	0.2	0.2	0.2	0.2	0.2
<i>Dendromus</i>	0.05	0.27	0.4	0.28	0
<i>Saccostomys</i>	0	0.33	0.33	0.33	0
<i>Otomys</i>	0	0.25	0.5	0.25	0
<i>Xerus</i>	0	0.33	0.66	0	0
<i>Heterocephalus</i>	0	0.2	0.3	0.4	0.1
<i>Acomys</i> *	0	0.17	0.17	0.17	0.5
<i>Dasymys</i> *	0	0	0.2	0.8	0
<i>Lemniscomys</i> *	0	0.1	0.1	0.5	0.3
<i>Praomys</i> *	0.8	0.2	0	0	0

in low abundance the probability of finding that species in Habitat 1, may be as low as 1 in 100, i.e.,  $p(H_1|T_A) = 0.01$ . The trapping records associated with most museum specimens provides a first approximation of habitat preferences, but due to predator preferences and other taphonomic factors it is better to calculate the niche model from coprocoenoses, such as those presented here.

Nesbit-Evans et al. (1981) focused on large mammals, but recently niche models were compiled for Olduvai fossil micromammals by Fernandez-Jalvo et al. (1998). Their niche models are reproduced here in Table 5. These authors use a slightly different set of habitat categories than did Nesbit-Evans et al. There are still five classes: forest, woodland, bushland, grassland, and semi-arid. The Aquatic-swamp category has been dropped and the woodland-bushland category split. The Olduvai fossil microfauna overlaps greatly with that of the modern Serengeti coprocoenoses, leaving only four genera that were not covered

by Fernandez-Jalvo et al. (1998) and for which new niche models were needed: *Acomys*, *Dasymys*, *Lemniscomys*, and *Praomys*.

To build the new niche models and validate the models developed by Fernandez-Jalvo et al. (1998), autecological summaries were compiled for all Serengeti genera based on Kingdon (1974a, b); and verified against other published descriptions (Vesey-Fitzgerald, 1966; Delany, 1972, 1986; Hubbard, 1972; Andrews et al., 1975; Avery, 1982). A summary is given in Table 6. Bats are excluded because they are very rare in owl assemblages and are not as intimately associated with land cover as are their non-volant cousins. Shrews are listed in the table, but they too are excluded from analyses because either too little is known about their autecology in East Africa (as is the case for *Suncus*) or there are too many species within the genus for it to be informative (*Crocidura*). The niche index values that appear in Table 6 are derived from the niche models for each taxon ( $t_i$ ) as

$$\text{Niche index}(t_i) = \sum_{j=1}^5 (R_j \cdot W_j) \quad (1)$$

where  $R_j$  is the habitat rank (1 for semi-arid, 2 for grassland, etc.) and  $W_j$  is the weighting for the taxon in the habitat. For example, *Arvicanthis* has a value of  $2.25 = (5 \times 0) + (4 \times 0) + (3 \times 0.25) + (2 \times 0.75) + (1 \times 0)$ . The niche index is used to give a simple ranking of habitat preferences with larger values indicating preference for more moist/closed habitats. Comparing the niche index against the habitat summary in the adjacent column of Table 6 serves as a check of the niche models.

Generally the summary of habits and habitat preferences given in Table 6 agree with the niche models developed by Fernandez-Jalvo et al. (1998) listed in Table 5. Gerbils (*Gerbillus* and *Tatera*) are characterized in the literature as arid adapted based on geographic distribution and habitat use within that distribution. Thus, they are expected to have a low niche index and heavy weighting on semi-arid and

grassland habitats in the niche model, which they do. Similarly, most of the other taxa are ordered sensibly, indicating that the niche models proposed by Fernandez-Jalvo et al. (1998) are reasonable. However, there are a few incongruencies.

*Dasymys* has a low niche index value because it favors grassland habitats; however, it is specific to wetlands and marshes. Similarly, *Arvicanthis* favors moist grasslands or woodlands with a moist-grass understory. Their position in part reflects the limitations of a simple linear index that combines dry and wet grasslands.

*Heterocephalus* is particularly indicative of arid environments (Kingdon, 1974a, b), yet it ranks rather high on the niche index due to partial weighting in woodland environments. Temperature and soil characteristics are probably more critical than woody vegetation cover or moisture, and again this taxon may differ on an independent axis of variation that is distorted by the linear niche scale.

Table 6. Body size and habitat summaries derived from Kingdon (1974) and others (see text). The niche index is a summary of habitat preference and ranges from open/xeric (1) to closed/mesic (5)

Taxa	Approx. body mass (g)	Habitat	Niche index
<i>Acomys</i>	23	Dry sav.—rocky	1.86
<i>Arvicanthis</i>	78	Grassl/dry—moist sav.	2.25
<i>Aethomys</i>	100	Dry—moist savanna	3.03
<i>Dasymys</i> *	103	Marsh/moist grassland	2.2
<i>Grammomys</i>	42	Dry—moist sav./sec. growth	4.05
<i>Lemniscomys</i> *	55	Grassl./dry—moist sav.	1.9
<i>Mastomys</i>	50	Dry—moist savanna	2.64
<i>Mus (Mus)</i>	10	Dry savanna	3.15
<i>Mus (Nannomys)</i>	12	Dry—moist savanna	3.15
<i>Oenomys</i>	90	Sec. growth	4.5
<i>Pelomys</i>	68	Grass/sec. growth	2.5
<i>Praomys</i>	35	Sec. growth/forest	3.8
<i>Thallomys</i>	68	Dry—moist savanna	3
<i>Zelotomys</i>	60	Dry—moist savanna	2.1
<i>Otomys</i>	157	Grassl/sec. growth	3
<i>Saccostomus</i>	63	Dry savanna	2.64
<i>Dendromus</i>	12	Grassl./dry—moist sav.	2.77
<i>Steatomys</i>	37	Grassl./dry savanna	2.6
<i>Gerbillus</i>	38	Grassland	1.6
<i>Tatera</i>	128	Grassl./dry savanna	2.4
<i>Xerus</i>	622	Grassl./dry savanna	3.3
<i>Heterocephalus</i>	55	Semi-arid	2.6

For *Steatomys*, Fernandez-Jalvo et al. (1998) propose a catholic habitat distribution with equal rankings in every habitat class. However, Kingdon (1974b) attributes this species to more xeric environments, and even at the most mesic edge of their distribution they favor moist woodland or "savanna" but not forest (Genest-Villard, 1979).

A revised niche model, making use of the comments above is beyond the scope of this chapter. For comparability I retain the niche models employed by Fernandez-Jalvo et al. (1999) but with the caveats described above.

#### PATTERNS IN THE DISTRIBUTION AND ABUNDANCE OF MICROMAMMALS BETWEEN ROOSTS

The niche models give *a priori* expectations as to where certain taxa should be most abundant. This section examines patterns of relative abundance between roosts to see if these expectations are manifested. The first question to address is whether relative abundance is significantly different from one roost to the next on a taxon-by-taxon basis. Here, a statistical test of independence using the Pearson's  $\chi^2$  (often called a chi-square test), examines whether changes in relative abundance of a taxon are significantly greater than would be expected by chance alone. The statistic examines a contingency table of abundance values (in this case MNI) and tests whether the observed values differ from what one would expect given the size of the sample. Or put another way, it tests whether the abundance of the taxon is independent of the roost examined. The proportion of a taxon at any one roost is tested against its global proportion across all roosts. This approach mitigates the effect of sample size differences between roosts. The Pearson statistic is compared against a chi-square probability distribution (Sokal and Rohlf, 1995). Significant values indicate the taxon is strongly associated with at

least one roost, and not randomly distributed across the roosts. Table 7 lists the results. Most taxa are not randomly distributed; however bats, *Elephantulus*, *Acomys*, *Lemniscomys*, *Praomys*, *Zelotomys*, *Dendromus* could not be distinguished from chance in their distribution across roosting sites and these taxa are thus excluded from subsequent analysis. The remaining 13 taxa were found to differ significantly from expected abundances.

The pattern of faunal associations is demonstrated on a per-roost basis using correspondence analysis (CA). Correspondence analysis is a multivariate ordination technique that maps the 13 dimensions of variability (one dimension for each taxon found significant in Table 7) onto a two-dimensional space. The analysis examines covariance between each of the dimensions and attempts to preserve the spatial relationships between the points (Greenacre and Vrba, 1984; Johnson and Wichern, 2002). The technique uses a chi-square distance measure and is thus amenable to count and frequency data among samples occurring along an ecological gradient (McCune and Grace, 2002). The technique also allows roosts to be mapped in the same space with the taxa so one can easily visualize both sets of variables. Taxon points that are closer together in the CA plot tend to appear together at the same roosts.

A contingency table of NISPn values is used for the CA to best represent the relative abundance of taxa (Figure 4). However, one obtains similar results using MNI, %MNI, or %NISPn. The first axis of variation splits roosts along a general gradient of dry/open to the left and more wet/closed roosts to the right. Taxa such as *Gerbillus*, *Steatomys*, and *Tatera* appear to the left, near grassland roosts 24 and 7. Shrubbed or partially wooded habitats in the dryer zones at roosts 3, 13, 18 are near the origin. Those roosts with the greatest woody cover and higher precipitation (4, 12, and 23) are to the right of the origin and associated with *Saccostomus* and *Thallomys*.

Table 7. Each row shows the results for a test of the independence of the taxon across all roosts, significant results indicate that the abundance of the taxon is not random from one roost to another. The critical value of 23.774 corresponds to an experiment-wide alpha of 0.5 adjusted for 20 unplanned comparisons;  $\alpha = 0.05/20 = 0.0025$ , with eight degrees of freedom. NS = not Significant, \* significant at  $\alpha > 0.001$ , \*\* significant at  $\alpha < 0.001$

Taxa	Chi-square	Probability	Result
<i>Crocidura</i>	53.8	0.00010	**
<i>Suncus</i>	29.8	0.00020	*
<i>Elephantulus</i>	16.8	0.03180	NS
<i>Microchiroptera gen. indet.</i>	21.8	0.00540	NS
<i>Acomys</i>	16.3	0.03770	NS
<i>Aethomys</i>	79.8	0.00010	**
<i>Arvicanthis</i>	104.1	0.00010	**
<i>Dasymys</i>	77.4	0.00010	**
<i>Lemniscomys</i>	14.2	0.07750	NS
<i>Mastomys</i>	111.2	0.00010	**
<i>Mus (Mus)</i>	42.3	0.00010	**
<i>Mus (Nannomys)</i>	70.3	0.00010	**
<i>Praomys</i>	15.7	0.04740	NS
<i>Thallomys</i>	231.9	0.00010	**
<i>Zelotomys</i>	9.4	0.31280	NS
<i>Saccostomus</i>	47.0	0.00010	**
<i>Dendromus</i>	15.6	0.04900	NS
<i>Steatomys</i>	84.8	0.00010	**
<i>Gerbillus</i>	103.1	0.00010	**
<i>Tatera</i>	183.1	0.00010	**

The taxa *Dasymys* and *Aethomys* are unique (or nearly so) to roost 44. *Dasymys* occurs only at this roost. *Aethomys* is most abundant here but a single specimen was also observed at roost 24. The uniqueness of roost 44 is most strongly expressed on Axis 2, indicating that it differs in its own way from roosts 24 and 23. *Mastomys* and *Arvicanthis* fall between roosts 23 and 44. These taxa share identical patterns of association. The remaining taxa are clustered about the origin.

taxon) and sample size (total NISP) for all taxa using both Pearson's and Kendall's rank correlation tests. NISP is appropriate here because the tests examine rank order of sample size, the size of the samples themselves does not affect the significance of the result. Given the large number of tests (13), a conservative significance level should be set at an alpha of  $0.05/13 = 0.0038$ . At this level none of the taxa show patterns of relative abundance that are correlated with sample size.

## SAMPLE SIZE EFFECTS

Grayson (1984) notes that faunal abundances may covary with sample sizes. The exact causes are not consistent across data sets but it is often the case that small samples have biased relative abundance values. As a simple precaution, tests were made on the correlation between relative abundance (%NISP for each

## PREDATOR EFFECTS

As mentioned earlier, the pattern of roost occupation shows a consistent segregation between two owl species. The barn owls, *Tyto alba affinis*, were commonly observed inside cavities, such as small vertical fissures of granitic rock outcroppings (kopjes) or the hollowed interior of baobab trees, *Adansonia digitata*. Alternately,

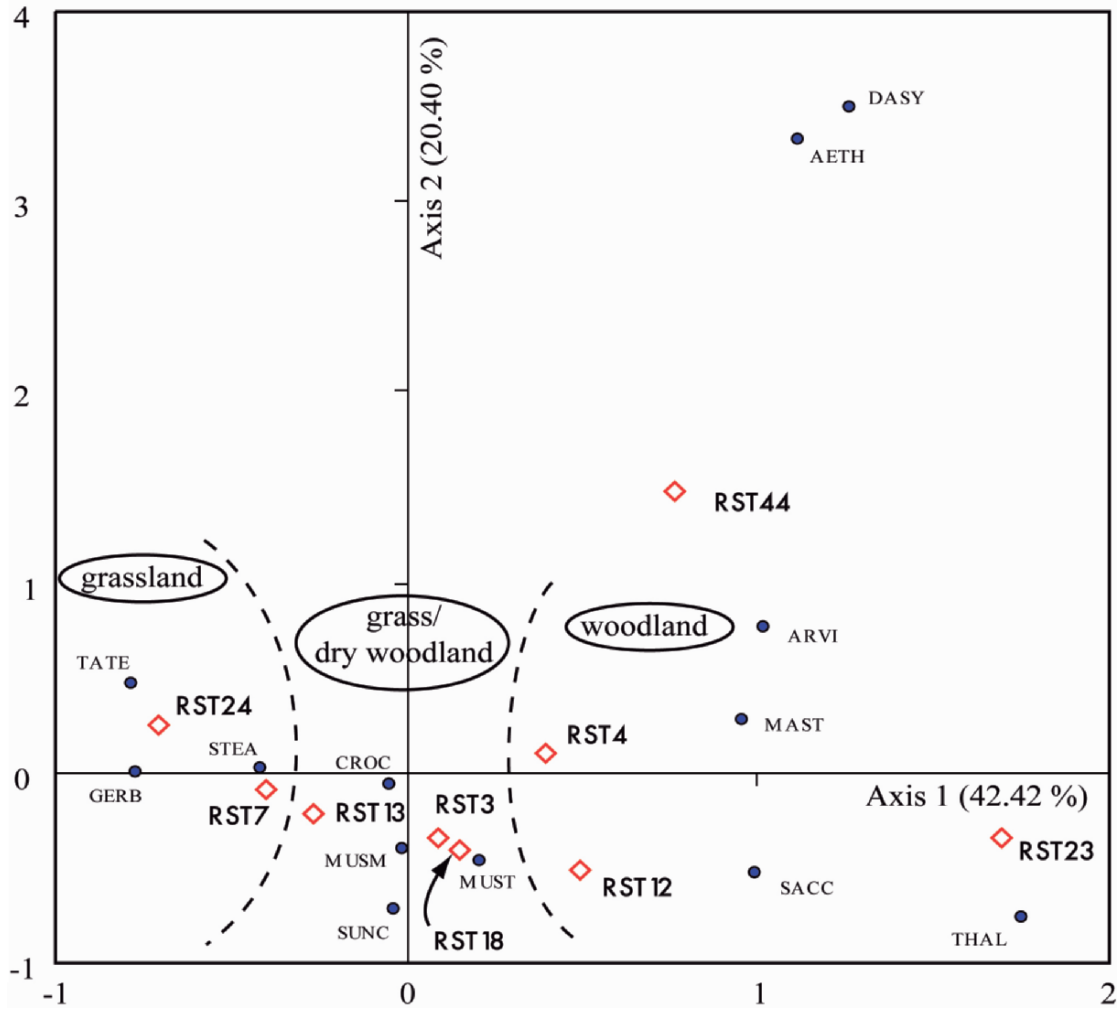


Figure 4. Correspondence analysis based on NISPn, Axes 1 and 2. The first two axes explain 62.8% of the inertia. Diamonds indicate roosts, and circles indicate taxa. Taxon codes are from the first four letters of the taxon name.

spotted eagle owls, *Bubo africanus* were found in exposed circumstances such as the sparse crowns of *Acacia* trees or roosting on the ground near rocks (Reed, 2003). These observations agree with other published reports on the roosting habits of these species (Brain, 1981; Demeter, 1982; Taylor, 1994). If the predators have very different prey preferences or hunting habits then strong differences are expected between assemblages even when they are accumulated in the same habitat. However, an analysis of the prey composition in regard to roost type (and hence predator species), when habitat is constrained, showed identical faunal composition (presence/absence)

between cavity and exposed roosts, but differences in the relative abundance of some taxa (Reed, 2005). Significant differences occurred in the relative abundance of *Lemniscomys*, and a strong shift in the rank abundance of *Thallomys*. In both cases these taxa were more common at exposed (eagle owl) roost than at cavity roosts. Additionally, exposed roosts demonstrated a significantly greater mean prey body mass than the cavity roosts. The prevalence of the arboreal, *Thallomys*, at exposed roosts is consistent with opportunistic predation by a tree-roosting eagle owl, and both *Thallomys* and *Lemniscomys* are larger taxa that may be preferred by the larger



predator, the eagle owl. However, these differences are insufficient to explain the patterns of faunal composition seen between roosts in different habitats.

#### SUMMARY OF FAUNAL ABUNDANCE PATTERNS

The CA plot gives a graphical representation of the relationships between species and roosts. The overall pattern of faunal distribution is in agreement with the niche models developed from the literature and presented in Tables 5 and 6. The dry, open grassland roosts (7 and 24) have the most significant associations with *Gerbillus*, the most arid-adapted taxon with the lowest niche index value (1.6). Both roosts also share strong negative associations with *Mastomys*, *Mus* (*Nannomys*), and *Thallomys*, all of which have high niche index values (2.64, 3.15, and 3 respectively). At the other extreme the mesic woodland roosts have different constellations of fauna, but all composed of species with more mesic habits such as *Thallomys* (niche index = 3), *Saccostomus* (n. i. = 2.64), *Mastomys* (n. i. = 2.64). Arid adapted fauna such as *Gerbillus* are negatively associated.

Roosts 3 and 44 do not neatly fit this pattern. Roost 3 is a grassland roost but at higher precipitation than 7 or 24 and right on the edge of the transition to woodlands. This roost is dominated by *Crocidura* and has very negative associations with the arid grassland fauna. Absent more detailed data on the habits of crociduran shrews this result remains enigmatic.

Roost 44 shows a negative association with dry grassland taxa consistent with its position at the wettest portion of the precipitation gradient. Semi-aquatic taxa such as *Dasymys* appear here as is expected since tributaries of the Mara River provide a perennial source of water. Likewise moist grassland taxa such as *Arvicanthis* are present beside other mesic taxa such as *Mastomys* and *Aethomys*. However, arboreal taxa, such as *Thallomys*, are con-

spicuously absent. Two explanations deserve consideration. Predator bias may explain the absence in part. *Thallomys* is more common at eagle owl roosts as was noted in the section Predator Effects. Roost 44 is a cavity roost and thus presumably the work of a barn owl. Another factor may be forest type. *Thallomys* prefers drier *Acacia* or *Brachystegia* woodland (Linzey and Kesner, 1997). The vegetation at roost 44 includes grasslands that abut dense riverine forests composed of broadleaf evergreen species (e.g., *Diospyros*, *Drypetes*, *Teclea*) and not *Acacia* (Herlocker, 1974). Thus, *Thallomys* may be absent from this habitat altogether, and not just absent from the owl pellets.

Returning to the questions that motivated this research the following points are emphasized: (1) The two species of owl examined here are capable of taking similar prey taxa, but with subtle biases in the relative abundances of prey items that may stem from prey size, with eagle owls preferring slightly larger prey. An alternate explanation is that roosting habits bias prey preferences. For example, the arboreal *Acacia* tree rat, *Thallomys*, may be opportunistically preferred by *Bubo africanus* since this owl roosts in tree crowns. (2) Over the subtle habitat transitions considered in this study, the relative abundance of the accumulated fauna differs significantly and predictably from roost to roost in different habitats. These differences agree with habitat predictions based on trapping studies and thus time-averaged, owl-accumulated taphonomic assemblages are good indicators of environments within a radius of 1.5 km surrounding the site of accumulation.

#### Calibration of Paleoecological Methods

Identifying the faunal differences between habitats as was the focus in the previous section remains one step removed from a paleoenvironmental reconstruction. Two techniques used to integrate data into composite paleoenvironmental reconstructions are reviewed below, taxonomic ratios

and the taxonomic habitat index. These methods are applied to the modern owl assemblages and the results compared against the existing vegetation.

### TAXONOMIC RATIOS

The use of ratios of indicator taxa is a popular method for interpreting the past. For example, Vrba (1980, 1985, 1995) has used the proportion of Alcelaphini and Antilopini bovid tribes as an indicator of open habitats. Similarly, the ratio of Gerbillinae to Murinae (both subfamilies in Rodentia, Muridae) has been proposed as an indicator of open habitats (Jaeger, 1976; Dauphin et al., 1994; Fernandez-Jalvo et al., 1998). Figure 5 shows the relationship between the Gerbillinae:Murinae (G:M) ratio and the percent woody vegetation surrounding the Serengeti roosting sites. A trend is evident toward decreasing proportions of gerbils as the roost environment becomes more wooded (Spearman rank correlation test,  $\rho = -0.0773$ ,  $p = 0.015$ ). The relationship is largely driven by the abundance of *Gerbillus*,

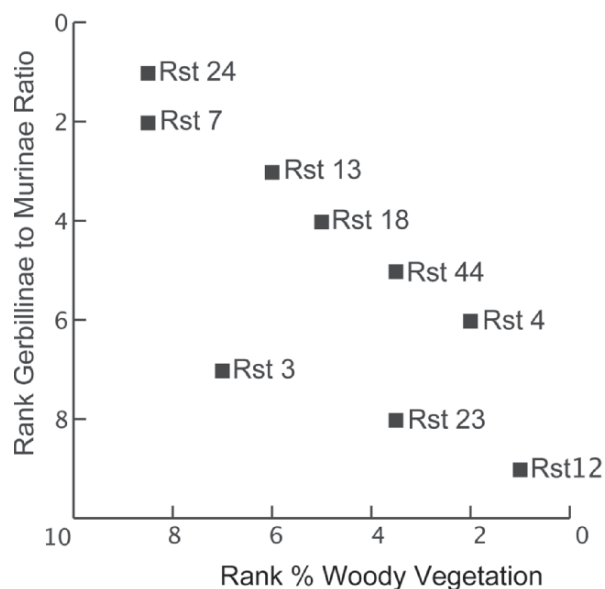


Figure 5. Bivariate rank plot of Gerbillinae:Murinae ratio against roost percent woody vegetation.

which accords with the niche model for this taxon. Similar patterns emerge from ratios of Soricidae:Murinae and Dendromurinae:Murinae (Table 8). The consistent direction of the relationship implies that murines tend to predominate in mesic woody vegetation. Roost 3 again appears as an outlier to the pattern, with a greater number of murines (especially *Mus* spp.) than would be expected for a grassland roost. As mentioned previously, roost 3 is a marginal grassland and may have been more wooded in the recent past. With this one exception, the G:M ratio performs well using the modern data.

### TAXONOMIC HABITAT INDEX

The taxonomic habitat index is a method for combining the niche models of each taxon into an overall picture of the habitat preferred by its constituents. The pooled value given to each habitat class is called the taxonomic habitat index (THI) and is defined by the following relationship:

$$THI_j = \frac{\sum_{i=1}^i w_{ij}}{i} \quad (2)$$

where  $w_{ij}$  is the habitat indication of the  $i$ th taxon for the  $j$ th habitat taken from the niche model. The analysis works from a contingency table of niche models with taxa as row headings and the different habitats as column headings (Table 9). The niche model proportions each species across habitats as was shown in Table 5.

Table 8. Spearman rank correlation,  $\rho$ , for three taxonomic ratios (rows), each tested against percent woody vegetation. Alpha values of 0.005 adjusted for three unplanned tests;  $0.05/3 = 0.015$

Ratio	$\rho$	$P$	Result
G:M	-0.773	0.015	*
D:M	-0.681	0.044	NS
S:M	-0.580	0.102	NS

Table 9. Example niche model contingency table

	Habitat 1	Habitat 2	...	Habitat $j$
Taxon 1	$w_{11}$	$w_{12}$		$w_{1j}$
Taxon 2	$w_{21}$			
...				
Taxon $i$	$w_{i1}$			$w_{ij}$

The values in the table are then summed by habitat type (i.e., down the columns) for those species present in the assemblage and divided by the total number of species to produce a habitat index. The results indicate which habitats are most strongly represented by the species in the assemblages (Nesbit-Evans et al., 1981; Andrews, 1990). A histogram charting the THIs for all habitats is called a habitat spectrum (van Couvering, 1980).

The quality of results from a THI analysis depends on several factors: the niche models for the taxa, the taxonomic rank that is used (species niche models are more specific than those for genera, family, etc.), and the assumption of taxonomic uniformity (i.e., transferred ecology). This assumption states that modern representatives are suitable analogues for the fossil taxa. Generally this assumption becomes less tenable with the older the fossil assemblage, and also depending on the evolutionary history of the lineages involved. Has the lineage experienced a recent radiation with the appearance of new species? If so, the assumption of transferred ecology is probably not as strong as for a lineage that has been morphologically stable.

Another factor to consider is how the taxa should be weighted with regard to their relative abundance. Equal weighting ignores relative abundance and assumes that each taxon is equally informative about the habitat. Weighting taxa by relative abundance assumes that the most abundant are best adapted to the surrounding habitat and should have a greater influence in the analysis. As a test, THI is applied to the modern coprocoenoses using both assumptions.

Taxonomic habitat spectra using equal weighting are shown in Figure 6. Given the broad niche breadth of most rodents, habitat spectra will usually have all habitat classes represented in at least some small amount, hence the presence of a habitat in the spectrum is not necessarily indicative of that in reality. This is clear, for example, at roost 24 where forest, woodland, and bushland habitats are indicated in the spectrum even though they are absent (or present in very small quantities) at that roost. Forest appears in the spectrum for every roost, but this landcover type is only present in significant quantities at roost 44.

The THI spectrum succeeds in returning indices in their proper rank order. For example, roost 24 yields grassland (36%) > bushland (~26%) > woodland (~15%) > semi-arid (~12%) > forest (~9%) in that order. This agrees with the remote-sensing habitat analysis that indicated 88% grasslands, and 12% bushed grasslands. The woody component at roost 24 is mostly low shrubs, with small numbers of trees at the kopjes themselves. Some bare ground is present both as part of the rocky kopjes and at salt flats. There is no forest.

This same rank order is returned by the THI spectra for each roost, except roost 12. From the perspective of accuracy this is appropriate as grassland is the dominant land cover category at all roosts. The only inaccurate result occurs at roost 12 where woody vegetation is over-represented in the analysis. However, at roost 12 the top three habitat indices are all very close to one another (26.1, 26.6, and 25.1), so the erroneous result may be due to that roost's small sample size.

The results are less consistent when comparing one roost to the next. Given the absence of woody vegetation from the area around roost 7 and 24, it is expected that these roosts should have the highest grassland and semi-arid values and the lowest forest values. Encouragingly, the four roosts at the drier/open end of the spectrum have the greatest values for the semi-arid

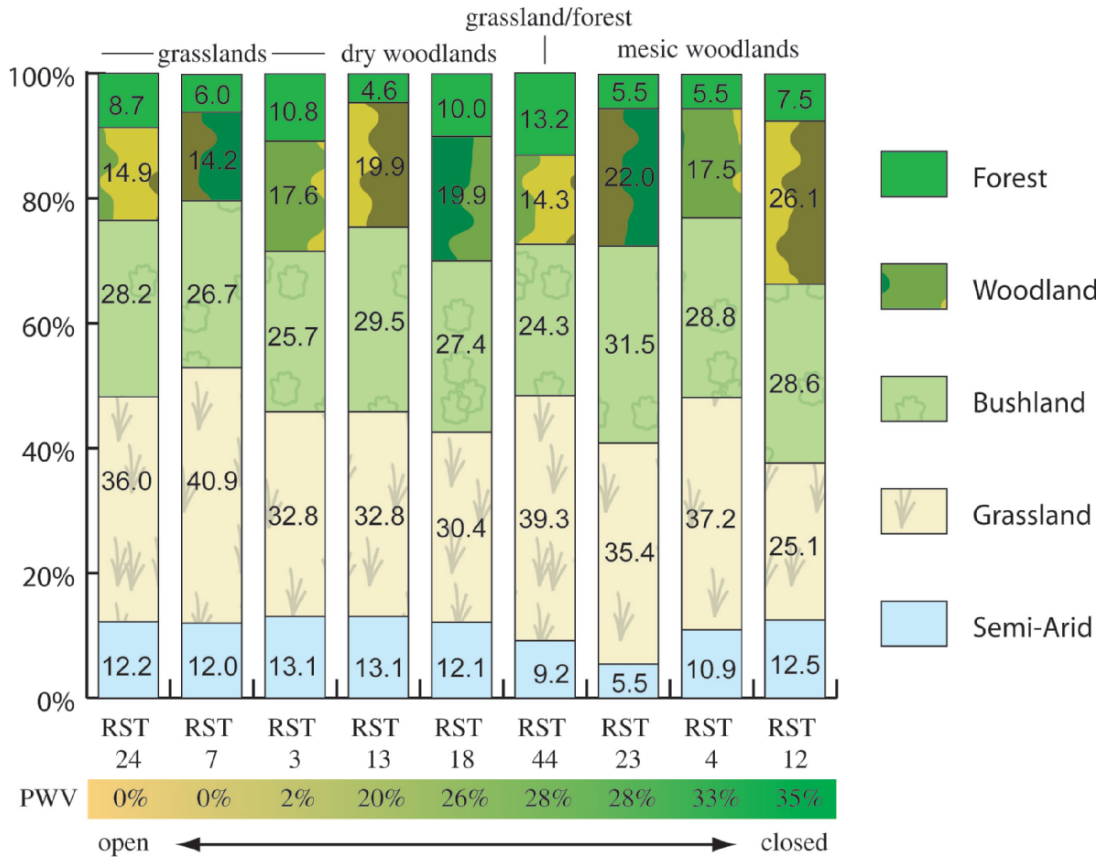


Figure 6. Taxonomic habitat spectra based on Serengeti taphonomic assemblages. Each bar shows cumulative percentages for each habitat index at the roost. Roosts are arranged from left to right in ascending order of percent woody vegetation cover. Each taxon is equally weighted in the analysis (abundance is not incorporated). General habitat descriptions are given across the top of the chart.

class; however, roost 12 has a value that is higher than expected. Similarly, for the grassland category roosts 7 and 24 have high values as expected but roosts 44 and 4 are also unexpectedly high. Combining the grassland and semi-arid categories, a generous observer may find a decreasing trend, but it is clearly disrupted by roosts 44 and 4.

The bushland category is very similar across all roosts while woodlands follow an increasing trend to the right as would be expected. Roost 44 has a small woodland component consistent with the actual habitat there (grasslands bordering forest). Furthermore, roost 44 has the largest value for forest. However, some of the other more closed roosts have very

small forest contributions. The fact that these values are small is not surprising given that true forests are not present in abundance, but it is surprising to find higher values at the grassland roosts.

Weighting by taxon abundance (NISP<sub>n</sub>) tends to amplify the results. THI values from the weighted analysis are illustrated in Figure 7. Grasslands remain the dominant vegetation type at roosts 24, 7, and 44, which accords with the actual habitat at these roosts, and roosts 24 and 7 retain high values for the semi-arid class, whereas this value drops off in the other woodland roosts. However, the forest class nearly disappears from roost 44. Woodland becomes the first ranking habitat class at all the remaining roosts.

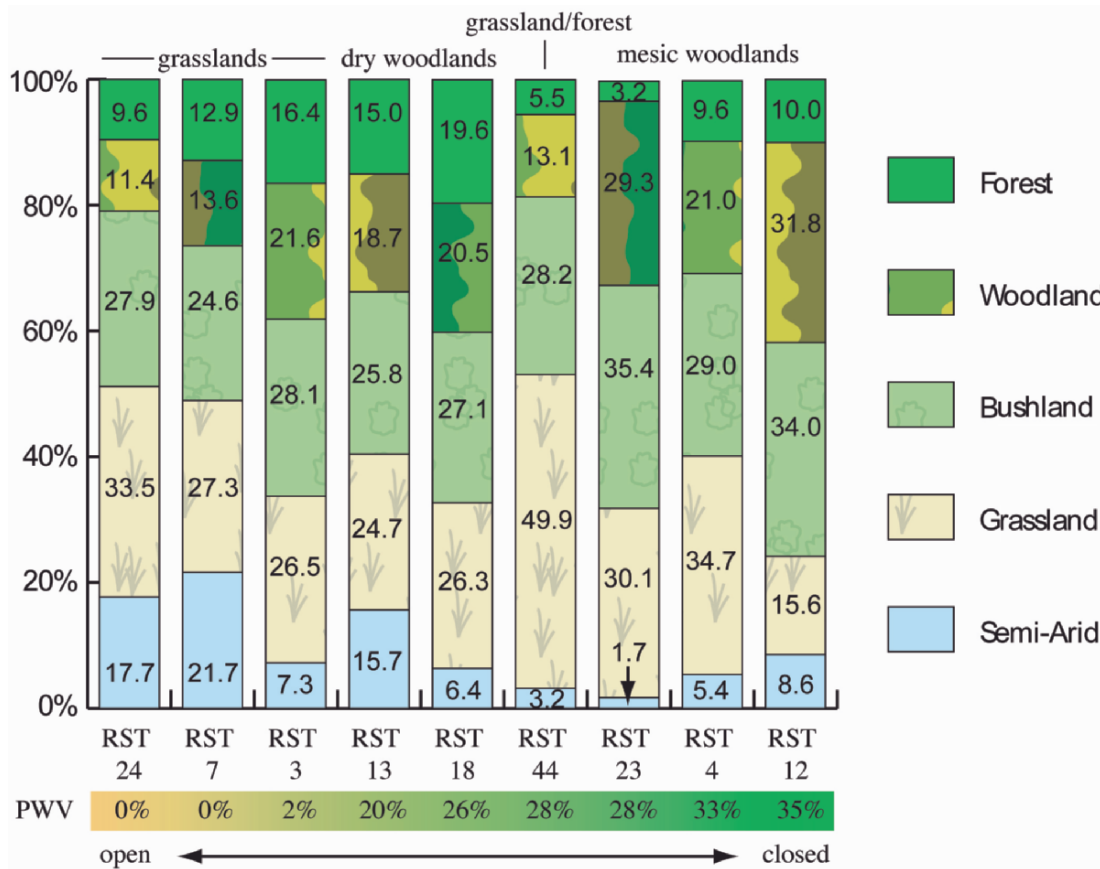


Figure 7. Taxonomic habitat spectra based on taxonomic habitat indices weighted by NISPn. Roosts are given in ascending order of woody vegetation starting with the least wooded roost on the left.

SUMMARY OF ANALYTICAL METHODS

Two common methods of micromammal faunal analysis are tested against modern assemblages. The taxonomic ratio of Gerbillinae to Murinae performs well. It returns rank order results consistent with the habitats observed around each roost. The dry, grassland roosts have G:M ratios greater than 1 with the exception of roost 3. This roost sits right on the border between grasslands and woodlands and it may at times in the past have been more wooded. Arid-adapted, Egyptian gerbils of the genus *Gerbillus* play a prominent role in determining this ratio, especially when found in association with other burrowing rodents such as *Steatomys* and *Tatera*. *Tatera* also occur in

woodlands that have a grass understory, making this genus a less reliable indicator of open grassland environments. *Steatomys*, though modeled as a catholic species, occurs predominantly in open grassland environments in Serengeti. All three species are burrowing, an adaptation that is crucial for predator avoidance in habitats with sparse vegetation cover. Burrowing is also an effective strategy against frequent fires. In the more mesic and wooded environments, the denser understory provides shelter for many of the murine species. Murine species such as *Dasymys* and *Arvicanthis* also filled the semi-aquatic edaphic grassland niche as evidenced at roost 44. Thus, non-burrowing murines come to replace burrowing gerbils and dendromurines in wet and water margin

environments. In the middle are burrowing rodents, such as *Arvicanthis* and *Lemniscomys* that also rely on runways through the herbage to avoid predation.

Results from the THI analysis were less robust and differed depending on whether the analysis used equal weighting or weighting by taxon abundance. Equal weighting returned results for which the dominant THI matched the prevailing habitat at the roost (grasslands in all cases) except for roost 12, where bushland was the dominant THI class. With equal weighting woodlands (areas with >20% woody canopy cover) have lower THI values for grassland and semi-arid classes compared to grasslands and generally higher values for forest and bushland classes. However, the differences are relatively small and there is some overlap that makes interpretation difficult. Weighting by abundance amplifies the differences but also produces results that appear less accurate, as for example, the small value of forest at roost 44.

Fernandez-Jalvo et al. (1998) compare THI values of fossil assemblages against results from modern faunas. The Serengeti data used here indicate that such comparisons are probably inappropriate because variability within a park or census area may be as great as the variability between them. For example, the three grassland areas (roost numbers 24, 7, 3) show a range of variability greater than that shown between grassland and woodland areas. The general trends in the data are encouraging, but the technique will need further refinement before confidence can be placed in the results.

### Olduvai Paleoenvironments

Olduvai Gorge lies on the southeastern edge of the Serengeti (35.3483° E, 2.9881° S), where the plains slope down to meet the foot of the volcanic highlands formed by the Ngorongoro caldera and neighboring volcanoes. This topographic depression forms a shallow basin now dissected by a seasonally flowing river that runs along the bottom of the gorge and flows

from two alkaline lakes further to the west (Lake Masek and Lake Ndutu). At its eastern edge the Gorge empties into the Ol'Balbal swamp. This swamp is also fed by freshwater streams coursing down from the volcanic highlands to the southeast (Figure 8).

Archaeological and paleontological sites are found throughout the gorge, including the FLK Bed I sequences at the crux between the main gorge and the side gorge. Exposures in the eastern portion of the gorge represent alternating fluvial and lacustrine sequences formed by fluctuating paleolake margins (Hay, 1976; Denys et al., 1996; Ashley and Driese, 2000). This region has been reconstructed as alkaline mudflats grading into moist grasslands and spring fed marshes along a volcanic piedmont between paleolake Olduvai and the adjacent highland to the southeast (Hay, 1976; Deocampo et al., 2002; Blumenschine et al., 2003). Archeological sites at FLK have yielded rich Plio-Pleistocene faunas including both large and small mammals (Butler and Greenwood, 1976; Jaeger, 1976; Gentry, 1978a, b). The oldest FLK sites occur in Middle and Upper Bed I deposits and span a time interval of approximately 50,000 years between Tuff IB at  $1.798 \pm 0.014$  Ma and Tuff IF at  $1.749 \pm 0.007$  Ma (Walter et al., 1991). Middle Bed I is represented at FLK North–North by three levels below Tuffs IC and ID (FLKNN1–3). Level FLKNN1 has few faunal remains but is considered contemporaneous with the “Zinjanthropus” floor at FLK 1 level 22, hereafter referred to as FLK-Zinj (Leakey et al., 1971). Above Tuff ID the Upper Bed I deposits include six levels at site FLK North, (FLKN1–6) extending up to Tuff IF.

### THE PLIO-PLEISTOCENE RODENT FAUNA AT OLDUVAI GORGE

Lavocat (1965) gave a brief description of the micromammals recovered from FLK. More detailed taxonomic treatments followed for the elephant shrews (Butler and Greenwood, 1976) and rodents (Jaeger, 1976; Denys, 1990,

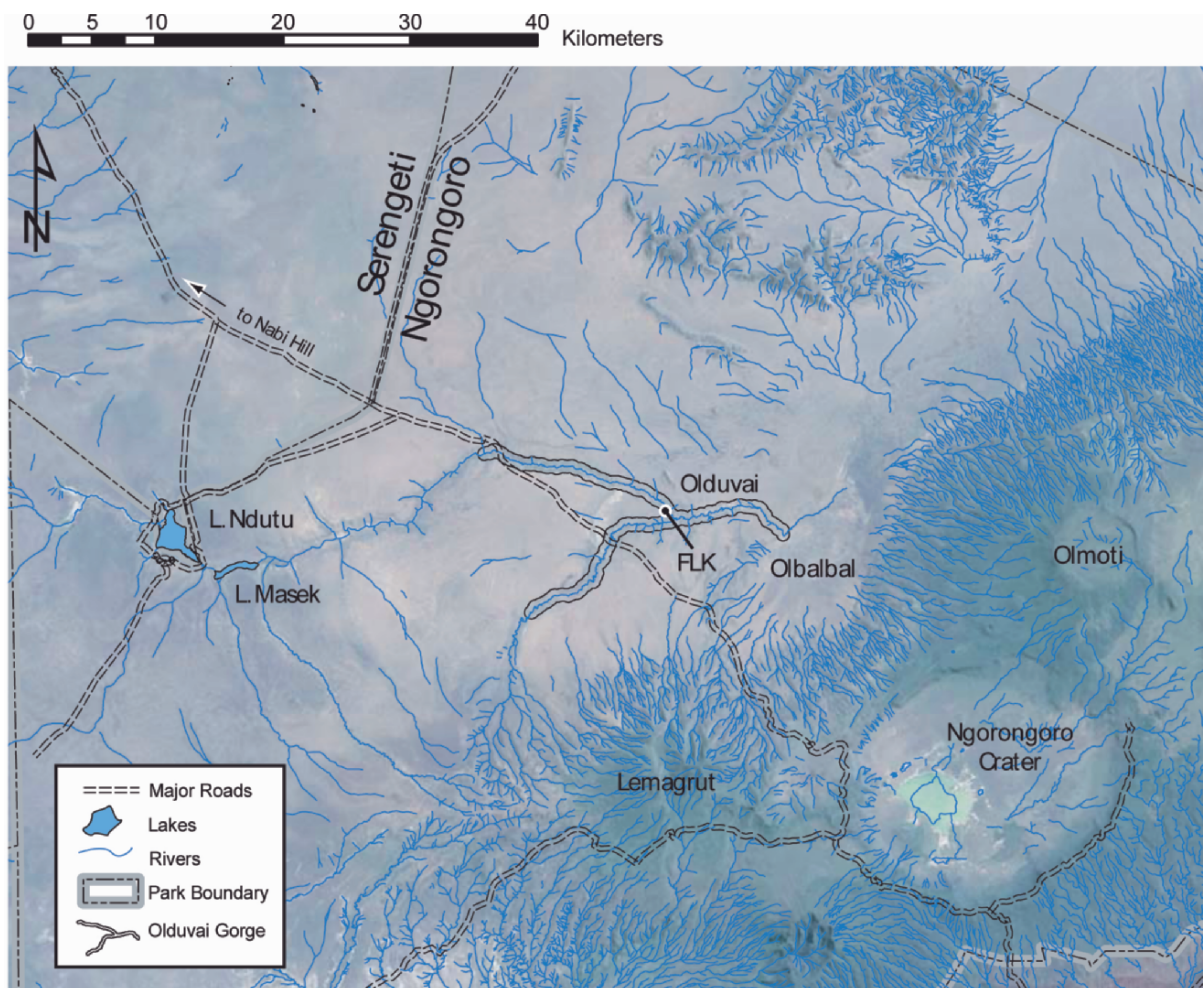


Figure 8. Satellite image background with map overlay showing the location of Olduvai Gorge and site FLK.

1999; Denys and Tranier, 1992. Table 10 lists the taxa occurring in the Bed I FLK sites at Olduvai Gorge.

The genera represented in the fossil Bed I assemblages overlap considerably with the taxa known from the modern Serengeti ecosystem and surrounding region. Of the 17 fossil rodent genera recovered at Olduvai, all but two, *Heterocephalus* and *Oenomys*, have been noted in the modern Serengeti ecosystem and Ngorongoro highlands either through owl pellet or trapping studies. The two extra-limital taxa are known from surrounding regions. The modern distribution of *Heterocephalus* includes the arid regions of Somalia, Ethiopia, and Kenya, while *Oenomys* is found in forest habitats

around Lake Victoria. Three genera: *Pelomys*, *Otomys*, *Grammomys*, have been recorded in the Serengeti through trapping studies or previous owl-pellet studies (Swynnerton, 1958; Andrews, 1983) but did not appear in the owl pellet assemblages analyzed for this project (Table 10). The consistency between fossil and modern assemblages implies a relatively stable metacommunity structure for East African rodents through the Pleistocene.

In East Africa, roughly contemporaneous Late Pliocene rodent faunas are known from the Peninj group of deposits at West Lake Natron (Denys, 1987a), the Koobi Fora Formation at East Turkana, between the KBS and Okote Tuffs (ca. 1.6 Ma) (Black, 1984; Black and Krishtalka,

1986), and Members D–H of the Omo Shungura Formation (Wesselman, 1982, 1984, 1995).

Clues to the origins and biogeographical history of these Late Pliocene rodent faunas can be found in older Pliocene deposits such as the Laetolil and Ndolanya Beds at Laetoli (Denys, 1987b) and the Ibol Member from the Manonga Valley in Tanzania (Winkler,

1997). In Kenya there are assemblages from the Chemeron Formation in the Tugen Hills (Winkler, 2002), the Mio-Pliocene deposits at Lothagam (Winkler, 2002), and as yet undescribed material from Kanapoi (Winkler, 1998). Further north along the rift valley are sizeable assemblages from Members B and C of the Omo Shungura Formation (Wesselman,

Table 10. Abundance (MNI) of Olduvai fossil rodents from FLK sites modified from Fernandez-Jalvo et al. (1998). Taxa are organized by niche index with the more arid-adapted taxa to the left. Presence or absence of taxa in modern roosts and trapping studies is indicated below each taxon. Asterisks next to taxon names indicate the taxon shows significant change in abundance between levels. The upper frame lists MNI values and the lower frame percent MNI

		Niche index >																		
		1.60	2.10	2.25	2.40	2.50	2.60	2.97	2.97	3.00	3.00	3.09	3.30	3.46	3.50	3.69	4.05	4.50		
Stratigraphic Level		<i>Gerbillus*</i>	<i>Zelotomys</i>	<i>Arvicanthis</i>	<i>Tatera</i>	<i>Pelomys</i>	<i>Heterocephalatus*</i>	<i>Mastomys*</i>	<i>Saccostomus</i>	<i>Steatomys</i>	<i>Otomys*</i>	<i>Dendromus</i>	<i>Xerus*</i>	<i>Aethomys</i>	<i>Thallomys*</i>	<i>Mus</i>	<i>Grammomys</i>	<i>Oenomys*</i>	Total MNI	
Trapping Owl Assemb.		+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+	-	-	
Absolute abundance (MNI)																				
Upper Bed I	FLKN1	21	10	0	10	0	0	2	3	16	27	10	0	3	0	3	0	0	105	
	FLKN2	12	8	0	11	0	0	1	10	13	17	2	0	8	2	2	0	0	86	
	FLKN3	6	3	0	14	0	2	0	9	8	19	2	5	10	1	0	0	0	79	
	Taphonomic shift																			
	FL KN4	16	3	1	7	1	11	9	4	9	16	1	0	11	1	1	0	0	91	
	FLKN5	8	2	0	3	1	8	11	1	4	8	1	0	3	0	1	0	0	51	
FLKN6	2	1	0	2	0	0	0	2	4	2	1	0	2	0	1	0	0	17		
Tuffs IC and ID																				
Middle Bed I	FLK-Zinj	0	3	2	3	1	0	2	2	3	0	1	0	16	11	1	0	1	46	
	FLKNN2	0	3	1	9	2	0	2	0	4	1	0	0	3	1	1	0	1	28	
	FLKNN3	0	2	2	3	0	0	1	0	9	15	0	0	4	1	1	1	4	43	
Percent abundance																				
Upper Bed I	FLKN1	20	10	-	10	-	-	2	3	15	<b>26</b>	10	-	3	-	3	-	-	100	
	FLKN2	14	9	-	13	-	-	1	12	15	20	2	-	9	2	2	-	-	100	
	FLKN3	8	4	-	18	-	3	-	11	10	<b>24</b>	3	6	13	1	-	-	-	100	
	Taphonomic shift																			
	FLKN4	18	3	1	8	1	12	10	4	10	18	1	-	12	1	1	-	-	100	
	FLKN5	16	4	-	6	2	16	<b>22</b>	2	8	16	2	-	6	-	2	-	-	100	
FLKN6	12	6	-	12	-	-	-	12	<b>24</b>	12	6	-	12	-	6	-	-	100		
Tuffs IC and ID																				
Middle Bed I	FLK-Zinj	-	7	4	7	2	-	4	4	7	-	2	-	<b>35</b>	<b>24</b>	2	-	2	100	
	FLKNN2	-	11	4	<b>32</b>	7	-	7	-	14	4	-	-	11	4	4	-	4	100	
	FLKNN3	-	5	5	7	-	-	2	-	<b>21</b>	<b>35</b>	-	-	9	2	2	2	9	100	



1982, 1984, 1995) and the Sidi Hakoma, Denen Dora, and Kada Hadar Members at Hadar, Ethiopia (Sabatier, 1982).

Taking a broader geographic perspective, one can compare the East African faunas to large assemblages from South African Pliocene localities including, Langebaanweg (Pocock, 1987; Denys, 1990), Makapansgat (Pocock, 1987), Kromdraai (de Graaff, 1961; Pocock, 1987), Taung (McKee, 1993), Sterkfontein and Swartkrans (Pocock, 1987; Avery, 1995, 1998, 2001). Two other micromammal sites are the Plio-Pleistocene fissure fillings at Humpata, Angola (Pickford et al., 1994) and the Lusso Beds in the Democratic Republic of Congo (formerly Zaire) (Boaz et al., 1992). Fossil micromammals also occur at numerous North African Mio-Pliocene localities, but these have greater affinities to European and circum-Mediterranean mammal communities than to those in eastern and southern Africa (Geraads, 1998).

In a review of the biogeography of East African rodents, Denys (1999) demonstrates that the Plio-Pleistocene and modern rodent faunas from Olduvai and Serengeti are typical of the Somali–Masai vegetation biome. This biome extends from northern Tanzania up through Kenya and the horn of Africa. Rift valley tectonic activity and volcanism increased paleobiodiversity in the region during the Pliocene by creating a mosaic of habitats ranging from arid environments along the valley floor to montane forests on the slopes of newly formed volcanoes. Transverse faults along the rift created mountain chains that segmented the rift valley into isolated basins, simultaneously restricting the movements and terrestrial animals and elevating the potential for fracturing (i.e., vicariance) of species' geographic ranges (Denys et al., 1986). East African rodent diversity was also influenced by migration from southern Africa. Shortly after the start of the Pliocene, ca. 4–3 Ma, southern Africa develops a differentiated Zambezian fauna that comes to influence the southern parts of

eastern Africa. For example, *Zelotomys* and *Otomys* are prevalent South African Pliocene taxa that appear in East Africa at Laetoli and Olduvai but are not recorded as far north as the Omo or Hadar (Denys, 1999).

#### PREDATOR INFLUENCE ON DIACHRONIC CHANGES IN OLDUVAI BED I RODENT FAUNAS

The general consensus among early studies of the Olduvai faunas was that the micromammals associated with Upper Bed I (especially FLKN level 1) represented a more xeric-adapted community than those associated with Middle Bed I (FLKNN level 3-2 and FLK-Zinj). Butler and Greenwood (1976) note that xeric-adapted macroscelideans, such as *Elephantulus*, become increasingly more abundant through Upper Bed I times. They observe that “a marked change takes place in the insectivore fauna between FLK NNI and FLK NI... This must imply a change of environment, and the most likely change would be a reduction in rainfall” (Butler and Greenwood, 1976, p. 48). However, Andrews (1983) proposed that some of these faunal shifts might reflect changes in the predators accumulating the assemblages rather than real environmental change. For example, the abundance of *Gerbillus* in the Upper Bed I deposits may be an artifact of eagle owls preferring gerbils over murines. Accounting for the bias led Andrews to conclude that the fauna at FLKN1–2 are “indicative of a wooded habitat that was perhaps closer to the denser and wetter woodlands of the northwestern part of the Serengeti ecosystem rather than to any of the habitats in the immediate vicinity of Olduvai Gorge today” (p. 84). Subsequent work on taphonomic processes affecting micromammal assemblages (Andrews, 1990) eventually led to a thorough investigation the taphonomy of Olduvai microfauna by Fernandez-Jalvo et al. (1998). One of their important contributions is the detailed analysis of bone breakage

and surface modification. Their findings are summarized in the “accumulator” and “modification” columns of Table 11. From this analysis the authors identify three intervals, each with different taphonomic biases. The oldest, Middle Bed I, assemblages at FLKNN and FLK-Zinj exhibit less breakage and less surface etching of the bones (Table 11). These patterns are consistent with owls, and the barn owl specifically in the case of FLKNN2. There is then a switch to a more destructive pattern of breakage and surface modification that the authors identify as a mammalian carnivore perhaps in combination with owls. This pattern maintains for levels 4–6 at FLKN. Further up the sequence (FLKN1–3), the assemblages exhibit moderate breakage consistent with an eagle owl.

One of the most important differences between Middle and Upper Bed I faunas is the absence of *Gerbillus* from the older members and its appearance in Upper Bed I. Is the appearance of *Gerbillus* in Middle Bed I the results of environmental change or a change in predator? This taxon has a very low niche index value (see Table 5) and is one of the best indicators of open and semi-arid habitats. Its abundance influences other types of analyses such as the ratio of Gerbillinae to Murinae, and THI

method discussed previously. Thus, taphonomic biases that affect *Gerbillus* can have a strong impact on any analysis. Fernandez-Jalvo et al. (1998, p. 166) argue that predator selectivity rather than environment “may produce changes in species composition... between FLKNN and FLKN.” They argue (ibid, p. 166) Middle Bed I (especially FLKNN2) was the work of a non-destructive accumulator such as the barn owl, *Tyto alba*, that “may favor murines against gerbils, as seen in modern assemblages (Laurie, 1971; Andrews, 1990).” Thus, they conclude that the absence of gerbils from the Middle Bed I assemblages is an artifact of barn owls selecting against gerbils. However, the modern Serengeti roost data does not appear to support this assertion. Gerbils are abundant in the drier grassland roosts of the current study (roosts 7 and 24). Both these roosts are very likely the work of barn owls. In both instances, barn owls were found as current occupants and both are “cavity” roosts, the type favored by barn owls to the near exclusion of eagle owls (Reed, 2003, 2005). At roost 7 in the current study *Gerbillus* was the third most abundant taxon (ca. 17% NISPn) behind the shrew *Crocidura* and the dendromurine *Steatomys*. The one previous pellet study in Serengeti by Laurie (1971) does not

Table 11. Stratigraphic summary of the Middle and Upper Bed I deposits including taphonomic interpretation for the microfauna. Accumulator and modification columns are taken from Fernandez-Jalvo et al. (1998)

	Level	Accumulator	Modification
Upper Bed I	Tuff IF	1.749 Ma	
	FLKN1	<i>Bubo leakeyae</i>	Intermediate
	FLKN2	<i>Bubo lacteus</i>	Low
	FLKN3	<i>Bubo lacteus</i>	Low
	FLKN4	Mammal + <i>B. lacteus</i>	Extreme + low
	FLKN5	mammalian carnivore	Extreme
	FLKN6	Unknown	Unknown
	Tuff ID	1.764 Ma	
	Tuff iC	1.761 Ma	
	FLK-Zinj	<i>Bubo?</i>	Intermediate
Bed I	FLKNN2	<i>Tyto alba</i>	Very low
	FLKNN3	Owl	Low
	Tuff IB	1.798 Ma	

report any *Gerbillus*. The discrepancy may be due to Laurie's emphasis on fresh pellets, which are sensitive to short-term population dynamics of the prey species. The current study relies on larger, time-averaged assemblages of decayed pellets that should provide a more robust representation of the biocoenosis. Also, pellet studies from western Africa, South Africa, and Israel indicate that barn owls take gerbils, including *Gerbillus*, as prey, and when available they are captured in abundance (Vernon, 1972; Rekasi and Hovel, 1997; Pokines and Peterhans, 1998; Ba et al., 2000). The modern data do not indicate a substantial bias against gerbils by barn owls as proposed by Fernandez-Jalvo et al. (1998). Rather, the available data support Andrews's (1990) summary of barn owl diet; "muri[n]es such as *Praomys* [are] the most common [prey] in Africa, replaced by *gerbils in drier regions*" (p. 179 emphasis added).

The abundance patterns in *Gerbillus* raise the issue of whether differences across levels at Olduvai are statistically significant and meaningful. Sample sizes of identifiable elements for the Olduvai micromammal assemblages range from very small (17 and 28 upper first molar specimens at FLKN6 and FLKNN2 respectively) to moderate (105 at FLKN1). With small, unequal samples it is possible that chance plays a large role in the shifting abundance values. Tests of independence using the Pearson  $\chi^2$  statistic reveal that 8 of the 17 taxa show significant differences across stratigraphic levels (probability threshold is adjusted for an experiment wide error rate of 0.05 with 17 unplanned comparisons;  $p < 0.003$ ,  $df = 8$ ). These taxa are highlighted in Table 10 and shown at right in Figure 9. *Gerbillus* is among the eight taxa with significant changes in relative abundance across levels at FLK but *Tatera* is not (though the  $\chi^2$  value for *Tatera* is nearly significant). Any argument incorporating the changing abundance between levels should emphasize these eight taxa.

Figure 9 shows trends in the Gerbillinae: Murinae ratio using the entire fauna (solid

line) and just the eight significant taxa (dashed line). Of the eight significant taxa, three make a first or last appearance at Tuff IC/D. The xeric-adapted taxa *Gerbillus* and *Heterocephalus* appear above Tuff IC/D while the mesic-adapted genus *Oenomys* disappears. No similar pattern appears in the interval between FLKN4–6 and FLKN1–3 as suggested by Fernandez-Jalvo et al. (1998). The ground squirrel, *Xerus* is the only taxon to appear at this transition and the environmental implications of this are not clear as the genus includes species that range from open to wooded environments.

Much of the prior taphonomic research into micromammal assemblages has focused on identifying different predators. The results of this study indicate that it is perhaps time to focus on the significance imposed by different predators once identified. The results from the modern Serengeti data indicate that barn owls do not exhibit a strong bias against gerbils and that at least some predators, such as barn owls and spotted eagle owls, have very similar trophic habits and limitations such that they may be treated as isotaphonomic under certain analyses (Reed, 2005).

## PALEOENVIRONMENT

Given the degree of faunal overlap between the fossil and extant assemblages, the modern results may serve as a model or starting point for evaluating the environmental signal indicated by the fossil faunas. Figure 10 shows a correspondence analysis using the intersection of taxa found in the modern and fossil assemblages. The plot illustrates associations between fossil and modern micromammal assemblages based on the abundance patterns of shared taxa. The first axis positions the more open, xeric, grassland roosts (7 and 24) to the left, grading into the more mesic, closed roosts to the right. The second axis separates modern from fossil roosts, but there is some overlap. FLK-Zinj is located furthest to the upper right, indicating a mesic environment most like that

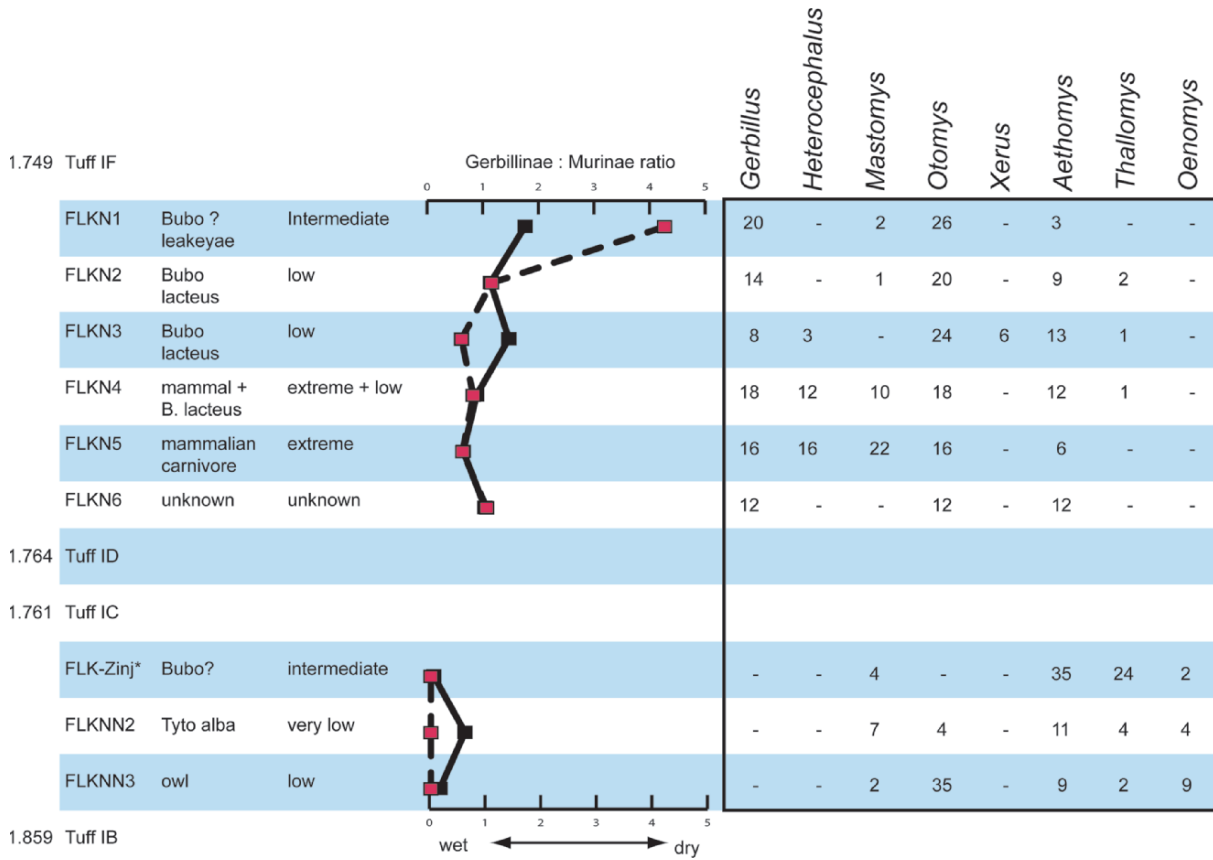


Figure 9. Temporal changes in the ratio of Gerbillinae to Murinae as reflected in the entire fauna (solid line). The right pane shows percent MNI of those eight taxa with significant interlevel differences in abundance (dashed line).

of modern roost 44. Its position is influenced largely by *Aethomys* and *Thallomys*. Both are *Acacia/Brachystegia* shrubland/woodland species. These taxa are found in the modern assemblages but not together in high abundance. The FLK-Zinj assemblage is consistent with a woodland environment, or moist savanna with evergreen gallery forest. Roost 44 occurs at higher rainfall with tall grasslands grading into relic evergreen, broadleaf forests. Extending this analogy to the paleo-Olduvai basin would produce a lake margin habitat hosting both dense and open woodland habitats that included some component of grass understory as habitat for *Tatera* and *Steatomys*.

At the other extreme, FLKN1 falls to the left along Axis 1. It also has the lowest position on Axis 2 indicating that this level has

the greatest affinity to the modern analogues. FLKN1 is most closely positioned to roost 24, the driest and most xeric of the modern analogues. The association is based on high abundances of two xeric-adapted taxa, *Gerbillus* and *Steatomys*. Both species shelter below ground, and *Steatomys* especially is an active burrower whose presence indicates soft, well-drained soils. However, the FLKN1 assemblages differ from all the modern assemblages in having *Otomys* as the dominant taxon. Modern species of *Otomys* are grazers that tolerate a broad variety of habitats including thicket and secondary growth to marshes and montane grasslands. Any interpretation of the paleoenvironment at FLKN1 must reconcile *Otomys* with the xeric affinities of the remaining taxa.

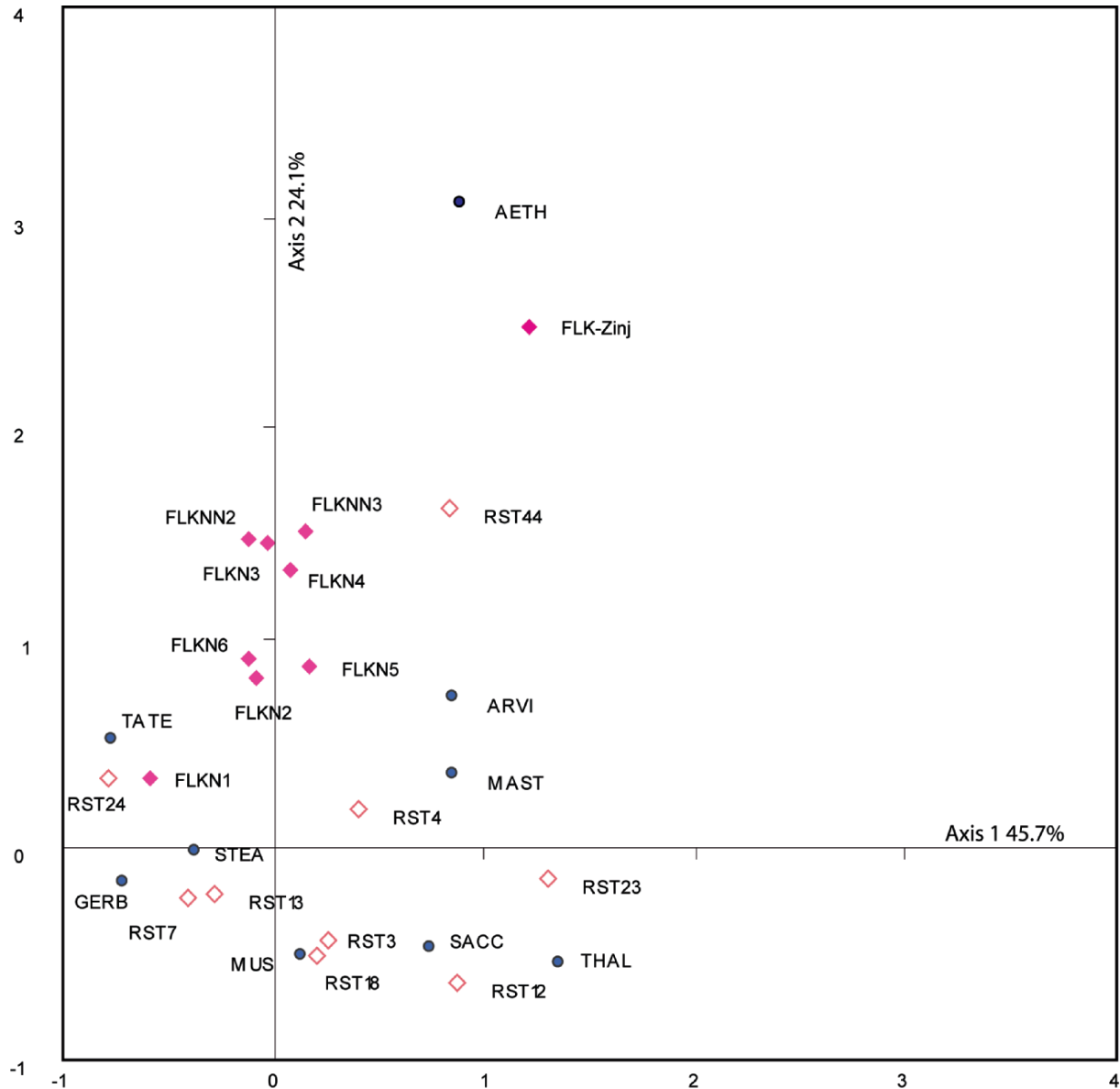


Figure 10. Correspondence analysis based on modern faunas (using NISPn abundance values). Fossil assemblages are included in the plot as ancillary data; fossil faunas were not used to calculate the topography of the plot. The position of the fossil assemblages is based only on those taxa that overlap with the modern assemblages. Modern data are shown as open diamonds, the taxa as closed circles, and the fossil assemblages as closed diamonds.

*Otomys* is present throughout the Bed I sequence. Its persistence may be associated with a stable moist grassland or marsh along the paleolake margin. It could also indicate lake margin or riparian bushland. However, none of the other taxa at FLKN1 give an indication of woody vegetation. Two closed

habitat taxa, *Aethomys* and *Mus*, are in low abundance, but similar low abundances of these taxa may be found in the modern grassland roosts (e.g., *Aethomys* and *Mus* both appear at roost 24). With the available data, it is not possible to rule out freshwater moist grasslands fed by montane streams,

surrounded by dry grassland. If a substantial woody environment existed around paleolake Olduvai during FLKN1 times, one would predict *Thallomys*, *Aethomys*, and *Mastomys* in greater abundance.

Despite the overlap in taxon representation between fossil and modern micromammal assemblages, the correspondence analysis also serves to illustrate that the fossil assemblages are all more like each other than they are to the modern assemblages and vice versa. It is certainly possible that the fossil assemblages are not analogous to any modern assemblage. The uniqueness of fossil Olduvai communities demonstrates that it is necessary both to expand the range of modern analogues and at the same time find more generalized factors for comparison than taxonomy, such as ecomorphology (Alexander, 1988; Damuth, 1992 or ecological structure analysis.

Although the THI analysis of the extant roost samples had difficulty differentiat-

ing some of the modern habitats, an analysis of the fossil assemblages is provided for completeness. Figures 11 and 12 show the results calculated under assumptions of even weighting and weighting by abundance, respectively. Proportions of forest decline through time with a concomitant increase in the semi-arid component. Bushland and grassland are the dominant habitat classes in every level except FLK-Zinj where the woodland component ranks second behind the bushland component when computed with abundance weighting. The pattern of results from the THI analysis follows the general drying trend already described. Under an assumption of even weighting, there is a marked increase in the abundance of the semi-arid class between Middle and Upper Bed I assemblages, and not a very marked change between FLKN4–5–6 and FLKN1–2–3 as reported by Fernandez-Jalvo et al. (1998). The same pattern appears when the analysis is run with abundance

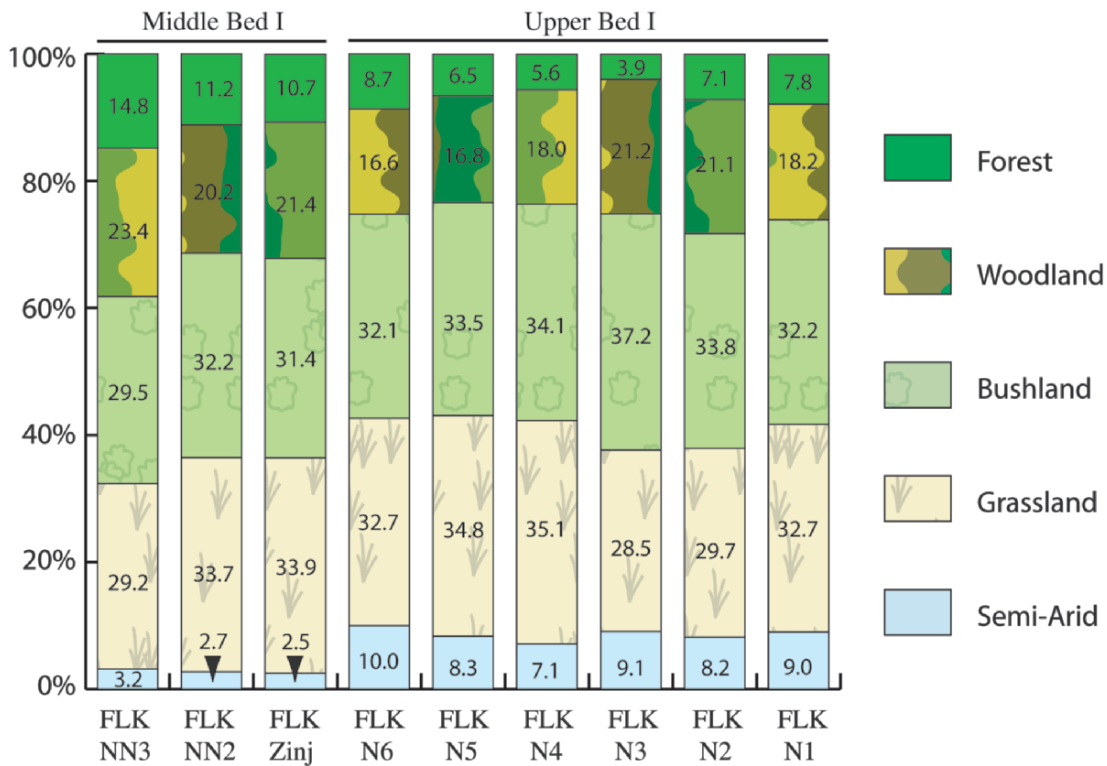


Figure 11. Taxonomic habitat spectra of Olduvai Bed I micromammal assemblages calculated with even weightings for all taxa.

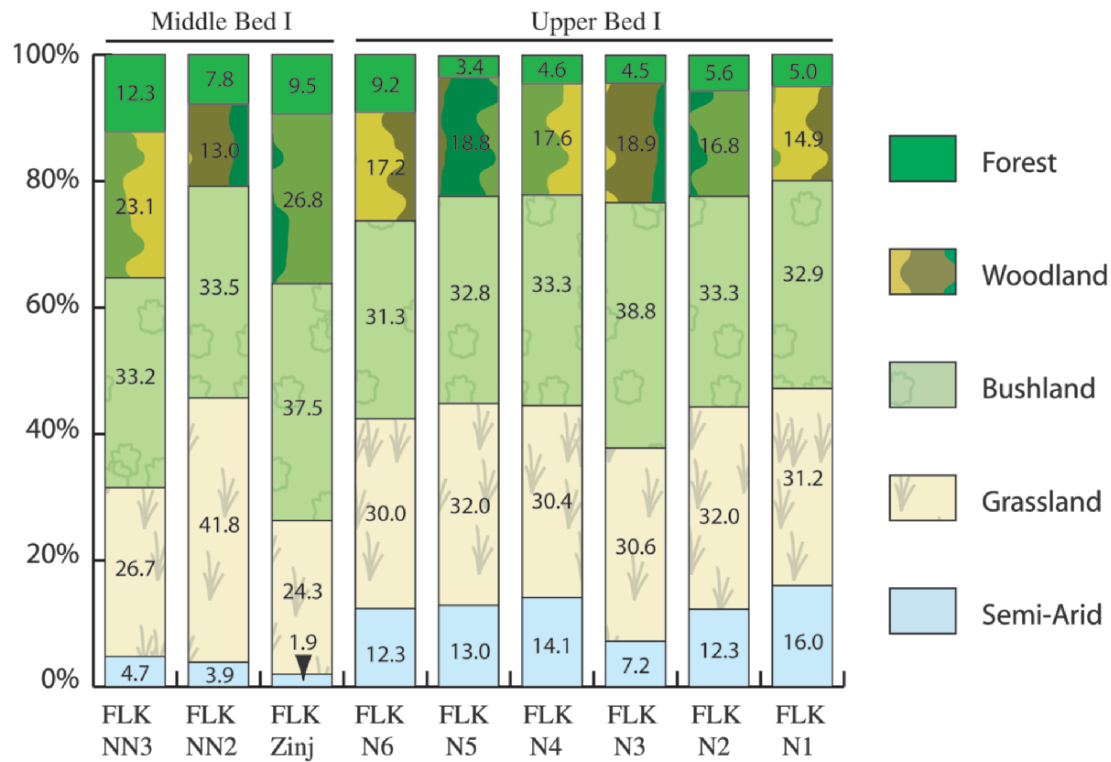


Figure 12. Taxonomic habitat spectra of Olduvai Bed I micromammal assemblages weighted by taxon abundance.

weighting, but in this analysis a change in the semi-arid category is more pronounced between FLKN4 and FLKN3. The same THI analysis was conducted by Fernandez-Jalvo et al. (1998) using the same data set. Their results show a similar pattern although forest values are much greater (see their Figure 8).

In summary, an analysis of the micromammals that incorporates modern data along with taphonomic analysis supports the initial interpretation that Middle Bed I represents a more wooded and mesic environment. This is followed by a transition to a drier phase in Upper Bed I. At this transition *Gerbillus* appears in the assemblages, *Thallomys* is lost or present at low abundance and *Grammomys* drops out as well, although the sample size for *Grammomys* is too small to say this definitively. This faunal transition occurs beside a change in the accumulating agent, but with current data we may reject the hypothesis that the low abundance

of *Gerbillus* in Middle Bed I (FLKNN and FLK-Zinj) was predator induced. The shift in the dominant predator may still influence the assemblages, but the effects need to be investigated with regard to specific methods of analysis. The ratio of Gerbillinae to Murinae increases throughout the Middle Bed I assemblages until they attain a community structure and composition similar to modern grassland assemblages, but with the addition of *Otomys* in high abundance. The best null hypothesis for the FLKN1 assemblage is that it represents a grassland environment with little woody vegetation cover but with some component of moist grassland or wetlands. This is a testable hypothesis. Should continued excavation in the FLKN1 level produce woodland species such as *Thallomys*, *Aethomys*, or forest species such as *Grammomys* the hypothesis should be rejected. True wetlands should also provide habitat for *Pelomys* or *Dasymys*. Without these

taxa, moist grassland remains the most likely landscape type.

### Summary and Conclusion

This chapter has examined the efficacy of micromammals for paleoenvironmental analysis with regard to predator bias, accuracy of habitat representation, and precision. The results indicate that faunal composition differs significantly one roost to the next along an ecological gradient despite biases owls have for hunting in open habitats, and a related study (Reed, 2005) demonstrates that at least two owl species (barn owls and spotted eagle owls) do not differ significantly in the proportions of most prey taxa that they take.

The prey composition and relative abundances noted in the modern Serengeti data appear to accurately represent the habitats that are present at the roost. The grassed plains are characterized by gerbils (especially *Gerbillus*), and the dendromurine *Steatomys* concurrent with the absence or very low abundance of arboreal or semi-arboreal taxa such as *Thallomys*. A reciprocal pattern occurs for *Acacia* woodland roosts, which are characterized by the absence or low abundance of *Gerbillus*, and the presence of *Thallomys* and *Mastomys*. Woodlands also provided habitat for moist grassland taxa such as *Arvicanthis*. Tall grasslands and evergreen forest occur in the northern extension where precipitation exceeds 800 mm annually and there are perennial water sources. Here suitable habitats exist for *Aethomys* and *Dasymys*. Ratios of Gerbillinae to Murinae were significantly correlated to percent woody vegetation cover along the ecological gradient and THI values calculated from previously devised niche models were consistent with the modern observed habitats.

Dominant prey taxa are those one would expect based on independent trapping studies reported in the ecology literature, and in no

instance did a taxon occur at a roost where an appropriate habitat for that taxon was not present within 1.5 km of the roost site. Given the broad niche tolerances of many rodents, and that limited data are available on the habitat use of African rodents and shrews, this result corroborates the accuracy of the method but probably does not represent the strongest test of accuracy one could perform. Accuracy can be better evaluated by improving how we document niche tolerance, collating published and unpublished data on micromammal distribution and abundances from museum collections, and by simultaneous, direct comparison between coprocoenoses and trapping results.

The nine analyzed roosts have largely overlapping taxonomic representation, and a simple taxonomic list would diagnose habitats at some roosts, but would overlook a great deal of meaningful ecological information. Using the relative abundance of taxa, it is possible to distinguish subtle differences in habitats over distances of tens of kilometers. This study demonstrates the potential of micromammal assemblages for depicting habitats within biomes at finer spatial scales.

Applying the general model to the Olduvai microfauna gives results that differ from the paleoenvironmental interpretations proposed by Fernandez-Jalvo et al. (1998) and corroborate earlier interpretations of the micromammals made by Jaeger (1976) and Butler and Greenwood (1976). Whereas Fernandez-Jalvo et al. (1998) argue that the faunal transition between Middle and Upper Bed I (specifically between FLKNN/Zinj and FLKN4–5–6) is the result of biases in the accumulating agent, this is not borne out by the modern data that indicate that barn owls hunting in open and arid habitats produce assemblages rich in *Gerbillus*. This finding does not rule out the possibility of a faunal transition during Upper Bed I (between FLKN4–5–6 and FLKN1–2–3) as they propose. The Gerbillinae to Murinae



ratio as well as the THI analysis both indicate a general drying trend over this interval. This pattern corroborates results from other, independent lines of evidence (Kappelman, 1984). Applying Vrba's (1980, 1985, 1995) Alcelaphini + Antilopini criteria (AAC) shows increases in the proportional representation of these arid-adapted bovid tribes through the sequence regardless of whether counts are done by minimum number of individuals (MNI) or numbers of individual specimens (NISP) (Gentry, 1978a, b; Kappelman, 1984; Potts, 1988; Plummer and Bishop, 1994) (Figure 13). One discrepancy appears at the FLK-Zinj locality. Among the bovids, FLK-Zinj has an AAC proportion intermediate to the FLKNN levels and the FLKN levels, but

among the micromammal assemblages this is the most wooded and mesic. The contrast may be due to differences in the scale of applicability between micro- and macrofauna, with the former applying to smaller and more local environments, while the bovids include fauna sampled from the region outside the immediate vicinity of paleolake Olduvai.

Using the data provided from modern Serengeti coprocoenoses, the relative, diachronic patterning at Olduvai is well established through multiple lines of evidence. More contentious, is determining the absolute paleoenvironments that occurred at various levels in Bed I, especially the maximum degree of aridity that is represented at FLKN1. The correspondence analysis shows low similarity

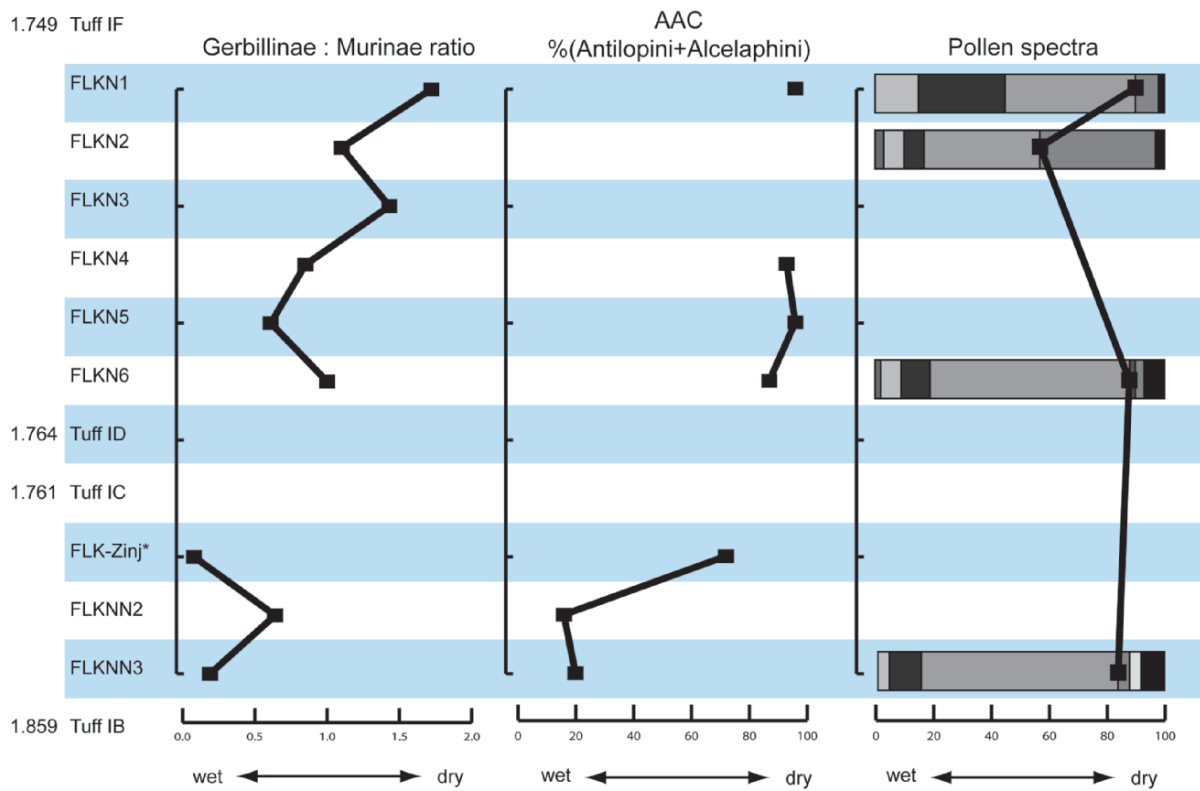


Figure 13. Paleoenviromental summary showing changes in three indices: proportions of fossil Gerbillinae to Murinae; percent abundance of arid adapted bovid tribes; and pollen spectra with points separating non-arboreal pollen (to left) from arboreal pollen (to right). Sources: Fernandez-Jalvo et al. (1998), Kappelman (1984), and Bonnefille (1984) for micromammals, macromammals, and pollen respectively.

between the mesic Middle Bed I localities and the modern Serengeti assemblages. The gallery forest habitat at roost 44 is the closest modern analogue, but the separation between modern roosts and fossil assemblages indicates the model is incomplete. Drawing upon the modern natural history of the genera found in Middle Bed I, one can infer a more forested and wooded environment based on the proportion of gerbils to murines and on the specific murine taxa that are present, such as the forest- and woodland-dwelling taxa *Oenomys* and *Thallomys* respectively. In contrast, the most arid-adapted assemblage found at FLKN1 shares taxa and a pattern of abundance similar to the drier, grassland roosts in the modern Serengeti, but with the addition of *Otomys* as the most abundant taxon. A plausible explanation for this pattern is a paleolake Olduvai surrounded by dry grassland and with a moist grassland or marsh habitat nearby. Small lakes of this sort exist in the Serengeti today (e.g., Lake Magadi, 70 km NE of Olduvai).

The nine owl-accumulated faunal assemblages presented here provide a foundation for interpreting assemblages with similar taphonomic histories in the fossil record. The scope of the model can be extended by adding owl taphocoenoses from novel habitats and replicating others both within the Serengeti from sites in other regions. The scope can also be extended by incorporating assemblages from different predators. Barn owls and spotted eagle owls were found to produce very similar assemblages, a result that may mitigate the complications induced by different predators. Determining agency will remain a key activity in taphonomic analysis but the discovery of multiple agencies need not mean that assemblages are incomparable. Furthermore, the availability of multiple lines of evidence is proving to be invaluable for paleoecological analysis and paleoenvironmental reconstructions. Simple linear summaries of relative diachronic

change such as the Alcelaphini and Antilopini criteria (AAC), or the Gerbillinae:Murinae ratio provide a simple means for comparing results from independent data sets. We lack similar, simple indices for synchronic habitat descriptions, which makes pooling data for habitat reconstruction more challenging than it is for inferring habitat change.

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## References

- Alexander, R., 1988. The scope and aims of functional and ecological morphology. *Netherlands Journal of Zoology*, 38, 3–22.
- Andrews, P., 1983. Small mammal faunal diversity at Olduvai Gorge, Tanzania. In: Clutton-Brock, J., Grigson, C. (Eds.), *Animals and Archaeology: 1 Hunters and their Prey*. BAR, Oxford.
- Andrews, P., 1990. *Owls, Caves and Fossils*. University of Chicago Press, Chicago.
- Andrews, P., Groves, C.P., Horne, J.F.M., 1975. Ecology of the lower Tana River flood plain (Kenya). *Journal of the East African Natural History Society of the National Museum* 151, 1–31.
- Ashley, G., Driese S., 2000. Paleopedology and paleohydrology of a volcanoclastic paleosol interval: implications for early Pleistocene stratigraphy and paleoclimate record, Olduvai Gorge, Tanzania. *Journal of Sedimentary Research* 70(5), 1065–1080.
- Avery, D.M., 1982. Micromammals as paleoenvironmental indicators and an interpretation of the late quaternary in the southern cape province, South Africa. *Annals of the South African Museum* 85, 183–374.
- Avery, D.M., 1987. Late Pleistocene coastal environment of the southern Cape Province of South Africa: micromammals from Klasies River Mouth. *Journal of Archaeological Science* 405–421.
- Avery, D.M., 1992. The environment of early modern humans at Border Cave, South Africa: micromammalian evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology* 91, 71–87.
- Avery, D.M., 1995. Southern savannas and Pleistocene hominid adaptations: The micromammalian perspective. In: Vrba, E., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven, pp. 459–478.
- Avery, D.M., 1998. An assessment of the Lower Pleistocene micromammalian fauna from Swartkrans Members 1–3, Gauteng, South Africa. *Geobios* 31(3), 393–414.
- Avery, D.M., 2001. The Plio-Pleistocene vegetation and climate of Sterkfontein and Swartkrans, South Africa, based on micromammals. *Journal of Human Evolution* 41, 113–132.
- Ba, K., Granjon, L., Hutterer, R., Duplantier, J., 2000. Les micromammifères du Djoudj (delta du Sénégal) par l'analyse du régime alimentaire de la chouette effraie, *Tyto alba*. *Bonner Zoologische Beiträge* 49, 31–38.
- Bell, R.H.V., 1969. The use of the herb layer by grazing ungulates in the Serengeti. In: Watson A. (Ed.), *Animal Populations in Relation to Their Food Resources*. Blackwell Publishers, Edinburgh, pp. 111–128.
- Bell, R.H.V., 1982. The effect of soil nutrient availability on community structure in African ecosystems. In: Huntley, B.J. and Walker, B.H. (eds.) *Ecology of Tropical Savannas*, Springer, pp. 193–216.
- Belsky, A.J., 1990. Tree/grass ratios in East African savannas: a comparison of existing models. *Journal of Biogeography* 17, 483–489.
- Belsky, A.J., 1995. Spatial and temporal landscape patterns in arid and semi-arid African savannas. In: Hansson L., Fahrig L., Merriam G. (Eds.), *Mosaic Landscapes and Ecological Processes*. Chapman and Hall, London, pp. 31–56.
- Black, C.C., 1984. Systematics and Paleoecology of Small Vertebrates from the Plio-Pleistocene Deposits East of Lake Turkana, Kenya. Research reports—National Geographic Society, Washington, D.C., pp. 111–113.
- Black, C., Krishtalka, L., 1986. Rodents, bats and insectivores from the Plio-Pleistocene sediments to the east of Lake Turkana, Kenya. *National History Museum of Los Angeles County Contributions in Science* 372, 1–15.
- Blumenschine, R.J., Masao, F.T., 1991. Living sites at Olduvai Gorge, Tanzania? Preliminary landscape archaeology results in the basal Bed II lake margin zone. *Journal of Human Evolution* 21, 451–462.
- Blumenschine, R.J., Peters, C.R., 1998. Archaeological predictions for hominid land-use in the paleo-Olduvai Basin, Tanzania, during lowermost Bed II times. *Journal of Human Evolution* 34, 565–607.
- Blumenschine, R., Peters, C.R., Masao, F.T., Clarke, R.J., Deino, A.L., Hay, R.L., Swisher, C.C., Stanistreet, I.G., Ashley, G.M., McHenry, L.J., Sikes, N.E., van der Merwe, N.J., Tactikos, J.C., Cushing, A.E., Deocampo, D.M., Njau, J.K., Ebert, J.I., 2003. Late Pliocene *Homo* and hominid land use from western Olduvai Gorge, Tanzania. *Science* 345(6), 565–607.
- Boaz, N.T., Bernor, R.L., Brooks, A.S., Cooke, H.B.S., de Heinzelin, J., Dechamps, R., Delson, E., Gentry, A., Harris, J., Meylan, P., Pavlakis, P., Sanders, W., Stewart, K., Verniers, J., Williamson, P., Winkler, A., 1992. A new evaluation of the significance of the Late Neogene Lusso Beds, Upper Semliki Valley, Zaire. *Journal of Human Evolution* 22, 505–517.

- Bonnefille, R., 1984. Palynological research at Olduvai Gorge. National Geographic Society Research Report, 17, 227–243.
- Brain, C.K., 1981. Hunters or the Hunted? An Introduction to African Cave Taphonomy. University of Chicago Press, Chicago.
- Butler, P.M., Greenwood, M., 1976. Elephant-shrews (Macroscelididae) from Olduvai and Makapansgat. In: Savage, R.J.G., Coryndon, S.C. (Eds.), Fossil Vertebrates of Africa. Academic Press, London, pp. 1–55.
- Coetzee, C.G., 1972. The identification of southern African small mammal remains in owl pellets. Cimbebasia 2(4), 54–62.
- Colvin, B.A., 1984. Barn Owl Foraging Behaviour and Secondary Poisoning Hazard from Rodenticide Use on Farms. Bowling Green State University, Bowling Green.
- Coughenour, M.B., Ellis, J., 1993. Landscape and climatic control of woody vegetation in a dry tropical ecosystem: Turkana District, Kenya. Journal of Biogeography 22, 107–122.
- Danuth, J., 1992. Taxon-free characterization of animal communities. In Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.A.; Potts, R.; Sues, H.; Wing, S.L. (eds.) Terrestrial Ecosystems Through Time; evolutionary Paleocology of terrestrial plants and animals, University of Chicago Press, pp. 183–204.
- Dauphin, Y., Kowalski, C., Denys, C., 1994. Assemblage data and bone and teeth modifications as an aid to paleoenvironmental interpretations of the open-air Pleistocene site of Tighenif (Algeria). Quaternary Research 42, 340–349.
- Dauphin, Y., Kowalski, C., Denys, C., 1997. Analysis of accumulations of rodent remains: role of the chemical composition of skeletal elements. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 203(3), 295–315.
- Davies, G., Berghe, E.V. (Eds.), 1994. Check-list of the Mammals of East Africa. East Africa Natural History Society, Nairobi.
- Davis, D.H.S., 1959. The barn owl's contribution to ecology and palaeoecology. Ostrich Supplement 3, 144–153.
- Davis, D.H.S., 1965. Classification problems with the African Muridae. Zoologica Africana 1, 121–145.
- Dawson, J., 1963. Carbonotitic volcanic ashes in northern Tanganyika. Bulletin Volcanologique 27, 1–11.
- de Graaff, G., 1960. A preliminary investigation of the mammalian microfauna in Pleistocene deposits of caves in the Transvaal system. Palaeontologia Africana 7, 59–117.
- de Graaff, G., 1961. On the fossil mammalian microfauna collected at Kromdraai by Draper in 1895. South African Journal of Science 57, 259–260.
- Delany, M.J., 1972. The ecology of small rodents in tropical Africa. Mammal Review 2, 1–42.
- Delany, M.J., 1975. The Rodents of Uganda. British Museum (Natural History), London.
- Delany, M.J., 1986. Ecology of small rodents in Africa. Mammal Review 16, 1–41.
- Demeter, A., 1982. Prey of the spotted eagle-owl *Bubo africanus* in the Awash National Park, Ethiopia. Bonner Zoologische Beiträge 33, 283–292.
- Denbow, D.M., 2000. Chapter 12. Gastrointestinal Anatomy and Physiology. Sturkie's Avian Physiology, fifth edn. Academic Press, New York, pp. 299–325.
- Denys, C., 1987a. Micromammals from the West Natron Pleistocene deposits (Tanzania). Sciences Géologiques Bulletin 40, 185–201.
- Denys, C., 1987b. Rodentia and Lagomorpha 6.1: Fossil rodents (other than Pedetidae) from Laetoli. In: Leakey, M.D., Harris, J.M. (Eds.), Laetoli: a Pliocene Site in Tanzania. Oxford University Press, London, pp. 118–170.
- Denys, C., 1990a. Deux nouvelles espèces d'*Aethomys* (Rodentia, Muridae) à Langebaanweg (Pliocène, Afrique du Sud): Implications phylogénétiques et paléoécologiques. Annals de Paléontologie 76, 41–69.
- Denys, C., 1990b. First occurrence of *Xerus* cf. *inauris* (Rodentia, Sciruridae) at Olduvai Bed I (Lower Pleistocene, Tanzania). Palaontologische Zeitschrift. Z64, 359–365.
- Denys, C., 1999. Of mice and men. In: Bromage, T., Shrenk, F. (Eds.), African Biogeography, Climate Change, and Early Hominid Evolution. Oxford University Press, Oxford.
- Denys, C., Tranier, M., 1992. Présence d'*Aethomys* (Mammalia, Rodentia, Muridae) au Tchad et analyse morphométrique préliminaire du complexe *A. hindei*. Mammalia 56(4), 625–656.
- Denys, C., Chorowicz, J., Tiercelin, J.J., 1986. Tectonic and environmental control on rodent diversity in the Plio-Pleistocene sediments of the African Rift System. In: Frostick, L.E. (Ed.), Sedimentation in the African Rifts. Geological Society Special Publication, pp. 363–372.
- Denys, C., Williams, C., Dauphin, Y., Andrews, P., Fernandez-Jalvo, Y., 1996. Diagenetical changes in Pleistocene small mammal bones from Olduvai Bed I. Palaeogeography, Palaeoclimatology, Palaeoecology 126, 121–134.
- Denys, C., Andrews, P., Dauphin, Y., Williams, T., Fernandez-Jalvo, Y., 1997. Towards a site classification: comparison of stratigraphic, taphonomic and

- diagenetic patterns and processes. *Bulletin de la société géologique de France* 168, 751–757.
- Deocampo, D.M., Blumenshine, R., Ashley, G.M., 2002. Wetland diagenesis and traces of early hominids, Olduvai Gorge, Tanzania. *Quaternary Research* 57, 271–281.
- Dublin, H.T., Douglas-Hamilton, I., 1987. Status and trends of elephants in the Serengeti-Mara ecosystem. *African Journal of Ecology* 25, 19–23.
- Dublin, H.T., Sinclair, A.R.E., McGlade, J., 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology* 59, 1147–1164.
- Fernandez-Jalvo, Y., Andrews, P., 1992. Small mammal taphonomy of Gran Dolina, Atapuerca (Burgos), Spain. *Journal of Archaeological Science* 19, 407–428.
- Fernandez-Jalvo, Y., Denys, C., Andrews, P., Williams, T., Dauphin, Y., Humphrey, L., 1998. Taphonomy and palaeoecology of Olduvai Bed-I (Pleistocene, Tanzania). *Journal of Human Evolution* 34(2), 137–172.
- Fernandez-Jalvo, Y., Andrews, P., Denys, C., 1999. Cut marks on small mammals at Olduvai. *Journal of Human Evolution* 36, 587–589.
- Foster, J.B., Duff-Mackay, A., 1966. Keys to the genera of Insectivora, Chiroptera and Rodentia of East Africa. *Journal of the East African Natural History Society* 15(3), 189–204.
- Fry, C.H., Kieth, S., Urban, E.K. (Eds.), 1988. *Birds of Africa*. Academic Press, London.
- Gawne, C.E., 1975. Rodents from the Zia sand, Miocene of New Mexico. *American Museum Novitates* 2586, 1–25.
- Genest-Villard, H., 1979. *Écologie de Steatomys opimus* Pousargues, 1894 (Rongeurs), Dendromuridés en Afrique Centrale. *Mammalia* 43(3), 275–294.
- Gentry, A., 1978a. Fossil Bovidae (Mammalia) of Olduvai Gorge, Tanzania. Part II. *Bulletin of the British Museum (Natural History) Geological Series* 30, 1–83.
- Gentry, A., 1978b. Fossil Bovidae (Mammalia) of Olduvai Gorge, Tanzania. Parts I. *Bulletin of the British Museum (Natural History) Geological Series* 29, 289–446.
- Geraads, D., 1998. Biogeography of circum-Mediterranean Miocene–Pliocene rodents; a revision using factor analysis and parsimony analysis of endemism. *Palaeogeography, Palaeoclimatology, Palaeoecology* 137, 273–288.
- Glue, D.E., 1970. Avian predator pellet analysis and the mammalogist. *Mammal Review* 1, 53–62.
- Grayson, D.K., 1984. *Quantitative Zooarchaeology: Topics in the Analysis of Archaeological Faunas*. Academic Press, New York.
- Greenacre, M.J., Vrba, E.S., 1984. Graphical display and interpretation of antelope census data in African wildlife areas, using correspondence analysis. *Ecology* 65(3), 984–997.
- Hay, R.L., 1976. *The Geology of the Olduvai Gorge*. University of California Press, Berkeley, CA.
- Herlocker, D., 1974. *Woody Vegetation of the Serengeti National Park*. Texas A&M University, College Station, Texas.
- Hubbard, C.A., 1972. Observations on the life histories and behaviour of some small rodents from Tanzania. *Zoologica Africana* 7, 419–449.
- Ihaka, T., Gentleman, R., 1996. R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics* 5(3), 299–314.
- Jaeger, J.-J., 1976. Les rongeurs (Mammalia, Rodentia) du Pléistocène inférieur d'Olduvai Bed I (Tanzanie). Ière Partie. In: Savage, R.J.G., Coryndon, S.C. (Eds.), *Fossil Vertebrates of Africa*. Academic Press, New York, pp. 58–120.
- Jager, T., 1982. *Soils of the Serengeti Woodlands, Tanzania*. Agricultural University, Wageningen, the Netherlands.
- Johnson, R., Wichern, D., 2002. *Applied Multivariate Statistical Analysis*. Prentice Hall, Upper Saddle River, New Jersey.
- Kappelman, J., 1984. Plio-Pleistocene of Bed I and Lower Bed II, Olduvai Gorge, Tanzania. *Palaeogeography, Palaeoclimatology, Palaeoecology* 48, 171–196.
- Kingdon, J., 1974a. *East African Mammals: Volume II A*. Chicago University Press, Chicago.
- Laurie, W.A., 1971. The food of the Barn Owl in the Serengeti National Park, Tanzania. *Journal of the East African Natural History Society* 28, 1–4.
- Lavocat, R., 1965. Rodents. In: Leakey, L.S.B. (Ed.), *Olduvai Gorge 1951–1961, 1: Fauna and Background*. Cambridge University Press, Cambridge, pp. 17–18.
- Leakey, M.D., Clarke, R.J., Leakey, L.S.B., 1971. New hominid skull from Bed I, Olduvai Gorge, Tanzania. *Nature* 232, 308–312.
- Levinson, M., 1982. Taphonomy of microvertebrates—from owl pellets to cave breccia. *Annals of the Transvaal Museum* 33(6), 115–121.
- Linzey, A.V., Kesner, M.H., 1997. Small mammals of a woodland-savannah ecosystem in Zimbabwe I. Density and habitat occupancy patterns. *Journal of the Zoological Society, London* 243, 137–152.
- Lyman, R.L., Power, E., 2003. Quantification and sampling of faunal remains in owl pellets. *Journal of Taphonomy* 1, 3–14.

- Maindonald, J., Braun, J., 2003. *Data Analysis and Graphics Using R*. Cambridge University Press, Cambridge.
- McCune, B., Grace, J.B., 2002. *Analysis of Ecological Communities*. MjM, Glendon Beach, OR.
- McKee, J., 1993. The faunal age of the Taung hominid deposits. *Journal of Human Evolution* 25, 363–376.
- McNaughton, S.J., 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. *Ecological Monographs* 53(3), 291–320.
- McNaughton, M.M., Banyikwa, F., 1995. Plant communities and herbivory. In: Sinclair, A.R.E., Arcese P. (Eds.), *Serengeti II: Dynamics, Management and Conservation of an Ecosystem*. Chicago University Press, Chicago, pp. 49–70.
- Meester, J., Setzer, H.W. (Eds.), 1971. *The Mammals of Africa: An Identification Manual*. Smithsonian Institution Press, Washington, DC.
- Milne, G., 1935. Some suggested units of classification and mapping, particularly for East African soils. *Soil Research* 4, 183–198.
- Nesbit-Evans, E.M., van Couvering, J.H., Andrews, P., 1981. Palaeoecology of Miocene sites in Western Kenya. *Journal of Human Evolution* 10, 35–48.
- Norton-Griffiths, M., Herlocker, D., Pennycuik, L., 1975. The patterns of rainfall in the Serengeti Ecosystem, Tanzania. *East African Wildlife Journal* 13, 347–374.
- Peters, C.R., Blumenshine, R.J., 1995. Landscape perspectives on possible land use patterns for early Pleistocene hominids in the Olduvai Basin, Tanzania. *Journal of Human Evolution* 29, 321–362.
- Pickford, M., Mein, P., Senut, B., 1994. Fossiliferous Neogene karst fillings in Angola, Botswana and Namibia. *South African Journal of Science* 90, 227–230.
- Plummer, T.W., Bishop, L.C., 1994. Hominid paleoecology at Olduvai Gorge, Tanzania as indicated by antelope remains. *Journal of Human Evolution* 27, 47–75.
- Pocock, T.N., 1987. Plio-Pleistocene fossil mammalian microfauna of southern Africa—a preliminary report including descriptions of two new fossil Muroid genera (Mammalia: Rodentia). *Palaeontologia Africana*. 26, 25–31.
- Pokines, J.T., Peterhans, J.C.K., 1998. Barn owl (*Tyto alba*) taphonomy in the Negev desert, Israel. *Israel Journal of Zoology* 44(1), 19–27.
- Potts, R., 1988. *Early Hominid Activities at Olduvai*. Aldine, Hawthorne, NY.
- Pratt, D.J., Gwynne, M.D., 1977. *Rangeland Management and Ecology in East Africa*. Hodder and Stoughton, London.
- Reed, D.N., 2003. *Micromammal Paleoecology: Past and Present Relationships between East African Small Mammals and Their Habitats*. Stony Brook University, Stony Brook, NY.
- Reed, D.N., 2005. Taphonomic implications of roosting behavior and trophic habits in two species of African owl. *Journal of Archaeological Science* 32, 1669–1676.
- Relethford, J.H., Harpending, H.C., 1995. Ancient differences in population size can mimic a recent African origin of modern humans. *American Journal of Physical Anthropology Supplement* 20, 180.
- Rogers, M., Stanley, W., 2003. *Tanzania Mammal Key*. Field Museum of Natural History, Chicago, <http://www.fieldmuseum.org/tanzania/>.
- Sabatier, M., 1979. Les rongeurs fossiles de la formation de Hadar et leur intérêt paléocéologique. *Bulletin de la Société de Géologie, France* 21(3), 309–311.
- Sabatier, M., 1982. Les rongeurs du site Pliocene a hominides de Hadar (Ethiopie). *Palaeovertebrata*, 12, 1–56.
- Sinclair, A.R.E., 1995a. Equilibria in plant–herbivore interactions. In: Sinclair, A.R.E., Arcese, P. (Eds.), *Serengeti II: Dynamics, Management and Conservation of an Ecosystem*. University of Chicago Press, Chicago, pp. 91–113.
- Sinclair, A.R.E., 1995b. Serengeti past and present. In: Sinclair, A.R.E., Arcese, P. (Eds.), *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem*. University of Chicago Press, Chicago, pp. 3–30.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry: The Principles and Practice of Statistics in Biological Research*, third edn. W. H. Freeman and Company, New York.
- Swynnerton, G., 1958. Fauna of the Serengeti National Park. *Mammalia* 22, 435–450.
- Taylor, I., 1994. *Barn Owls*. Cambridge University Press, Cambridge.
- Tchernov, E., 1992. Eurasian–African biotic exchanges through the levantine corridor during the neogene and quaternary. *Courier Forschungsinstitut Senckenberg* 153, 103–123.
- van Couvering, J.A., 1980. Community evolution in East Africa. In: Behrensmeyer, A.K., Hill, A.P. (Eds.), *Fossils in the Making*. Chicago University Press, Chicago, pp. 272–298.
- Vernon, C.J., 1972. An analysis of owl pellets collected in southern Africa. *Ostrich* 43, 109–124.

- Vesey-Fitzgerald, D.F., 1966. The habits and habitats of small rodents in the Congo River catchment region of Zambia and Tanzania. *Zoolologica Africana* 2, 111–122.
- Vrba, E.S., 1980. The significance of bovid remains as indicators of environment and predation patterns. In: Behrensmeyer, A., Hill, A.P. (Eds.), *Fossils in the Making*. University of Chicago Press, Chicago, pp. 247–271.
- Vrba, E.S., 1985. Ecological and adaptive changes associated with early hominid evolution. In: Delson, E. (Ed.), *Ancestors: The Hard Evidence*. Alan R. Liss, New York, pp. 63–71.
- Vrba, E.S., 1992. Mammals as a key to evolutionary theory. *Journal of Mammalogy* 73, 1–28.
- Vrba, E.S., 1995. Fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), *Paleoclimate and Evolution with Emphasis on Human Origins*. Yale University Press, New Haven, pp. 385–424.
- Walter, R.C., Manega, P.C., Hay, R.L., Drake, R.E., Curtis, G.H., 1991. Laser-fusion  $^{40}\text{Ar}/^{39}\text{Ar}$  dating of Bed I, Olduvai Gorge, Tanzania. *Nature* 354, 145–149.
- Wesselman, H.B., 1982. Pliocene Micromammals from the Lower Omo Valley, Ethiopia: Systematics and Paleocology. University of California, Berkeley.
- Wesselman, H.B., 1984. The Omo Micromammals: Systematics and Paleocology of Early Man Sites from Ethiopia. S. Karger, Basel.
- Wesselman, H.B., 1995. Of mice and almost-men: Regional paleoecology and human evolution in the Turkana Basin. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), *Paleoclimate and Evolution with Emphasis on Human Origins*. Yale University Press, New Haven, pp. 356–368.
- Wilson, D., Reeder, D.M. (Eds.), 1993. *Mammal Species of the World*. Smithsonian Institution Press, Washington, DC.
- Winkler, A., 1997. Systematics, paleobiogeography and paleoenvironmental significance of rodents from the Ibole Member, Manonga Valley, Tanzania. In: Harrison, T. (Ed.), *Neogene Paleontology of the Manonga Valley, Tanzania: A Window into the Evolutionary History of East Africa*. Plenum Press, New York, pp. 311–332.
- Winkler, A., 1998. New small mammal discoveries from the early Pliocene at Kanapoi, West Turkana, Kenya. *Journal of Vertebrate Paleontology* 18(Supplement), 87.
- Winkler, A., 2002. Neogene paleobiogeography and East African Paleoenvironments: contributions from the Tugen Hills rodents and lagomorphs. *Journal of Human Evolution* 42, 237–256.
- Zimmerman, D., Turner, D.A., Pearson, D.J., Willis, I., Pratt, H.D., 1996. *Birds of Kenya and Northern Tanzania*. A&C Black, London.