Micromammal Paleoecology: Past and present relationships between African small mammals and their habitats

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Chapter 1

Background and Introduction

The role of climate on the evolutionary trajectory of African mammals during Pliocene and Pleistocene remains an active topic of research in paleobiology, and especially paleoanthropology. At least three models have been proposed to explain the pattern exhibited by mammals in response to climate change. Vrba (1985, 1995) proposed a model of abrupt faunal transition instigated by vicariance of populations that experience climatic stress. Vrba (1995) includes predictions of how fauna should respond to climatic change. However, tests of this model against fossil evidence show gradual turnover but do not reveal pulses of faunal change as predicted (Behrensmeyer et al. 1997). Many of the original ideas about climate forcing were reconsidered in light of improved paleoclimatic records indicating changes in climate and climate variability (deMenocal 1995; Zachos et al. 2001), and it is variability that has captured the most interest recently, including the proposal for a new species of evolutionary process, variability selection (Potts et al. 1999; Potts 1996).

The Plio-Pleistocene is a promising time interval in which to address questions of climatic influence on hominin evolution. It marks the transition between the more stable climatic regimes of the Pliocene and the chaotic episodes of Pleistocene glaciation. Micromammals hold unique promise for testing models of Plio-Pleistocene faunal responses. They are very speciose and embody a rich array of adaptations ranging from dedicated faunivory to hyper-grazing. Furthermore, their comparatively short lifespans make for an interesting comparison with hominins. Most micromammals have life history strategies that are the polar opposite to hominoids. Micromammals are small, short lived and occupy small home

ranges. Hominoids, by comparison are three to four orders of magnitude larger in body size, long-lived, behaviorally complex and capable of using much larger home ranges. The responses of these two life-history extremes to habitat fragmentation, gradual climate change, and climatic variability are expected to differ significantly. Trapped as they are in a confined geographical region, individual populations of small mammals must confront climatic and environmental change either by adapting or going locally extinct. Given their short life-spans, small mammals do not have the time during ontogeny to develop behavioral flexibility so their adaptations must be physiological. For these reasons micromammals may be more likely to exhibit patterns of faunal turnover that are not apparent in larger mammals. On the other hand behavioral flexibility is the hallmark of hominoid response to environmental change. Studying hominoids and micromammals together provides stark contrast and possibly better power for interpreting evolutionary processes. For example, intense faunal turnover in the microfauna may indicate climatic extremes that would trigger either speciation events or behavioral adaptations in hominoids.

Yet, to produce reliable interpretations of micromammal fossil assemblages it is important to consider how the assemblages were created and the taphonomic factors that may have altered it. Taphonomy proves to be particularly important for microvertebrate assemblages because these are often accumulated by predators whose behavior alters the composition of the assemblage. Owls are one of the primary predators of small mammals, and this predator-prey system is vitally important to understanding the formation of fossil assemblages. By way of a general introduction, an overview of the relationship between owls and small mammals is given below.

1.1 Background

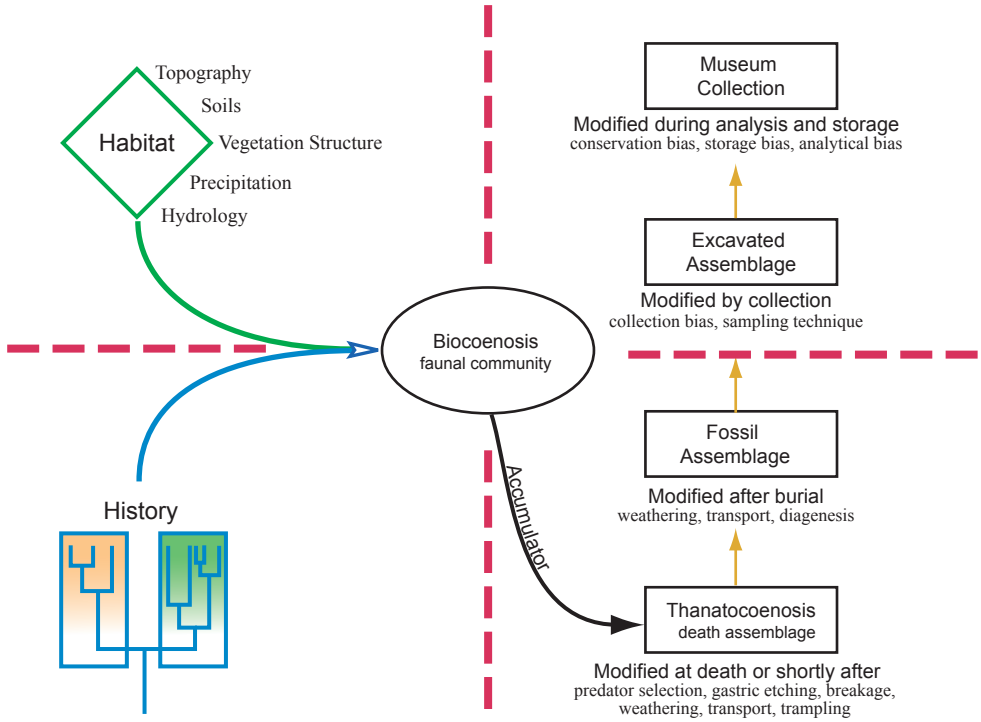
For many years, mammalogists and ornithologists have benefited from the hunting and digestive processes of owls (Glue 1971). Owls routinely regurgitate the undigested remains of consumed prey in a compact package of bone wrapped in fur (Grimm and Whithouse 1963). These egested pellets not only provide a non-invasive way to study the diet of owls they also aid paleontologists by concentrating small mammal faunas (Davis 1959). As efficient predators of small animals, owls

sample the faunal community (or biocoenosis) in their hunting range and return to selected roosting spots where they deposit pellets. At some fossil localities the remains of small mammals occur in densities so great that the most reasonable explanation is that they were accumulated by owls. The phenomenon is common to many cave sites and rock shelters (Andrews 1990; Avery 1987, 1992b; de Graaff 1960, 1961; Levinson 1982), but similar dense concentrations are also known from open-air sites. Further support that owls were accumulating fossil faunas comes from the discovery of fossilized impressions of pellets (Denys 1987; Gawne 1975), and from detailed taphonomic analysis of micromammal bones (Andrews 1990; Denys et al. 1997; Dauphin et al. 1994, 1997; Fernandez-Jalvo and Andrews 1992; Fernandez-Jalvo et al. 1998).

Multiple interacting processes influence which species are accumulated in owl assemblages. An overview of these processes is given in Figure 1.1. The faunal community of a region is influenced both by the habitat and the history of the region. History determines the unique lineage of species present in that region. Convergent and parallel evolution, however, generate communities which may share few taxa but in which there are organisms fulfilling similar roles (Cody and Mooney 1978; Fleming 1973; Glanz 1982; Harrison 1962). By focusing on the roles available to organisms living in a region, that is by analyzing the available niches, the regions become comparable despite their singular histories (Andrews et al. 1979; Reed 1998).

A region may be divided into niches across several environmental factors such as, topography, soils, rainfall, temperature or vegetation structure. Of these variables, vegetation structure most influences the distribution and abundance of non-volant, non-fossorial small mammals (Batzli 1991). Andrews and O'Brien (2000) found small mammal (0-1kg) biodiversity to be significantly correlated with woody plant diversity across southern Africa ($r = 0.718$, $P < 0.0001$). Bats make a substantial contribution to the strength of the correlation. Excluding bats, terrestrial small mammals were reported having a Pearson product-moment correlation coefficients of $r = 0.481$. However, terrestrial micromammals in the size range most often taken by owls (0-100g) were better correlated with woody plant diversity ($r = 0.596$). Woody plant species diversity is not synonymous with vegetation structure, but greater plant diversity implies greater heterogeneity in the vegetation and more niches available for small mammals.

Figure 1.1: Overview of the processes resulting in taphonomic and fossil assemblages of micromammals. The biocoenosis is influenced both by ecological factors shaping local niches and historical contingencies influencing what lineage are present to exploit the niches. Often owls, or some other predator, sample the biocoenosis and accumulate prey remains at a site such as a roost or latrine (curved arrow). Repetitive use of these sites results in a taphocoenosis or death assemblage. This may become buried and eventually form a fossil assemblage which is recovered and analyzed. Alterations to the assemblage may accrue along the way and some examples are listed below the boxes representing the different stages.



This point was not lost on Avery (1982, p. 238) who remarked that, "generally speaking...small mammal distribution is influenced by vegetation type. Correlation with other factors is likely to be coincidental, except in so far as those factors will probably be affecting the vegetation upon which the animals are dependent." Thus, terrestrial, non-fossorial, small mammals indicate best the type of vegetation in a region. The physical structure of sediments becomes a dominant factor in the distribution of fossorial and burrowing species such as moles, and gerbils and some murine rodents (Genest-Villard 1967; Kingdon 1974).

Predators, such as owls, eagles, jackals and genets sample a biocoenosis and deposit prey remains via regurgitated pellets or scats in a confined area such as a roosting place, or latrine. Emphasis is given to owls because they routinely ingest the entirety of their prey (Andrews 1990; Dodson and Wexlar 1979), tend to induce less damage to the bones than mammalian and diurnal avian predators (Andrews 1990; Andrews and Nesbit-Evans 1983), habitually occupy a roost for long periods (Taylor 1994), and thus develop dense assemblages which provide the best sample sizes. The prey collected by an owl forms the death assemblage or thanatocoenosis. The death assemblage is the best modern approximation of what will appear in the fossil record, it is of intermediate age, very young in geological terms but old in ecological time. The intermediate age averages out short term biases, such as seasonality, which has been noted to alter the composition of pellet assemblages (Avery 1992a).

With a little luck, the thanatocoenosis survives its tenure as a surface collection and becomes a fossil assemblage. The likelihood of survival and burial may be increased by predator behavior, such as the roosting habits of the owls. Some owl species prefer to roost in cavities such as caves and fissures, where their pellets are protected from weathering, trampling and fluviatile activity. Species roosting near rivers may deposit bones on overbank deposits that become buried quickly. Once buried, the assemblages may be exposed to numerous biotic and abiotic modifications ranging from tooth etching to chemical diagenesis. At some point recovery brings them to light and they become the object of an analysis.

Humans are also predators of small and micro- mammals. There's no shortage of anecdotes about people eating small mammals such as rabbits. In Africa larger rodents such as the cane rat, *Thryonomys*, are being considered as protein staples (Kingdon 1974). Nor are small rodents exempt. Vesey-Fitzgerald (1966) reports

that the fat mouse, *Steatomys*, is "greatly relished by Africans, and such large numbers are excavated [from their burrows] in some areas that it is becoming scarce" (p. 119). Exploitation of small mammals extends deep in time as well. Fernandez-Jalvo et al. (1999) observed cut-marks on the mandibles of *Erinaceous broomei*, a Plio-Pleistocene species of hedgehog, recovered from Bed I deposits at Olduvai Gorge, Tanzania. Despite these examples, compared to mega-fauna, micromammals are seldom the focus of studies on human subsistence strategies, and most often, taphonomic examination reveals micromammalian accumulations are the result of non-human agency. This independence incurs an important benefit to micromammals in many zooarchaeological contexts when it may be desirable to have a measure of paleoenvironment not linked to hominid subsistence.

The general aim of this dissertation is to investigate the relationships between modern taphonomic assemblages of micromammals from a tropical African environment and to associate the community structure of these assemblages with ecological and environmental factors relevant to the study of human evolution. Referring back to Figure 1.1 one can visualize this aim as trying to forge a link between the analyzed assemblage, depicted by the box in the upper right, and the vegetation structure and related parameters of interest depicted in the upper left. These two endpoints are connected by a long chain of inferences, and though cliché, the adage holds that confidence in paleoenvironmental reconstructions is limited by the weakest link in the chain.

The factors appearing in the upper right quadrant of Figure 1.1, such as sampling effort, curation bias, storage bias and analytical bias, are active in the present. Most are within the control of the investigator and reflect compromises to time and resources. More problematic are those in the lower right. These are the cumulative effects of biotic and abiotic natural processes acting before the assemblage has even been observed. Direct observation of these historic events is not possible for fossil assemblages, but modern predator-prey systems provide valuable insights. In this study the focus is placed on modern taphonomic assemblages of micromammals accumulated by owls. Numerous studies have investigated owl pellet assemblages, but the current effort is unique in focusing on the aggregate assemblages resulting from the decay of many pellets, what I term ossuaries. Ossuaries are time-averaged palimpsests resulting from one or many birds over years, decades, perhaps centuries. Such assemblages are generally disregarded or de-

precated by neontologists focusing on the ecology of owls or micromammals (for example see Lyman and Power 2003). Ornithologists prefer to establish that pellets come from a particular bird. Additionally, they desire to track prey contents in individual pellets, and to measure trophic variability over seasonal and annual time intervals.

Mammalogists, at times have also been reluctant to consider ossuaries. They prefer the experimental control afforded by trapping. To the mammalogists, trapping also provides whole animals, which are easier to identify and suitable for museum reference collections. However, the benefits to mammalogy have been noted (Glue 1971), and more recent work demonstrates the usefulness of owl pellets in biodiversity surveys (Avery 1977; Avery et al. 2002). Furthermore, careful comparisons between ossuaries and trapping studies may also reveal significant correlations that permit translation between the two. Live-dead comparisons in marine ecosystems have shown marine death assemblages to provide reliable rank-order abundance data (Kidwell 2001). Within the constraints set by the accumulating agent on prey size and activity patterns, tandem studies of pellets assemblages and trapping show good correspondence (Hanney 1963; Perrin 1982), and given the sampling biases associated with trapping, it is often difficult to determine which is more accurate, the traps or the pellets. Thus investigation of ossuaries can provide neontologists with important biodiversity data as it does in the marine realm.

Whereas ossuaries can pose problems for neontologists, for the paleobiologists or zooarchaeologist, the bone detritus of an ossuary is the appropriate unit of analysis. Time averaging buffers many short term fluctuations resulting in an assemblage more like the fossil record. Also of interest here is their position in the chain of inference. Through the analysis of ossuaries one can study the processes active between the biocoenosis and the taphocoenosis. Such an analysis provides two routes to improving paleoenvironmental analysis. By one route, studying how taphocoenoses form improves our ability to undo taphonomic biases and reconstruct the biocoenosis from taphonomic data. This route is difficult because so many interacting factors are in play, and at present we know very little about these processes. Furthermore, if the object of interest is the environment influencing the biocoenosis then we must also contend with interpreting the ecological and biogeographical factors as well.

A more direct route, is to study correlations between the taphocoenosis 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 analogs, and exploring correlations, while prying open the box to understand the causal mechanisms responsible for the associations between thanatocoenoses and the environments from which they were derived. this general approach adopted here, and either route is preferable to simply ignoring taphonomic biases on micromammal assemblages altogether.

1.2 Overview of Materials and Methods

Each chapter provides details of data collection methods, tabular summaries of the data, and brief descriptions of the analytical techniques used on those data. Here I provide an overview of the data that were collected. The data are summarized verbally; quantitative summaries are left to the individual chapters. Broad issues of sampling, such as sample size and sample independence are discussed here along with descriptions of the common statistical and analytical techniques employed throughout.

1.2.1 Materials

Field research was conducted continuously from November 1998 through April 2000. Two principal types of field data were collected; land cover data from ground surveys, and faunal data from owl roosting sites. The vegetation data come from 216 ground surveys throughout the Serengeti ecosystem. These data are augmented by similar ground survey data provided from other researchers working in Serengeti at the same time or shortly after my field season. The combined data set features 869 ground survey points. Additional vegetation and land cover data were derived from satellite imagery, published maps, and unpublished databases. All these data were combined in a geographical information system (GIS), from which a census of the land cover around each roost could be obtained. The GIS includes maps and linked databases describing the regional hydrology; topography; precipitation; and

physiognomic vegetation cover. Land cover is given in two classification schemes. The simpler scheme has two classes, wooded and non-wooded. The more complex has five land cover classes. In addition to land cover the following ecological variables are also examined: mean annual precipitation, mean elevation, standard deviation of elevation, mean percent slope, standard deviation in slope.

The faunal data come from dense ossuaries found at owl roosting sites. A total of sixty-one roosting sites were located in the Serengeti. Most of these sites had ossuaries along with fresh pellets. The fresh pellets were collected and stored separately. Of the sixty-one roosts, eight were selected for detailed faunal analysis. The number of roosts analyzed simply reflects limitations of time and resources. Terrestrial small mammal specimens were identified to genus and entered into a database along with the geographical location of the roosting sites. With the geographical information, the fauna could be incorporated into the GIS and compared directly with the land cover data. In total 19 taxa of non-volant small mammals are analyzed.

The category, "small mammals", generally refers to animals under 5 kg in mass (Andrews 1990). The term micromammals is used interchangeably with small mammals, but emphasizing those weighing less than a few hundred grams. In Africa, Rodents (Order Rodentia) and shrews (Order Insectivora) are the most abundant small mammals, 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.

1.2.2 Data representation

Roosting sites are the pivot points for comparing fauna with the associated land cover and ecological variables. From the faunal perspective roosts can be characterized by the taxa present and their abundances. Similarly, from the vegetation standpoint roosts can be characterized by the different land cover categories and their abundances. These data may be presented in a matrix of r rows by c columns, with taxa, land cover and ecological variables occupying the rows, and the sampling units – the roosting localities – occupying the columns. There are three main variables each divided into categories: the fauna divided into taxa, land cover divided into classes, and sundry ecological variables such as precipitation, elevation etc.

Table 1.1: Example r x c data matrix with taxa as rows and roosts as columns.

	Sampling Units = Roosts							
	Roost 1	Roost 2	Roost 3	Roost 4	Roost 5	Roost 6	...	Roost p
Taxon A	x_{A1}	x_{A2}	...					x_{Ac}
Taxon B	x_{B1}	$\ddots$						
Taxon C	$\vdots$							
Taxon D								
Taxon E								
$\vdots$								
Taxon r	x_t							x_{rc}

Table 1.2: The general arrangement of a 2 x 2 contingency table. Presence of Taxon B indicates counts of that taxon, while absence indicates observations of all other taxa, i.e. all observations that were *not* Taxon B. Each row and column is summed to give margin totals, and the grand total is the sum of the margin totals.

	Roosts		
Taxon B	Roost 1	Roost 2	Taxon Total
Presence	a	b	a+b
Absence	c	d	c+d
Roost Total	a+c	b+d	Total a+b+c+d

The data matrix itself is filled with the observations made on each variable, with the observations presented as frequencies (counts of an occurrence), proportions (frequencies divided by the total) or percentages (proportions times 100). The r x c data matrix, or a subset of the matrix is also called a contingency table.

A common use of contingency tables is to test for the association between rows and columns, for example Taxon B at Roost 2. In this case the association can be summed up in a 2 x 2 contingency table listing the presence/absence of taxa where absence is indicated by observations of taxa other than Taxon B, and observations at roosts other than Roost 2. An example is given in Table 1.2. The concept of a contingency table may be expanded to any number of rows and columns back to the full data matrix. An example of differences in the abundance of *Arvicanthis* at two roosts sites is shown in Table 1.3.

Table 1.4: Expected frequency values of *Arvicanthis* at roosts 3 and 4.

	3	4	Total
ARVI	12.458	13.542	26
OTHER	240.542	261.458	502
Total	253	275	528

Table 1.3: Contingency table of observed frequencies.

	Roost 3	Roost 4	Total
ARVI	5	21	26
OTHER	248	254	502
Total	253	275	528

Contingency tables test for independence between column variables and row variables. Observed cell values are compared against expected values derived from the marginal totals in the contingency table. Using table 1.3 as an example, 26 individuals of *Arvicanthis* were observed out of a total 528 specimens. Similarly, 253 and 275 individuals were observed at roosts 3 and 4 respectively. The expected frequency of *Arvicanthis* at roost 3 is thus given by the product of the margin totals,

$$f_{Arvi,Rst3} = np_{Arvi,Rst3} = np_{Arvi} \times p_{Rst3} = 528\left(\frac{26}{528}\right)\left(\frac{253}{528}\right) = 12.458 \qquad (1.1)$$

Differences in sample sizes between the roosts is accounted for by the margin totals for each roost and appear as the second probability term p_{Rst} in equation 1.1. Following equation 1.1 the expected frequency values of *Arvicanthis* at roosts 3 and 4 are shown in Table 1.4 . A test of independence addresses whether there is an association between two variables, in this case taxon and roosting site. Differences between observed and expected values are expected to approximate a chi-square distribution with one degree of freedom (Sokal and Rohlf 1995). A Model I contingency table applies when neither of the margin totals (i.e. the sample size at the roost, or the number of individuals from each species) is controlled by the investigator. Pearson's statistic, X^2, and the G statistic are the appropriate tests for independence between the row and column variables under a Model 1 design (Sokal and Rohlf 1995).

1.2.3 Tests of independence and association

Independence and association measure the degree of interaction between row and column variables in a contingency table. Association is simply the opposite of independence; a test for one is a test for the other. The degree of independence between variables in a contingency table may be assessed using the Pearson statistic for goodness of fit X^2, commonly referred to as a chi-square test. The X^2 statistic tests for independence of the contingency table cells using the following relationship,

$$X^2 = \frac{(f_{obs} - f_{exp})^2}{f_{exp}}$$

where f_{obs} is the observed frequency value of the cell, f_{exp} is the expected frequency value of the cell. In a test of independence the observed values occurring in each cell are compared against the expected values derived from the margin totals (Ludwig and Reynolds 1988). The expected cell values are simply the products of the margin totals divided by the grand total. One can also consider the grand total as being partitioned among the cells according to the proportions of the margin totals if the variables are independent. For example, referring back to Table 1.2, the expected value Taxon A at Roost 1 is

$$f_{exp} = \frac{(a+b)(a+c)}{n}$$

However, if Taxon A is more likely to occur at Roost 1 then cell "a" will be disproportionately large (and cells "b" and "c" smaller). Whether these differences are significant is determined by comparing the Pearson statistic, X^2 against a chi-square distribution.

The chi-square distribution is a probability density function. Its shape is different from the familiar normal or Gaussian distribution in that values are always positive and it is skewed, with a single peak near 0 and a long tail toward higher values as shown in Figure 1.2 (see also Appendix B.1.5). Many phenomena in addition to the Pearson statistic are modeled by a chi-square distribution.

The G statistic, also known as a log likelihood statistic, is another measure of independence; it too is expected to follow a chi-square distribution. The Pearson statistic appears more frequently in the literature, however, Sokal and Rohlf (1995) recommend the G statistic because it more closely approximates the chi-square

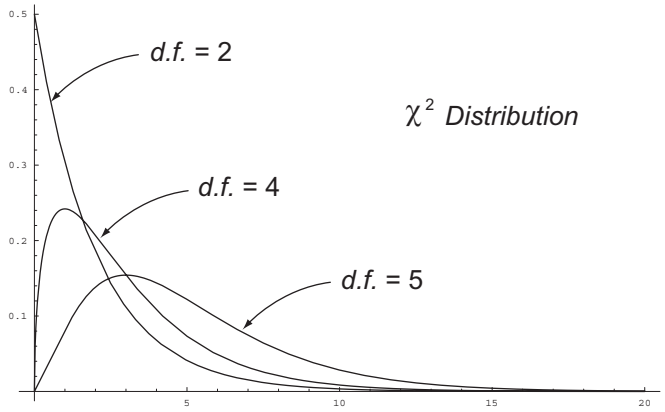


Figure 1.2: Plots of the chi-square probability density functions for several values of ν= d.f. When ν is small the curve is uniformly decreasing with greater chi-square values (x axis). Greater values of ν reveal a unimodal shape.

distribution and has additive properties that allow a G value to be partitioned into parts. Under most circumstances the two yield very similar results. Application of one or the other in the current study is determined in part by availability in the statistical software.

Tests of independence applied to a 2 x 2 contingency table, like the example in Figure 1.2, can be expanded to tables of arbitrary size and dimension. In this case, a test for independence checks the entire table. If a significant result is found one does not immediately know which cells are contributing to the significant result. A table of partial X^2 reveals all pairwise tests of independence and reports those that are significant.

1.2.4 Correlations

In many cases we wish to test for correlations between two rows or two columns in the table. The abundances of the taxa and land cover are given as counts, or derivatives of counts (proportions and percentages) for which certain analytical techniques are not appropriate. First, abundance data have a closed sum, such that for any given sample of N specimens, changes in the proportion of one taxon must influence the abundance of another. This interdependence causes abundances to shift depending on how samples are aggregated (Grayson 1984). One solution is to treat abundances as ordinal data (ranks) rather than measurement data (con-

tinuous or discrete values). As ordinal data, correlations between abundances may be compared using nonparametric tests such as the Spearman rank correlation statistic, rho, or the Kendall rank correlation statistic, tau. The formulae and summaries of these statistics appear in Appendix B.1.

If abundances are treated as measurement data in a parametric test it is often necessary to transform the data in order to correct for heterogeneity of the variance (i.e. heteroscedasticity). Heterogeneity arises when the variance of an abundance measurement increases with the size of the measurement. A taxon that is 2% of the assemblage varies less than one that is 50%. The arcsine transformation applied to proportions will often correct heteroscedasticity (Sokal and Rohlf 1995).

1.2.5 Similarity Coefficients

Coefficients of similarity and dissimilarity provide a measure of the proximity of points in multidimensional space. Two of these are particularly useful for comparing presence/absence records, as in a comparison of two roosts based on the presence or absence of species. The Czekanowski coefficient of similarity (also known as the Dice or Sorensen coefficient) weighs joint occurrences more than mismatches (Etter 1999). It is calculated as,

$$C_s = \frac{2a}{2a + b + c}$$

where a is the number of joint occurrences between sampling units B and C, b and c are the number of occurrences unique to sampling units B and C respectively.

Using the same notation as above, the Jaccard coefficient of similarity lacks special weighting for joint matches,

$$J_s = \frac{a}{a + b + c}$$

The similarity coefficients were originally developed to measure species overlap, that is to measure the dependence between rows of a data matrix, or what is referred to as R-mode analysis. They have also been employed to measure similarity between the independent elements in the columns of a data matrix, what ecologists refer to as Q-mode analysis. Both applications are acceptable for these indices (Ludwig and Reynolds 1988)

1.2.6 Runs Test

A runs test looks for patterns in sequences of data. A common application of the runs test is to see if the residuals around a regression follow a random pattern. Fitting a linear model, to a slightly non-linear data set will cause a long string of residuals either above or below the line. By examining runs of residuals we test the null hypothesis that the sequence of points above (+) and below (-) the line is random. Rejecting the null hypothesis implies that the model is inappropriate.

1.2.7 Correspondence analysis

The pattern of association between categories of the row and column variables is often complex. Correspondence analysis (CA) is a multivariate ordination technique that maps the data to a reduced number of dimensions, making it easier to visualize and interpret. The full matrix has 8 sampling units (roosts) and as many as 32 rows representing 20 taxa (though bats and shrews are often excluded for reasons described later, reducing the number of taxa to 19 or 17 for many analyses), up to 7 land cover classes and 5 ecological variables (precipitation, elevation etc.). A geometrical interpretation of the data matrix may represent roosts as points in an s-dimensional space where s is the number of species, up to 20 in the current example. Conversely the species may be plotted in an 8-dimensional roost-space. The two spaces, species-space and roost-space are merely different representation of the same data and both retain the full information content of the original data matrix (Gauch 1982; Etter 1999). However, visualizing such relationships is difficult if not impossible. To interpret the relationships between points we must reduce the reduce the dimensionality of the data. If the distribution of data points on the various axes is not completely independent, that is if some axes are correlated, then it is often possible to project the data points onto a reduced number of axes while preserving the relationships between the points. This is the general objective of multivariate ordination techniques.

Correspondence analysis (CA) is an ordination technique, similar to principal components analysis, but more appropriate for frequency data of categorical variables such as taxa or vegetation types (Greenacre and Vrba 1984; Johnson and Wichern 2002). CA starts with a data matrix or contingency table. The margin totals of the input contingency table are referred to as the mass of that category.

Different mass values result in weightings of the respective rows and columns. Thus large roosts will have a greater influence on the orientation of the points than smaller roosts, and abundant taxa will have more influence than rare taxa. One can balance the mass weightings by entering relative abundances into the original data matrix instead of frequencies. This has the effect of giving equal weight to each roost regardless of sample size (Greenacre and Vrba 1984).

Results from a CA are presented in bivariate plots with each axis representing some fraction of the total inertia explained by that axis. The position of points is an indication of their similarity. A particularly useful feature of CA is that row categories and column categories can be plotted in the same space and associations between them interpreted by their position in the space. Points that are close together have similar profiles, i.e. they have similar patterns in the distribution of values along rows or columns. The total amount of dispersion present in the table is characterized by the "inertia" of the table. The axes of the plots are ranked according to the amount of information or inertia explained by each axis. The greatest inertia is loaded on the first axis and decreases with each additional axis.

1.2.8 Statistical Software

Most statistical tests, including correspondence analysis, were performed with XLstat software version 6.1.9 by Addinsoft. The software package, Palaeontological Statistics (PAST) version 1.06 (Hammer et al. 2001) was used for the calculation of diversity indices and coefficients of association. Mathematica version 4.1.1 (Wolfram 1999) was used for the calculation of nonparametric correlations and runs tests.

1.2.9 Data independence

Each roost is generally considered an independent sample, but the row variables, such as taxonomic abundance and land cover abundance are not assumed independent. Many row variables are expected to correlate. Taxa may cluster together at some roosts resulting in positive correlations, while competition may prevent some taxa from occurring together and result in negative correlations.

At another level each observation that contributes to the cell values (specimen counts of fauna, pixel counts of land cover types) is assumed to be independent

from one another. The unit used to tally occurrences may violate the assumption of data independence. For example, in the analysis of fauna the unit of interest is the individual organism, but the basic unit of observation is the number of identified specimens (NISP). Individuals may be represented by multiple specimens. If each individual is represented by the same number of specimens there will be no effect on the relative abundances of the taxa, but there will be an inflation of sample size and a spurious increase in the sensitivity of statistical tests (Grayson 1984). Two derived measures of faunal abundance were calculated in order to address this issue, the normalized NISP (NISPn) and the minimum number of individuals (MNI). NISPn simply divides the NISP by the expected number of elements for each individual of a taxon. For most taxa, the expected number of elements is 3, one skull and two mandibles. For shrews, only the skulls were identified and so the expected number of elements is 1. MNI values represent the minimum estimate of abundance. MNIs were tallied by counting sub-elements, in this case the individual teeth in the dentition, and taking the maximum value for any one sub-element (for example upper left M1) as the MNI for that taxa. Using sub-elements allowed unbiased estimation with both jaws, and isolated teeth. Many researchers further refine MNI values by comparing additional factors such as tooth wear. To expedite the analysis tooth wear was not evaluated here.

While NISPn values address the bias of element representation, breakage will also artificially increase NISPn. For this reason MNI is preferred for some statistical analyses. However abundances represented by MNI values will vary depending on how the assemblages are aggregated (Grayson 1984). Aggregation does not affect NISPn, so this measure of abundance is preferred in direct comparisons of relative abundances.

A similar phenomenon may occur in the analysis of land cover. Land cover is measured by counting the number of pixels belonging to each land cover class. Pixels in a land cover map represent a fixed area on the ground. The size of the pixel is determined by the spatial resolution of the underlying data sets. The smallest spatial resolution used in the analysis of land cover is 30 square meters. Data point independence becomes an issue when spatial resolution exceeds the dimensions of the feature being measured, in this case a tree, or shrub. If the resolution is too great then multiple pixels will count the same feature, just as multiple element represent the same animal. Few trees in the Serengeti ecosystem have canopies

that exceed 30 square meters and thus this is a suitable spatial resolution for the analysis. It is also clear from the land cover maps that land cover classes can vary from one pixel to the next and often do. There are many solitary pixels classified as woody vegetation, and thus land cover pixels are independent measurements of vegetation.

The assumption of independence of roosts is also challenged when the analysis area surrounding the roosts is expanded beyond a 1.5 km radius. If we assume that 1.5 km measures the maximum extent of the owl hunting radius, or the maximum extent used most often by the owls, then the roosts are mostly independent from one another as the areas within these boundaries do not overlap. Though at the 1.5 km level there is a small amount of overlap between roosts 4 and 12. If the owls are assumed to use a larger area then roost 4 and 12 and roosts 13 and 18 overlap considerably and the roosts are no longer independent. Under this assumption, the number of roosts that can be considered independent is reduced to 6: roosts 24, 3, 4, 18, 23, 44.

1.2.10 Sample size

Among the samples collected for this analysis, numbers of identified specimens (NISP) range from 37 specimens at roost 12 to several hundred specimens at the other roosts. Many statistical procedures are sensitive to small or unequal sample sizes. Even basic enumeration of taxon abundances may be biased by sample size. For example, Grayson (1984) noted that faunal abundance may shift with sample size depending on how counts of individuals are made or samples aggregated. Many metrics of species richness and diversity are also sensitive to sample size (May 1975; Magurran 1988; Rosenzweig 1995). Problems may also arise from the application of parametric statistical techniques to percentages and proportions. When taxonomic counts are expressed as proportions the values sum to one. Unlike standard measurement variables which are independent, this closed sum reduces by one the number of values that can vary freely.

These differences must be taken into account when applying statistical tests and interpreting results. Statistical procedures were selected with these limitations in mind. Tests of independence using the Pearson's statistic, X^2 and the G statistic are generally robust to sample size differences as these are incorporated in the margin totals that determine the expected values in each cell. Sokal and Rohlf

(1995) provide examples of these tests performed on unequal samples as well as corrections that should be applied to small samples such as the Yates correction and Williams correction. The corrections reduce the value of X^2 or G, resulting in a more conservative test . Adjusted statistics are noted in the text and symbolized by subscripts, such as $X^2_{adj.}$. Correspondence analysis is appropriate for presence/absence data, counts and proportions for many of the same reasons as the Pearson's and G tests.

The statistical techniques described above have been chosen in part to contend with uncertainties arising from variation in samples sizes. For example, relative abundance of taxa may not be precise but the rank correlation of taxa is likely to be more robust to variation in sample size so rank correlation statistics are used to test relationships between taxa. The influence of sample size on taxon relative abundance is examined carefully in Chapter 3.

Faunal richness and diversity are considered in Chapter 5. Various species diversity indices are employed some of which are more sensitive to sample size than others. Rarefaction is used to compare assemblage at different sample sizes. The same technique also produces a nonparametric confidence interval for the taxonomic richness at different samples sizes.

1.3 Chapter Summaries

Micromammal accumulations contain a great deal of information that is otherwise difficult to gather. Owl roosts may aggregate tens of thousands of specimens in dense mats several inches thick below a roosting or nesting place (personal observation). Guerin (1928) reports that one barn owl captured over 1100 prey items in the span of 90 days. By comparison, in areas with high densities of small mammals, trapping seldom yields greater than 10% success; at that rate it would take 100 days of continuous trapping with 100 traps to match what a barn owl collects over roughly the same period. The returns are equally efficient in paleontological contexts. The breccias from South African cave sites contain very dense accumulations of microfauna as do some open air sites; for example Sabatier (1982) describes more than 1218 microvertebrate specimens from a concentrated assemblage at Hadar locality A.L. 327. To analyze microfaunal assemblages in paleoecological context we require:

1. a reliable method of identifying micromammals from osteological remains
2. a model of the taphonomic process
3. a set of quantitative procedures for describing and comparing assemblages
4. a model of ecosystem process linking small mammal community structure to ecosystem variables of interest (vegetation structure, precipitation, temperature etc.)

These steps form the foundation for micromammal paleoecology. My aim is to improve aspects of this foundation and highlight those areas requiring additional investigation.

Chapter 2: Study Area, is an introduction to the study ecosystem. I describe the methods used for developing a landcover/physiognomic vegetation classification of the study area and summarize other climatic and ecological parameters at work in the ecosystem and their interactions. The landcover map is a quantitative summary of the habitat for comparison with the spatial distribution of microfauna, and an attempt to reduce the dimensionality of the ecological data into a smaller set of covarying factors.

Chapter 3: Fauna describes the faunal analysis including methods for identifying and processing taphonomic micromammal assemblages. The different morphotypes are described and attributed to taxa. The habitat proclivities of the taxa are summarized and the correlations between taxa are examined.

Chapter 4: Taphonomy examines the process by which micromammal assemblages enter into the fossil record and the taphonomic biases that may be imposed. The behavior of two species of owl, the Barn Owl, *Tyto alba* and the Spotted Eagle Owl, *Bubo africanus* are compared and contrasted. Faunal composition under two taphonomic modes, cavity roosts and open roosts, are compared. Differences in roost type are shown to associate with the two different predators.

Chapter 5: Paleoenvironmental Analysis assesses the relationships between faunal composition and physiognomic vegetation/landcover. This chapter synthesizes the results of previous chapters and answers the fundamental

questions that motivated the overall project: How well, if at all, do owl-accumulated micromammal assemblages represent local vegetation land cover?

Chapter 2

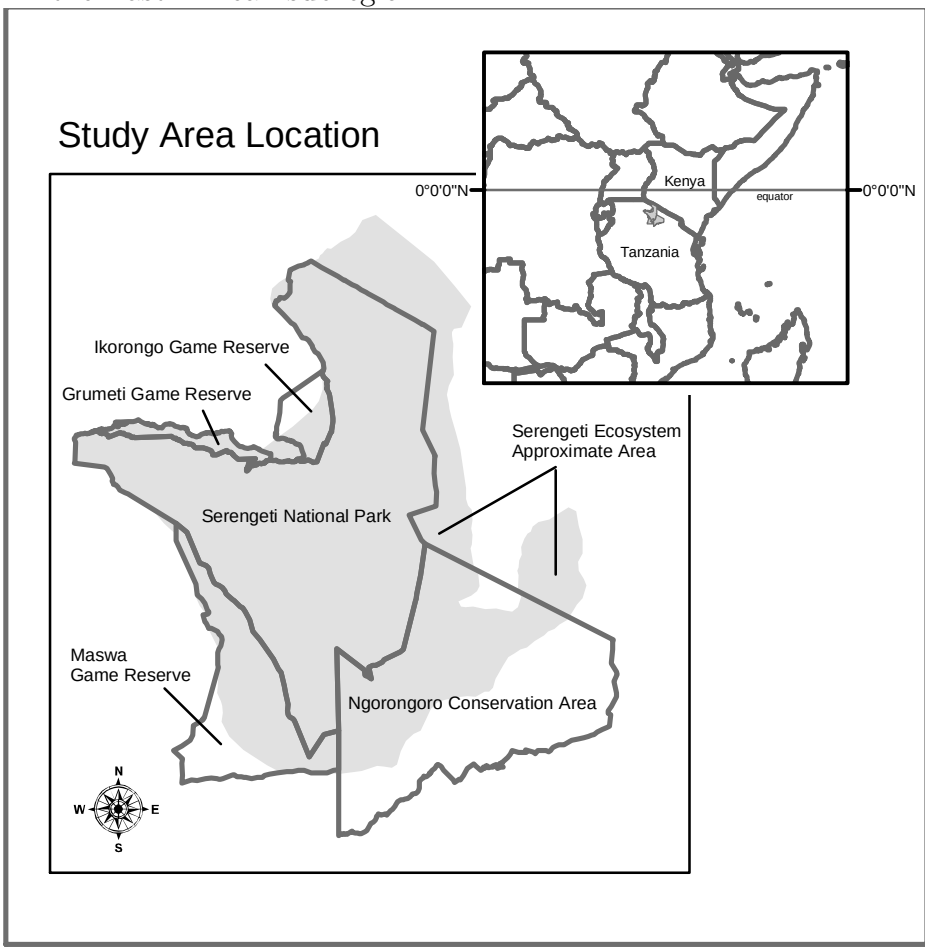
Study Area

2.1 Introduction

As a World Heritage Site and home to some of the largest free-ranging ungulate herds, the Serengeti-Masai Mara ecosystem is not only a treasure of global biodiversity and conservation, it is also one of the best studied natural laboratories in the paleotropics. The ecosystem straddles the Tanzania-Kenya border in East Africa between $34° - 36°$E longitude and $1° - 2°$S latitude. Serengeti National Park in Tanzania encompasses an area of 14,763 square kilometers but the larger ecosystem – defined as the area covered by the wildebeest migration – extends into neighboring Masai Mara National Reserve (1,510 km^2) to the north in Kenya, Ngorongoro Conservation Area (8,094 km^2)to the southeast, the Loliondo Game Controlled Area (4,000 km^2) to the east, Maswa Game Reserve (2,200 km^2) to the southwest and the Ikoronogo and Grumeti Game Controlled Areas (5,000 km^2) to the northwest (Sinclair 1995c). In total, the ecosystem covers an expanse of roughly 24,000 square kilometers as shown in Figure 2.1.

Land cover and vegetation patterning are important to management and conservation of the ecosystem as well as scientific understanding of ecosystem processes across varying spatial and temporal scales. A unique aspect of the Serengeti – Masai Mara ecosystem is its relevance to modern ecosystem studies (Sinclair and Norton-Griffiths 1979; Sinclair and Arcese 1995), paleoecosystem studies (Blumenschine and Peters 1998; Leakey and Harris 1987; Bower 1979), and actualistic research that bridges the two (Blumenschine 1987; Cavallo and Blumenschine 1989). Understanding the modern macroecology along with empirical analysis of

Figure 2.1: 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.



vegetation structure is critical for testing and validating models of paleoenvironmental reconstruction as is the purpose here.

Intense scientific exploration during the 1970's produced many cartographic descriptions of the ecosystem. Herlocker (1976) prepared a woody plant species map of the Serengeti National Park. This work was an extension of earlier efforts to map regions of similar land cover types, such as the zonal land classification scheme of Gerresheim (1974). Two soil maps followed these efforts. One for the Serengeti plains (de Wit 1978) and another for the woody regions of the western corridor and the northern extension (Jager 1982). Climate patterns and precipitation were also described in detail during this time (Norton-Griffiths et al. 1975). The Herlocker map is quite detailed, especially as regards species composition, but focuses only on the wooded areas of the park. Moreover, none are geographically precise, and as printed maps they are not easily compared against each other or other data sets. Digital image interpretation, as used in this study, solves the data integration problem and produces more geographically precise results. More recently, digital vegetation maps have been produced by Hunting Services, UK; the Tanzania National Resource Information Center (TANRIC); and the FAO's Africover project. The Hunting Services and TANRIC maps both derive from satellite imagery, but use unsupervised classification without detailed ground truth data. The Africover maps are based on manual image interpretation and at a relatively small scale (1:200,000 or 1:100:000). This study improves on these previous efforts by employing extensive ground survey stemming from roughly four years of cumulative field experience in the study area. The results are also presented at a larger scale than the Africover maps.

The goal of this chapter is to organize existing ecological, and climatological data relevant to the Serengeti-Masai Mara ecosystem and produce a physiognomic vegetation GIS of the study area suitable for investigating faunal-floral relationships. This task included digitizing paper maps, updating existing digital coverages, compiling meteorological data and synthesizing ground survey data sets to a common format. The resulting land cover/physiognomic vegetation GIS is based primarily on Landsat Enhanced Thematic Mapper (ETM+) imagery using a fuzzy-classification approach with the ancillary data used to stratify the image but not to predict vegetation classes. A brief primer on Geographic Information System (GIS) and Remote Sensing (RS) is provided for background on common

jargon and techniques, followed by methods, results and discussion of the land cover classification map. The effort of vegetation mapping was mitigated in part by data exchange with other researchers. I present ground survey data collected by five researchers (including myself) who participated in a workshop dedicated to the task of vegetation mapping of the Serengeti.

2.1.1 GIS and remote sensing fundamentals

A geographical information system (GIS) is a tool for integrating geographical data (objects and features that appear in maps) with attributes about those features stored in databases. Most paleobiological and archeological investigations have a spatial as well as temporal component for which GIS is the best analysis environment. Early GIS software stored feature information separately from the attributes about the features. Geodatabases pursue a more integrated approach – placing both in a common database management environment that can serve features and attributes to multiple clients (MacDonald 2001).

Remote sensing is the practice of visualizing the earth's surface from sensors mounted on high altitude platforms such as balloons, airplanes or satellites. Remote sensing is particularly well suited for regional exploration of ecological and climatological phenomena and in this role is an important tool for actualistic research. The utility of remotely sensed data varies with the type of sensor carried by the platform. ETM+ is a generalized sensor package suitable for a broad suite of earth surface mapping applications including terrestrial vegetation mapping, geology and geophysical mapping to oceanic mapping.

The regions of the electromagnetic spectrum that a sensor can detect is called a "band." The ETM+ sensor has eight: bands 1-3 detect reflected visible light in the wavelengths corresponding approximately to blue, green and red respectively. Bands 4, 5, 7 detect reflected electromagnetic radiation in the longer-wavelength, infrared portions of the spectrum. Band 6 detects thermal rather than reflected radiation. Finally band 8 detects a broad swath of the spectrum (panchromatic) at higher spatial resolution. There is a trade-off between spatial resolution, radiometric resolution and spectral resolution (Lillesand and Kiefer 1994). Spatial resolution indicates the smallest area that is imaged instantaneously, i.e. the size of the picture elements (pixels) in ground surface area. Spectral resolution refers to the frequency range and number of bands, while radiometric resolution refers

to the differences in energy that can be detected within each band. If spatial and spectral resolution are increased then less total energy is striking the sensor and it is more difficult to detect subtle differences in the amount of energy, thus radiometric resolution is reduced. Landsat imagery has constant radiometric resolution (8 bits or $2^8 = 256$ shades) with differing spatial and spectral resolution. The panchromatic band for example has a spatial resolution of 15 m^2 but covers a much broader area of the spectrum while the other bands (save band 6) have 30 m^2 resolution. The thermal band has 60 m^2 resolution.

2.1.1.1 Raster versus vector data.

Two data formats are common to GIS and remote sensing applications: rasters and vectors. Raster data sets store information in a geographical grid. The area covered by a raster data set is divided into many small squares (or rectangles) called pixels and each pixel stored a discrete value, sometimes called a digital number (DN). Satellite imagery is an example of a raster data set. The area covered by a single scene may be divided up into a grid thousands of pixels to a side. The size of the pixels and their density defines the spatial resolution of the image. The more pixels that are packed into a given area the higher the spatial resolution. The value stored in a single pixel of a satellite image records the amount of reflected (or emitted) energy of a certain wavelength detected by the sensor at that point on the ground. Continuous phenomena are rendered and stored as discrete data in digital format, hence the use of summation rather than integration in most algorithms. Raster data layers, if properly registered to each other, may be combined in stacks so that a given point on the ground is represented by a measurement vector (not to be confused with vector data, see below) with each element corresponding to one band of the image or layer in the stack of raster data (see also B.3).

Vector data layers do not use a grid format to store information but rather record the location of features to be displayed in a database. Thus one difference between raster and vector layers is that grids have information about every point represented within the extent of the image (null values must still be recorded in the raster) whereas the vector format stores only information about what is present. Vector data may be stored as a series of points, points connected into lines, or points surrounding areas that form polygons. Vector coverages may also be stores as mathematical equations depicting the shapes of curves. In the following

discussions, references to point coverages, line coverages and polygon coverages refer to vector data types. A rivers map is an example of a line coverage. Rivers are represented by lines, that in turn are stored as a series of connected points. Many other types of vector coverages have been developed including networks, routes and triangular integrated networks. These are largely modifications of the basic types described above.

2.1.1.2 Map projections and geographical coordinate systems

Coordinate systems provide a reference framework for geographic positions. The geodetic coordinate system of longitude, latitude and altitude describes positions on the surface of a sphere in terms of degrees east or west of a meridian passing through Greenwich England, above or below the equator and at some altitude. However the earth is not a perfect sphere, it bulges slightly at the equator. Accounting for this distortion, map coordinates need to reference a model of the earth's three-dimensional shape called a spheroid. The earth-centered earth-fixed coordinate system (ECEF) is a Cartesian polar system with heights measured relative to the earth's center of mass. The World Geodetic System 1984 (AKA WGS 1984 and detailed in a report by NIMA 2000) combines the ECEF origin with a spheroid (also called WGS 1984). The combination of a spheroid and origin is called the coordinate system datum. The WGS 1984 datum provides a global approximation of the earth's surface but more precise models are often used for regional and local mapping. Kenya and Tanzania share a datum called Arc 1960 which is based on the Clarke 1880 spheroid. Unless stated otherwise, all coordinates and locations are provided in this datum.

It is often necessary to map the earth's surface onto a plane (as in a paper map). To do so requires a projection of the spherical surface onto the plane. Imagine a clear plastic sphere with surface features drawn on its surface and a light bulb in the middle. By illuminating the bulb an image of the surface features can be projected onto a nearby wall. Any such projection invokes some distortion and the many varieties of geographical projection systems are meant to limit or select one type of distortion over another. Universal Transverse Mercator (UTM) is both a projection and coordinate system. Transverse Mercator is a cylindrical-tangential projection system with the projection plane intersecting the sphere at a single point. UTM divides the globe into 60 zones along the equator, each 6° wide and centered on a

meridian where the plane is tangential to the sphere. Serengeti, for example falls in UTM Zone 36 South which is centered on the 33rd meridian. Distortion is lowest at the equator and at the central meridian of each zone. UTM is widely used for field work (and artillery range-finding) because positions are recorded in meters relative to the origin. The equator is given a value of 10,000,000 meters and values descend toward the poles; the central meridian is given a value of 500,000 meters with values increasing to the east and decreasing to the west.

2.1.1.3 Global positioning systems

Global Positioning Technology (GPS) links a surface based receiver with a constellation of 24 orbiting satellites to provide geographical coordinates to the receiver. At the most basic level, a GPS receiver is little more than a very accurate clock. The receiver uses the lag time in radio communication to measure distances to the satellites and triangulate a position. All coordinates provided in this study were obtained with a consumer-grade 12 Channel Garmin 12XL GPS receiver (Garmin International Inc., Olathe, KS).

The GPS satellite constellation is maintained and operated by the United States Department of Defense, primarily for military purposes, but with a civilian channel available at reduced accuracy. Accuracy reduction of the civilian GPS signal was implemented by the DoD through a system called selective availability (SA). Generally, SA reduces the accuracy of a GPS reading by an order of magnitude, from roughly 3-5 m without SA to 30-50 m with SA. SA induces a bias that affects both accuracy and precision that cannot be countered by simply averaging repeated measurements. Given a known position, such as a benchmark, and additional GPS equipment, GPS accuracy can be greatly improved (down to sub-meter accuracy) using a technique called differential correction. However, the means to employ differential correction were never available in the field. On 1 May 2000, President Clinton signed an executive order eliminating SA. All GPS readings presented here, unless otherwise noted, were made without differential correction and thus subject to selective availability if taken prior to 1 May 2000. GPS measurement were averaged in order to increase the precision of readings. Without averaging, one-time readings under SA may be off by as much as 100 m.

2.1.2 Image classification

Classification is the process of mapping the members of a large set with either continuous or discretely varying members (e.g. the pixels in an image) to a smaller array of thematic sets or classes (see Appendix B.4). Humans are naturally adept at classification since the brain automatically integrates color tones, textures, contrast, position and context to identify features and cluster similar elements. Computers are not so adept but they are tirelessly efficient. Supervised classification requires one to train computer software to recognize vegetation classes by providing example areas in the imagery termed training sites. Training sites are based on reference data – independent information about the vegetation at that spot on the ground. Reference data may include higher resolution imagery such as large-scale aerial photographs or in this case, places that have been visited in person, a process called ground truthing. In the imagery, regions of pixels are selected at and around the ground truth points as training areas and the software stores these pixel values and their key statistics as the signature for that class of ground cover. With some experience, one may also develop signatures at areas that were not ground truthed based on visual interpretation of the imagery alone or in concert with ancillary data sources such as aerial photographs, soil maps etc. The terms "truthed" and "untruthed" distinguish signatures developed with and without ground truth data. Many of the classification algorithms are parametric, that is they assume variability of the pixels comprising a training set to be normally distributed. This assumption applies to maximum likelihood classification and fuzzy-classification based on a maximum-likelihood decision rule. The sensors are often capable of detecting subtle differences in soil characteristics that do not impact the physiognomic structure of the vegetation, but do give the same vegetation very different spectral reflectance properties. Grouping these training sites into a common signature results in a bimodal (or worse) distribution of pixel values that interfere with the performance of the classification algorithms. Thus, it is necessary to create training subclasses – multiple signatures that represent the same class. For example there are numerous signatures for low open grassland because the substrate is easily visible through the vegetation canopy and has a greater influence (especially in the longer wavelengths) than the vegetation itself.

Natural vegetation is difficult to classify because boundaries tend to be gradual and because different vegetation covers have very similar spectral properties or they

co-occur. Grasslands with a few trees, for example, will be spectrally similar to light woodlands with grass understory. This is the challenge of forcing an *a priori* classification schema onto a natural vegetation regime, often the class boundaries and spectral boundaries do not coincide. One solution is to use ancillary data such as precipitation, soil mapping, and topography to predict the presence of different vegetation types. However, predictive modeling of this nature is at odds with the current objective which is to produce a land cover map *independent* of those variables against which to test predictive models that employ them. Another strategy for improving map quality and accuracy is to stratify the image into zones where certain vegetation types are known not to occur. Years of extensive survey, and our own ground truth data indicate southern areas where trees are rare, and a boundary, north of which they become much more prevalent. This is illustrated in Figure 2.11. This knowledge comes inductively, from experience and thorough observation, and it is used to stratify the image into a woodland zone and a grassland zone. The signature sets for woodland and grassland zones largely overlap, but those woodland signatures that are poorly separated from grassland signatures are omitted in the analysis of the grassland region and vice-verse for the woodland region. Each zone was analyzed using its own signature set, though the majority of signatures overlapped across sets.

2.2 Data Sources and Methods

Two Landsat 7 ETM+ scenes serve as the principal data source and these were supplemented by ancillary coverages derived from paper maps. The ancillary data cover hydrology, elevation and topography, precipitation and soils. Description of the ancillary data sources is provided first, followed by the analysis and interpretation of satellite data. The ancillary coverages were used to establish zonation but were not input to the classification algorithms. Figure 2.6 illustrates the work flow.

2.2.1 Hydrology

Rivers and drainage lines greatly influence physiognomic vegetation patterns and the classification seeks to distinguish riverine and wet land cover. The hydrology GIS was compiled from 55 government produced 1:50,000 scale quarter degree topographic maps. Hydrology lines for individual map sheets were digitized by

the Tanzanian Wildlife Conservation Monitoring Program in Arusha, Tanzania. The individual map sheets were edgematched and stitched together to form the ecosystem-wide GIS coverage using tools in Arc/Info v. 8 (ESRI Inc., Redmond, CA). A drainage density grid was derived from the hydrology GIS by calculating the number of lines intersecting pixels inside a 300 meter search radius around each pixel using the line density function in the Arc/Info GRID module. These maps are depicted in Figure 2.2.

2.2.2 Elevation and topography

A GIS of elevation contours was constructed in the same manner as the hydrology GIS and is illustrated in Figure 2.3. All elevation units were converted to meters. The entirety of the Serengeti National Park (SNP) has elevation contour intervals at 20 m. The adjacent Ngorongoro Conservation Area (NCA) and Loliondo region were digitized at 100 m intervals. The contour GIS was then combined with the hydrology map to generate a raster Digital Elevation Model (DEM) with 30 m cells. A Secondary raster coverage depicting percent slope was derived from the DEM. Derivative DEM and slope grids were generated in Arc/Info.

2.2.3 Precipitation

Weather monitoring stations established by various national agencies including the Tanzanian Wildlife Research Institute (TAWIRI) and the Tanzanian National Parks (TANAPA) are distributed throughout the study area as shown in Figure 2.4. Precipitation data gathered from these stations was interpolated from the points using ordinary kriging to produce the raster surface model of mean annual precipitation shown in Figure 2.5. Only those monthly precipitation measurements that were part of a complete annual rain cycle beginning in November were used (i.e. no missing data), and only those rain gauges that had at least ten years of data were incorporated. Kriging is a method of interpolation that incorporates distance between measurement points as well as spatial autocorrelation of the data.

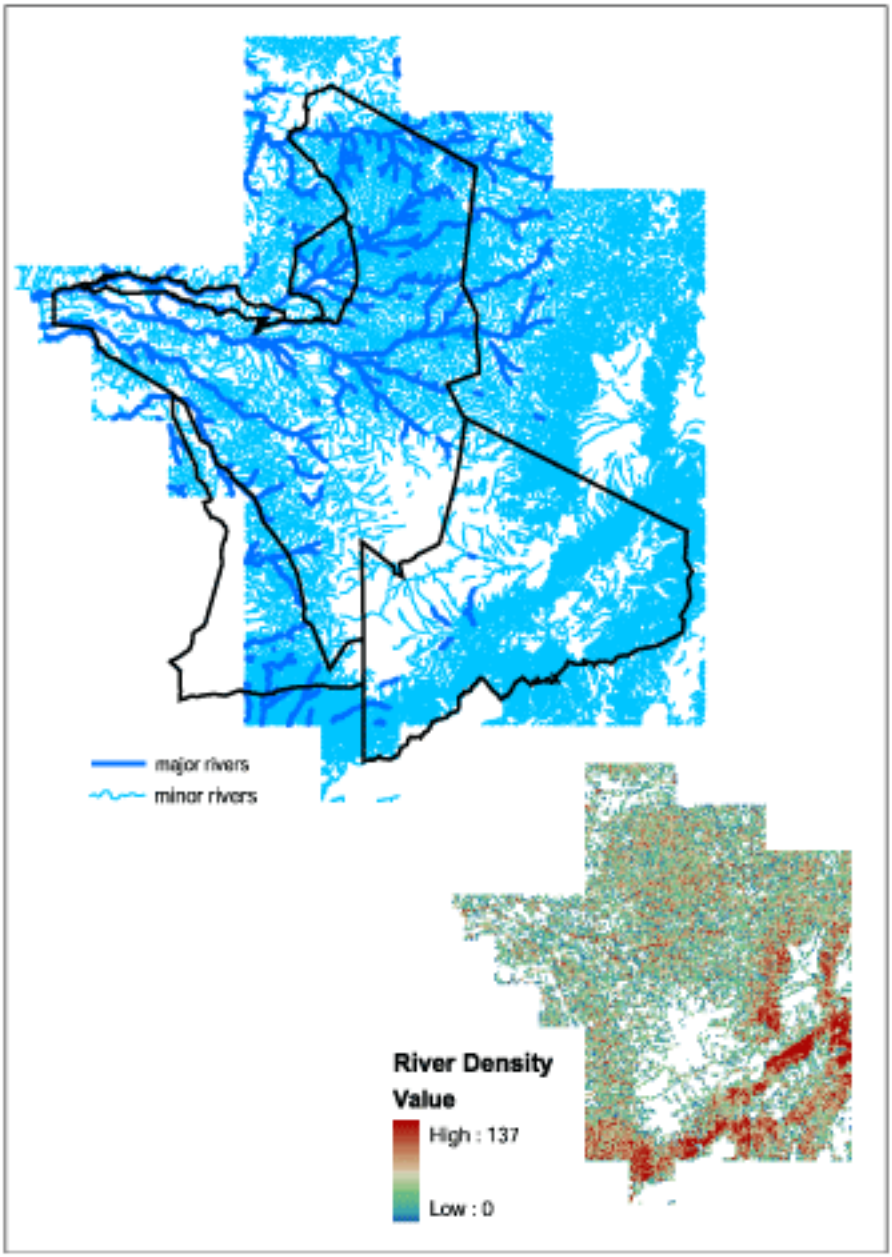


Figure 2.2: Regional hydrology and river density. Dark blue lines indicate major rivers, these are usually flowing year-round. Light blue lines indicate seasonal rivers and drainages. A river density image, derived from they hydrology coverage is plotted in the lower right. White spaces in both maps indicate the absence of rivers altogether. From both it is clear that few rivers dissect the plains in the southeastern portion of Serengeti.

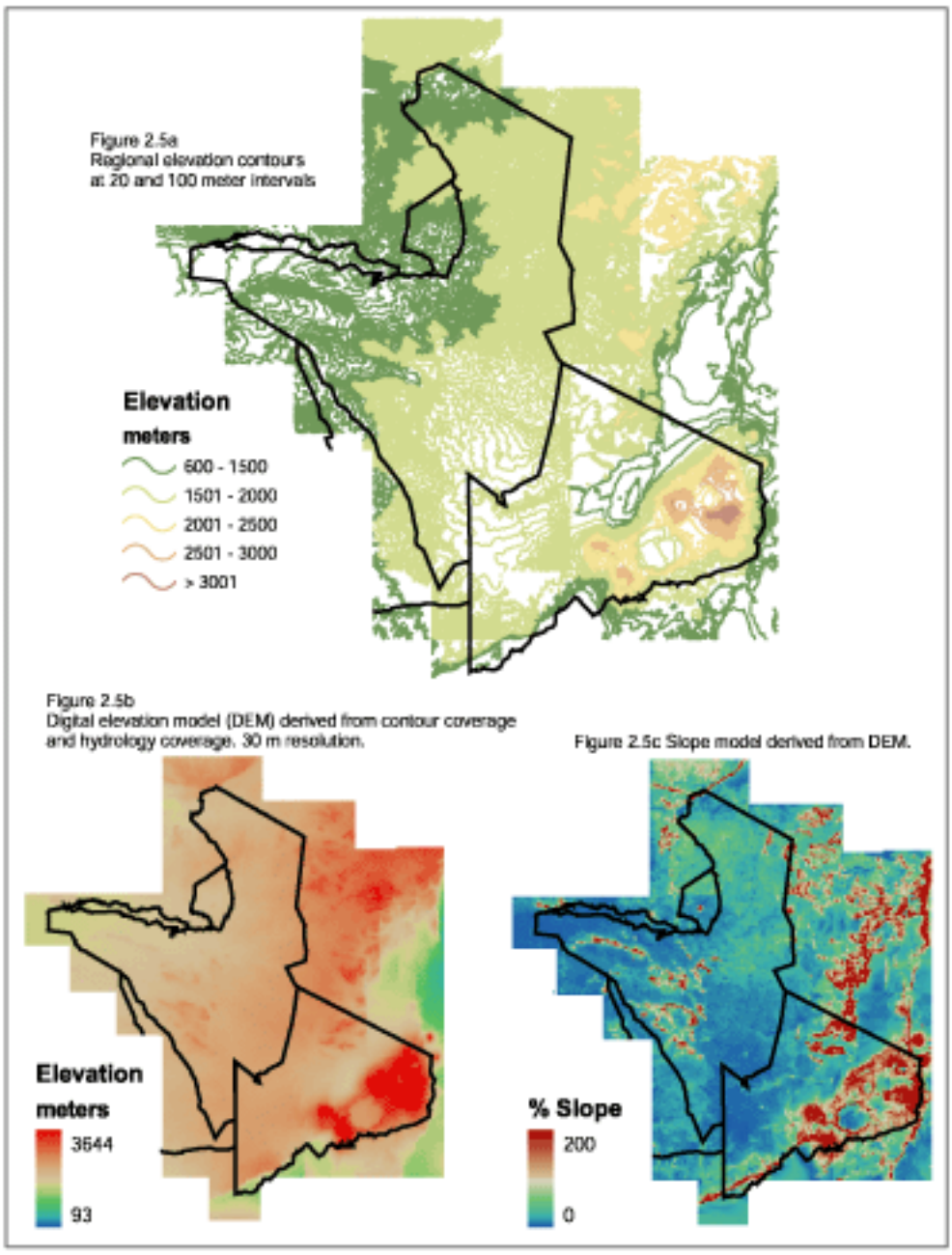
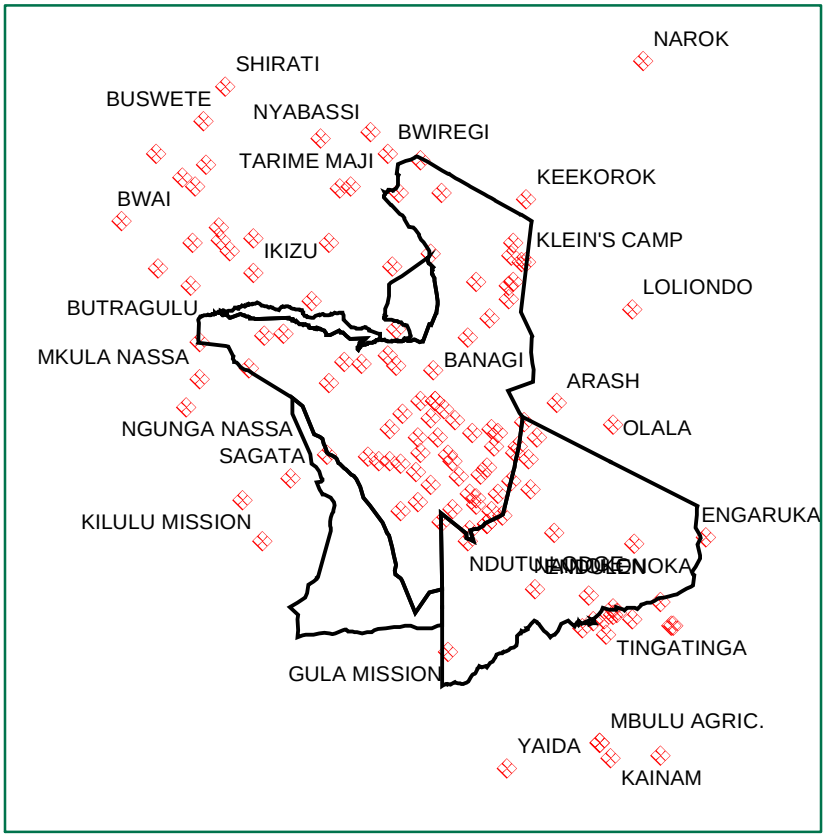


Figure 2.3: Regional elevation contours, digital elevation model and slope model. Percent slope values range from a flat surface (0% slope), to a vertical surface (200% slope). An incline of 45 degrees will have a 100% slope.

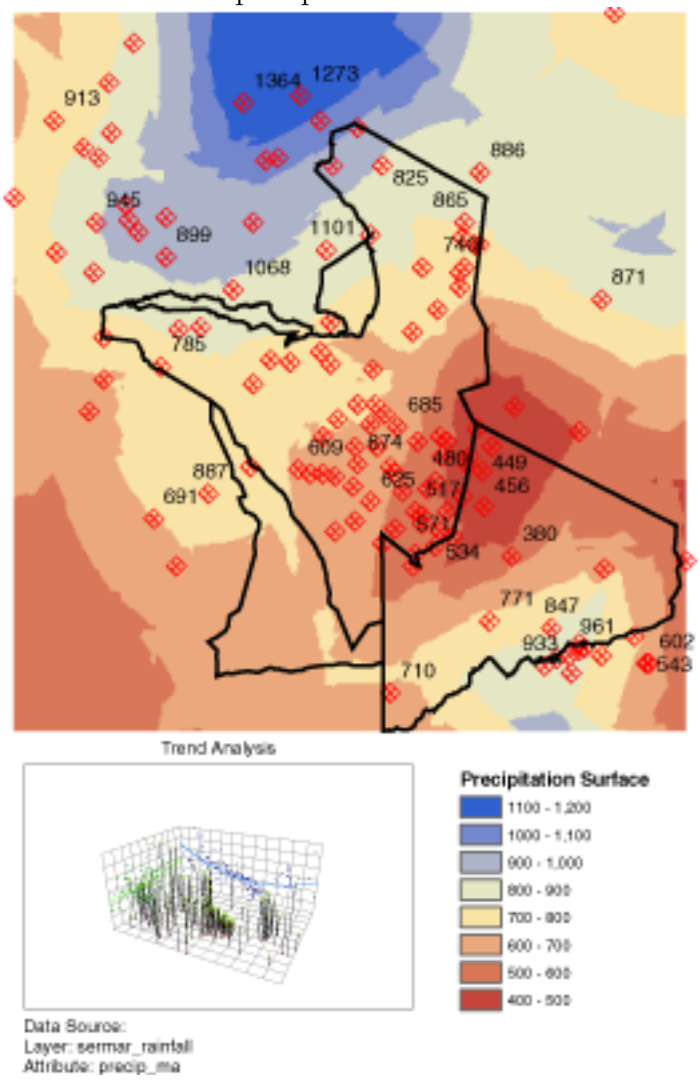
Figure 2.4: Distribution of rain measurement stations in the study area. Rain measurements are recorded monthly. Labels indicate place-names for the gauges.



2.2.4 Soils

Two soil maps have been developed for the Serengeti, one focusing on the southern grasslands (de Wit 1978) and another for the woodland regions of the central Serengeti, western corridor and northern extension (Jager 1982). Printed maps were digitized by Dr. K. Metzger and georectified to the hydrology GIS by D. Reed. The base map used as the armature for both soils studies was not planimetrically correct, and thus it was not possible to produce a distortion free digital version of the soil maps. However, the digitized maps are accurate enough for visual inspection of soil patterns.

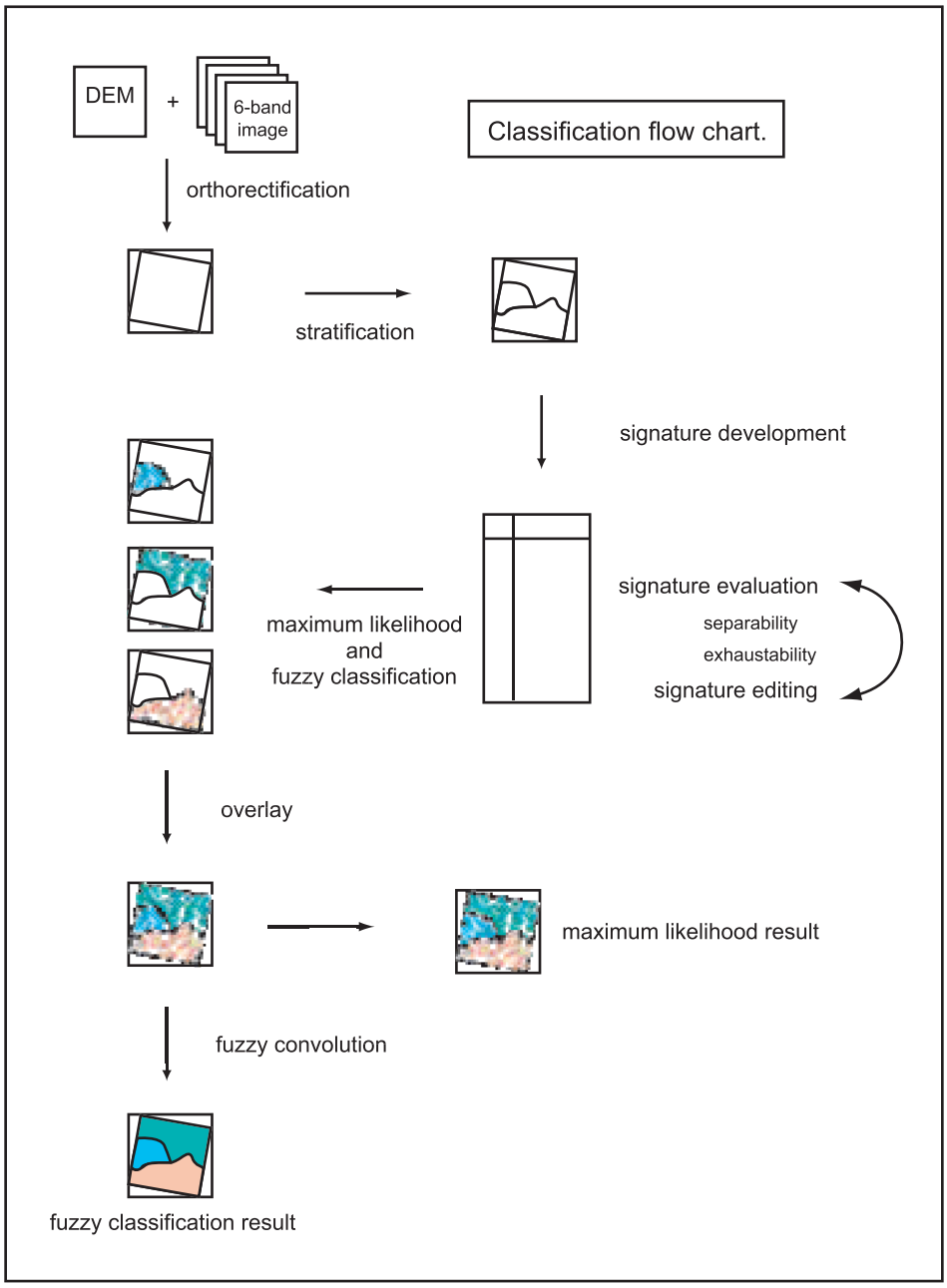
Figure 2.5: Interpolated surface of mean annual precipitation (MAP) derived by ordinary kriging from the point coverage of rainguages. 3D point plot at bottom shows the NW-SE precipitation trend.



2.2.5 Land cover classification

The classification uses a stratified fuzzy-classification approach with post-classification fuzzy convolution. Figure 2.6 provides an overview of the analysis flow. Each Landsat scene was first orthorectified and then stratified into as many as three zones: lakes; grasslands; woodlands. Each zone was classified separately using a largely overlapping signature set (see Appendix A.1). The overlapping training sites helped reduce edge matching errors in the final output. Signatures were evaluated iteratively for separability and exhaustability then applied to the image using a fuzzy-classification algorithm that stored three membership grades per pixel (see Section 2.2.5.7 and Appendix B.7 for further discussion on fuzzy classification) .

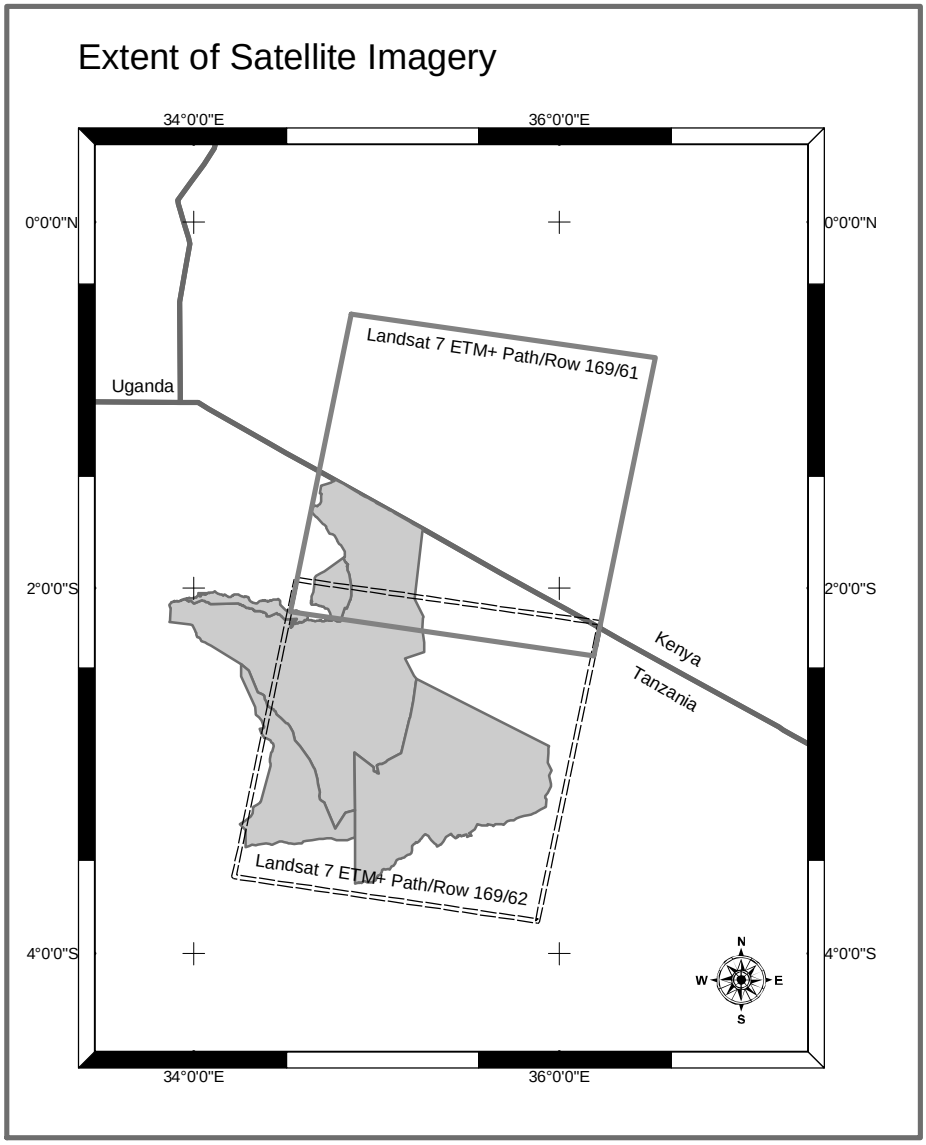
Figure 2.6: Flow chart of steps taken during image classification.



2.2.5.1 Image preparation

The primary input data sources were two Landsat 7 Enhanced Thematic Mapper scenes (ETM+). Table 2.1 gives the details on the imagery used, Figure 2.7 illustrates the coverage of each scene over the study area. The images were delivered from the Earth Resources Observation Systems (EROS) Data Center as radiometrically and geometrically corrected level-1G products in geotiff format.

Figure 2.7: Area covered by the Landsat 7 scenes purchased for this study.



For each scene, bands 1-5 and 7 were imported to ERDAS Imagine version

Table 2.1: Primary Imagery

Path/Row	Date Captured	Longitude at Center	Latitude at Center
169/61	2 February 2000	1.44° S	35.52° E
169/62	2 February 2000	2.88° S	35.22° E

8.4 (Atlanta, GA) and combined into a layer stack. Band 6 primarily represents emitted thermal radiation, and it was excluded due to its lower spatial resolution and low performance in separability measures. The images are largely cloud and haze free. Small clouds dot the eastern margins of path 169 but these fall outside the ecosystem study area.

Rectification is the processes of warping an image to align with a geographical coordinate system, and orthorectification applies an additional correction to account for the topographic distortions induced by hills and mountains. I applied the Landsat georeferencing model within Imagine, which uses a second order polynomial to transform the input Landsat coordinates to the proper geographical coordinates. The coefficients of the transformation polynomial are determined by matching points in the Landsat imagery to ground control points in a georeferenced image. Reference points were gathered either from scanned 1:50,000 scale topographic maps or from a detailed hydrology GIS layer derived from 1:50,000 topographic maps. The Landsat georeferencing model can also accept elevation values, which were provided from a digital elevation model of the study area. All the cartographic input layers and the resulting orthorectified imagery were projected to UTM coordinates, using the ARC 1960 datum (mean solution for Kenya and Tanzania) with the Clarke 1880 spheroid. The imagery was reprojected using a nearest neighbor algorithm in order to preserve original pixel values. The root mean square error – a measure of rectification precision – is reported in Table 2.2. In both images, the RMS error was slightly greater than the dimensions of one pixel (30m). Figure 2.8 shows a mosaic of the georectified landsat scenes.

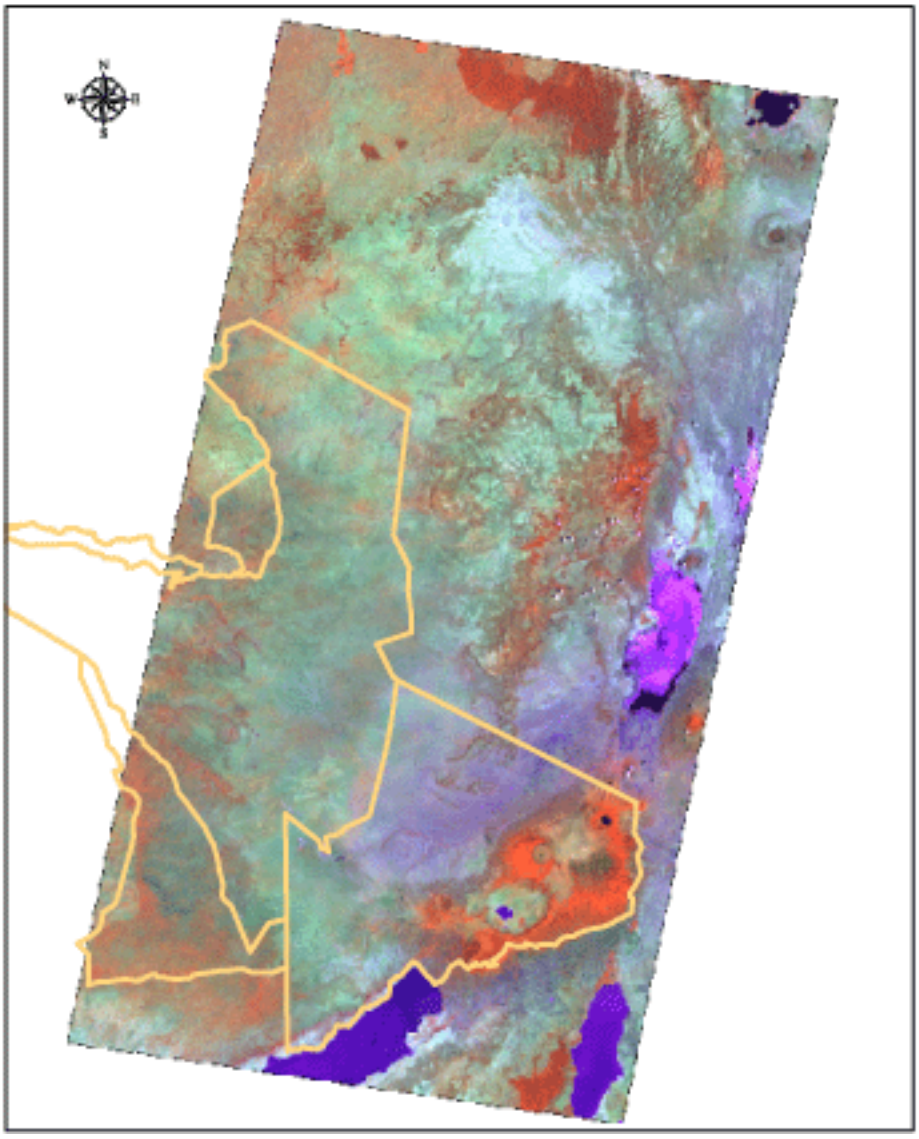


Figure 2.8: False color image of Landsat 7 ETM+ scene, path 169 row 62: Red near infrared (band 4), Green mid infrared (band 5), Blue red visible light (band 3. With this color combination dense vegetation appears red, and moderate vegetation appears dark green. Sparse vegetation appears blue as does shallow water. Deep water appears darker blue or black.

2.2.5.2 DRSRS land cover classification system

The land cover classification system developed by Grunblatt et al. (1989) for the Kenyan Department of Resource Surveys and Remote Sensing (DRSRS) is hier-

Table 2.2: Geometric Correction Results

Path/Row	Number of Points	Total RMS Error
169/61	48	41.5m
169/62	36	39.5m

archical in that different levels of precision can be applied depending on the data available and more specific classes can be telescoped inside broader classes and vice-verse. The hierarchy has four levels. At the highest and broadest level (Level 1), the vegetation is described in terms of the primary life form and its density, e.g. open grassland (oG), or dense Forest (dF). The four primary life forms are

Forest (F) / Woodland (W) land cover dominated by trees. Trees are defined as single stem woody plants. Many plants in the study area have a low, shrubbed growth form (typically under a meter) that develops later into a true tree growth form. Many species in the genera *Acacia* and *Comiphora* are good examples. In general such plants that were in their low, shrub growth-form when the plots were surveyed were recorded as shrubs. Two terms are provided for treed land cover as a concession to custom. Sparse or open treed land cover is called "Woodland" while dense and closed tree cover are called "Forest".

Shrubland (S) land cover dominated by multistemed woody plant cover. As mentioned above this may include the low growth form of some tree species.

Grassland (G) land cover dominated by herbaceous vegetation including grass and sedges.

Bare (B) Areas with less than 2% vegetation cover.

In general candidates for the primary life form must have a percent canopy cover greater than 20% and within those, preference is given to trees over shrubs, shrubs over grass and grass over bare ground. The Level 1 adjective describes the primary life forms' canopy density.

Closed (c) 80-100% canopy cover

Dense (d) 50-79% canopy cover

Open (o) 20-49% canopy cover

Sparse (s) 2-19% canopy cover.

For example, a plot with 25% trees, 14% shrubs, 30% grass and 70% bare ground is an open woodland (oW). If an area has no life form with a percent canopy cover greater than 20% but some greater than 2% then the life form with the greatest canopy cover is used along with the sparse modifier, e.g. canopy coverage of 0% trees, 2% shrubs 10% grass and 90% bare ground would be classified as sparse grassland (sG, not to be confused with shrubbed grassland SG – see below).

Level 2 designations include a secondary life form as a descriptive modifier to the primary life form. The terms for the secondary life form are similar those for the primary: Treed, Shrubbed and Grassed. The level 2 life form may be used when a form other than the primary form attains 20% density with preference following the same order as earlier (trees, shrubs, grass). The plot described in the first example above (T25%,S14%,G30%,B70%) would have a Level 2 classification of open grassed woodland (oGW), while another with slightly greater shrub cover (e.g. T25%,S22%,G30%,B70%) would be an open shrubbed woodland (oSW). One should be careful to remember that the density adjective and secondary life form are both descriptors of the primary life form. The system of Grunblatt et al. (1989) affords an emphasis to wooded and shrubbed categories, allowing them to be included as secondary descriptors if they are present at levels between 2 and 19% when no other life form is present as a true secondary candidate (i.e. greater than 20%). To illustrate, if a plot has T5%, S15%, G70%, B30% it would be a dense treed grassland (dTG).

Level 3 and 4 include additional information on height and plant taxon names respectively. The general height categories are, dwarf (D), Low (L) and Tall (T). Lastly, adjectives may be added to a code at any level. These include: Multistory (M), Riverine (R) and Wet (W). These optional modifiers would prefix the level 3 height descriptors. The overall form of any code is: species description + optional modifier + height modifier + canopy modifier + secondary life form name + primary life form name. For example, *"Acacia xanthophloea* RToSW" is riverine tall open shrubbed woodland with fever trees of the species *Acacia xanthophloea* as the dominant species.

All ground truth points have data suitable for determining a level 2 code and many have additional data allowing level 4 designations. Each signature is annot-

Table 2.3: Summary of Ground Truth Data. Survey methodologies include 30 meter square plots (30m), 9 point plots (9P) and modified Whittaker plots(MW). See text for details.

Collector	Dates	Ground Truth Points	Method
Denné Reed	1998 - 2000	216	30m
Kristine Metzger	1999 - 2000	405	9P,MW
Michael Anderson	2000, 2002	103	MW
Jan Dempewolf and Suzanne Serneels	2003	145	30m+

ated with information about the ground truth points that went into its development and the most detailed description that is possible from a consensus of the training data.

2.2.5.3 Ground truth data

Four ground truth data sets were combined into the larger dataset used for this analysis. Table 2.3 summarizes the data sources and times of acquisition. Three ground truthing methodologies were used. KM and MA employed modified Whittaker (MW) plots (Stohlgren 1995). These are intensive surveys selectively conducted at 1000 m^2 grassland plots in which the hierarchical structure of the plant species community is examined through overlapping plots of different sizes. MW plots include data on species composition in addition to physiognomic structure. Plant specimens from MW plots were identified by KM and MA using the herbarium collections at the Mweka Wildlife Research College, Mweka and the Serengeti Wildlife Research Institute, Seronera. A total of 133 MW plots are in the dataset (103 from MA and 29 from KM). The remaining 376 plots by KM are nine-point plots (9P). Like the modified Whittaker plots, the 9P plots have a nested structure. The main sampling area is 100 m x 100 m (10,000 m^2= 1 ha), this plot is subdivided into 9 subplots with measurements taken from a circular region 8 meters in diameter at the center of each subplot and then averaged over the entire plot. Placement of the MW and 9P was random to pseudo-random. General locations were chosen from randomly generated geographic coordinates, but the specific placement of the plot might be altered to avoid local hazards.

A different methodology was used by the remaining contributors. All of DR's

216 plots sampled a 30 m^2 area that was divided into quadrats. The percent canopy cover of trees and shrubs was estimated visually as the area in each quadrat that would be shaded at noon and then averaged over all quadrats. Grass density was measured by visual inspection of a fixed-area 1 m^2, metal rectangle (AKA Daubenmire plot) randomly placed throughout the 30 meter plot. Bare ground was taken as the converse of the grass density (1-grass). Notes on species composition and Hi8 video supplement these data. JD and SS followed a very similar protocol to DR but without the fixed area grass measures, and their 145 plots were documented in digital photographs. Initial placement of these plots was partly random, and often conducted in transects. Later plots were chosen interactively by consulting the satellite imagery and preliminary iterations of the supervised classification to target areas not yet classified.

All five of the primary data contributors met together in person at a workshop in Washington D.C. for the specific purpose of comparing the sampling methodologies and generating a unified data structure. All MW and 9P ground plots were recoded as percentage canopy cover of four main canopy levels, trees, shrubs, herb and bare ground to match the more general data structure of the DR, JD, SS methodology. The percent canopy cover estimates were then used to derive a vegetation class name based on the scheme developed by the Kenya DRSRS and described in section 2.2.5.2.

Consistency across the data sets is a concern as data were collected independently by researchers asking different questions. The independence is mitigated in part by overlapping field experiences. DR and KM had overlapping tenure in the study area and were able to coordinate data acquisition and methodology within the constraints of their research agendas. Similarly, MA adopted the same modified Whittaker methodology as KM and data collections by JD and SS followed consultation on methodology with DR. This inter-observer variability is dwarfed by the spatial and temporal variability of the landscape and the limitations of the remotely sensed data sets.

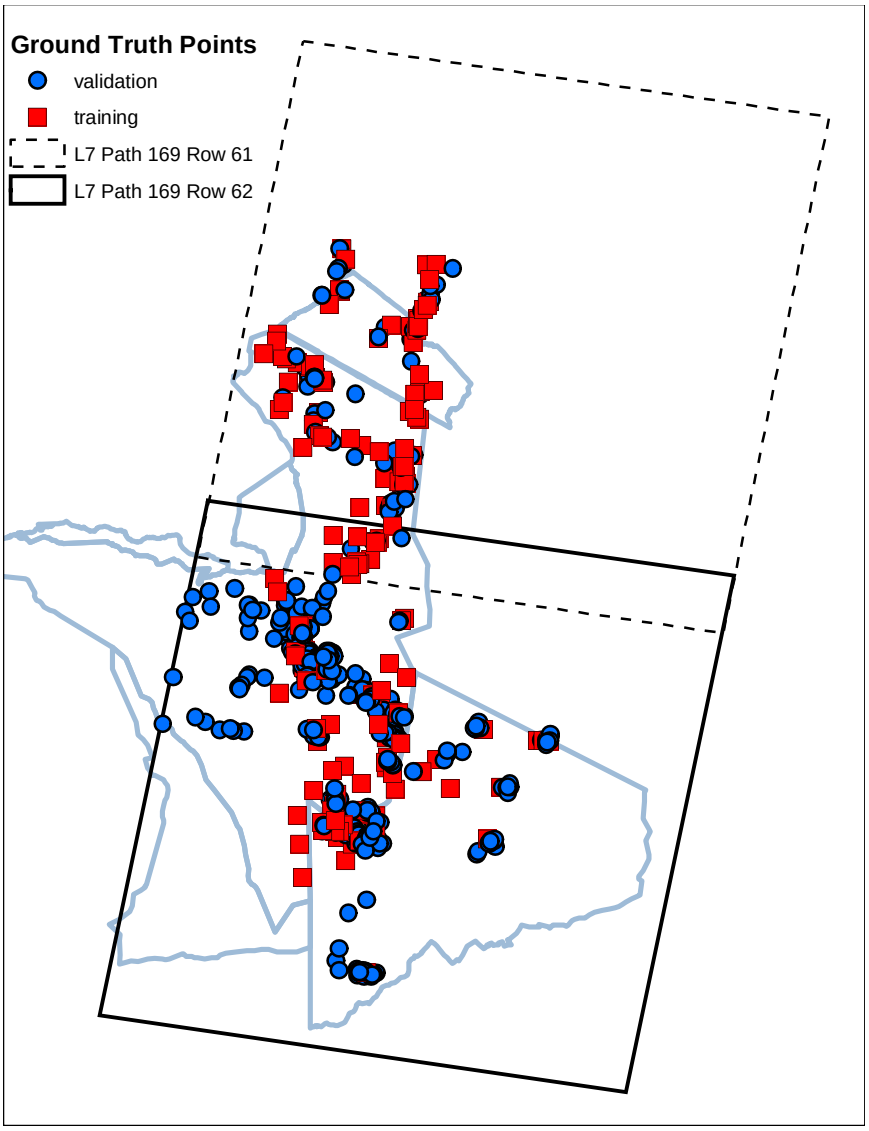


Figure 2.9: Distribution of Ground Truth Points. A total of 869 ground truth points were surveyed across the ecosystem. 620 overlap with the Path 169 imagery and were incorporated in this study.

Ground truth data cover the entirety of the Serengeti National Park as shown in Figure 2.9. These data extend into Ngorongoro to the south, and Masai Mara and Narok Districts to the north. For the current analysis data were limited to those points overlapping the image and within Serengeti National Park, Masai Mara National Reserve and the plains of Ngorongoro Conservation Area.

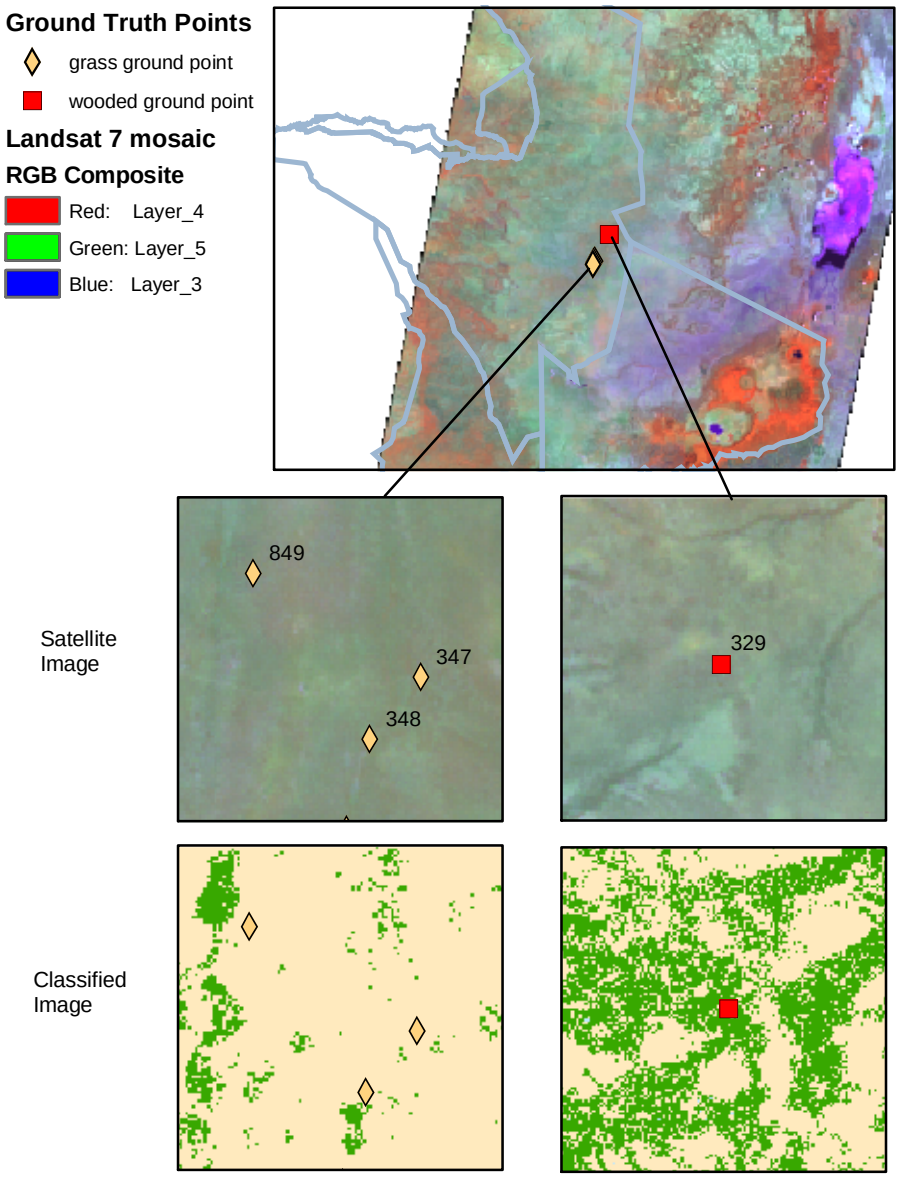
2.2.5.4 Additional reference data sources

Several reference data sources supported interpretation of the imagery and the development of classification signatures. Scanned aerial photographs taken during reconnaissance flights of the late 1960's and early 1970's provided imagery with greater spatial resolution. Nearly complete coverage of the Serengeti region was available in this format. The aerial photographs also provide time depth to the image interpretation and this aspect was supported further by MSS and Landsat 5 imagery captured in 1975, 1976, 1987, 1995 and 1999. Temporal depth is important for interpreting burn scars, and sudden flushes of new green growth that accompany local rainfall.

2.2.5.5 Image texture

Per pixel classifiers like maximum-likelihood classification (MLC) do not interpret the context in which a pixel occurs. Image texture provides a way of incorporating information about neighboring pixels into the classification. Texture provides a means to distinguish classes with very similar spectral characteristics such as dense grassland and dense grassed woodland growing on similar substrates. Woodland areas generally have higher pixel heterogeneity while grasslands are much more homogeneous, as is illustrated in Figure 2.10. A texture layer was generated from the first principal component of the six band ETM+ image. A water mask was then used to exclude lakes and and lake margins from the image and standard deviation was calculated at each pixel from a five by five pixel window. A seven by seven pixel low-pass convolution filter was then applied to the output to smooth the image.

Figure 2.10: The challenge of separating grassland and woodland land cover is shown here. Grassland and woodland areas have similar tones but differ in texture. Two areas in Serengeti are shown; one in the grasslands and one in the woodlands. Upper inserts show the satellite imagery, lower inserts the resulting classification.



2.2.5.6 Image stratification and signature development

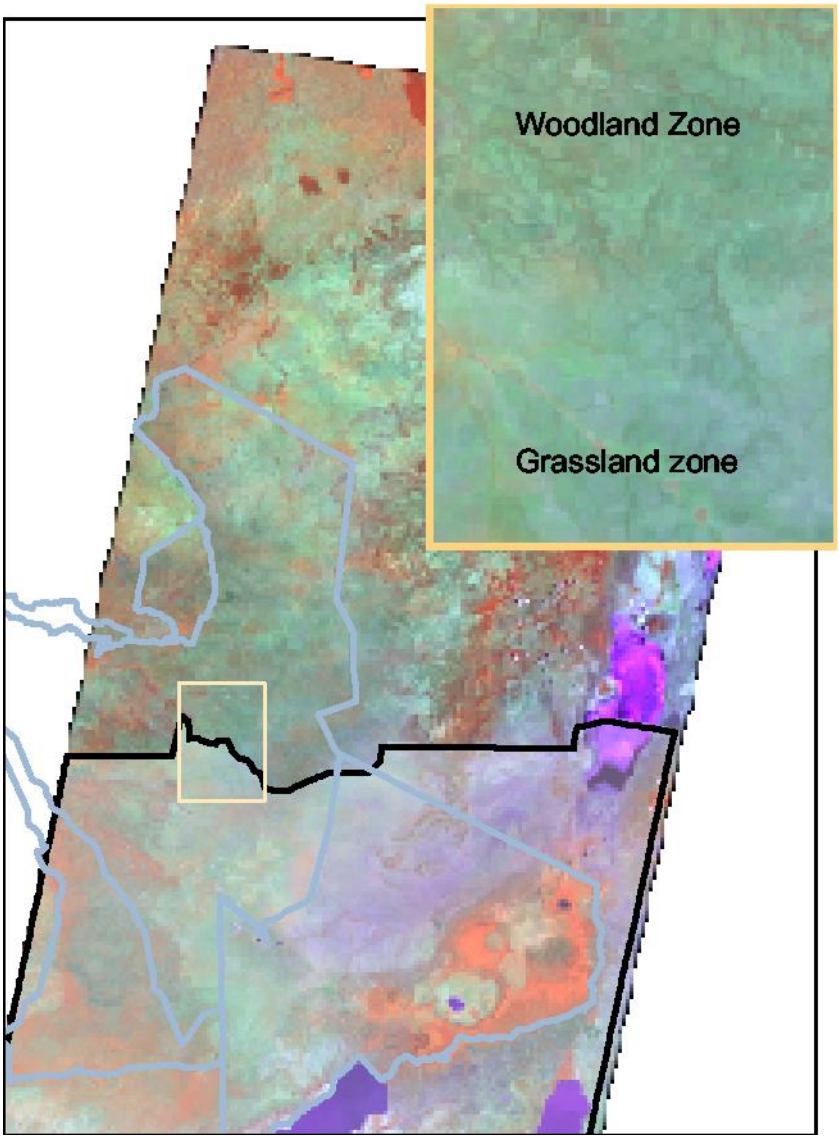


Figure 2.11: False color image of Landsat 7 scene, path 169 rows 61 and 62: near infrared (band 4) is depicted as red, mid infrared (band 5) as green and red visible light (band 3) as blue. Detail shows the transition between the grassland zone and the woodland zone and the accompanying shift in image tones and texture.

The images were stratified into grassland, woodland, and lake zones (see A.1). The grassland and woodland zones were stratified along an east-west line running below the first woodland ground truth points as shown in Figure 2.11. A water mask was developed from a preliminary classification of the image using untruthed training

areas on known lakes.

A GIS point coverage of the ground truth points was projected over the Landsat imagery, and training areas were developed at selected ground truth points. Most training areas were developed by region growing with a spectral euclidean distance threshold set interactively by the analyst. [1] Signatures were tested for separability using a transformed divergence measure. Similar signatures were merged and retained if the merged result was a normally distributed set of training pixels. Otherwise, separate signatures were retained. In this way several sub-classes were developed for each signature class in order to meet the parametric assumptions for the MLC decision rule. Preliminary classifications were run to test for feature space exhaustability, i.e. the completeness with which the signature set covered the hyper-dimensional space of the imagery, and new signature developed as needed.

2.2.5.7 Fuzzy classification and fuzzy convolution filtering

Ecotonal boundaries are seldom very strong in natural settings.Transitions are gradual or arranged in complex recurring patterns that follow edaphic conditions and often create a mosaic of land cover types over several different spatial scales. Additionally, homogeneous land cover pixels are rare and differences between land cover classes are often subtle. Fuzzy classification increases the information content of a classification relative to standard MLC and copes better with pixels of mixed makeup and complex spatial disposition. The general routine of fuzzy classification is very similar to that of standard maximum-likelihood. Training samples are collected and a maximum-likelihood estimation is calculated for each pixel. However, whereas standard maximum-likelihood classification assigns each pixel to a single class, fuzzy classification assigns class grades or likelihoods, to each pixel. In this study, each pixel was assigned a grade for the three closest classes, returning a three band image with each band containing the primary, secondary and tertiary class assignments respectively. A related, three band distance file records the class

[1] Region growing starts from a seed pixel, in this case the ground truth point, and selects neighboring pixels if their multidimensional euclidean distance (see B.5) is below the threshold declared by the analyst. The process continues from pixel to pixel until the algorithm either fails to find suitable neighboring pixels, or it encounters a maximum count of pixels or maximum distance from the seed ascribed by the analyst. Euclidean distance values were individually adjusted for each training area in order to capture a region of adequate size and homogeneity from the image. In some areas of high pixel heterogeneity, such as grassed woodlands, training areas were digitized by hand to insure a unimodal distribution of pixel values in a the training sample.

grades for each pixel as well, so a record is maintained of class assignment along with a statistical measure of how well that pixel is classified to the different classes.

Fuzzy convolution moves pixel by pixel through the image and at each examines neighboring pixels in a N x N window surrounding the focal pixel and across each band. A three pixel square convolution window was applied across the three-band fuzzy-classification resulting in a 3x3x3 convolution cube (see B.7 for additional details). The class assignment of the center pixel is evaluated in light of the surrounding pixels, and weighted by their spatial distance to the focal pixel and the grade values (or spectral distance) to their respective classes. The class assignment of the focal pixel may be changed if there are enough, well classified surrounding pixels. Fuzzy convolution is thus a contextual filter, with the results generally producing a much smoother image than MLC.

2.2.6 Thresholding

Thresholding is a technique to eliminate poorly classified pixels. MLC returns both a classified image and a distance file in which each pixel records the distance to the class to which that pixel was assigned. Pixel distances within a class are expected to be approximately chi-square distributed. The chi-square distribution is a probability density function ranging from zero to infinity and typically skewed (see Section B.1.5). Most pixels lie close to the class mean and their distance values are near zero. Poorly classified pixels are far from the sample mean and the have large distance values. Plots of the distances converted to chi-square values help identify those pixels that lie far from the sample mean and are the most likely to be misclassified (ERDAS 1999). The MLC classification developed for this analysis was interactively thresholded by examination of output distance histograms. All class distance histograms exhibited unimodal, chi-square shaped curves. A single mode is a positive indication that the signature for that class is properly developed and is not drawing in many pixels of a different land cover type. The threshold value was selected at the inflections point in the tail of the curve. All classes had similar histograms and a single value approximated the break point for all.

2.3 Classification Results L7 Path 169 Row 61 and 62

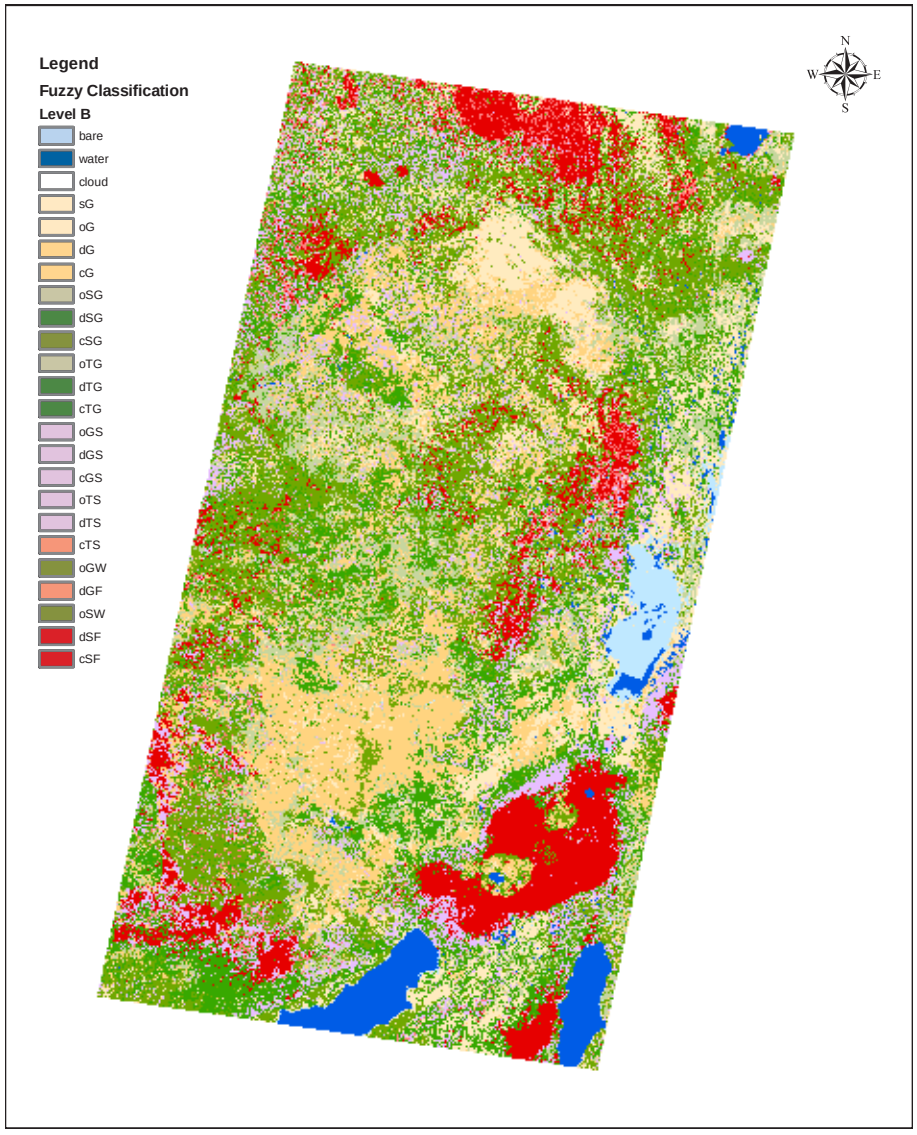


Figure 2.12: Level B supervised fuzzy classification of central-southern Serengeti and Ngorongoro Conservation Area. The legend codes are described in Table 2.6.

A false-color composite of the landsat image mosaic of path 169 rows 61 and 62 is shown in Figure 2.8 followed by the fuzzy classified version of the image in Figure 2.12. A subset of the available reference data was used to seed training areas leaving a majority as validation data for the resulting classification. To this

Table 2.4: Maximum Likelihood Classification accuracy matrix for L7 path 169 rows 61- 62 Vegetation coding at Level 1 with five classes.

	Reference Data						**Accuracy**	
Classification	Bare	Water	Grass	Shrub	Tree	**Total**	Producer's	User's
Bare	6	4	1	0	0	**11**	60.0%	54.6%
Water	0	94	0	0	0	**94**	94.0%	100.6%
Grass	4	1	356	12	27	**400**	90.8%	89.0%
Shrub	0	0	21	1	12	**34**	6.3%	2.9%
Tree	0	1	14	3	42	**60**	51.6%	70.0%
Col Total	**10**	**100**	**392**	**16**	**81**	**599**		

Total Correct: 499 Total Accuracy: 83.31%

number were added additional random reference points for water and bare ground. Table 2.4 gives an accuracy assessment of the thresholded image using straight maximum likelihood classification, at the broadest level (Level 1). Reference classes are given in the columns and the classification results along each row. General accuracy is measured as the percentage of properly classified pixels (sum of the diagonal) relative to the total number of reference points, N (row or column totals). Producer's accuracy is the proportion of correctly classified pixels in a given class relative to the number of reference pixels in that class (Row total). It is a measure of number of reference pixels that were properly classified. The converse, user's accuracy, is the percentage of map pixels that represent the correct class.

Of the major vegetation types, shrubs are the most poorly classified, followed by trees and grasses. The difficulty in identifying shrubs stems from a few factors; first they are infrequently represented in the training data. Out of the 538 ground truth points available for training in the images only 32 are shrublands and 12 of these occur in the highlands, leaving only 20 potential training sites. Shrubs are rare as a dominant vegetation types because those areas that support shrub vegetation usually have a woody canopy cover as well and the trees take precedence in defining the class. As a land cover dominant shrubs most frequently occur discontinuously along drainage lines and thus finding homogeneous patches ideal for training is difficult. Given these circumstances it is not surprising that shrubs are so poorly classified.

Treed areas are generally better classified. Dense and closed forests are eas-

Table 2.5: Maximum Likelihood Classification accuracy matrix for L7 path 169 rows 61-62. Vegetation coding at Level 1 with four classes (shrubs and trees combined)

	Reference Data					**Accuracy**	
Classification	Bare	Water	Grass	Tree	**Row Total**	Producer's	User's
Bare	6	4	1	0	**11**	60.0%	54.6%
Water	0	94	0	0	**94**	94.0%	100.6%
Grass	4	1	346	27	**378**	89.2%	91.5%
Tree	10	1	41	48	**90**	64.0%	53.3%
Col Total	**10**	**100**	**388**	**75**	**599**		

Total Correct: 499 Total Accuracy: 86.21%

ily distinguished by their high infrared reflectance (bands 4 and 5) compared to grasslands, though they can be mistaken for closed tall wet herbaceous vegetation. Woodlands are more difficult as their reflectance properties overlap that of grasslands and shrublands. *Acacia* and *Comiphora* woodlands are challenging in particular as they have very thin canopies with grass and shrub understories. They are best identified by their stippled patterning (alternating trees and grass patches), but this is often mimicked in grasslands, presumably by edaphic factors such as termitaria. An example is shown in Figure 2.10.

Given the poor classification of shrubs, this class was grouped with woodlands to form a more basic classification (Level A) with four classes: bare ground, grass, wooded vegetation (shrubs and trees combined), and water. The resulting classified image is shown in Figure 2.13 and the accuracy matrix is given in Table 2.5.

A classification schema intermediate to Level 1 and Level 2 was developed (Level B). This represents the most detail with reasonable accuracy that could be obtained from this data set using the current methods. Table 2.6 lists the correspondence between the four classification schemes. Importantly, the term "Bushland" is introduced to refer to woody vegetation ranging in stature from shrub to treed ground cover. This usage is broader than the definition of bush given by Pratt and Gwynne (1977) and discarded by Grunblatt et al. (1989).

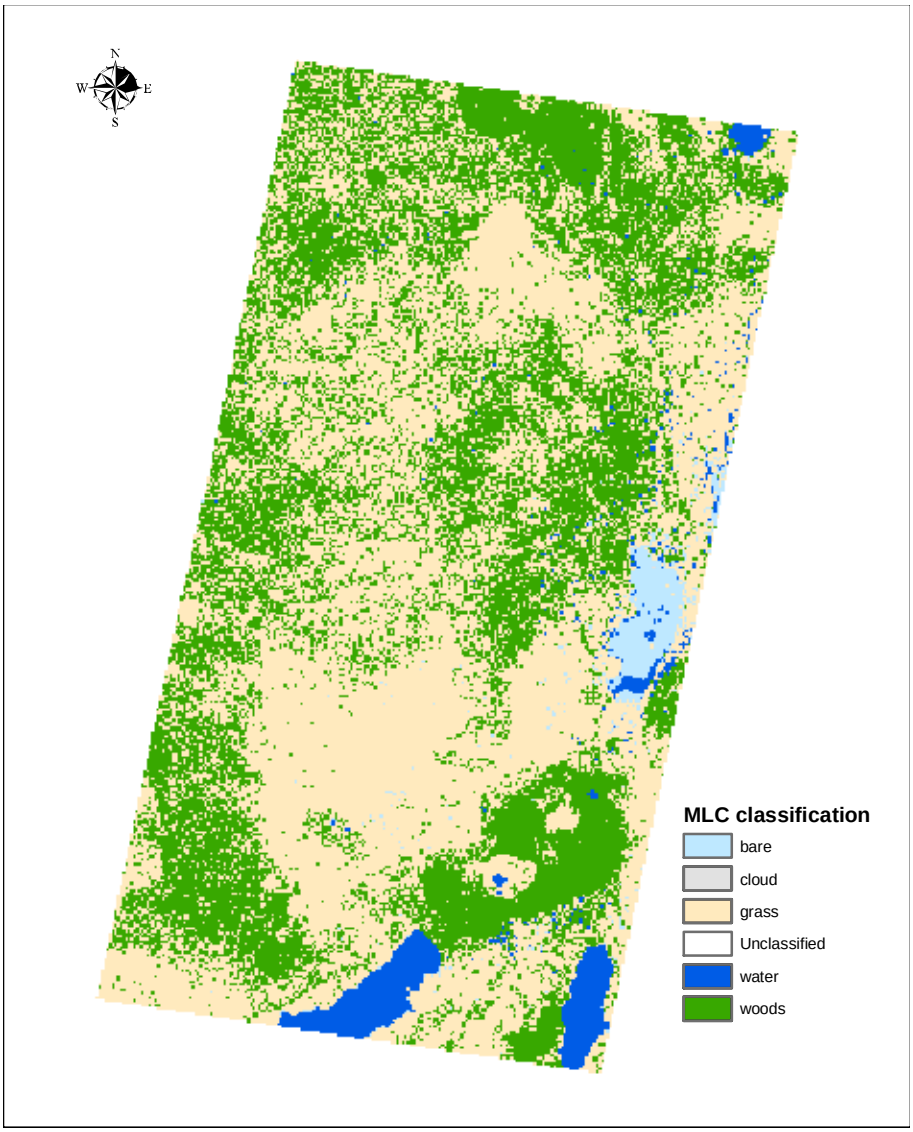


Figure 2.13: Maximum likelihood classification with five classes.

Table 2.6: Vegetation Classification Schemes. The first two column list the Level 1 and Level 2 codes from as proposed by Grunblatt et al. (though without the density code for Level 1). The two columns to the right list modified versions (A and B) that better match what is detectable in the imagery.

Level 1	**Level 2**	**Level A**	**Level B**	**Description**
U	U	U	U	Unclassified
bare	bare	bare	bare	bare
water	water	water	water	water
G	sG	G	s-oG	sparse to open grasslands
G	oG	G	s-oG	sparse to open grasslands
G	dG	G	d-cG	dense to close grasslands
G	cG	G	d-cG	dense to close grasslands
G	sSG	G	s-oBG	sparse-open shrubbed (bushed) grassland
G	oSG	G	s-oBG	sparse-open shrubbed (bushed) grassland
G	dSG	G	d-cBG	dense-closed shrubbed (bushed) grassland
G	cSG	G	d-cBG	dense-closed shrubbed (bushed) grassland
G	sTG	G	s-oBG	sparse-open treed (bushed) grassland
G	oTG	G	s-oBG	sparse-open treed (bushed) grassland
G	dTG	G	d-cBG	dense-closed treed (bushed) grassland
G	cTG	G	d-cBG	dense-closed treed (bushed) grassland
S	sS	B	s-dGB	sparse-dense (grassed) shrubland (bushland)
S	oS	B	s-dGB	sparse-dense (grassed) shrubland (bushland)
S	dS	B	d-cGB	dense-closed (grassed) shrubland (bushland)
S	cS	B	d-cGB	dense-closed (grassed) shrubland (bushland)
S	sGS	B	s-dGB	sparse-dense (grassed) shrubland (bushland)
S	oGS	B	s-dGB	sparse-dense (grassed) shrubland (bushland)
S	dGS	B	s-dGB	sparse-dense (grassed) shrubland (bushland)
S	cGS	B	d-cGB	dense-closed (grassed) shrubland (bushland)
S	sTS	B	s-dGB	sparse-dense (grassed) shrubland (bushland)
S	oTS	B	s-dGB	sparse-dense (grassed) shrubland (bushland)
S	dTS	B	s-dGB	sparse-dense (grassed) shrubland (bushland)
S	cTS	B	d-cGB	dense-closed (grassed) shrubland (bushland)
T	sW	B	s-dGB	sparse-dense (grassed) shrubland (bushland)
T	oW	B	s-dGB	sparse-dense (grassed) shrubland (bushland)
T	dF	B	d-cGB	dense-closed (grassed) shrubland (bushland)
T	cF	B	d-cF	dense to closed forest
T	sGW	B	s-dGB	sparse-dense (grassed) shrubland (bushland)
T	oGW	B	s-dGB	sparse-dense (grassed) shrubland (bushland)
T	dGF	B	d-cGB	dense-closed (grassed) shrubland (bushland)
T	cGF	B	d-cF	dense to closed forest
T	sSW	B	s-dGB	sparse-dense (grassed) shrubland (bushland)
T	oSW	B	s-dGB	sparse-dense (grassed) shrubland (bushland)
T	dSF	B	d-cF	dense to closed forest
T	cSF	B	d-cF	dense to closed forest

2.4 General Vegetation Patterns

Interpretation of roost vegetation benefits from the larger context of landscape patterns which are reviewed briefly here. Explaining the causes of vegetation patterning in response to biotic and abiotic factors is beyond the scope of this thesis. However, many of these factors covary and it is heuristically valuable to examine the contending factors in order to understand the larger picture of habit patterns in the study area. The general trends stem from three major classes of influence:

1. climatic influences, principally precipitation but also temperature and winds.
2. topographic and edaphic factors including soil origin, degree of weathering, topography and mineral composition.
3. disturbance factors, including grazing and fire.

Perhaps the most important point to make about these factors is that they are interrelated, and frequently in such a way as to produce predictable gradients (as with precipitation and temperature with respect to topography) or landscape patterns that are repeated over the landscape and reiterated at different spatial scales (as with the caternary sequence of soils and the patterns of drainage). Many ecological factors in Serengeti covary spatially forming what Whittaker (1975) terms a "complex gradient." Without experimentation it is often difficult to weigh the relative significance each factor has on the coenoclines, i.e. the distribution of organisms along the gradient. However, complex gradients may be beneficial by reducing the complexity of the problem. It may be difficult to resolve elements within a complex gradient but there are fewer gradients to consider. The emphasis in this study is on whether taphocoenoses record faunal response to the dominant ecosystem gradient.

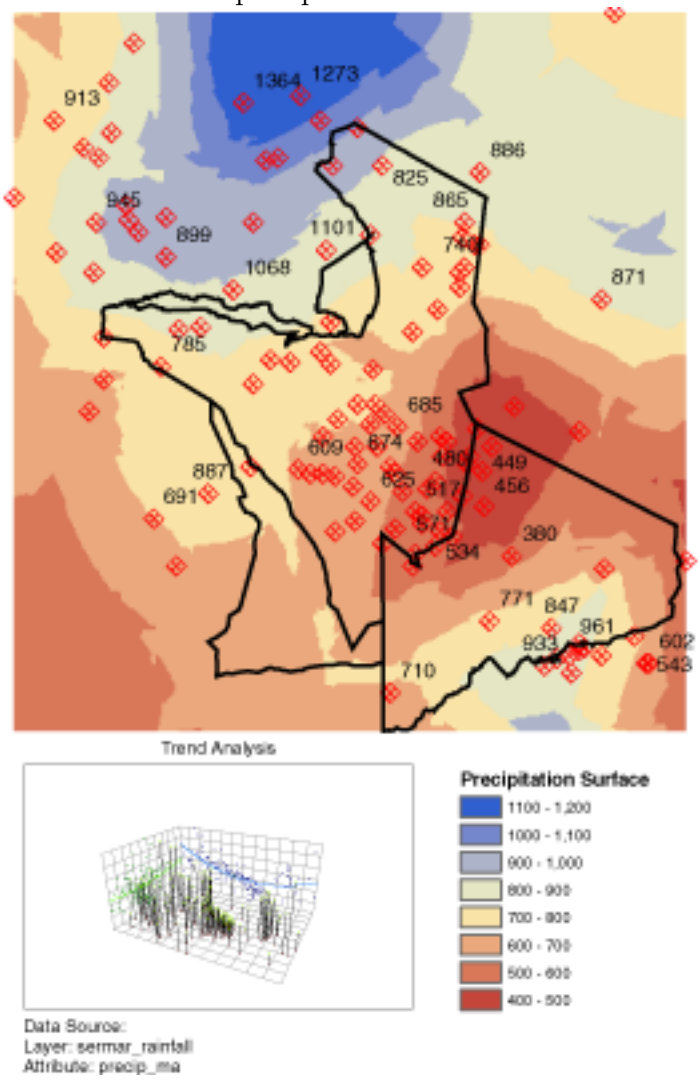
2.4.1 Climate

In general terms the Serengeti ecosystem is a semi-arid to dry sub-humid grassland grading into woodlands and punctuated by marshes, alkaline lakes, and ribbons of dense shrubs, thickets and forests along waterways and drainage lines. The region is traditionally referred to as 'savanna' a catchall term to describe tropical C_4 grassland biomes with varying degrees of woody vegetation cover (Belsky 1990).

Temperatures in Serengeti are relatvely stable. Mean annual temperature ranges between $15 - 23°C$ (Jager 1982; Hay 1976).

Rainfall is the primary form of precipitation in the ecosystem and in the Serengeti it follows a complex pattern. The annual rain cycle commences in November with a peak in December and another more pronounced peak in April (Norton-Griffiths et al. 1975) though there is considerable variability. The rains then taper out in late May and the dry season runs from June through the end of October with July representing the driest month. Rainfall patterns are influenced by the inter-tropical convergence zone (I.T.C.Z.), which moves north and south relative to the equator as the seasons change. The I.T.C.Z. is a zone of low pressure cells created by the merging of trade winds from the northern and southern hemispheres. Its position is influenced by seasonal changes in solar insolation but it lags behind the solstices by approximately five weeks (Norton-Griffiths et al. 1975). At the height of the dry season in July, the I.T.C.Z. is at its most northernly position. During its wanderings the I.T.C.Z. is positioned over the Serengeti in April and October and "differences in rainfall between the two months are related to differences in winds." (Jager 1982, p. 3). During the wet season, the predominant winds come from the southeast. These winds, laden with moisture from the Indian Ocean encounter the Ngorongoro highlands, which induce precipitation and thus cast a rain shadow over the southeastern portion of the Serengeti-Masai Mara ecosystem. The winds shift direction during the dry season, bringing moist air from Lake Victoria and the Congo weather systems in the northwest. The dry season northerlies do not appear to be strongly influenced by the I.T.C.Z. but rather by "the convergence between two high level wind regimes" (Norton-Griffiths et al. 1975, p. 359) that interact with Lake Victoria's own convergence zone to bring rain to the northwestern parts of the ecosystem during the dry season. The result of decreased wet season rainfall in the SE and increased wet and dry season rainfall in the NW is an annual precipitation gradient with a low of approximately 400 mm in the SE ranging up to 1100 or 1200 mm in the northwest as shown in Figure 2.14. The rainfall gradient produces a dramatic effect on the vegetation that is readily visible in the satellite imagery. Plains along the northwestern foot of the Ngorongoro highlands are covered with very short grasslands and thus the underlying substrate penetrates the grass canopy and give the image a deep blue tinge when viewing bands 4R, 5G, 3B. These spatial trends appear in both the wet and dry season though

Figure 2.14: Interpolated surface of mean annual precipitation (MAP) derived by ordinary kriging from the point coverage of rainguages. 3D point plot at bottom shows the NW-SE precipitation trend.



their orientation is slightly more northernly during the dry season. The trend in annual precipitation is augmented by increased variability (Norton-Griffiths et al. 1975). The north and northwest experience a bimodal regime, typical of equatorial regions, with strong peaks in December and April; this degrades into a unimodal pattern in the southeast (December). Thus precipitation trends from a highly variable, unimodal, low precipitation regime in the SE to a less variable, bimodal moderate rainfall regime in the NW (Jager 1982; Norton-Griffiths et al. 1975). The general effect of climate on vegetation structure in the African tropics is for grassland dominated ecosystems, such as savanna, to exist in arid and sub arid climate regimes (ca. 400-700 mm mean annual rainfall) from which they grade into woodland in more humid climes where trees begin to shade out grasses in the understory, and thorn scrub and dwarf shrub habitats at the arid extreme (Belsky 1990, 1995; Pratt and Gwynne 1977; Whittaker 1975). Climate provides the broad conditions that determine biome level habitat differences (Andrews and O'Brien 2000; O'Brien 1993; Whittaker 1975). Operating beneath this umbrella are local topographic and soil characteristics that interact with disturbance factors such as fire and grazing to determine the specific tree/grass ratio that appears at a given place and time.

2.4.2 Topography and soils

Already, we have seen that local topography has an important impact on precipitation through the creation of rainshadows. The major topographic features in the region include the Ngorongoro highlands to the southeast, which are perched at the edge of the rift valley further southeast, and a series of low broad hills running along the eastern flank of the ecosystem called the Gol mountains. Several smaller hill systems punctuate the terrain. A slope map of the region (see Figure 2.3c) reveals a roughly north-south divide in the amount of topographic relief, with the southern plains comprising a gently undulating terrain that gives way to more a more dissected terrain to the north. Here we see the influence of precipitation on terrain, as higher rainfall regimes to the north cause greater runoff and stream erosion leading to the more dissected terrain (Jager 1982). Topography's most blatant influence on vegetation structure is the dendritic patterns of riparian vegetation. The diffusion and retention of moisture associated with perennial rivers as well as seasonal drainages supports strong ecotones between riparian habitats

and their surroundings, and allows woody vegetation to penetrate otherwise strictly grassland habitats on the plains.

Hydrodynamic activity in conjunction with gravity creates local variability in soil characteristics along the repeated pattern of hills and valleys formed by drainage lines. This edaphic pattern – termed a catena (Milne 1935; Pratt and Gwynne 1977) – influences the vegetation structure and vegetation communities that occur along its profile (Herlocker 1974; McNaughton 1983; Vesey-Fitzgerald 1973). Well drained eluvial soils tend to dominate hill tops giving way to finer textured, shallow illuvial soils on hill slopes and deeper, poorly drained, fine textured soils on lower slopes and valley bottoms (Jager 1982; de Wit 1978). Local caternary patterns influence species composition (McNaughton 1983; McNaughton and Banyikwa 1995) and vegetation structure as soil moisture availability changes with soil texture (Jager 1982). The specific physiognomy of the vegetation in a given caternary sequence depends upon the larger context. Among the more dissected terrain (steeper caternary sequences) and higher precipitation in the north of the park, well-drained ridge top soils tend to host woodlands and grassed woodlands. Open grasslands dominate the ridge slopes and valley margins then give way to the dense woody vegetation and forests along the rivers (Jager 1982). In the plains, a more undulating topography supports grasslands along ridge tops and ridge slopes which grade into riparian shrubs and woodlands along valley bottoms or at the base of hills.

Interactions between climate and topography create gradients in soil depth and soil texture. The parent materials underlying the Serengeti grasslands derive from pyroclastic natrocarbonatites expelled by Pleistocene eruptions of volcanoes in the Ngorongoro highlands (Dawson 1964; Hay 1976). Low mean annual precipitation and its concentration during a short interval leads to a ustic soil moisture regime – one in which the soils are wet continuously for at least 90 days out of the year then allowed to dry completely. The repeated cycle of wetting and drying causes soluble soil minerals to be leached from the soil surface and subsurface, then precipitated at depth creating petrolithic horizons that may inhibit root growth in shallow soils (de Wit 1978). The depth at which these "hard pans" occur depends on soil texture, the amount of precipitation and temperature. Temperature regimes in the Serengeti are relatively stable, so variability in the depth and continuity of petrolithic horizons depend primarily on the first two factors. Low precipitation

on the grassy plains in the south and eastern parts of the ecosystem help produce a nearly continuous petrocalcic horizon at shallow depth, since evaporation quickly overtakes soil moisture (Norton-Griffiths et al. 1975; de Wit 1978). This horizon becomes less continuous and occurs at greater depth as one travels north and west, away from the rain shadows and toward the higher, and less seasonal rainfall regimes.

A similar phenomenon occurs along hill tops in the northern region of the Serengeti Park. Here petroplinthic horizons form under hill and ridge crests though at much greater depths than in the grasslands (Jager 1982) and often in conjunction with pebbles and coarse material that are slightly more durable to erosion. As streams dissect the terrain the petroplinthic layers are exposed beneath the ridge tops and form a distinct boundary between ridge top and upper slopes called the "seepage line," because of the tendency for water filtering through the well drained ridge top soils to encounter the hard pan and drain laterally over it and out onto upper ridge slopes (Herlocker 1976; Jager 1982). Seepage lines form a distinct landmark feature in aerial photographs and satellite imagery of the northern Serengeti Park as seen in Figure 2.15. Seepage lines are very useful for delineating between woodland and treed grassland along ridge tops, and grasslands occurring along slopes. Well drained soils along ridge crests support woody vegetation because water penetrates further and increases soil moisture availability. Finer textured soils downslope receive water but do not retain it as well. Thus slopes host grasslands. The recurring dendritic pattern of seepage lines resembles that described and illustrated by Michelmore (1939).

Mineral concentrations also track the dominant NW-SE gradient since precipitation leaches soluble minerals from soils. Low precipitation regions closest to the eruptive origin of the parent material are the most alkaline and saline (de Wit 1978). Belsky (1990, 1995) argues that these mineral concentrations (in conjunction with soil depth) are the most important proximal cause excluding woody growth on the Serengeti plains.

2.4.3 Disturbance

Fire, burrowing, browsing and grazing play important roles in determining landscape structure. Infrequent fires fueled by greater ground litter are generally hotter and more destructive to woody vegetation while more frequent, cooler burns are en-

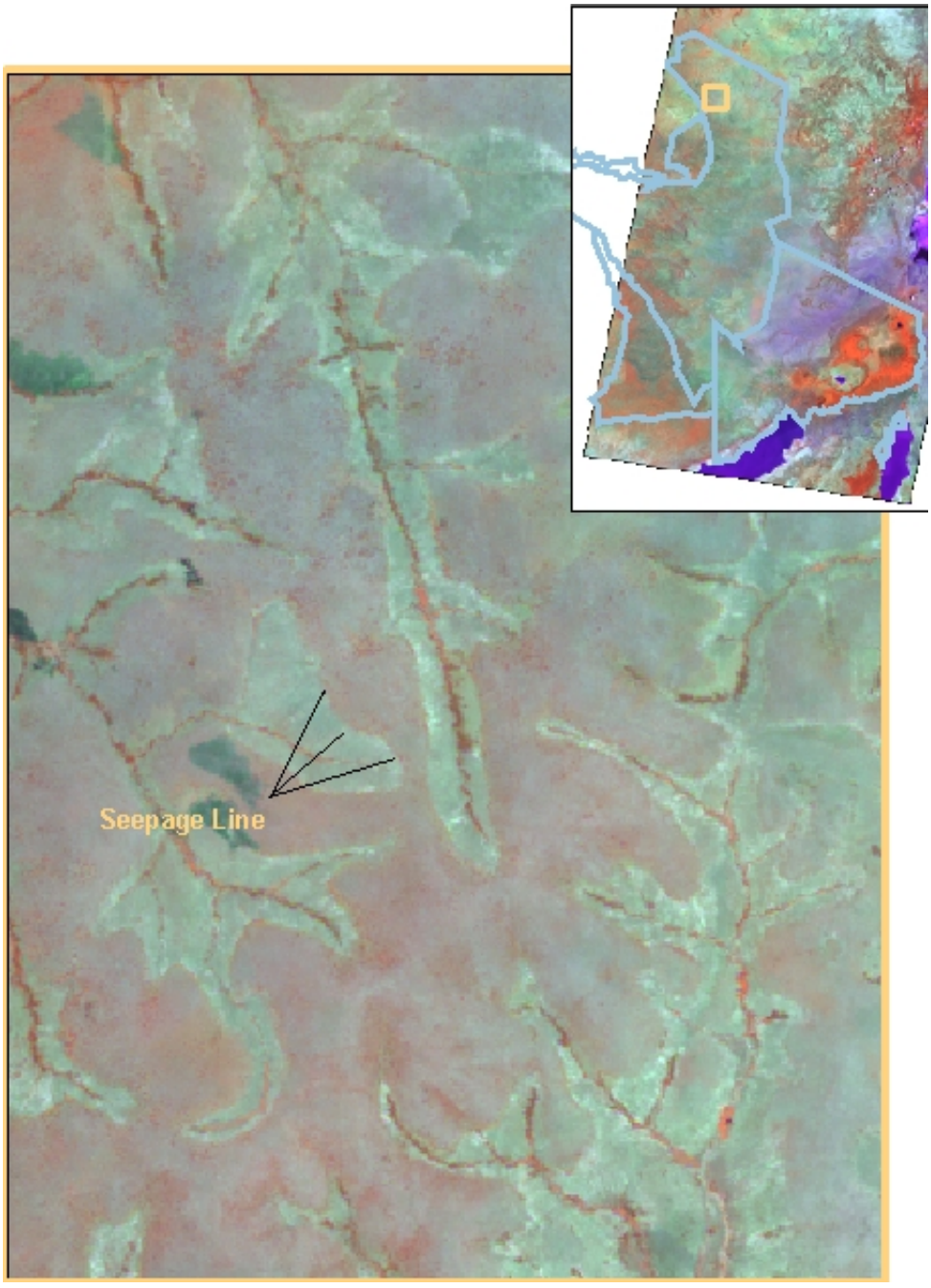


Figure 2.15: False color landsat 7 insert demonstrating seepage lines. Bands as in Figure 2.8.

dured by fire tolerant woody plant species (Frost and Robertson 1987). Burn scars in various stages of recovery are evident throughout the satellite imagery and create extensive variability in the reflectance properties of different land cover types. In the north, burning down ridge slopes also acts to accentuate the ecotonal boundaries between slope grasslands and evergreen forest along river margins (Jager 1982). The impact of fires in the northern part of the ecosystem is inversely proportional to the density of the wildebeest population. The resurgence of wildebeest following the rinderpest pandemic of the 1960's greatly reduced standing grass biomass and thus the amount of dry litter to fuel fires (Norton-Griffiths 1979).

Burrowing animals ranging in size from termites, to warthogs, influence the spatial patterning of soil properties (mineral composition, texture, moisture) through the act of creating their burrows (Belsky 1995; Jager 1982). And on a larger scale grazing plays an important role in the maintenance of grasslands as such. Cropping of grasses induces them to grow anew, in turn prompting more grazing and resulting in very high above ground plant productivity (McNaughton and Banyikwa 1995). Large ungulates break soil crusts and facilitate soil moisture infiltration rates, increasing soil moisture availability (de Wit 1978). Also, ungulates replenish soil nutrients by depositing dung and urine (McNaughton 1983). All these factors facilitate a very productive grass ecosystem, raising the question of whether grasslands would be the climax vegetation in the absence of grazing (Bell 1982). Exclosure experiments support the idea that grasslands would continue (at least over the short term) but with a dramatic difference in grass height, species composition, and species diversity. Similarly, browsing mammals such as giraffe and especially elephants influence woody plant distributions (Dublin et al. 1990).

The compound effect of these interacting "disturbance" factors is not completely understood, but in conjunction with historical evidence, they indicate fluctuations in the amount of woody vegetation present in the park (Dublin et al. 1990; Sinclair 1995a). Fire, and animal disturbance are clearly important to determining the plant community structure, and have an influence on the mosaic structure of wooded grasslands (Cole 1986). However, these factors seem to be secondary determinants of woody/grass ratios compared with more pervasive climatic factors – such as precipitation, temperature, winds – and edaphic factors including soil moisture availability, mineral composition, texture (Belsky 1990, 1995; Coughenour and Ellis 1993).

2.5 Vegetation Patterns at the Individual Roosts

The following sections summarize the land cover, hydrology and soil characteristics around the eight analyzed roosting sites. The verbal descriptions are derived from analysis of the GIS coverages in an area buffered by 1.5 km around the roost locations. The roosts are in approximate order from north to south and east to west, thus roughly following the precipitation gradient. Figure 2.16 shows the distribution of roosting sites along with precipitation and the Level A maximum likelihood classification.

2.5.1 Roost 24 – Gol Kopjes

Roost 24 is situated at Gol Kopjes in the southeastern corner of the Serengeti National Park, amidst the short- to mid-grass plains. The Gol Kopje complex is a small archipelago of kopjes (granitic outcroppings) surrounded in all directions by expanses of grassy plains. The roost is a cavity formed in a vertical fissure in the kopjes. A barn owl was sighted roosting in residence and the floor of the roost was littered with many fresh pellets and a dense surface assemblage of bones.

Gol receives an estimated 527 mm average rainfall in a year. As a result, the terrain is not strongly dissected, but instead has a gently undulated topography with slope values ranging between 0.5 -4.33% and a mean of 1%. The most common soil units include loamy soils of ridges and the gently undulating plain, with a petrocalcic horizon deeper than 50 cm or without a petrocalcic horizon. The absence of a calcified hardpan is relevant to the distribution of burrowing genera such as *Gerbillus*, *Tatera* and *Steatomys*. While plant species diversity may in some places be quite high due to complex interactions of grazing and fire (McNaughton and Banyikwa 1995), the physiognomic provinces around Gol are very homogeneous. The larger kopjes at Gol and at the other kopjes nearby host tree and shrub vegetation including species of *Ficus* and *Euphorbea*, accounting for the fractional percent of a hectare that is classified as woody vegetation in the analysis radius, but the remaining area is herbaceous vegetation with some dwarf shrubs mixed in the herb layer. No perennial surface water is present near the roost, only seasonally flooded drainage lines.

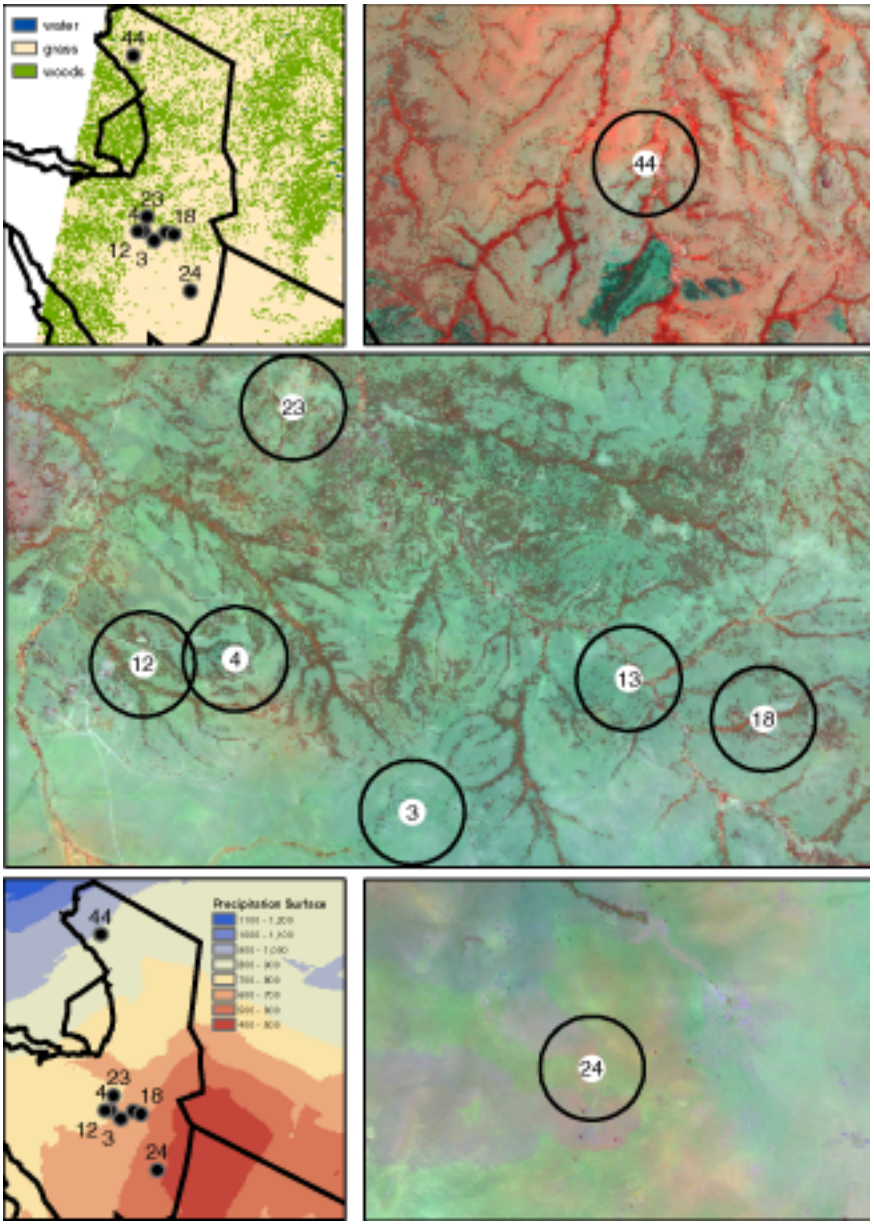


Figure 2.16: Distribution of analyzed roost sites. The upper left pane shows the roosts against a background map of woody vegetation, and against precipitation in the lower left. Remaining panes show close-ups of roosts outlined by 1.5 km buffer against a landsat background. The background includes a semi-transparent overlay of the vegetation classification to highlight woody vegetation.

2.5.2 Roost 3 – Wandamu River Kopjes

Six roosts cluster within 10 km of each other in the area around Seronera at the boundary between the grasslands to the south and the treed grasslands and grassed woodlands to the north and west. Roost 3 is the southernmost in this cluster. Roost 3 occurs in a small kopje with a tall vertical fissure. A barn owl was observed roosting and nesting on a ledge in the side of the fissure approximately four meters above the ground. Bones covered the floor of the fissure over an area of approximately a square meter.

Roost 3 is surrounded by mid-height grasslands intruded by seasonal rivers flanked with *Acacia xanthophloea* woodlands and an understory of shrubs. The smaller tributaries and drainages are filled with dense shrub and herbaceous vegetation. The most proximal of these is a headwater of the Wandamu River. The larger and perennial, Nyamara River lies about three kilometers to the east.

Soils in the analysis radius are deep and loamy along ridge tops fining into deep clayey soils on the slopes and clayey bottomland soils lining drainages. A petrocalcic horizon underlies parts of the area but generally at greater depth than on the short grass plains to the south. The mean annual precipitation is 679 mm producing a slightly more dissected terrain with low hills and wide valleys and a more pronounced caternary sequence in the region just 2-3 km to the north, however the area within the analysis radius is very level terrain. Slope values range from 0.03 - 2.21%. Hilltops are dotted with low trees and shrubs, grading into grasslands along the bottom of hill slopes and then into denser woody vegetation along the drainage lines.

2.5.3 Roost 13 - Turner Spring Kopjes

The Turner Springs kopje complex is situated 16 km east of Seronera near the banks of the Ngare Nanyuki River. Roost 13 is inside a narrow slanting fissure in the main kopje. A hyrax colony currently occupies the kopje with no indication of an owl or fresh pellets. Dense concentrations of micromammal bones were discovered in the base of the fissure under a layer of hyrax pellets. The region is generally treed grassland grading into open woodland, but the woodland is very thin and the trees uniformly short statured with few exceeding 2 meters. Denser woody vegetation occurs along the river and drainage lines. Charred trees and grass are

in evidence.

Roost 13 receives 655 mm average precipitation per annum and is situated in more dissected terrain of alternating valleys and ridges. The kopje is situated on a gentle 3-4% slope leading northeast down to the river and southeast to a small but densely vegetated drainage line. Most of the analysis area is underlain by deep clay-loam soils. The average slope in the analysis area is 3% with little variation. The kopje itself hosts dense shrub and tree vegetation. The Ngare Nanyuki is a perennial river and one of the larger tributaries to the Grumeti via the Orangi.

2.5.4 Roost 18 – Ngare Nanyuki

Across the Ngare Nanyuki river from roost 13 squats a complex of kopjes on the slopes leading down to a tributary of the Ngare Nanyuki. The collection at roost 18 comes from an open space about 2 m^2 at the base of a large rock and beneath a short bushy tree. Bones were concentrated near the rock and many are blackened and appear to have been burned. Charred grass tufts and branches are also evident. No owls were observed though one fresh pellet of indeterminate origin was recovered.

The vegetation surrounding roost 18 is similar to that around roost 13, generally treed grassland, but with a higher proportion of dense riparian vegetation in the immediate vicinity of the roost and cutting through the center of the analysis area. Like roost 13, the soils are deep or very deep and occur on sloping terrain along with a substantial component of bottomland soils associated with tributaries and drainages. The roost itself is on a hillslope of roughly 3% slope and average slope over the analysis area is 2%. The tributary running just to the north of the roost is seasonally flowing but the perennial Ngare Nanyuki is less than two kilometers to the southwest.

2.5.5 Roost 4 – SRI-Oloserian

Just outside the entrance to the main facilities of the Serengeti Research Center is a small kopje that is home to at least one nesting pair of barn owls. The kopje actually has at least three or four roosting and nesting sites. Two are separate, and the third is at the confluence of two vertical fissures that open in different directions. Numerous fresh pellets and dense bone concentrations were found at each sub-roost.

The SRI roost is among a large complex of kopjes and low buildings that make up the research institute, all of which are situated in a mosaic of open grasslands and woodlands. The SRC headquarters and residences are all within the analysis area and commensal species may influence the assemblage. Patches of weathered granites and gneisses forming sandy soils surround many of the kopjes but the majority of the substrate comprises deep clay-loam soils. The topography is made up of rolling hills and valleys weakly dissected with an average slope of 3% and maximum slope of 7%. The SRC sits at 1536 meters elevation and receives just over 700 mm of rainfall. Several small drainages pass through the analysis area with associated riparian woodlands along their banks and some woodland stands extending out onto ridge tops. Dense shrubs and trees vegetate the numerous kopjes. Gravel roads transect much of this area and owls were observed flighting from the road where they may prefer to hunt crossing prey.

2.5.6 Roost 12 – Seronera

At least three spotted eagle owls were found roosting on rocks and trees on the kopje between the park headquarters at Seronera and the Serengeti Research Center. Fresh pellets and bone detritus were collected over a wide area beneath the trees. The pellets are longer and thinner than barn owl pellets and generally more grey in color.

Roost 12 lies on the flanks of a low ridge between two small, seasonal drainages. The terrain slopes at just 2% and is dotted with treed grasslands, grading into riparian woodlands. The density of drainages and woody vegetation along ridge tops makes this the roost with the greatest amount of woody land cover, though little of it is at very great density. The park headquarters and residences are within the analysis area and commensal species are an issue here as they are at roost 4. Also similar to roost 4 is the presence of gravel roads transecting the analysis area. Mean annual precipitation is 708 mm at an elevation of 1509 meters.

2.5.7 Roost 23 – Pipeline Kopje

Heading northwest from Seronera through patches of dense bushland and woodland a track follows the pipeline that brings water from the springs at Bolagonga to the park headquarters and research institute. Roost 23 is in one of a complex of

kopjes along this track. Pellets and bone detritus were collected from beneath two trees about 30 meters apart. Both locations were nestled among the rocks of the kopje. At first only fresh pellets were visible on the surface, but closer inspection revealed dense bone concentrations mixed with litter and sub-surface humus especially where rocks channeled the material into a confined area. No owls were observed but fresh pellets of the color and dimension of eagle owl pellets from roost 12 are recorded.

The terrain surrounding roost 23 is more topographically complex and dissected than the southern roosts on or near the plains. The kopje hosting roost 12 is at the base of a long slope at a 3% grade that flattens out onto a large, grassy plain to the north. The southern portion of the analysis area is a topographically complex sequence of small hills with slope values ranging up to 23%. A dense mosaic of bushland and low open woodland occupy this southern region. Dense woody vegetation occurs along a seasonal drainage to the west. No persistent surface water is present but the perennial Ngare Nanyuki lies two kilometers to the east and north.

2.5.8 Roost 44 – Kogatende

Roost 44 is found at the northern end of the park among the hilly terrain of the northern extension, south of the Mara River. The roost occurs inside the hollowed trunk of a dead tree that is situated on the lower, grassy slopes beneath a ridge and bordering dense gallery forest that line the Nyanjogo River, a tributary of the Mara River system. Mean annual precipitation is approximately 850 mm. The Mara river system is one of the few areas in the study area where lowland, dense canopy evergreen forests are present. The dense forests occur along the alluvial banks of the rivers. Relic stands also occur in small patches on deep, well drained ridge-top soils or at spring heads, implying that perhaps forest biomes were once more widespread (Herlocker 1976). Near roost 44 the ecotonal transition between gallery forest and lower slope grasslands is abrupt, and it is believed that fire plays an important role in establishing this pattern (Jager 1982; Herlocker 1976). Fire, however, augments physiognomic patterns induced by edaphic factors of the soil catena. In this moderately dissected region of hills and valleys, the ridges are covered with coarse textured soils that are well drained and underlain by a plinthite horizon formed from the leaching of iron. Water is able to infiltrate

the soils down to the plinthite then travel laterally over it and drain where the plinthite is exposed by erosion along upper hill slopes forming seepage lines that are clearly visible in aerial photographs and satellite imagery (Jager 1982). The seepage lines mark the boundary between treed and shrubbed vegetation growing on the well drained ridge-tops versus the grasslands covering slopes that start below the seepage line and are underlain by more poorly drained illuvial soils. The more dissected terrain means greater spatial heterogeneity in slope and soil characteristics leading to greater heterogeneity in plant physiognomy. The region surrounding roost 44 hosts treed and shrubbed grasslands grading into grassed woodlands along the ridge slopes, treed grasslands on upper ridge slopes grading into grasslands on lower slopes and then abruptly into dense evergreen forest at the river margin. The river itself is perennial and hosts patches of dense wet grasslands and marshes. Roost 44 is therefore situated in the most spatially and ecologically heterogeneous environment.

2.6 Summary and Conclusions

Satellite imagery in conjunction with ancillary data were compiled in a GIS and used to map woody plant vegetation in the Serengeti ecosystem. The distributions of woody and herbaceous plant cover in the resulting map follow familiar trends and patterns. These patterns result from the influences of climate, topography and disturbances. 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 with the lowest mean annual precipitation (ca 400 mm) and a more unimodal pattern of 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. Rainfall influences the grade of the caternary sequences by causing a more dissected terrain in the north than in the south. Soil substrates follow the same gradient. Much of the southern Serengeti ecosystem is blanketed by natrocarbonatitic ash falls from volcanoes in the Ngorongoro highlands. The pattern of ashfall follows from 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. Augmenting

the compound gradient, are the local topographical or caternary gradients. These also influence soil texture, mineral composition and hence soil moisture availability. The caternary gradients are linked in part to the precipitation gradient as the topography becomes more dissected in areas with higher rainfall. Disturbance factors such as fire, grazing, browsing and burrowing have important local influence on plant species composition and community structure, but are generally of secondary importance relative to climatic and edaphic factors.

Chapter 3

Fauna

3.1 Introduction

Beginning with the first aerial surveys (Grzimek and Grzimek 1960; Talbot and Stewart 1974) interest in Serengeti biodiversity has led to detailed study of most large mammal species. A survey of the literature finds studies on wildebeest (Talbot and Talbot 1963; Watson 1967; Murray 1995), buffalo (Sinclair 1977), elephant (Dublin and Douglas-Hamilton 1987), impala (Jarman and Jarman 1973), oribi (Mduma 1995), topi (Duncan 1975), lions (Bertram 1975; Hanby and Bygott 1979; Schaller 1972; Scheel and Packer 1995), leopard (Bertram 1974), cheetah (Schaller 1968), hyena (Kruuk 1972), jackals (Wyman 1967), wild dogs (Frame and Frame 1976; Malcolm and van Lawick 1975), resident herbivores (such as topi, kongoni, giraffe, warthog), and others (Sinclair 1995b).

By comparison, Serengeti small mammal ecology and biodiversity have received far less attention. Fortunately there is sufficient research on East African small mammals outside Serengeti to afford a reasonable assessment of the autecology of the various taxa. The bulk of this work was conducted during ecological surveys of the 1960's and '70's (Delany 1972, 1975, 1986; Kingdon 1974; Misonne and Verschuren 1966; Vesey-Fitzgerald 1966; Hubbard 1972; Andrews et al. 1975). At last count there were approximately 2015 species in the Rodentia, 925 species of bats, and 428 species of Insectivora (Wilson and Reeder 1993) and each of these is represented by numerous regional variants or races that are frequently shifting in and out of species rank as a result of molecular and morphometric investigation.

Taphonomic assemblages, such as those accumulated by owls, are a potentially

excellent resource for tracking species distributions and relative abundances (Glue 1971; Avery et al. 2002). The utility of predator assemblages for this type of research is limited in part by the challenge of identifying species from partially preserved skeletal remains. Museum reference collections provide the best resource for the identification of skulls and teeth, but they have several limitations. Not least is that the best collections are immobile and often housed far from where field research is conducted. Diagnosis requires large series of animals in order to assess variability within species, and even the most complete reference collections of African rodents and shrews lack a full representation of the species that occur in East Africa. Thus there is no single place where one can simultaneously view all the species of East African rodents or shrews. For these reasons, taxonomic diagnosis of small mammals relies in large part on diagnostic keys. Several keys cover African rodents and insectivores, including the Smithsonian key edited by Meester and Setzer (1971) or those included with regional studies (Delany 1975; Foster and Duff-Mackay 1966; Smithers 1971). There is also a digital key for Tanzania mammals created by Rogers and Stanley (2003). These keys, while helpful are unsatisfactory for use with fragmented taphonomic material. Two papers specifically address this limitation, but focus on the South African faunas (Coetzee 1972; Davis 1965). A thorough key is needed for the identification of small mammals in taphonomic and paleontological assemblages.

The remainder of the chapter describes how specimens were collected, how they were identified and presents the fauna and their abundances as the basic results. Brief summaries of the different taxa are provided to familiarize the reader with the systematics and habitat proclivities of the animals under consideration. A preliminary key, derived from published materials is presented in section 3.2. Additional notes on diagnostic traits for the different taxa are given in their summaries. The discussion of the fauna begins by comparing the fauna recovered in this study against previous reports on Serengeti small mammals published in the literature, including one previous analysis of owl pellets by Laurie (1971). From there I turn to examining how the different genera are distributed within the study area and the patterns of relative abundances across the different roosting sites.

Table 3.1: Summary of the roosts selected for analysis. Where owls were witnessed at the roost, the species is listed. Geographical coordinates are given in decimal degrees.

Roost ID	Collection ID	Collection Date	Owl Species	Latitude (dd)	Longitude (dd)
12	88	02-Dec-98	Bubo africanus	-2.43268	34.82940
23	90	06-Jan-99		-2.36593	34.86813
18	92	30-Dec-98		-2.44666	34.98977
44	93	18-Sep-99		-1.64596	34.80920
3	94	26-Oct-98	Tyto alba	-2.47109	34.89905
13	95	19-Dec-98		-2.43625	34.95496
4	146	01-Nov-98	Tyto alba	-2.43132	34.85326
24	158	09-Jan-99	Tyto alba	-2.69849	35.06356

3.2 Methods

One hundred eighty-nine collections were made from 61 roosting sites in and around the Serengeti National Park. Roost locations were recorded on a Garmin XL12 GPS receiver and given sequential numbers (roost ID). Collections made from each roosting site were entered into a database. Roosts may have multiple collections (and hence Collection IDs) to designate samples made on different dates and to distinguish fresh pellet samples from samples of bone detritus. A subset of eight roosts was selected for faunal analysis. The roosts were selected based on several factors. Sample size was an important criteria, as was distribution along the complex gradient. It was also desirable to include roosts from both owl species in order to determine whether there were differences between them. The resulting test set included one dry grassland roost (roost 24), one moist shrub grassland roost (3), one moist (treed) grassland roost bordering evergreen forest (roost 44) and four woodland roosts (4, 12, 13, 18, 23). All the selected roosts have reasonably large sample sizes except for roost 12, which was selected by virtue of being an eagle owl roost (along with roosts 18 and 23 though these are inferred from indirect evidence such as roost type). Roost 12 also provides a good foil to roost 4 as the two are just three kilometers apart and in very similar habitats. Table 3.1 provides summary information on the analyzed roosts.

The geographical distribution of the roosts is shown in Figure 3.1. Roost 24 is

located to the south, in the mid-grass plains. Roost 44 is located in the northern extension along the tributaries of the Mara River system. The remaining six roosts are clustered near Seronera in roughly a cross pattern. Roost 23 to the north is firmly established in the shrubbed woodlands. Opposite this is roost 3 located to the south, in the grasslands, but just at the border between the transition from grasslands to woodlands. Roosts 13 and 18 are to the east in the catchment of the Ngare Nanyuki River. The remaining two roosts, 4 and 12, are in the vicinity of the research institute and park headquarters. This area is a woodland grassland mosaic.

Bulk samples of the bone detritus below each roost were made from surface scrapes and stored, separately from the fresh pellets, in sealed plastic bags. Samples were frozen for two weeks prior to analysis to kill invertebrates. The loose bone assemblages, or ossuaries, were picked and sorted with the aid of a 4-10x magnifying lens. Osteological material was sorted into six classes:

1. maxillae and maxillary fragments, including skulls
2. mandibles and mandibular fragments
3. isolated cheek teeth
4. edentulous mandibles and maxillae
5. isolated incisors
6. auditory bullae
7. post-cranial bones

All mandibles, maxillae and isolated check teeth were affixed to nickel plated straight pins with Duco Cement (TM). Adhesive labels documenting roost site, collection date and collection type (pellet or ossuary) were then attached to the pins. Each sorted collection was processed, stored and transported separately to avoid any risk of mixing samples. Identifications were made on the pinned mandibles, maxillae and isolated molars. Post-cranial specimens, isolated incisors, bullae and edentulous jaws are not easily diagnosed to genus and were not analyzed.

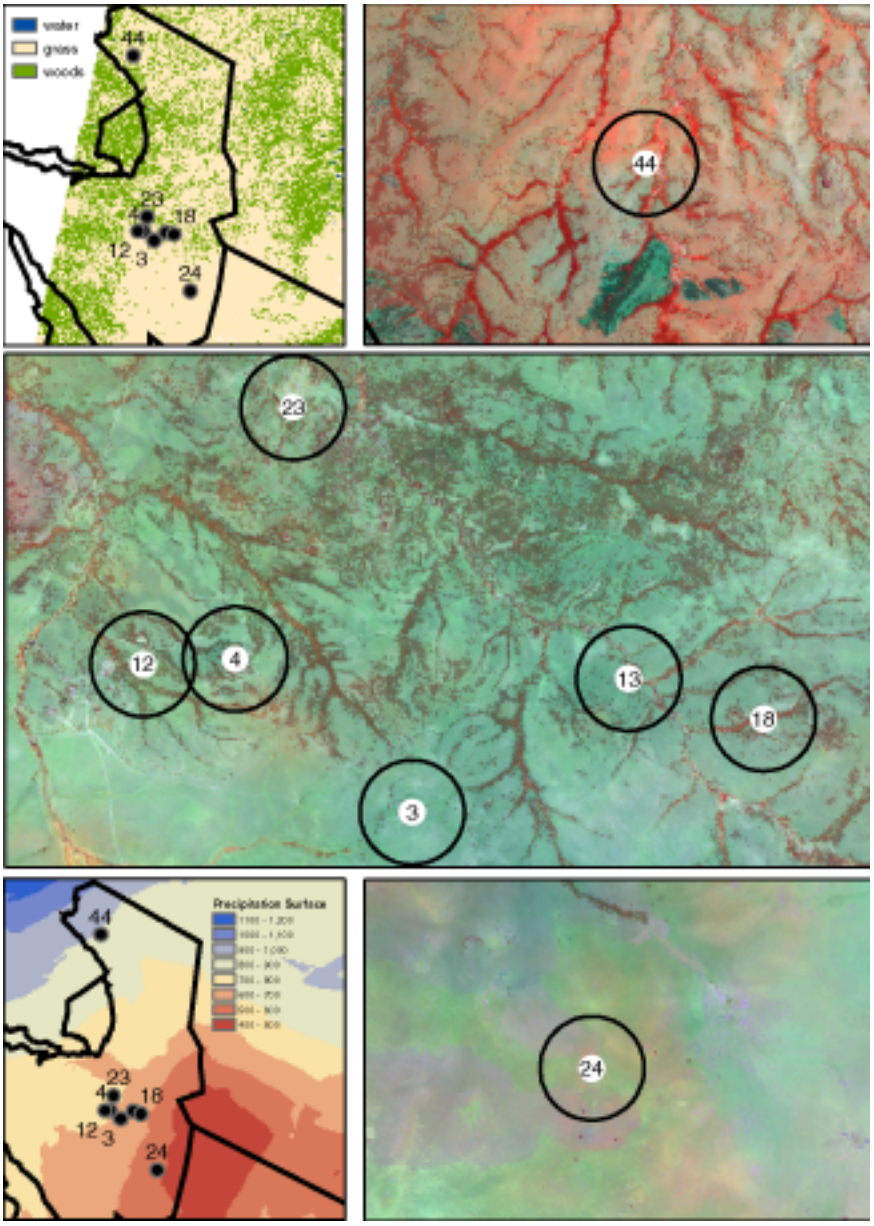


Figure 3.1: Distribution of analyzed roost sites. The upper left pane shows the roosts against a background map of woody vegetation, and against precipitation in the lower left. Remaining panes show close-ups of roosts outlined by 1.5 km buffer against a landsat background. The background includes a semi-transparent overlay of the vegetation classification to highlight woody vegetation.

3.2.1 Identification

Specimens were iteratively sorted into taxonomic categories starting from Order and working down to Subfamily with the aid of printed and digital identification keys (Coetzee 1972; Davis 1965; Foster and Duff-Mackay 1966; Rogers and Stanley 2003; Delany 1975). Final taxonomic assignments were made by comparison with collections at the American Museum of Natural History (AMNH); Field Museum, Chicago (FMNH); National Museum of Natural History, Smithsonian Institution (NMNH) and the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK).

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). Separate identification criteria were developed for upper and lower dentitions and subsequently merged for analysis. Thus *maxillae* assigned to *Thallomys* are presumed to represent the same species as the *mandibles* assigned to *Thallomys.* Shrews were identified only by maxillary specimens as the mandibles and lower dentition between some genera cannot be distinguished readily.

The analysis is conducted at the generic level. For many groups, taxa could be delimited to species or groups of species. However, genera were chosen for analysis, because they are the lowest common ranking at which all specimens can be identified accurately and efficiently from discrete diagnostic criteria. An exception is made for two forms of *Mus*, since maxillae and mandibles were easily diagnosed for two forms in this genus. Figure 3.2 diagrams the decision tree used to diagnose genera. The tree is based on the key developed by Rogers and Stanley (2003) and supplemented by cranio-dental characters from other published sources and museum collections.

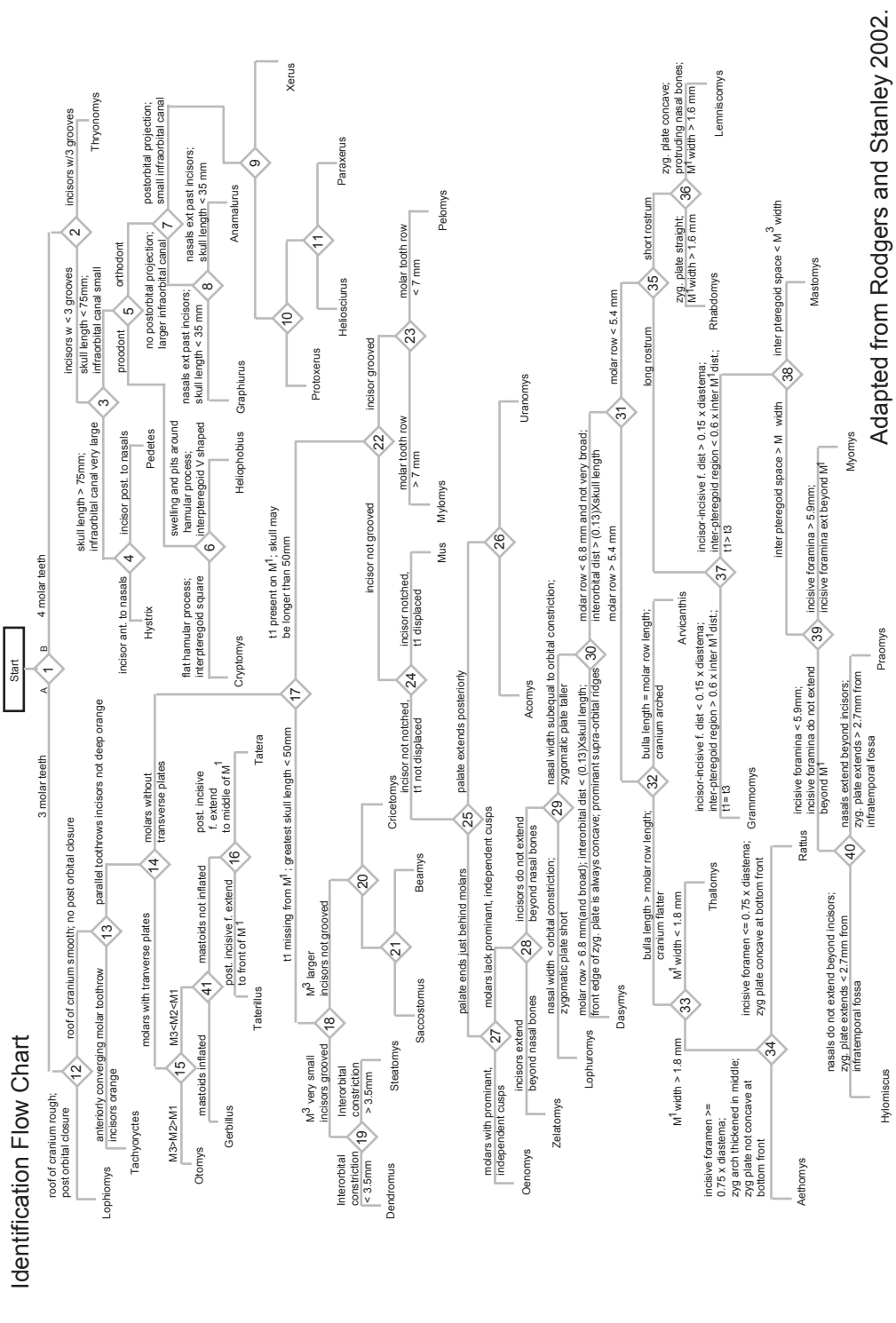
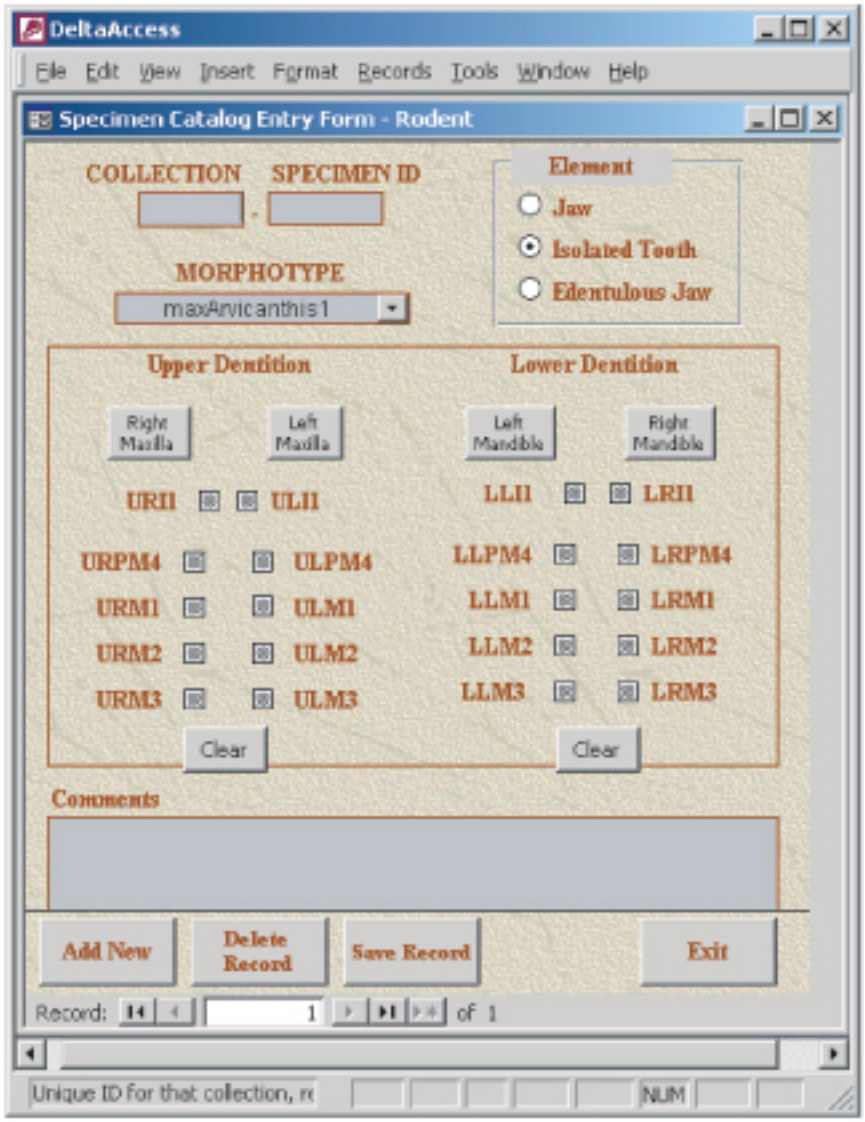


Figure 3.2: Identification Flow Chart

Figure 3.3: Example rodent specimen data entry form. Check boxes track the presence/absence of individual teeth and a separate field tracks whether the specimen is an isolated tooth or still part of the jaw. Edentulous specimens were not analyzed but the option is available in the interface.



3.2.2 Faunal Database

A database application was developed in Microsoft Access 2000 to catalog specimens. The database tracks specimen identification, geographic location and element representation for the entire dentition of each specimen. An example data entry form is shown in Figure 3.3. Abundances were tabulated in two ways. First by counting the number of identified specimens (NISP), entered into the database. A specimen includes any bone, tooth or fragment thereof, while the term element is reserved for complete, unbroken, unfused anatomical parts. Some flexibility is required for discussing skulls and the dentition. Whole teeth are considered an element, but they are a subset of a complete mandible. Thus a mandible element includes the dentary and all the teeth while a specimen of a mandible may have teeth missing.

3.2.3 Quantification and Aggregation

Two metrics were derived from the raw NISP values. The minimum number of individuals, MNI, was tabulated by counting the number of occurrences of each dental element (e.g. left upper M1) and taking the maximum value across all elements as the MNI value for that taxon. No attempt was made to separate specimens based on wear stage, but side was taken into account.

The normed number of identified specimens, NISPn, was calculated by dividing the raw NISP values for each taxon by the expected number of elements for that taxon. The number of expected elements for most taxa was three, a skull and two mandibles. Shrews of the genus *Crocidura* and *Suncus* were identified by maxillae only, so their expected value is one. Plotting MNI against raw NISP as is shown in Figure 3.4, reveals the discordance in shrews immediately. The plot of MNI vs NISPn in Figure 3.5 shows the correction to be effective.

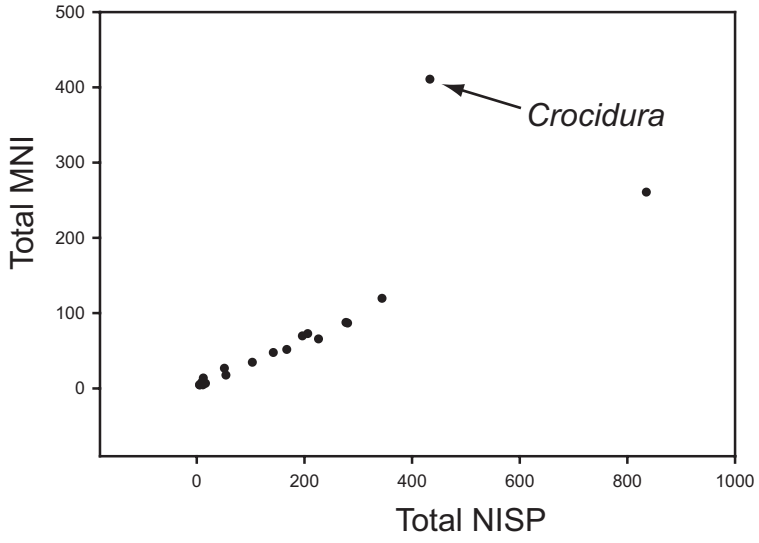


Figure 3.4: Bivariate scatter plot of MNI vs. NISP for 20 taxa. The outlying point represents the genus *Crocidura*.

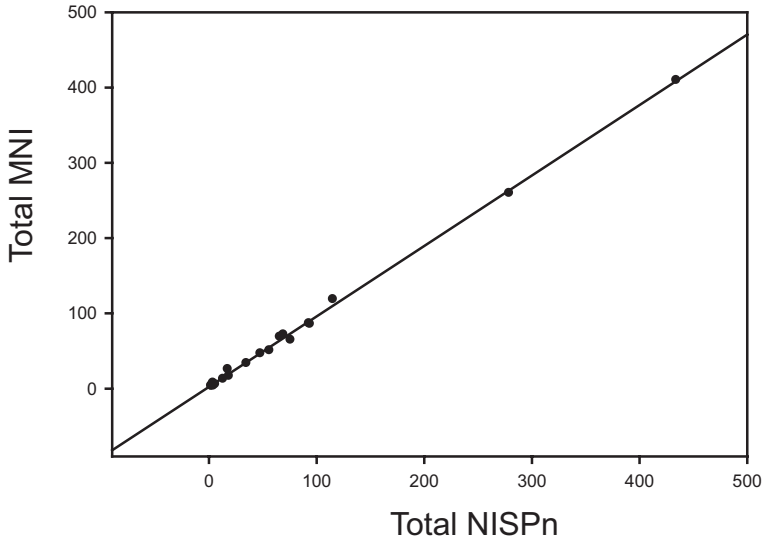


Figure 3.5: Least-squares regression of MNI on NISPn for 20 taxa ($r = 0.999$, $P < 0.001$).

Both NISP and MNI values are estimates of the number of organisms represented in the assemblage. NISP represents the upper limit and MNI the lower limit.

Grayson (1984) has shown that both estimates are problematic but in different ways. NISP values increase as a function of the number of elements per animal, and as the assemblage becomes more fragmented; for example a hemi-fractured skull and two mandibles from one individual will be recorded as four specimens. Since individual organisms are the unit of analysis in this study, counting individual specimens from the same individual violates statistical assumptions of data independence and artificially inflates sample sizes. Even if breakage is constant across all taxa, the artificial increase in sample size will inappropriately boost the power of statistical tests. For example, a Pearson's X^2 test on a sample of 100 items may be non-significant, but a test on 1000 may be significant even when the proportions between cells in the contingency tables are constant.

MNIs on the other hand, are biased depending on how samples are aggregated. Roosting sites form natural units, and if each is treated as a single aggregate one can be reasonably certain that MNI values are independent. I say reasonably, because individual prey sometimes become divided between multiple pellets (Raczynski and Ruprecht 1974), creating the possibility of depositing part of one prey individual, e.g. the mandible, at one roost while depositing the maxilla at another. Most prey items are egested in the same pellet, and most pellets at the same roost, so the probability of bias resulting from fractionation of the skeleton is slim.

Even with independence between roosts there is still the issue of aggregation within a roost. As a minimum value, MNIs underestimate the number of individuals because each roost is itself an aggregate of pellets even if the divisions are not apparent. Distribution of elements, such as the right mandible of an individual from one pellet and the left mandible of another individual will lead to aggregation of the MNI counts. If the element destruction varies across taxa then the MNI values will not be accurate representations of relative abundance. As Grayson (1984) noted, "the fact that there is no choice to be made as to how aggregate [sic] the [assemblage] does not mean that aggregation effects are absent; it just means that they cannot be detected" (p. 91). Unless each element experiences aggregation in the same way, MNIs will distort relative abundances. NISP and NISPn values do not experience this type of bias.

Thus, neither NISP nor MNI perfectly reflects the true abundance of individuals. Due to the sample inflation issue raw NISP values are clearly inappropriate for statistical tests, and NISPn or MNI are preferred. However, the aggregation

issue favors NISP or NISPn as the best measure for non-statistical comparisons of relative abundances. These general guidelines are followed for subsequent analyses.

For many archeological assemblages, plots of NISP against MNI show curvilinear or log-linear relationships (Grayson 1984), but the Serengeti ossuaries show a good fit with a simple linear model. Regressing MNI against raw NISP, yields a model with a relatively good fit, ($r = 0.813$, $P < 0.001$), while using the adjusted values and regressing MNI against NISPn greatly improves the fit ($r = 0.999$, $P < 0.001$). The model for the second curve is $MNI = 0.91395 \cdot NISPn + 9.9412$. The slope of this curve, $b = 0.91395$, is very close to 1 indicating that, once adjusted for the number of elements per individual, there are few additional specimens that are not also new individuals. In other words there is little breakage, and new specimens introduce new individuals. The breakage is underestimated in part because edentulous jaws were not counted, but isolated teeth were.

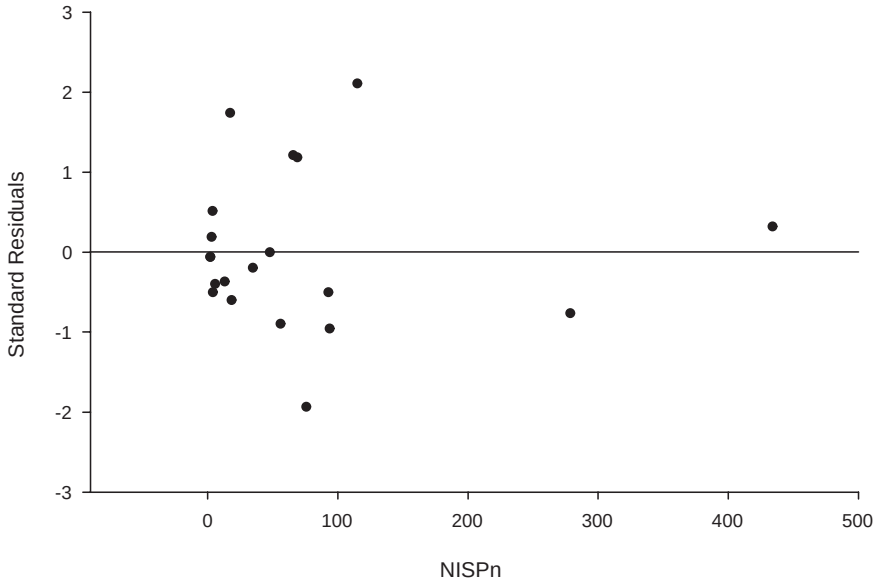


Figure 3.6: Standard residuals from the regression of MNI on NISPn. A runs test on the pattern of negative and positive residuals is non-significant at the 0.05 level.

The goodness of fit to a linear model may be tested by examining the residuals. These are shown in Figure 3.6. A runs test on the residuals results in a non-significant pattern at the 0.05 significance level (10 runs observed, lower boundary 5 runs, upper boundary 10 runs). We must accept the null hypothesis that points

are distributed randomly above and below the regression line. This supports the propriety of a linear fit.

The relationship between MNI, NISP and NISPn is not surprising given that MNI is derived from NISP. However the strength of the linear fit is generally better than that reported for large mammals, most likely due to the fact that only craniodental specimens are tabulated (Grayson 1984). Furthermore, as a modern sample breakage is not as great as would be expected in a fossil assemblage and thus NISPn values are close to MNI values. Lyman and Power (2003) report similar results in the analysis of an owl pellet assemblage though they test the relationship between MNI and NISP *per pellet*.

3.3 Results

Complete listings of the mammalian fauna and frequencies for each taxon as number of identified specimens (NISP), normalized number of identified specimens (NISPn), and minimum number of individuals (MNI) are given in Tables 3.2, 3.4, and 3.5. The fauna is dominated by small mammals though passerine birds, insects, and reptiles were also observed. The distribution of reptiles and birds is shown in Table 3.6. Relative abundance histograms of all taxa are plotted in Figure 3.7 , and a histogram showing the total abundances from all assemblages treated together is shown in Figure 3.8.

The histogram of the total fauna shows that crociduran shrews are the most abundant taxon. The abundance of *Crocidura* results from the patterning of diversity between generic and species ranks in shrews and rodents. Among the 59 species of soricid shrews in East Africa, 42 belong to the genus *Crocidura*. A different pattern occurs in rodents where 113 species are distributed among 40 genera and none have more than 10 species. Taxonomic counts are taken from the mammal checklist for East Africa published by Davies and Berghe (1994). Thus, much of the biodiversity in shrews occurs at the species level, while in rodents the diversity is partitioned among genera. At the ordinal level, rodents are nearly twice as abundant as insectivores, as shown in Table 3.7.

Table 3.2: Taxonomic representation presented as the number of identified specimens (NISP). Taxa grouped by Order and the Rodentia are further grouped into Subfamilies.

				Roost ID					Total
Taxa	**3**	**4**	**12**	**13**	**18**	**23**	**24**	**44**	**NISP**
Insectivora									
Crocidura	114	91	9	66	47	5	75	27	434
Suncus	8	0	0	4	1	0	0	0	13
Subtotal Insectivora	122	91	9	70	48	5	75	27	447
Macroscelidea									
Elephantulus	0	0	0	1	1	4	0	0	6
Chiroptera									
Microchiroptera gen. Indet	5	0	0	0	4	2	0	0	11
Rodentia									
Murinae									
Acomys	1	0	1	3	2	0	0	2	9
Aethomys	0	0	0	0	0	0	1	16	17
Arvicanthis	15	79	0	4	11	48	2	68	227
Dasysmys	0	0	0	0	0	0	0	12	12
Lemniscomys	8	8	1	4	11	14	5	1	52
Mastomys	27	140	1	9	6	56	8	34	281
Mus cf. musculoides	69	37	3	29	33	15	11	0	197
Mus cf. triton	47	39	0	46	61	8	2	4	207
Praomys	1	0	0	0	4	0	0	1	6
Thallomys	18	9	10	11	10	85	0	0	143
Zelotomys	13	22	0	17	1	1	0	1	55
Subtotal Murinae	199	334	16	123	139	227	29	139	1206
Cricetomyinae									
Saccostomus	18	24	1	8	17	36	0	0	104
Dendromurinae									
Dendromus	67	104	3	79	23	7	52	10	345
Steatomys	97	137	8	216	44	3	309	22	836
Subtotal Dendromurinae	164	241	11	295	67	10	361	32	1181
Gerbillinae									
Gerbillus	8	2	0	48	3	0	107	0	168
Tatera	2	15	0	13	8	7	223	10	278
Subtotal Gerbillinae	10	17	0	61	11	7	330	10	446
Subtotal Rodentia	391	616	28	487	234	280	720	181	2937
Totals	**518**	**707**	**37**	**558**	**287**	**291**	**795**	**208**	**3401**

Table 3.3: Taxonomic representation presented as normed number of identified specimens (NISPn). Taxa grouped by Order and the Rodentia are further grouped into Subfamilies.

				Roost ID					Total
Insectivora									
Crocidura	114.0	91.0	9.0	66.0	47.0	5.0	75.0	27.0	434.0
Suncus	8.0	0.0	0.0	4.0	1.0	0.0	0.0	0.0	13.0
Subtotal Insectivora	122.0	91.0	9.0	70.0	48.0	5.0	75.0	27.0	447.0
Macroscelidea									
Elephantulus	0.0	0.0	0.0	0.3	0.3	1.3	0.0	0.0	2.0
Chiroptera									
Microchiroptera gen. Indet	1.7	0.0	0.0	0.0	1.3	0.7	0.0	0.0	3.7
Rodentia									
Murinae									
Acomys	0.3	0.0	0.3	1.0	0.7	0.0	0.0	0.7	3.0
Aethomys	0.0	0.0	0.0	0.0	0.0	0.0	0.3	5.3	5.7
Arvicanthis	5.0	26.3	0.0	1.3	3.7	16.0	0.7	22.7	75.7
Dasysmys	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0	4.0
Lemniscomys	2.7	2.7	0.3	1.3	3.7	4.7	1.7	0.3	17.3
Mastomys	9.0	46.7	0.3	3.0	2.0	18.7	2.7	11.3	93.7
Mus cf.musculoides	23.0	12.3	1.0	9.7	11.0	5.0	3.7	0.0	65.7
Mus cf. triton	15.7	13.0	0.0	15.3	20.3	2.7	0.7	1.3	69.0
Praomys	0.3	0.0	0.0	0.0	1.3	0.0	0.0	0.3	2.0
Thallomys	6.0	3.0	3.3	3.7	3.3	28.3	0.0	0.0	47.7
Zelotomys	4.3	7.3	0.0	5.7	0.3	0.3	0.0	0.3	18.3
Subtotal Murinae	66.3	111.3	5.3	41.0	46.3	75.7	9.7	46.3	402.0
Cricetomyinae									
Saccostomus	6.0	8.0	0.3	2.7	5.7	12.0	0.0	0.0	34.7
Dendromurinae									
Dendromus	22.3	34.7	1.0	26.3	7.7	2.3	17.3	3.3	115.0
Steatomys	32.3	45.7	2.7	72.0	14.7	1.0	103.0	7.3	278.7
Subtotal Dendromurinae	54.7	80.3	3.7	98.3	22.3	3.3	120.3	10.7	393.7
Gerbillinae									
Gerbillus	2.7	0.7	0.0	16.0	1.0	0.0	35.7	0.0	56.0
Tatera	0.7	5.0	0.0	4.3	2.7	2.3	74.3	3.3	92.7
Subtotal Gerbillinae	3.3	5.7	0.0	20.3	3.7	2.3	110.0	3.3	148.7
Subtotal Rodentia	130.3	205.3	9.3	162.3	78.0	93.3	240.0	60.3	979.0
Totals	**254**	**296**	**18**	**233**	**128**	**100**	**315**	**87**	**1432**
Taxa	**3**	**4**	**12**	**13**	**18**	**23**	**24**	**44**	**NISPn**

Table 3.5: Taxonomic representation presented as the minimum number of individuals (MNI). Taxa grouped by Order and the Rodentia are further grouped into Subfamilies.

	Roost ID								Total
Taxa	**3**	**4**	**12**	**13**	**18**	**23**	**24**	**44**	**MNI**
Insectivora									
Crocidura	104	89	9	63	40	5	73	27	410
Suncus	8	0	0	4	1	0	0	0	13
Subtotal Insectivora	112	89	9	67	41	5	73	27	423
Macroscelidea									
Elephantulus	0	0	0	1	1	2	0	0	4
Chiroptera									
Microchiroptera gen. Indet	4	0	0	0	3	1	0	0	8
Rodentia									
Murinae									
Acomys	1	0	1	2	1	0	0	1	6
Aethomys	0	0	0	0	0	0	1	5	6
Arvicanthis	5	21	0	3	4	14	1	17	65
Dasysmys	0	0	0	0	0	0	0	4	4
Lemniscomys	4	3	1	2	5	6	4	1	26
Mastomys	9	35	1	4	2	21	4	10	86
Mus cf. musculoides	21	14	2	11	9	7	5	0	69
Mus cf. triton	20	13	0	13	21	3	1	1	72
Praomys	1	0	0	0	2	0	0	1	4
Thallomys	7	2	5	4	3	26	0	0	47
Zelotomys	3	6	0	5	1	1	0	1	17
Subtotal Murinae									
Cricetomyinae									
Saccostomus	6	7	1	2	7	11	0	0	34
Dendromurinae									
Dendromus	24	33	2	26	9	4	17	4	119
Steatomys	32	44	4	64	14	2	93	7	260
Subtotal Dendromurinae	56	77	6	90	23	6	110	11	379
Gerbillinae									
Gerbillus	3	1	0	15	3	0	29	0	51
Tatera	1	7	0	4	3	3	66	3	87
Subtotal Gerbillinae	4	8	0	19	6	3	95	3	138
Subtotal Rodentia	137	186	17	155	84	98	221	55	953
Totals	**253**	**275**	**26**	**223**	**129**	**106**	**294**	**82**	**1388**

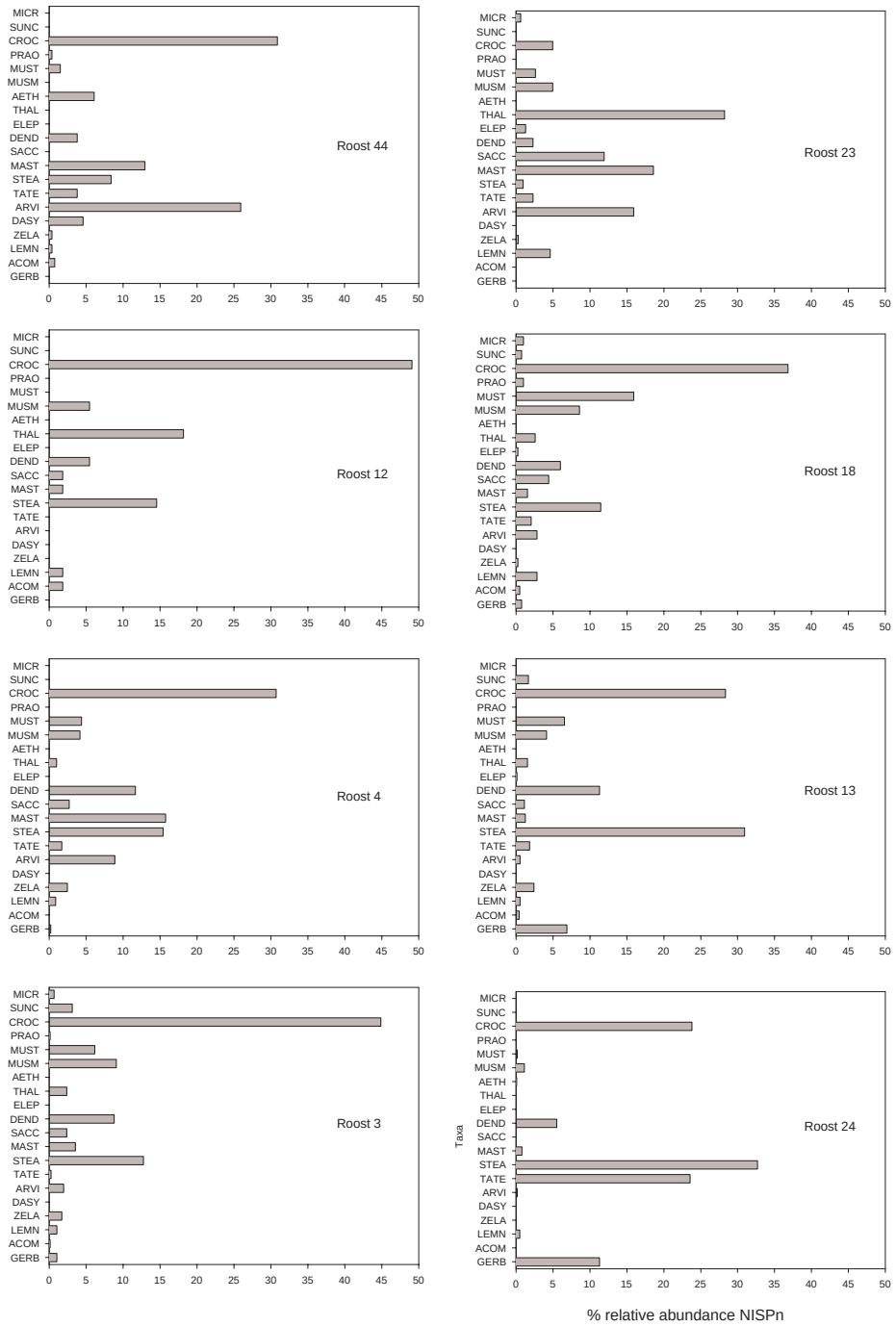


Figure 3.7: Relative abundances (%NISPn) of all mammalian taxa at each of the eight roosts.

Table 3.6: Presence-Absence of birds and reptiles.

	Roost ID							
	3	**4**	**12**	**13**	**18**	**23**	**24**	**44**
Birds	+	0	0	+	+	0	0	+
Reptiles	+	0	+	0	+	+	0	0

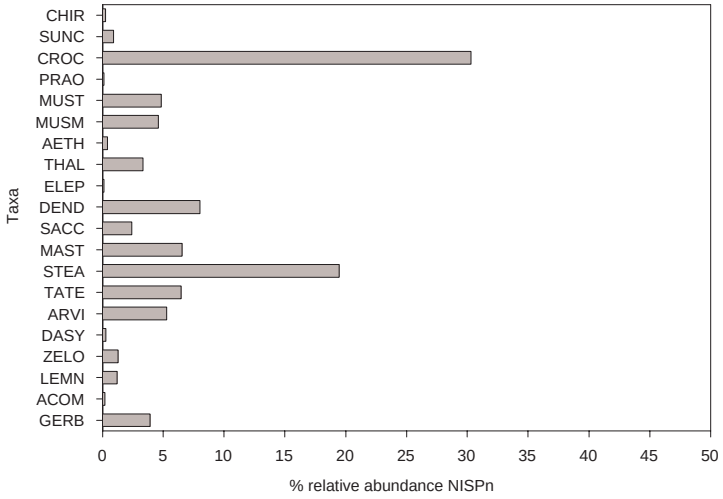


Figure 3.8: Relative abundances (%NISPn) of all mammalian taxa from all roosts combined.

3.4 Discussion

Within Serengeti, an early survey of animal diversity by then Tanganyika Game Warden G. Swynnerton (1958) included most of the small mammals known from the park today. The report groups animals under five headings: swamps, plains, bushland, mountain mist forest and heath. The distribution of small mammals among these classes is suspect as Swynnerton includes no rodents for the plains, and lumps most of them into the bushlands. The current study and others (Senzota 1978, 1983) clearly show rodents inhabiting the grasslands. Subsequently, Misonne and Verschuren (1966) reported the results from trapping conducted at 27 locations in and around Serengeti National Park. These authors express an interest in competition between large and small herbivores (p. 517), an idea that may extend from earlier writings by Verschuren (e.g. 1964 as cited in Senzota 1978). Shortly

after, Hendrichs (1969) conducted small mammal trapping as part of an analysis of herbivore biomass and carrying capacity of grassland ecosystems. The faunal list provided in Hendrichs's report includes summaries of species previously reported in the study area, though curiously it omits the records of *Otomys* and *Thryonomys* reported by Swynnerton (1958) despite the fact that the latter paper is cited by Hendrichs. Laurie (1971) produced a small study of owl pellet assemblages in Serengeti. He described three assemblages, one of these sites, Oloserian, is replicated in this study (roost 4).

The aforementioned studies are general surveys, providing little detailed information on autecology, community structure, population dynamics or microhabitat use. The first, and really only, in depth studies on small mammal species in Serengeti were conducted by Senzota (1978; 1983; 1990). These studies focused on two abundant rodent taxa *Arvicanthis* and *Tatera.* Beyond this the distribution, biodiversity, microhabitat use and community structure of Serengeti small mammals is unknown.

3.4.1 Autecological profiles of Serengeti micromammals

In order to facilitate discussion of the fauna, brief summaries of the different genera are provided in this section. These summaries are derived from a review of the literature on East African micromammals. The current state of knowledge regarding different genera is very uneven. Some taxa such as *Arvicanthis* and *Acomys* are used in medical research, and as a result there is a rich literature on their biodiversity and systematics. Others, such as *Mastomys* are ubiquitous crop pests and disease vectors. The population biology of *Mastomys* has thus been well studied

Table 3.7: Taxonomic abundance (NISPn) of specimens grouped by Order.

	Roost ID								**Total**
Order	**3**	**4**	**12**	**13**	**18**	**23**	**24**	**44**	**NISPn**
Insectivora	122	91	9	70	48	5	75	27	447
Macroscelidea	0	0	0	0	0	1	0	0	2
Chiroptera	2	0	0	0	1	1	0	0	4
Rodentia	130	205	9	162	78	93	240	60	979
Totals	**254**	**296**	**18**	**233**	**128**	**100**	**315**	**87**	**1432**

in an effort to predict outbreaks. I attempt to provide an overview that includes information on systematics, morphology and most importantly, ecological habits. A few sources were particularly informative. Jonathan Kingdon's seminal work on East African mammals (Kingdon 1974) remains the single best compendium of ecological data on East African small mammals. Musser and Carleton (1993) has become the defacto consensus regarding taxonomic classification. With the large biodiversity present in small mammals, a standard classification is a great benefit. Delany (1972, 1986) wrote two very useful summaries of rodent ecology in Africa. These provide a useful framework for understanding the broad outlines of rodent community structure and their relations to African biomes. Two papers focusing on Tanzania, one by Vesey-Fitzgerald (1966) and another by Hubbard (1972) provide very helpful observations on Tanzanian rodents, and studies in Kenya, such as Andrews et al. (1975), are also relevant. These references form the foundation for the summaries below. The summaries include comments on morphology useful in the diagnosis of the taxa. Anatomical comments employ the Cope-Osborn system of dental nomenclature for Insectivores and Macroscelideans, but a specialized nomenclature is followed for the rodents. Figure 3.9 illustrates a rodent toothrow to demonstrate the nomenclature.

Rodentia

A*comys* – *Spiny Mice*

These small nocturnal rodents are dispersed through a wide range of habitats, being more closely associated with rocky microhabitats within arid to sub-humid climes hosting scrub to grassland to grassed woodland habitats. Their association with rocky substrates may make them the target of opportunistic predation by owls roosting on or in kopjes. However, their presence in predator assemblages is mitigated in part by the development in this genus of stiff, spine-like dorsal hairs.

Musser and Carleton (1993) recognize 14 species, though the taxonomy needs revision, especially for the East African representatives, of which there are 11 species:

A. cineraceus

A. ignitus

A. kempi

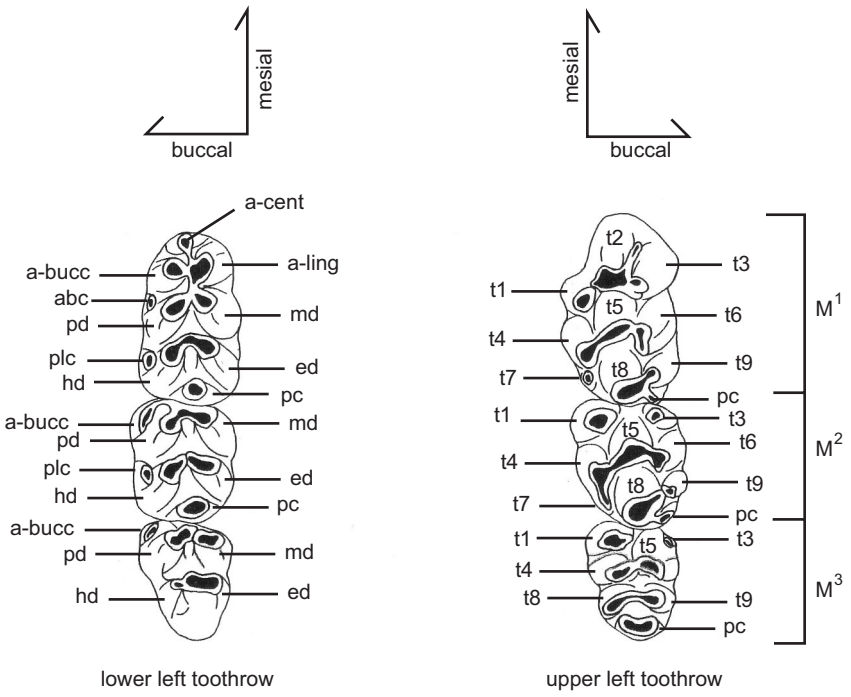


Figure 3.9: Murine dental nomenclature modified from Musser (1987). Illustration shows upper and lower left tooth rows. Upper cusp numberings follow Miller 1912. Lower terminology modified from van de Weerd 1976: a-ling, antero-lingual cusp; a-cent, antero-central cusp; a-bucc, antero-uccal cusp; abc, antero-buccal cusplet; pd, protoconid; pbc, postero-buccal cusplet; hd, hypoconid; pc, posterior cingulum; ed, entoconid; md, metaconid.

A. louisae

A. mullah

A. percivali

A. spinosissimus

A. subspinosus

A. wilsoni

Comparisons with published descriptions is complicated by shifting names and complex synonymy (Jeremy and Bates 1994). Their distribution includes most tropical grassland, treed grassland and open woodland habitats but does not extend into the forested regions of the Congo basin nor the mesic highland of Uganda.

Aethomys – Bush Rats

Aethomys resembles *Arvicanthis* in size and in the bunodont shape of the tooth cusps. *Aethomys* also shares characteristics with *Thallomys*, including a tendency toward stephanodonty[1], with crests extending distally from cusps t4 and t6 on the upper molars. *Aethomys* is readily distinguished from both *Arvicanthis* and *Thallomys* in having a single large lingual root under t1 and t4 on the first and second upper molars as opposed to two smaller lingual roots in the latter taxa. Of the ten recognized *Aethomys* species none live outside Africa. Within Africa they have a broad distribution and three species are known for East Africa:

A. chrysophilus

A. hindei

A. kaiseri

A medium sized, generalist rodent, *Aethomys* shows propensities for grasslands, bushlands, and woodlands. *Aethomys* is often associated with *Acomys* on rocky substrates (Vesey-Fitzgerald 1966). Of the three species *A. chrysophilus* is proposed to inhabit more wooded areas and *A. hindei* more open grassland habitats. *Aethomys* are mainly nocturnal and vegetarian, though *A. chrysophilus* is claimed to have a more omnivorous diet that includes insects (Gliwicz 1987). On the basis of this dietary distinction Denys (1994) argues for a link between the more "vegetarian" diet *A. namaquensis* and the greater degree of stephanodonty that appears in this species relative to the more "omnivorous" *A. chrysophilus*. However, the

[1]stephanodonty describes a molar crown with distinct cusps joined by narrow crests in arch like arrangements.

argument assumes that the correlation between diet and stephanodonty demonstrates a causation. Without further functional analysis this proposition must remain speculative. Furthermore Denys (1994) implies a link between stephanodonty and folivory,

> According to Gliwicz (1985, 1987) in Mozambique, *A. namaquensis* is primarily a folivore and grass eater. The latter feature could explain the existence of small "stephanodont" crests...During the dry season, *A. namaquensis* does not eat any insects in contrast to A. chrysophilus, which has a wider spectrum of food. The development of longitudinal crests and of supplementary labial cingular cusps can be put in relation with a mainly vegetarian diet. (pp. 362-362)

As an explanation for stephanodonty, a vegetarian diet is unsatisfactorily vague, nor is it clear how folivory would be served by stephanodonty. Stephanodonty is characterized by the development of tall, but rounded cusps linked together by crests in an arc. This arrangement reduces the amount of linear shearing area formed at the edge of dentine lakes – a feature that is optimized in other grazers such as *Otomys* and *Arvicanthis*. By comparison with other grazers, stephanodonty does not appear to be an optimization for grazing. It may be beneficial for hard object feeding, as in grannivory, and this idea is proposed by Fernandez-Jalvo et al. (1998).

Arvicanthis – Grass Rats

Arvicanthis niloticus is a sub-humid grassland specialist. The species type locality is in the Nile Valley of Egypt but the name has been applied to forms over a vast range, though specimens from western Africa are probably different species.

The three species known from Kenya and Tanzania form a size gradient with *A. neumanni* < *A. nairobae* < *A. niloticus* and have very similar cranio-dental morphology. *A. neumanni* is markedly smaller but the latter two approach each other in size and are difficult to diagnose using discrete characters. All taphonomic specimens attributed to *Arvicanthis* fall into the size range of *A. niloticus* though the possibility that the smallest specimens represent examples of *A. nairobae* cannot be eliminated.

Arvicanthis is a grazer feeding on grass shoots, leaves and seeds. The derived dentition reflects this adaptation. As the cusps wear they quickly merge to form lophs with exposed dentine lakes, as the dentine lakes merge they form repeated transverse lamellar patterns of enamel and dentine much like the selenodont patterns in ungulates but rotated from that pattern by ninety degrees to accommodate a retromolar (antero-posterior) chewing motion. This adaptation is taken to its extreme in *Otomys*, and recent molecular studies point to *Arvicanthis* as the likely sister clade to *Otomys* (Ducroz et al. 2001).

Arvicanthis is reported to favor lush, green grasses such as *Digitaria abyssinica*, *Imperata*, *Amaranthus polygamus* and *Bidens pilosa* (Kingdon 1974). It is claimed to be the most abundant rodent on Serengeti grasslands where it avoids resource competition with large bodied herbivores by feeding on less palatable grasses such as *Pennisetum* and *Cymbopogon* (Senzota 1983). It prefers a dense herb mat and soils soft enough to burrow, or seasonally cracked to allow creation of short tunnels (Vesey-Fitzgerald 1966). *Arvicanthis* may inhabit grasslands, treed grasslands and grassed woodlands as well as mesic peri-lacustrine habitats with rank herbage.

Despite its wide abundance in Serengeti, it often does not rank as numerically dominant in owl assemblages. This is likely a result of activity patterns. Most individuals are active during the day in both laboratory and natural settings (Blanchong and Smale 2000) though some individuals are nocturnal. The differences in this study along with other field reports of nocturnality may indicate the existence of a nocturnal morph in the wild.

Arvicanthis competes with *Lemniscomys* and *Otomys* in grasslands. Its competitive and community relation to the former is poorly documented. *Arvicanthis* gives way to *Otomys* in more mesic and more temperate (higher elevation) habitats.

Dasymys – Shaggy Swamp Rat

The broad, robust upper molars of this genus are similar to *Arvicanthis*, except whereas *Arvicanthis* tends to have a t9 cusp that is connected to t8 but not linked to t6 (that is it lacks a longitudinal crest), *Dasymys* does not have a very distinct t9, in its place is a crest linking t8 and t6. *Dasymys* also exhibits greater hypsodonty, part of its adaptation to grazing. The lower molars are easily recognized by the presence of a large antero-central cusp and accessory buccal cusplets.

Two species of *Dasymys* occur in East Africa. One, *D. montanus*, is a montane

Western Rift Endemic (Musser and Carleton 1993), leaving *D. incomtus* as the single species in much of East Africa.

Very little is documented about the autecology of *Dasymys*. It is consistently associated with wet habitats such as marshes, river margins, and lake margins. Vesey-Fitzgerald (1966) describes *Dasymys* as a common inhabitant of drainage lines, a habitat it shares with *Pelomys, Otomys* and sometimes *Arvicanthis*. Hubbard (1972) notes catching this species "on the river in the city park of Eldoret [Kenya] which is only 10 miles south-west of the type locality" (p. 429). Delany (1986) describes *Dasymys* as part of the flood plain community along the Kafue River along with *Pelomys*, *Mastomys*, *Mus minutoides* and *Arvicanthis*.

Grammomys – Narrow-footed Thicket Rats

These thicket and shrub dwelling arboreal rodents inhabit a broad range of vegetation types from tall grass to forest margins. Vesey-Fitzgerald (1966) mentions three sympatric varieties of *G. dolichurus* inhabiting ecological grades from forest to woodland to thicket. Musser and Carleton (1993) recognize twelve species of which five appear in Kenya or Tanzania:

G. caniceps

G. dolichurus

G. gigas

G. ibeanus

G. macmillani

Another species, *G. dryas* is restricted to Uganda. Misonne and Verschuren (1966) note that *Grammomys* like *Praomys jacksoni* is a form peripheral to the Serengeti, preferring more closed and moist habitats[2]. Although morphological adaptations, such as the lengthy tail, indicate an arboreal adaptation Hubbard (1972) reports catching them in grasslands some distance from trees.

Grammomy was originally grouped under *Thamnomys* but was asserted to be an independent genus by Ellerman (1941). The teeth resemble *Thamnomys* except that the t7 is reduced to a crest only. Overall the dentition of *Grammomys* is very similar to *Thallomys*, though smaller.

[2]"*Grammomys* est, comme *Praomys jacksoni*, une forme marginale dans la région du Serengeti; il affectionne particulièrement les milieux fermés et humides" (p. 522)

Lemniscomys – Striped Grass Rats

Lemniscomys is a complex of species occupying varying grades of xeric to mesic grassy habitats up to elevations of 3500 m (Kingdon 1974). Like *Arvicanthis* these species are mostly diurnal but with some nocturnal activity as well. Musser and Carleton (1993) recognize 10 species, of which three occur in the Kenya and Tanzania:

L. barbarus

L. rosalia

L. striatus

Where they are sympatric *L. striatus* tends to occupy the more mesic microhabitats such shrubbed grasslands along drainage lines, while *L. barbarus* is displaced to higher ground and more open vegetation. *L. rosalia* (= *L. griselda* and *L. macculosus* of Kingdon, 1974) occurs in *Brachystegia* woodlands and is common on the grassy borders of pans and where it co-occurs with *L. striatus* again the latter is found in the denser vegetation. Thus *L. striatus* appears the most mesic adapted, while *L. barbarus* and *L. griselda* are the more open and xeric adapted. *Lemniscomys* competes with *Arvicanthis* and *Otomys*.

Mus – Mice

Mus is easily diagnosed by its small size and distinctive molar morphology, though it may be confused for *Steatomys*. In *Mus*, the t1 of the upper first molar is offset distally from the t2 and t3, but the base of the cusp remains connected to the anterior loph. The same is true for the next loph, where t4 is offset from t5 and t6. Superficially the molar has the appearance of only two cusps in the anterior loph as is the condition in Dendromurinae such as *Dendromus* and *Steatomys*.

Two forms are readily distinguishable in the taphonomic collections. The smaller form is characterized by a prominent cingulum on the mesial aspect of t2 on the upper first molar. It also has a well developed masseteric knob. The larger form lacks the masseteric knob and cingulum on the upper first molar, it also has a more proodont dentition with the lower incisor forming a much wider arc than in the smaller form.

Numerous species must have been described, though many of the East African forms have been lumped into the subgenus *Nannomys*, including:

M. (Nannomys) mahomet
M. (N.) minutoides
M. (N.) musculoides
M. (N.) neavi
M. (N.) setulosus
M. (N.) tenellus
M. (N.) triton

An exception is the commensal house mouse, *Mus (Mus) musculus*. For two forms recovered in Serengeti the smaller resembles either *M. (N.) Minutoides* or *M. (N.) musculoides*, while the larger may be *M. (N.) tenellus* or *M. (N.) triton*. Nannomys is associated with a very broad range of habitats though not often with closed forest or desert.

Mastomys – Multimammate Mice

The multimammate mouse is one of the most common and ubiquitous taxa in the study area. They are widely associated with disturbed vegetation and cultivation and many populations are commensal or semi-commensal. The widespread and ubiquitous nature of the genus poses problems for diagnosing species, along with their morphological and geographical boundaries. *Mastomys* is one of the most numerous murine genera collected by the owls, and the genus shows some morphological variability with occasional specimens exhibiting additional cusps.

The ecology of this genus varies along the entire continuum, but avoiding the extremes of rain forest. Hubbard (1972) notes that *Mastomys* have been found at altitudes ranging from sea level to 8,500 ft and "in both dry bushy country and swampland," (p. 436) but not in closed forest. However, Vesey-Fitzgerald (1966) reports that *Mastomys* has been caught on the floor of forests with *Praomys jacksoni* and "along drainage lines with *Otomys*, *Pelomys* and *Dasymys*, in flood plain grassland with *Arvicanthis*, among rocks with *Aethomys chrysophilus* and *Acomys*, in warrens of *Tatera* and in villages and houses with *Rattus*" (p. 115). Clearly *Mastomys* has a very broad niche. Yet, in competition with other rodents, their realized niche may be limited. Linzey and Kesner (1997) report that while some taxa in their study area were caught in as many as four different habitats, *Mastomys* was restricted to riverine grassland. The success of *Mastomys* may lie in its ability to shift between any of several available niches based on the presence

or absence of competitors.

Praomys – Soft-furred Rats

The soft furred rats are medium to small sized with dental morphology most similar to *Mastomys*, which until recently was considered a subgenus of *Praomys*. Three species of *Praomys* are known from East Africa (Musser and Carleton 1993):

P. delectorum

P. jacksoni

P. misonnei

Praomys inhabits closed and shady habitats including forest and dense shrub in areas with relatively high precipitation. According to Vesey-Fitzgerald (1966) *Praomys jacksoni* is confined to forest but can survive in very small relic blocks and in gallery forests along streams. They possess long tails and are at least partly arboreal.

Thallomys – Acacia Tree Rats

Thallomys is a mid sized arboreal specialist preferring *Acacia* or *Brachystigia* woodlands. Two species of *Thallomys* are known from East Africa,

T. paedulcus

T. loringi.

The two are commonly confused or conflated in the literature, but comparison among specimens in the NMNH shows *T. loringi* to be slightly larger and to have a much better developed posterior cingulum on the upper first and second molars.

Upper molars are easily diagnosed by a strongly stephanodont cusp pattern in which cusps are pointed, and separated from one another by deep grooves but united by a narrow arcing crest along the distal aspect of the cusps. To a creative eye the pattern resembles jewels in a crown or tiara, hence the term stephanodont (= crown toothed). The arcing crests bridge cusps in the standard murine transverse loph, but also extend distally on the buccal and lingual margins to link cusps in the middle and posterior lophs.

The lower molars are arranged in three pairs front to back with the wear facets of the first two sets facing each other in a clover-like pattern common to many murines. *Thallomys* is recognized by the additional well-developed antero-central

cusp at the anterior margin of the M_1. Buccal and lingual cusps are well separated from each other by a well developed trench running longitudinally down the center of the tooth and cusps tend to wear to a tear-shaped pattern with the apex developing along the median trench. The posterior cingulum is very well developed on both the lower first and second molars and these are also decorated with a very well-developed posterior buccal cusplet.

Acacia buds, leaves, seeds and gums appear to be the staple diet, these are supplemented with grass, seeds, berries and occasional insects (Kingdon 1974). *Thallomys* forage for food in and below their host tree, venturing out onto terminal branches, down the trunks of trees and out among the grass understory beneath trees. *Acacias* do not seem to be preferred habitat for squirrels and *Thallomys* thus occupies an important open niche in sparsely canopied *Acacia* woodlands.

Thallomys is an arboreal species adapted to life in open woodland environments. It possesses adaptations for climbing including longer, broader feet with raised pads on the soles, recurved claws and partially opposable outer digits (Herskovitz 1969). The same study suggests that the tail hairs in arboreal species such as *Thallomys* and *Praomys* function as tactile organs. Climbing behavior of captive *Thallomys* reveal it is well adapted to arboreal life and can move up and down trunks head first, while using the tail as a prehensile organ (Earl and Nel 1976).

Kingdon (1974) and others (Skinner 1990; Hubbard 1972; Vesey-Fitzgerald 1964) describe *Thallomys* as an *Acacia* woodland specialist, preferring tall *Acacia* such as *A. xanthophloea* and *A. tortilis*. However this may be an oversimplification as there are also reports of *Thallomys paedulcus* being trapped in Miombo woodland characterized by the genera *Brachystegia* and *Julbernardia* growing on sandy soils (i.e. the upper part of the catena) as well as Mopane woodland characterized by *Colophospermum mopane* growing on clays and often with a dense grass understory (ie catena bottoms) (Linzey and Kesner 1997).

Thallomys resides in nests built at ground level or above ground in tree hollows or in the forks or branches. Large ground shelters of piled leaves and twigs may serve as nests but also expansive shade and predation shelters during ground foraging.

Zelotomys – Broad-headed Rats

Zelotomys is a medium sized rodent. The dentition is less robust than *Arvicanthis* and has a superficial resemblance to *Mastomys*. The t1 is offset from t2 and t3 but not to the degree of *Mus*. The M^3 is much smaller than M^2 as in *Mus* and very different from *Arvicanthis*. Longitudinal crests are weakly developed on the lingual aspect of the tooth between t4 and t8. The t9 is a very prominent and distinct cusp.

The anterior incisive foramen is large and extends well past the anterior alveolus of M^1 and extending down to the level of the t1. The a.i.f is also very broad along its entire length. The lower dentition is simple. Small posterior cingula decorate the distal margins of the $M_{1\text{-}2}$. Very small postero-buccal cusplets may be present.

Two species are known: *Z. woosnami* and *Z. hildegardae* (Musser and Carleton 1993). The former has an arid to semi-desert distribution in the Kalahari region of Southern Africa (Skinner 1990). The second, *Z. hildegardae* has a distribution that includes more semi-arid to subhumid regions extending into Uganda, Sudan and the Central African Republic. This small to medium sized rodent is associated with moist, tall grasslands and grassed shrublands to grassed woodlands (Kingdon 1974; Cheeseman 1977). *Zelotomys* is a specialized omnivore and seldom appears to reach very high densities .

Steatomys – Fat Mice

According to Musser and Carleton (1993) there are six species

S. caurinus

S. cuppedius

S. jacksoni

S. krebsii

S. parvus

S. pratensis

of which the first three are West African species. *S. krebsii* and *S. pratensis* are listed only for southern Africa, leaving *S. parvus* with an East African distribution.

Little is known about the ecology or niche of this group. The genus is widespread in savanna woodland, forest clearings, cultivated fields, and semi-desert areas. *Steatomys* is a burrowing rodent preferring softer substrates such as sands

and cultivated soils (Vesey-Fitzgerald 1966). It creates burrows at least 40 cm deep and can go down as deep as one meter (Kingdon 1974). *Steatomys* is described by Kingdon (1974) as primarily gramnivorous, but it also feeds on ground bulbs, groundnuts and insects. Perrin and Curtis (1979) note that, "the short gut, small caecum and long small intestine" are indicative of a high protein diet, but, "the decreased number of liver lobes and loss of a gall bladder are atypical of a seed-eater" and perhaps related to fat storage or estivation (Perrin and Curtis 1979, p. 28). Their common name derives from the ability to lay down thick layers of body fat, and then estivate for long periods. Linzey and Kesner (1997) report trapping *S. pratensis* predominantly in riverine grasslands in Zimbabwe (93% of captures), and also in Miombo woodland. Similarly Smithers (1971) reports the genus occurring in a variety of habitats ranging from riverine floodplain and woodland, dry open scrub but predominantly from sandy scrub or sandy alluvium.

Dendromus – Climbing Mice

Adapted for climbing thin supports these mice have prehensile tails and a specialized grasp. They are widely distributed throughout subsaharan Africa occurring in moderate environments to the exclusion of true forests and the most arid regions (Kingdon 1974). Eleven species are recognized by Musser and Carleton (1993) of which six occur in Kenya or Tanzania:

D. insignis
D. melanotis
D. mesomelas
D. messorius
D. mystacalis
D. nyikae

though only a single of these, *D. melanotis*, is known from Serengeti (Hendrichs 1969). All build nests though in different ways that may be related to their niches. Those inhabiting more mesic habitats with a moist herb layer build grass nests up to a meter off the ground Vesey-Fitzgerald (1966). Those in areas more prone to fire may nest in burrows.

Saccostomus – Pouched Rats

The single East African species, *Saccostomus mearnsi*, derives its common name from the practice of hoarding seeds and other food items in its capacious cheeks, much like a cercopithecine monkey stores leaves. In *Saccostomus* this adaptation facilitates foraging. The animals spends its active time searching for food then returns to its burrow to feed in safety.

Vesey-Fitzgerald (1966) reports finding *Saccostomus* in grasslands, previously cultivated lands and various types of mixed woodlands. *Saccostomus* is nocturnal and resides in burrows dug by other rodents, thus it may necessarily associate with larger burrowing species such as *Tatera* or *Arvicanthis*. Pettifer and Nel (1977) observed larder hoarding behavior – the storage of food in one place at the burrow – during feeding experiments on wild caught individuals. Another experiment in the same lab supports the view that *Saccostomus* is not an especially agile climber, as compared to *Thallomys* and *Praomys*.

Specimens of *Saccostomus* are readily identified by their size and superficial similarity to dendromurines in the upper dentition, while the lower molars somewhat resemble *Tatera*. The M^1 has a cusp pattern similar to dendromurines with only a single pair of cusps in the anterior loph. The lower molars are lophed and nearly laminate as in *Tatera*, but the lower M_3 is more complex than in *Tatera*. The mental foramen is also diagnostic in *Saccostomus*, being positioned inferiorly and laterally on the mandibular corpus compared to other murines.

Tatera - Gerbils

Tatera is a widespread genus of rodents with at least 7 species occurring in East Africa:

T. boehmi
T. inclusa
T. leucogaster
T. nigricauda
T. philipsi
T. robusta
T. valida

All species prefer loose sandy ground in open well drained areas for constructing

elaborate burrows (Avery 1982; Kingdon 1974; Vesey-Fitzgerald 1966). Burrowing is part of their adaptation to generally xeric conditions where these species are most successful (Dauphin et al. 1994; Kingdon 1974). Some species such as *T. leucogaster* prefer woodlands and bushland areas provided the substrate is suitable (Linzey and Kesner 1997; Vesey-Fitzgerald 1966).

Gerbillus - Egyptian Gerbils

Smaller than *Tatera* these gerbils are common to more xeric environments. There are 60 species according to Musser and Carleton (1993) of which at least three occur in Kenya or Tanzania:

G. harwoodi

G. pulvinatus

G. pusillus

The bulk of the diversity is found in the more arid biomes of North African, Arabia, the Levant and into India. *G. harwoodi* and *G. pusillus* are previously reported for Serengeti (Hendrichs 1969). They prefer loose sandy substrate for burrowing, especially near seasonally flooded areas where deep soil cracks form during the dry season and aid in the construction of their burrows. Burrows are reported to be less complex than in other gerbils (Kingdon 1974). A single specimen of this genus was found (but not trapped) at the edge of the short grass plains by (Misonne and Verschuren 1966).

Macroscelidea

Elephantulus – Elephant Shrews

Three species are known for East Africa

E. rufescens

E. brachyrhynchus

E. fuscipes

Inhabiting open habitats but generally requiring some shrub or fire resistant vegetation to provide cover. Found along drainage lines, bomas etc.

3.4.2 Micromammal niche models

The autecological summaries provided in section 3.4.1 may be distilled into niche models for each of the taxa. A niche model is a numerical summary of the habitat and ecological preferences of that taxa. Niche models, though not termed as such, were developed by Andrews and Nesbit-Evans[3] (Nesbit-Evans et al. 1981) as a component of the taxonomic habitat index. This method of faunal analysis is addressed more closely in Chapter 5, but it is useful to introduce the niche model concept here as it provides a consistent structure for organizing and interpreting the fauna.

Nesbit-Evans et al. (1981) acknowledged five major habitat types in Africa. These are: forest, woodland-bushland, grassland, desert and semi-desert, and wet or swamp habitats. Taxa were ascribed to each of these habitat types according to descriptions of the taxa by Meester and Setzer (1971) and Kingdon (1971, 1974). Each taxon is apportioned to the habitat classes so that the total value across classes for each taxon sums to 1. In their example Nesbit-Evans et al. (1981) score the African elephant, "0.33 forest, 0.33 woodland-bushland, 0.23 grassland and 0.11 semi-desert" (p. 102). This set of closed-sum numerical weights for a given taxon is what I refer to as a niche model.

A shortfall of this method is that no clear guidelines are given for how to distribute the values in the niche model across the habitat classes. The great advantage of this method, however, is that the analyst is forced to produce an explicit model of habitat weightings for the taxon. This is an improvement over subjective and vague statements of habitat preference. Using niche models at least provides a concrete system for discussing differences of opinion about a taxon and for comparing results across studies.

For the current study, niche models are taken from a recent analysis of the Olduvai microfauna conducted by Fernandez-Jalvo et al. (1999). These authors use a slightly different set of habitat categories than did Nesbit-Evans et al. (1981). There are still five classes: forest, woodland, bushland, grassland, and semi-desert. The Aquatic-swamp category has been dropped and the Woodland-bushland category split up. The Olduvai Bed I microfauna overlaps greatly with that of the Serengeti ossuaries, leaving only four genera that were not covered by their ana-

[3]The order of attribution follows the order given in the paper, which happens to be reversed from the order of authorship.

Table 3.8: Niche models for Serengeti rodents.

		Land Cover				
	Code	Forest	Woodland	Bushland	Grassland	Semi-Arid
Arvicanthis	ARVI	0	0	0.25	0.75	0
Aethomys	AETH	0.18	0.25	0.4	0.18	0
Mastomys	MAST	0	0.33	0.33	0.33	0
Mus	MUS	0.35	0.19	0.26	0.2	0
Oenomys	OENO	0.5	0.5	0	0	0
Pelomys	PELO	0	0	0.5	0.5	0
Thallomys	THAL	0	0.5	0.5	0	0
Grammomys	GRAM	0.4	0.35	0.2	0	0.05
Zelotomys	ZELA	0	0	0.2	0.7	0.1
Gerbillus	GERB	0	0	0.2	0.2	0.6
Tatera	TATE	0	0	0.4	0.6	0
Steatomys	STEA	0.2	0.2	0.2	0.2	0.2
Dendromus	DEND	0.05	0.27	0.4	0.28	0
Saccostomus	SACC	0	0.33	0.33	0.33	0
Otomys	OTOM	0	0.25	0.5	0.25	0
Xerus	XERU	0	0.33	0.66	0	0
Heterocephalus	HETE	0	0.2	0.3	0.4	0.1
*Acomys**	ACOM	0	0.17	0.17	0.17	0.5
*Dasysmys**	DASY	0	0	0.2	0.8	0
*Lemniscomys**	LEMN	0	0.1	0.1	0.5	0.3
*Praomys**	PRAO	0.8	0.2	0	0	0

* new niche models not included in Fernandez-Jalvo (1998)

lysis and for which new niche models were constructed: *Acomys*, *Dasymys*, *Lemniscomys* and *Praomys*. Table 5.7 lists the niche models. A version with four habitat classes matching the Level B land cover classes developed for the current study was also constructed and appears in Table 3.9 . This table was derived from the five category table simply by combining woodlands and bushlands. Unfortunately, neither Fernandez-Jalvo et al. (1999) nor Nesbit-Evans et al. (1981) provide detailed definitions for their habitat classes and thus translation to the landcover classes developed for this study may be imperfect. A summary of the autecology of Serengeti small mammals is given in Table 3.10. Bats are excluded because they are very rare in owl assemblages, are rarely preserved in fossil 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 many analyses because either too little is known about their autecology in East Africa (as is the case

Table 3.9: Niche models for Serengeti rodents using 4 land cover classes. Short codes are given to each taxon based on the first four letters of the genus name. These codes are used to symbolize the taxa in subsequent analyses.

		Land Cover			
	Code	Forest	Wood/Bush	Grassland	Bare
Arvicanthis	ARVI	0	0.25	0.75	0
Aethomys	AETH	0.18	0.65	0.18	0
Mastomys	MAST	0	0.66	0.33	0
Mus	MUS	0.35	0.45	0.2	0
Oenomys	OENO	0.5	0.5	0	0
Pelomys	PELO	0	0.5	0.5	0
Thallomys	THAL	0	1	0	0
Grammomys	GRAM	0.4	0.55	0	0.05
Zelotomys	ZELA	0	0.2	0.7	0.1
Gerbillus	GERB	0	0.2	0.2	0.6
Tatera	TATE	0	0.4	0.6	0
Steatomys	STEA	0.2	0.4	0.2	0.2
Dendromus	DEND	0.05	0.67	0.28	0
Saccostomus	SACC	0	0.66	0.33	0
Otomys	OTOM	0	0.75	0.25	0
Xerus	XERU	0	0.99	0	0
Heterocephalus	HETE	0	0.5	0.4	0.1
*Acomys**	ACOM	0	0.34	0.17	0.5
*Dasysmys**	DASY	0	0.2	0.8	0
*Lemniscomys**	LEMN	0	0.2	0.5	0.3
*Praomys**	PRAO	0.8	0.2	0	0

* new niche models not included in Fernandez-Jalvo (1998)

Table 3.10: Autecological summary of taxa. Column heading abbreviations stand for taxon code, body mass, activity patterns, diet, locomotion, habitat summary and niche index. See text for a description of the niche index. Habitat summaries are taken from Kingdon (1974).

Code	Body Mass	Act.	Diet	Loc	Habitat	Niche
GERB	38	N	H/G*	T***	Grassland	1.6
ACOM	23	N	O	T	Dry sav. - rocky	1.86
LEMN	55	D	H	T	Grassl./Dry-moist sav.	1.9
ZELO	60	N	O/I	T	Dry-moist savanna	2.1
DASY	103	N/D	H	T	Marsh/Moist grassland	2.2
ARVI	78	D	H	T/B	Grassl./Dry-moist sav.	2.25
TATE	128	N	H/G	T/B	Grassl./Dry savanna	2.4
STEA	37	N	O	T/B	Grassl./Dry savanna	2.6
MAST	50	N	O/H	T	Dry-moist savanna	2.64
SACC	63	N	H	T	Dry savanna	2.64
DEND	12	N	O	T/A	Grassl./Dry-moist sav.	2.77
THAL	68	N	O/H	A/T	Dry-moist savanna	3
ELEP	43	D	I	T***	Dry-moist savanna	3
AETH	100	N	O/H	T	Dry-moist savanna	3.03
MUSM	10	N	O	T	Dry savanna	3.15
MUST	12	N	O	T	Dry-moist savanna	3.15
PRAO	35	N	O	T/A	Sec. growth/Forest	3.8
CROC	12	N	C	T	N/A	
SUNC	9	N	C	T	N/A	

* C = Carnivore, G = Gramnivore, H = Herbivore, I = Insectivore, O = Omnivore
**B = Burrowing, T = Terrestrial, A = Arboreal
***Ricochetal

for *Suncus*) or there are too many species within the genus for it to be informative (*Crocidura*). Table 3.10 includes a column for a niche index. This number is derived from the niche models for each taxa as, $Niche\,index = \Sigma(R_i \cdot W_i)$ where R is the rank of the habitat class and W is the weighting for that taxon in that habitat. Habitats were ranked from 1 for Semi-arid up to 5 for Forest. 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.

The niche models are introduced here so that they may be compared with the verbal summaries in section 3.4.1. Also, the niche index is the basis for organizing taxa on the axes of the abundance histograms. More xeric adapted species occur toward the bottom and more mesic species toward the top. Shrews and bats are included in the histograms but are not part of this ordering. The following sections examine the presence of taxa compared to previous studies, followed by an examination of the distribution of taxa at different roosts. The causes for the patterning of faunal distributions is taken up in Chapters 4 and 5. Chapter 4 looks at the influence of the accumulating agents, while Chapter 5 examines relationships with ecological variables, and at that point the niche models presented here will be taken up again.

3.4.3 Comparison with previous Serengeti small mammal studies

Table 3.11 compares the published mammalian faunal lists for the Serengeti against the current study. The correspondence across published studies for the region is good, as indicated by coefficient of similarity measures shown in Table 3.12 . Considering all the fauna purported to occur in Serengeti, twelve genera were not recorded in the owl assemblages that I surveyed:

1. *Hystrix*
2. *Pedetes*
3. *Thryonomys*
4. *Cricetomys*

Table 3.11: Comparison of reports on Serengeti rodents and shrews

	Current Study	**Swynnerton 1958**	**Mis. & Ver. 1966**	**Hendrichs 1969**	**Laurie 1971**
Insectivora					
Crocidura	1	1			1
Suncus	1	1			
Macroscelidea					
Elephantulus	1	1			1
Rodentia					
Acomys	1	1	1	1	
Aethomys	1	1	1		
Lemniscomys	1	1	1	1	
Arvicanthis	1	1	1	1	1
Dasymys	1			1	
Mastomys	1	1	1	1	1
Mus	1	1	1	1	1
Praomys	1	1	1	1	
Thallomys	1	1	1	1	1
Zelotomys	1		1		1
Saccostomus	1		1		1
Dendromus	1	1			
Steatomys	1	1			1
Gerbillus	1	1	1	1	
Tatera	1	1	1	1	1
Paraxerus		1		1	
Graphiurus		1	1	1	
Grammomys		1	1		
Pelomys		1	1		1
Rhabdomys		1			
Lophuromys		1	1	1	
Tachyoryctes		1	1		1
Otomys		1			
> 400 grams					
Hystrix		1	1	1	
Pedetes		1	1	1	
Thryonomys		1			
Cricetomys			1		
Total	**18**	**26**	**20**	**15**	**13**
Total < 400 g	**18**	**23**	**17**	**13**	**13**

Table 3.12: Coefficients of similarity between reports on Serengeti small mammals. The upper right portion of the matrix shows the Jaccard index and the lower left the Czekanowski index (see Section 1.2.5 for details). Values closer to 1 indicate greater similarity across studies. The current study (Reed 2003) shows the greatest similarity to Laurie 1971 according to both indices.

	Reed 2003	**Swynnerton 1958**	**Mis. & Ver. 1966**	**Hendrichs 1969**	**Laurie 1971**
Reed	-	0.500	0.444	0.417	0.524
Swynnerton	0.667	-	0.586	0.519	0.345
Mis, & Ver.	0.615	0.739	-	0.591	0.375
Hendrichs	0.588	0.683	0.743	-	0.217
Laurie	0.688	0.513	0.545	0.357	-

5. *Paraxerus*
6. *Graphiurus*
7. *Grammomys*
8. *Pelomys*
9. *Rhabdomys*
10. *Otomys*
11. *Lophuromys*
12. *Tachyoryctes*

Many of these omissions can be attributed to body size and activity patterns. *Hystrix*, *Pedetes, Thryonomys and Cricetomys* all exceed the maximum prey size for barn owls and likely the spotted eagle owls as well. *Paraxerus* lies at the upper limit of the barn owl prey size range and is diurnal. *Graphiurus* is an agile, scansorial species, so its absence may be attributed in part to not inhabiting the open vegetation that is the preferred hunting habitats of the owls. *Rhabdomys* is closely related to *Lemniscomys* and *Arvicanthis*, grazing species with whom they are presumed to compete. Thus *Rhabdomys* tends to be limited to highlands and sub-alpine zones that were not sampled by any of the roosting locations (Kingdon 1974). Similar conditions may hold for *Otomys*, which too is associated with more mesic or montane environments. The absence of the remaining genera is

unexplained. *Grammomys* is well within the prey size range for an owl and though it often prefers moister habitats, it has been reported from dry scrub areas such as the Athi Plains of Kenya (Kingdon 1974). *Lophuromys* is expected to inhabit mesic grasslands free of closed canopy forest. Its absence from roost 44 in the north is somewhat surprising. The last two genera, *Tachyoryctes* and *Pelomys* were absent from the current study but were recorded by Laurie. *Tachyorcytes* is fossorial and thus expected to be rare in owl accumulated assemblages. Laurie reports only a single specimen out of a combined sample of 1267 individuals. *Pelomys* inhabits rank grasslands and shrub vegetation associated with river margins. Its habitat is sampled by the owls in the current study and is expected to occur. It is rare (three specimens in Laurie's sample) and may be absent by chance.

Not surprisingly the current study has overlaps greatly with that of Laurie (1971) who also examined owl pellet assemblages. However, seven genera appear in the current study that were not observed in the pellets collected by Laurie:

1. *Suncus*
2. *Acomys*
3. *Aethomys*
4. *Dasymys*
5. *Lemniscomys*
6. *Praomys*
7. *Dendromus*

Suncus is a small shrew that differs from species of *Crocidura* in having one additional, and very small, upper unicuspid. The genus was recovered from roosts 3, 13 and 8. roost 3 is very near to Laurie's Masai Kopjes site and may be expected there, so its absence from Laurie's study is unexpected. At 1% abundance overall this genus may have been missed in Laurie's collections because it is too rare. *Acomys* and *Lemniscomys* were absent from pellets in Laurie's study but were caught in live traps near the roosts. As mentioned earlier *Lemniscomys* is diurnal, and even if abundant in the biocoenosis, appears rarely in the owl accumulated assemblages. *Acomys* is also rare in owl assemblages, perhaps because it

has stiff, spine-like dorsal hairs that may discourage owls. Thus the absence of these species from Laurie's study is not surprising, but it is rewarding to discover them in current study.

Though never dominant, *Dendromus* was recovered from every roost in the current study at abundances ranging from 2-10%. The molars bear a superficial similarity to *Steatomys*, and confusion with that genus is the only likely explanation for its absence from Laurie's study. The remaining genera, *Aethomys, Dasymys and Praomys* are all rare and appear in areas not sampled by Laurie.

In comparing the results with trapping studies it is clear that the owl assemblages are biased toward small, nocturnal rodents, but despite this they still obtain predominantly diurnal species (e.g. *Arvicanthis* and *Lemniscomys*), and manage to catch most of the known diversity at the generic level.

3.4.4 Patterns of faunal association between roosts

At this point we can turn to an examination of the distribution of species across the different roosting sites. One strategy for exploring faunal relationships would be to use the abundance histogram for the total assemblage given in Figure 3.8 as a benchmark against which the abundances at each roost could be compared. One could overlay the histogram from a single roost on top of the combined histogram and see whether each taxa fell below or above the expected abundance value. A similar such test is made using Pearson X^2 tests of independence (hereafter just chi-square tests) for each taxon taken one at a time across all roosts. Each of the nineteen tests (bats are excluded) asks whether the pattern of abundance across all roosts for that taxon differs significantly from random. The observed frequencies for each taxon across the roosts are compared against the margin totals and tested for significant departure from expectations. Significant values indicate the taxon is strongly associated with at least one roost, and not randomly distributed across the roosts. Table 3.13 lists the results, first with roost 12 omitted and then with all roosts included. Most taxa are not randomly distributed. The taxa: *Acomys, Elephantulus, Lemniscomys, Mus cf. musculoides, Praomys, Zelotomys, Dendromus* could not be distinguished from random in their distribution across roosting sites. The remaining genera are associated with one or more roosts. For those taxa that were found to be significantly associated with at least one roost, I explored the associations in more detail by constructing a table of partial chi-squares.

Table 3.13: Tests of independence by species made across all roosts. Each row shows chi-square values from a test of independence made on the hypothesis that each species is independently distributed across all roosts. The first column lists results with roost 12 excluded, the second column shows the probability of the observed result (d.f. = 6). Results for tests made on all roosts are given in the next two columns (d.f. = 7). Significant results are indicated in the last column. Alpha is adjusted for 19 unplanned comparisons; alpha = 0.05/19 = 0.0026.

Taxa	**chi-square rst12 excl.**	**p**	**chi-square all roosts**	**p**	**sig**
Crocidura	53.8847	0.0001	54.0912	0.0001	**
Suncus	22.2840	0.0011	22.9597	0.0019	*
Elephantulus	13.1385	0.0409	13.4671	0.0615	NS
Acomys	6.4203	0.3778	12.5804	0.0830	NS
Aethomys	63.8513	0.0001	65.1877	0.0001	**
Arvicanthis	90.7075	0.0001	93.6714	0.0001	**
Dasymys	62.2326	0.0001	63.5011	0.0001	**
Lemniscomys	14.4134	0.2530	14.6825	0.0403	NS
Mastomys	85.3429	0.0001	86.1863	0.0001	**
Mus cf. musculoides	19.2542	0.0038	19.4698	0.0068	NS
Mus cf. triton	54.6490	0.0001	57.0982	0.0001	**
Praomys	12.2698	0.0562	12.5817	0.0830	NS
Thallomys	182.6462	0.0001	187.0452	0.0001	**
Zelotomys	7.6929	0.2615	8.1693	0.3179	NS
Saccostomus	45.3223	0.0001	45.0569	0.0001	**
Dendromus	14.7947	0.0219	14.8516	0.0379	NS
Steatomys	83.0145	0.0001	83.4458	0.0001	**
Gerbillus	56.8246	0.0001	58.8900	0.0001	**
Tatera	162.1121	0.0001	166.7946	0.0001	**

NS:Chi-square by row test non-significant at the level of significance alpha=0.0026
*:Chi-square by row significant at the level of significance alpha=0.0026
**:Chi-square by row significant at the level of significance alpha=0.0001

Table 3.14: Contingency table of fauna MNI. Taxon codes are from the first for letters of the taxon name.

	Rst3	Rst4	Rst12	Rst13	Rst18	Rst23	Rst24	Rst44	MNI
CROC	104	89	9	63	40	5	73	27	410
SUNC	8	0	0	4	1	0	0	0	13
ELEP	0	0	0	1	1	2	0	0	4
ACOM	1	0	1	2	1	0	0	1	6
AETH	0	0	0	0	0	0	1	5	6
ARVI	5	21	0	3	4	14	1	17	65
DASY	0	0	0	0	0	0	0	4	4
LEMN	4	3	1	2	5	6	4	1	26
MAST	9	35	1	4	2	21	4	10	86
MUSM	21	14	2	11	9	7	5	0	69
MUST	20	13	0	13	21	3	1	1	72
PRAO	1	0	0	0	2	0	0	1	4
THAL	7	2	5	4	3	26	0	0	47
ZELO	3	6	0	5	1	1	0	1	17
SACC	6	7	1	2	7	11	0	0	34
DEND	24	33	2	26	9	4	17	4	119
STEA	32	44	4	64	14	2	93	7	260
GERB	3	1	0	15	3	0	29	0	51
TATE	1	7	0	4	3	3	66	3	87
Total	249	275	26	223	126	105	294	82	1380

Table 3.15: Table of partial chi-squares for faunal MNI. Cell values indicate the result of a chi-square test of independence between the taxa and the roost. (+) indicate associations and (-) dissociations. Significance levels are given at the bottom of the table. Taxon codes are from the first for letters of the taxon name.

	Rst3	Rst4	Rst12	Rst13	Rst18	Rst23	Rst24	Rst44
CROC	(+) ***	(+) NS	(+) NS	(-) NS	(+) NS	(-) ***	(-) **	(+) NS
SUNC	(+) ***	(-) NS	(-) NS	(+) NS	(-) NS	(-) NS	(-) NS	(-) NS
AETH	(-) NS	(-) NS	(-) NS	(-) NS	(-) NS	(-) NS	(-) NS	(+) ***
ARVI	(-) **	(+) **	(-) NS	(-) **	(-) NS	(+) ***	(-) ***	(+) ***
DASY	(-) NS	(-) NS	(-) NS	(-) NS	(-) NS	(-) NS	(-) NS	(+) ***
MAST	(-) *	(+) ***	(-) NS	(-) ***	(-) **	(+) ***	(-) ***	(+) **
MUST	(+) **	(-) NS	(-) NS	(+) NS	(+) ***	(-) NS	(-) ***	(-) NS
THAL	(-) NS	(-) **	(+) ***	(-) NS	(-) NS	(+) ***	(-) ***	(-) NS
SACC	(-) NS	(+) NS	(+) NS	(-) NS	(+) **	(+) ***	(-) ***	(-) NS
STEA	(-) ***	(-) NS	(-) NS	(+) ***	(-) **	(-) ***	(+) ***	(-) **
GERB	(-) **	(-) ***	(-) NS	(+) **	(-) NS	(-) *	(+) ***	(-) NS
TATE	(-) ***	(-) ***	(-) NS	(-) ***	(-) *	(-) NS	(+) ***	(-) NS

(+): observed frequency > expected frequency
(-): observed frequency < expected frequency
NS: Chi-square by cell test non significant at the level of significance alpha=0.100
*: Chi-square by cell test significant at the level of significance alpha=0.100
**: Chi-square by cell test significant at the level of significance alpha=0.050
***: Chi-square by cell test significant at the level of significance alpha=0.010

Table 3.14 presents the basic MNI contingency table that was tested. The cells of Table 3.15 shows the results of the partial chi-square tests based on MNI for each taxon at each roost. MNI was used as a measure of abundance in order to avoid the effects of sample size inflation. The tests were replicated using NISPn with qualitatively similar results (not shown) though some taxa are more significant as a result of the larger sample sizes.

Some patterns are readily apparent in the partial chi-square table. For example the three genera at the bottom of the list, *Steatomys*, *Gerbillus* and *Tatera* all have a very similar patterns of distribution. Other species may also covary but it is difficult to find these patterns by inspection of the table. A better method is to use correspondence analysis (CA) to ordinate the data in order to better visualize the relationships. CA helps show the geometry of associations but it does not test the significance of the association, as does the chi-square table. Using the two together provides a useful means of exploring the data.

The same contingency table that was used for the chi-square tests is used for the correspondence analysis shown in Figure 3.10 , though percent MNI was employed instead of raw MNI. This has the effect of giving equal weight to each of the roost regardless of sample size (Greenacre and Vrba 1984). Similar results are obtained using MNI, NISPn or percent NISPn. The upper left quadrant of Figure 3.10a shows a close association between roost 24 and the genera *Gerbillus*, *Tatera* and to a lesser extent *Steatomys,* as was noted in the table of partial chi-squares. The chi-squares indicate that these associations are significant. This same pattern is apparent in the histograms.

The abundance histograms in Figure 3.7 also show *Thallomys* to be markedly abundant at roost 23. This association appears in the CA and is highly significant in the chi-square table. *Arvicanthis*, *Saccostomus*, *Mastomys* are closely grouped and also significantly associated with roost 23.

Arvicanthis and *Mastomys* are significantly associated with roost 44 as are two species which are unique (or nearly so) to roost 44 *Dasymys* and *Aethomys*. *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 the third axis indicating that it differs in its own way from roosts 24 and 23. Axes 2 and 3 are nearly equivalent in their information content, 22 and 21% respectively, so the differences in roost 44 are as significant as those for 24 or

Figure 3.10: Correspondence analysis of %MNI values, The first two axes explain 64% of the inertia. The first three axes together explain 82% of the inertia. Red diamonds indicate roosts, and blue circles indicate taxa. Taxa codes are from the first four letters of the taxon name.

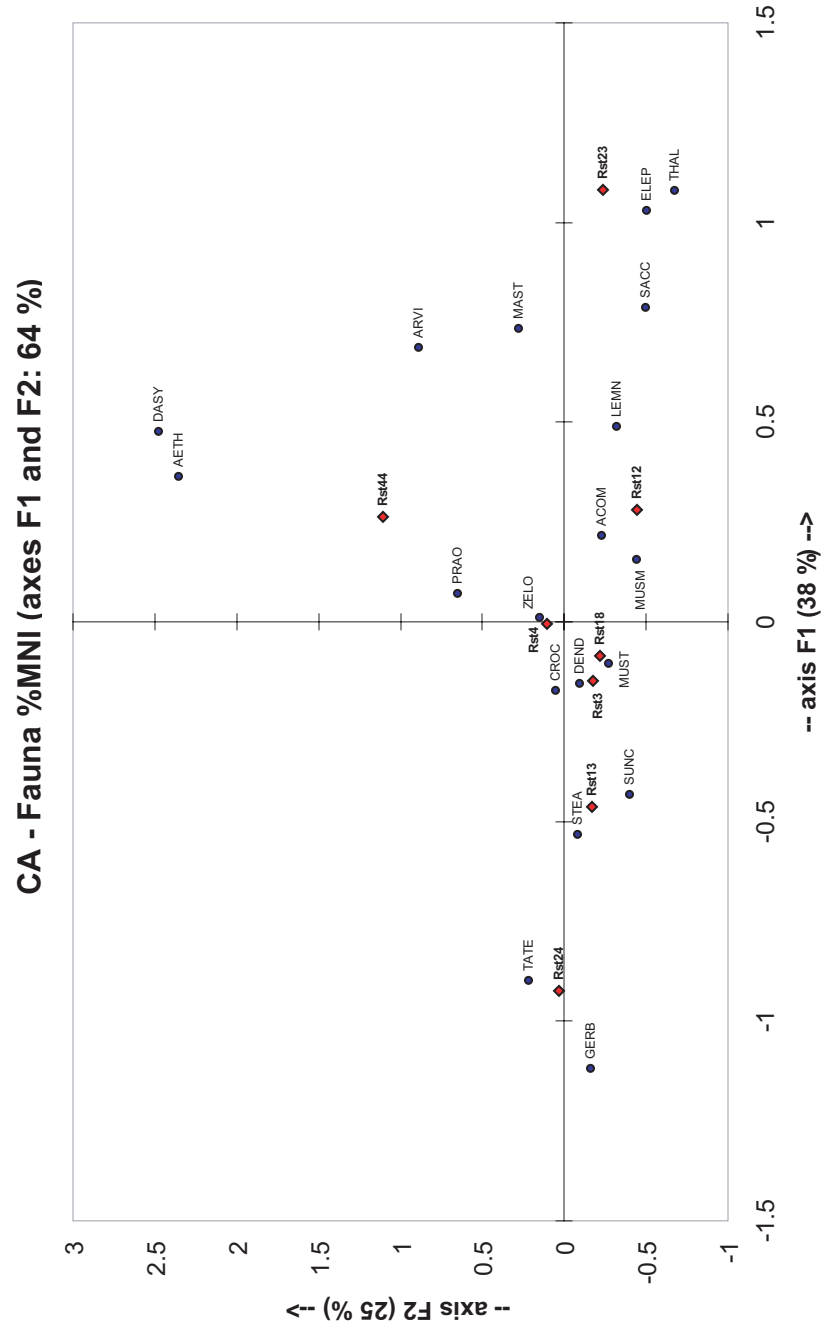
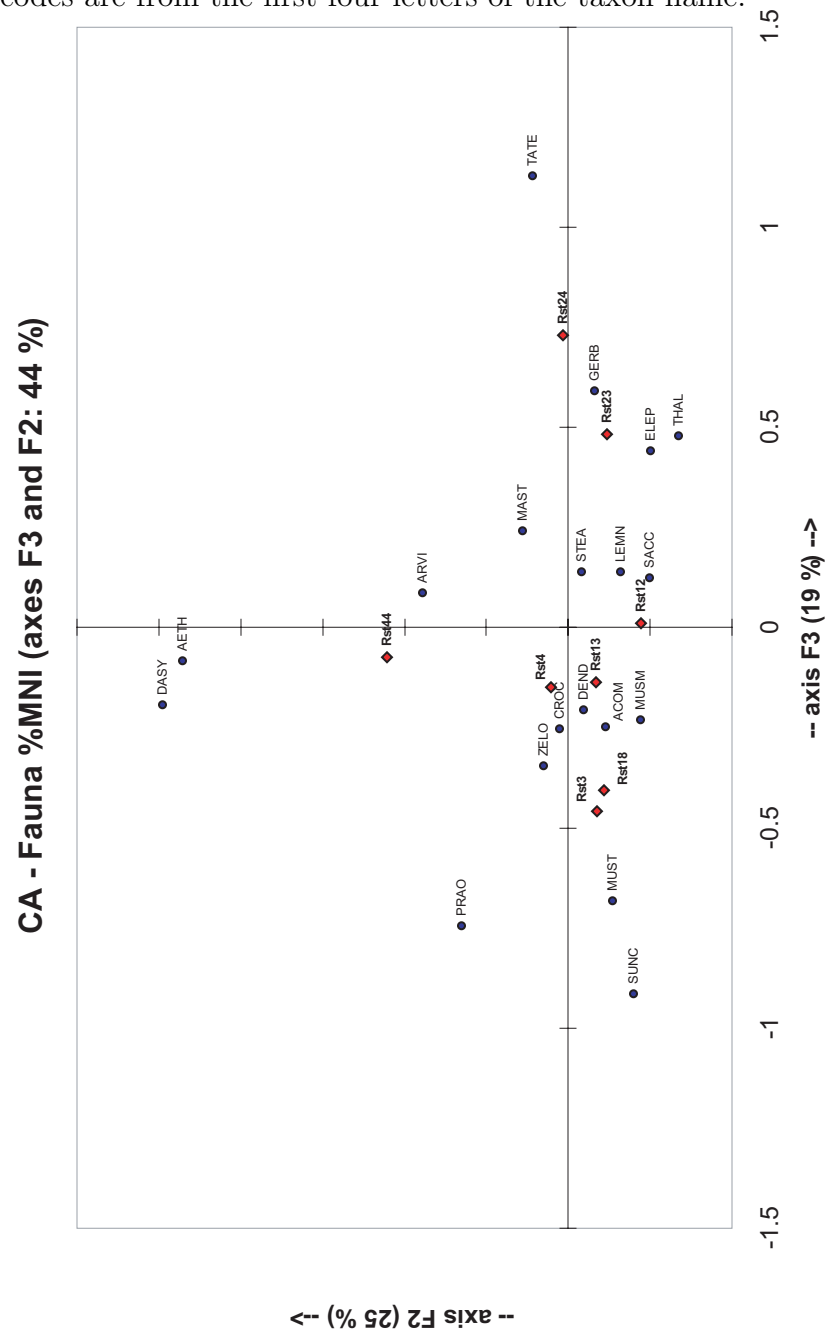


Figure 3.11: Correspondence analysis of %MNI values. Axes 2 and 3 explain 44% of the inertia. Red diamonds indicate roosts, and blue circles indicate taxa. Taxa codes are from the first four letters of the taxon name.



23.

The remaining roosts and taxa are more tightly clustered together though there are some interesting subtleties to their arrangement. Roost 12 lies slightly apart and closer to roost 44 and 23 in the upper right quadrant of Figure 3.7a, indicative of the common presence of *Thallomys*. Roosts 3 and 18 have very close association with each other and with the taxa *Zelotomys* and *Acomys* those these associations are not statistically significant. Roosts 3 and 4 are also associated with roosts 13 and 18 but opposite each other, with 4 having a greater affinity to the more closed roosts such as 12, 23, 18, while 3 leans in the direction of 24.

In summary, correspondence analysis and the chi-square tables show a large cluster around the origin, and three or four roosts that are outlying. Roost 24 is distinct and with it are associated *Gerbillus*, *Tatera* and *Steatomys*. Roost 23 represents the opposite extreme, with *Thallomys*, *Saccostomus* and positively associated here. These taxa also show strong dissociation from roost 24. Roost 44 occupies a third axis of variation, with *Dasymys* and *Aethomys* uniquely (or nearly so) associated here. *Arvicanthis* and *Mastomys* are very significantly associated with both roosts 23 and 44 while being strongly dissociated with roost 24. Finally roost 12 appears falls toward roost 23, but it is closer to the origin. The general pattern of faunal distribution are consistent regardless of whether CA is conducted with MNI or NISPn. Normally CA gives added weight to larger samples, thus roosts, and roost 13 will have more influence on the topology of the constellation than roost 12. Using proportional abundances in the contingency matrix given to the CA will induce even weightings between the roosts. The result is a shift in the distances between some points but the overall pattern remains consistent.

Given these differences in the faunal composition between roosts, what are the probable causes? Two sources should be addressed first, sample size differences and potential biases induced by different taphonomic modes. The sample size issue is address in the remainder of this chapter while taphonomic modes are discussed in Chapter 4.

3.4.5 Correlations of sample size and faunal abundances

Correspondence analysis and chi-square tests were selected in part because they do not assume equality in sample sizes. The tests are made against expected values intrinsic to the data sets rather than *a priori* probability distributions. However

Table 3.16: Rank correlations between abundance and sample size in *Acomys* and *Gerbillus*.

Roost	MNI	*GERB*	*ACOM*
12	26	0.00%	3.85%
44	82	0.00%	1.22%
23	106	0.00%	0.00%
18	129	2.33%	0.78%
13	223	6.73%	0.90%
3	253	1.19%	0.40%
4	275	0.36%	0.00%
24	294	9.86%	0.00%
Spearman's rho		0.756	-0.732
probability		0.030	0.039
Kendall's tau		0.567	-0.643
probability		0.050	0.026

the associations that are detected have many potential causes. Sample size may be one of them. 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. A simple precaution is to test rank correlations of taxon abundance against sample size. Pearson's and Kendall's rank correlation tests were conducted between %NISP, %NISPn and %MNI for all taxa. At the 0.05 significance level, the results were non-significant for all taxa save two, *Acomys* and *Gerbillus*. Correlation results for these taxa are given in Table 3.16 . The cause of the correlation is not readily apparent. In both cases the probability values are only weakly significant and removing the smallest sample, roost 12, also removes the correlation as shown in Table 3.17 . Grayson (1984) notes that small samples are often the cause of spurious correlations.

3.5 Conclusions

The faunal analysis reveals an assemblage of 20 taxa that is in accord with what has previously been reported for the Serengeti region. No species occur in the assemblages that were not previously reported but a few that are known to occur in Serengeti are not found in this study. The most apparent biases are the absence

Table 3.17: Rank correlations between abundance and sample size in *Acomys* and *Gerbillus*. Roost 12 excluded.

Roost	MNI	*GERB*	ACOM
44	82	0.00%	1.22%
23	106	0.00%	0.00%
18	129	2.33%	0.78%
13	223	6.73%	0.90%
3	253	1.19%	0.40%
4	275	0.36%	0.00%
24	294	9.86%	0.00%
Spearman's rho		0.667	-0.593
probability		0.102	0.161
Kendall's tau		0.488	-0.514
probability		0.124	0.105

of larger taxa such as *Pedetes*, *Hystrix* and *Thryonomys*, as well as some diurnal species. These omissions are consistent with the habits of the accumulating agent, as is discussed in Chapter 4. Not surprisingly, the best agreement in taxonomic representation was found with Laurie's (1971) owl pellet study.

Tchernov (1992) has argued that habitat selection is very strong in owls, especially the barn owl, such that comparisons between modern barn owl assemblages will show strong similarities in faunal composition due to the owl concentrating its hunting effort in a particular microhabitat. His position has been that diversity appears in fossil assemblages through the activity of a guild of raptors contributing to the assemblage. The proposition that owls collect identical assemblages regardless of the surrounding habitat is not supported by these data. Differences appear between roosting sites. As yet the cause of the differences is not established but the patterning between roosts suggests associations with the surrounding habitat. Comparing species abundances with their ecological proclivities as summarized in this chapter we find that semi-arid and dry savanna species such as *Gerbillus*, *Tatera*, and *Steatomys* are strongly associated with roost 24 which lies in the mid-grass plains and has the lowest mean annual precipitation. Conversely more mesic woodland species such as *Thallomys*, and *Elephantulus* are associated with roost 23 which occurs amidst the woodlands. *Dasymys* is a specialist that favors wet environments. It appears at roost 44 which is one of the only roosts with perennial

water that can sustain marsh environments.

The distribution of taxa may be influenced by many factors, including intrinsic correlations that do not have ecological meaning. Tests of rank correlations with sample size reveal two taxa whose abundances were weakly correlated with sample size. Removing the very small sample at roost 12 was sufficient to remove the correlation. Roost 12 has a similar effect on the relationship between sample size and diversity as will be seen in Chapter 5.

Chapter 4

Taphonomy

4.1 Introduction

Taphonomic models provide the background to questions of evolutionary biology addressed by the fossil record. In one respect this entire thesis lies in the realm of taphonomy – the study of the processes that produce fossil accumulations, or in the words of its christener, "the study of the transition ... of animal remains from the biosphere into the lithosphere" (Efremov 1940, p. 85). Taphonomy has many domains, this chapter examines site formation processes under the influences of two sympatric species of owl inhabiting and roosting in an open environment. These two species, the Barn Owl and Spotted Eagle Owl (from here on just barn owls and spotted eagle owls) are likely the most important agents for accumulating dense microvertebrate assemblages in Africa. Examining their roosting and trophic behavior in a sympatric context provides the most direct comparison of the two species yet published. Owls are common inhabitants of caves, for which there is a growing body of literature regarding their taphonomy, including the recent seminal work by Andrews (1990). Their activities outside of caves is poorly understood by comparison and is explored here.

A general structure for taphonomic models developed by Gifford (1981) begins with a biologic stage followed by biostratinomic, diagenetic, recovery and analytic stages. The biologic stage refers to the assemblage of living organisms, the biostratinomic phase to the processes that alter the assemblage at the time of death and after, up to the point of surface contact and burial at which time diagenetic processes take over. Diagenesis – chemical and physical alteration while in contact

with sediment – continues until the assemblage is recovered and analyzed (the last two stages). The biostratinomic phase is unique and particularly important in the analysis of terrestrial microvertebrate assemblages because dense fossil aggregations may result from the activities of predators (Andrews and Nesbit-Evans 1983; Andrews 1990; Brain 1981; Davis 1959; Denys 1985; Mayhew 1977; Mellet 1974).

The processes following the death of an animal can be divided into abiotic and biotic categories, with a wide variety of possible sequences. Animals may be killed in pit traps (abiotic) then scavenged (biotic) and deposited in aggregate assemblages derived from scats (biotic). Subsequently, the scats may be transported, size sorted and distributed by water (abiotic). The permutations of possible scenarios is large, but in the case of microvertebrate assemblages the focus is on aggregating phenomenon, for which there is a finite and relatively small number of postulated processes. Micromammal bones are fragile and their appearance in fossil assemblages is most common under conditions where the material accumulates in dense quantities and is protected from weathering, trampling and fluviatile activity (Andrews 1990; Korth 1979). The involvement of predators as accumulating agents for fossil assemblages is well supported by comparison to modern analogues in which modifications such as bone breakage patterns match what is observed in many fossil assemblages (Andrews and Nesbit-Evans 1983; Andrews 1990; Fernandez-Jalvo and Andrews 1992). The involvement of predators is further supported by fossilized coprolites and owl pellets (Denys 1987; Gawne 1975). Those dense microvertebrate assemblages characterized by little to moderate bone breakage, minimal and predictable loss of skeletal elements, slight to moderate bone surface modification such as rounding salient edges (i.e. Andrews [1990] modification categories 1 and 2) fit the characteristics observed in modern owl assemblages, especially the larger species of owls. Well preserved, dense concentrations of microfaunal remains, fossil *and modern,* characterize many caves, karst fissures, and rock shelters that harbor owls; and it is the owls that are implicated as the primary collecting agent for these assemblages (Andrews 1990; Brain 1981; Davis 1959). For this reason, the interrelations between modern owls and micromammals has garnered interest as a system for understanding the background to fossil and subfossil micromammal assemblages. Given the roosting proclivities of owls, emphasis has rested on caves (Andrews 1990; Brain 1981), however owls can also produce dense assemblages in open-air settings (e.g. Andrews 1983; Sabatier 1982) but

actualistic research on this aspect of their taphonomy has been limited.

The larger species of owl are efficient predators of small mammals (Guerin 1928). They routinely ingest the entirety of their prey, either whole or in parts, enzymatically digest the flesh and some bone then regurgitate the undigested prey remains in a compact bolus, called a pellet (Denbow 2000; Glue 1967; Grimm and Whithouse 1963; Raczynski and Ruprecht 1974; Reed and Reed 1928). The undigested elements consist of durable materials such as bones, fur, feathers, chitin, seeds etc. too large to pass through the small, superiorly positioned pyloris (Denbow 2000; Grimm and Whithouse 1963). Pellets may contain the remains of one or more prey with larger prey taking up the whole of one pellet or even spread among multiple pellets (Raczynski and Ruprecht 1974; Yom-Tov and Wool 1997). Approximately one to two pellets are ejected per meal or roughly 1.4 pellets per day (Dodson and Wexlar 1979; Hoffman 1988). Given time, the accumulated pellets fall beneath a roost, disaggregate and form carpets of bone (personal observation).

Taphonomic stability is a key assumption when analyzing microfauna, especially when exploring environmental change – is the change a function of climate or a shift in taphonomic mode, such as the accumulating agent? Throughout the literature on micromammal taphonomy one frequently encounters the refrain that it is crucial to diagnose the predator responsible for generating an assemblage (Andrews and Nesbit-Evans 1983; Andrews 1990; Fernandez-Jalvo et al. 1998; Hoffman 1988; Marean et al. 1994; Matthews 2000). The importance given to predator diagnosis stems from the recognition that the predators' prey preferences, activity patterns, and hunting habits will bias species composition of the resulting prey assemblage. The resulting bias is expected to impact phylogeographic interpretations, analysis of biodiversity, and chemical alterations of bone in relation to diagenesis (Dauphin et al. 1997; Denys et al. 1997; Fernandez-Jalvo and Andrews 1992; Fernandez-Jalvo et al. 1998), thereby prompting investigations into methods for distinguishing different predator assemblages (Andrews 1990; Dauphin et al. 1997; Dodson and Wexlar 1979; Hoffman 1988; Kusmar 1990; Saavedra and Simonetti 1998). While it is certainly beneficial to develop as complete and comprehensive a taphonomic understanding as possible for any fossil assemblage this research overlooks two important questions. First, how sensitive or robust are the analytical methodologies in distinguishing ecological change independent of species change? Diurnal and nocturnal predators may return prey assemblages that differ in the species present

but with species representing very similar ecology and habitat preferences because they were sampled from the same area. Secondly, are there predators that have a high degree of trophic overlap that may be considered taphonomically equivalent? A preliminary analysis by Brain (1981) on small pellet assemblages from a sympatric barn owl and spotted eagle owl showed very close similarity between the two, suggesting they may create assemblages that are identical in faunal composition and abundance.

In this chapter I present field observations on the roosting and trophic habits of these two sympatric species of owl in the Serengeti region of northern Tanzania that further corroborate the hypothesis that they produce similar assemblages. The barn owl and spotted eagle owl are found to segregate by roosting habit. This has important implications for the taphonomy of open-air sites or those derived from small fissures and tree stumps. An analysis of faunal composition between roosting types is also conducted and indicates only slight differences in relative abundances across roosting types, in turn implying that species abundances may be robust to certain taphonomic circumstances.

4.2 Methods

Owl 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[1] as well as hollowed trees and woodland thickets.

Many of the roosts had owls in residence. Only those observations in which a clear visual identification could be made are reported. Barn owls were identified by their white face disk; dark eyes; orange-buff colored uppers with dark speckles or patches; and white, or lightly spotted breasts. Eagle Owls have uppers of buff-grey with irregular dark grey or beige patches; yellow eyes; grey breast with bars and 'ear' tufts. These two species as they appear in northern Tanzania are similar in size, with the spotted eagle owls perhaps just slightly larger. Faunal analysis was conducted on eight roosts across ecotones in Serengeti National Park. Methods of identification and faunal analysis are described in Chapter 3: Fauna.

[1] see Section 4.4 for a description of the geological features.

Table 4.1: Roost preference by species

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

4.3 Results

Sixty-one owl roosting sites were discovered in the course of the survey; 8 in or near Tarangire National Park, 1 on the escarpment above Lake Manyara National Park, 6 in the Ngoorongoro Conservation Area, 46 in or near the Serengeti National Park. Of the 61 roosts, 29 had one or more owls in residence: The Spotted Eagle Owl, *Bubo africanus*, was observed roosting in 10 locations and the Barn Owl, *Tyto alba* at 19 as illustrated in Figure 4.1. Roosts were always monotypic and the two species appear to exploit very different types of roosts as discussed below.

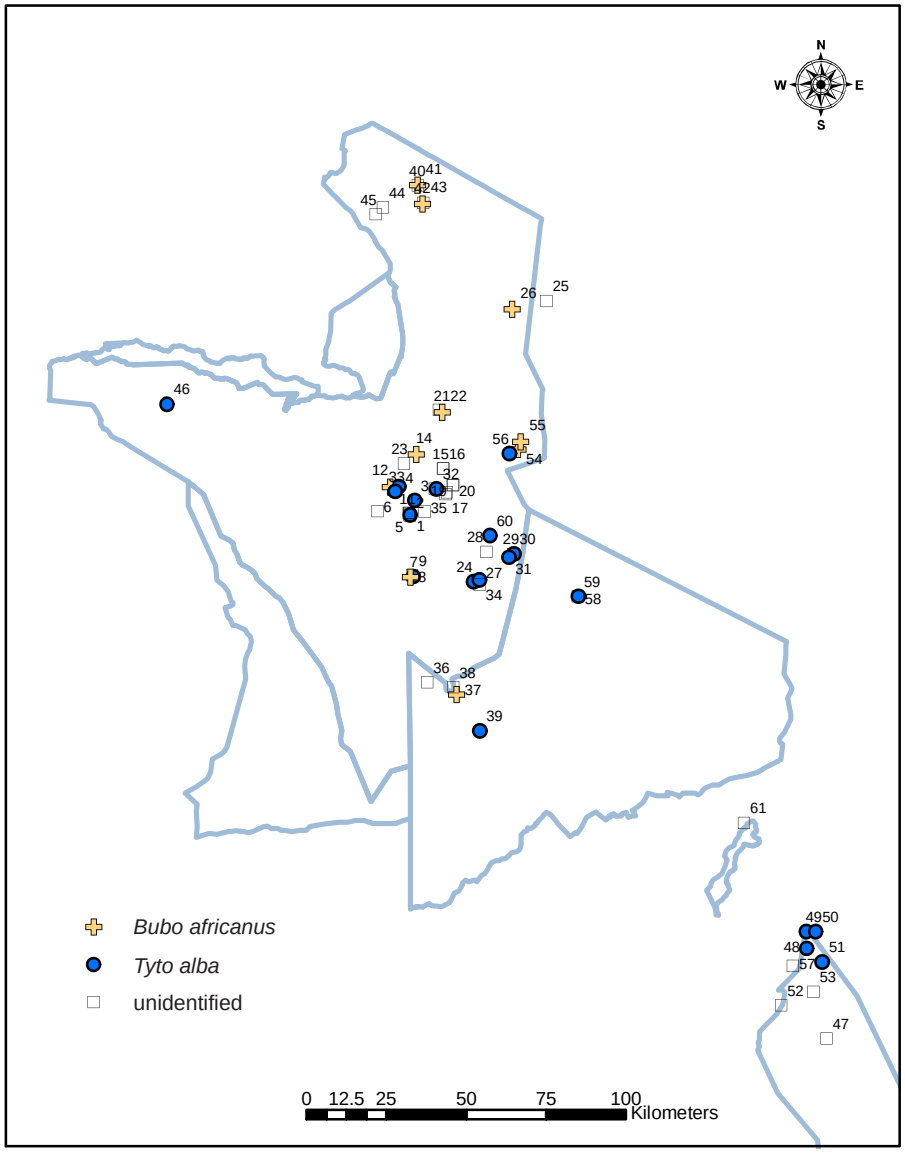
4.3.1 Roosting Type

Spotted eagle owls and barn owls were seen to occupy very different types of roosting environments. The former was observed to use open roosts: tree crowns and rocky outcrops. Barn owls were observed to occupy closed roosts: for example sequestered in the twilight regions of rock fissures or the hollowed interior of trees. In three cases barn owls were observed in open type roosts. Table 4.1 presents a contingency table of owl roosting preferences from which we can safely reject the hypothesis that the two owls utilize the same types of roosts (chi-square test of independence, $X^2 = 18.87$, Yate's corrected chi-square test of independence, $X^2_{adj} = 15.5348$, $p < 0.01$; Yate's corrected G test of independence, $G_{adj} = 17.768\, p < 0.01$).

4.3.2 Prey Preference

Prey selectivity is a poorly understood source of taphonomic bias. Prey selectivity by owls is difficult to assess in modern samples as it requires independent measurement of prey abundance beyond what is observed in the owl's diet (Andrews 1990). This study did not attempt to measure prey abundance at large, nor is it

Figure 4.1: Owl roosting sites in northern Tanzania.



possible to verify that the bone assemblages analyzed in this study were generated by a single species of owl. Instead I compare prey abundance between closed and open roost types. The pattern of roosting suggests segregation between barn owls and spotted eagle owls in the use of closed versus open roosts respectively. However, other owls large enough to prey on small mammals are known to occur in the study area, including: Verreaux's eagle owls, *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 (Fry et al. 1988; Vernon 1972). It is possible that all of these species may have contributed to the open roosts analyzed here though it is considered unlikely for various reasons. First, *Bubo africanus* is the most abundant, open roosting owl in the study area based on the observations made during this study. Second, of the eight roosts for which faunal analysis was undertaken, half had owls in residence and the species followed the predicted pattern (three barn owls occurring in cavities, one spotted eagle owl tree roosting.) Third, the prey items are all in the size range expected for *Tyto alba* and *Bubo africanus* with no evidence of larger species, especially hedgehogs, that are preferred prey of *Bubo lacteus* (Fry et al. 1988). For these reasons it is reasonable to tentatively presume that cavity roosts contain prey primarily accumulated by barn owls, and that open roosts are primarily the work of spotted eagle owls.

The fauna from eight roosts was analyzed, three open roosts and five cavity roosts. A total of 20 different mammalian taxa were identified from the eight roosts, as shown in Table 4.2. All the species that appear in cavity roosts also appear in open roosts with the exception of two, *Aethomys hindei* and *Dasymys incomtus*. Both are rare species (first and fifth rarest respectively) so the difference cannot be distinguished from chance. To better detect subtle differences in relative abundances, single classification analysis of variance (ANOVA) was performed on each species with the taphonomic context (cavity vs. open) serving as the treatment (Sokal and Rohlf 1995). On the raw MNI data, only *Crocidura spp.* approach significant difference. However, sampling effort is not constant across roosts. Cavity roosts have consistently larger samples than do open roosts, a bias that will influence the ANOVA. MNI values were converted to proportions (pMNI) in order to standardize the means, and an arcsine transformation, $x_{tr} = sin^{-1}\sqrt{x}$, was used to standardize the variance (Sokal and Rohlf 1995). Following the trans-

formations, *Lemniscomys*, showed a strong bias toward open roosting sites (p = 0.000191). Two other taxa, *Saccostomus* and *Thallomys* also exhibit suspiciously low values, 0.020615 and 0.019351 respectively. Differences in relative abundance may also result from differences in vegetation. Examining the spatial distribution of the roosts, two are obvious outliers, roosts 24 and 44, excluding these yields a similar pattern of results though all the values are less significant.

4.4 Review of the predators

Discussion of the results will benefit from a short review of the two predator species. Despite being one of the best studied owl species, comparatively little is known about the African barn owl subspecies and even less about the spotted eagle owls. The African Barn Owl, *Tyto alba affinis* and the Spotted Eagle Owl, *Bubo africanus* are sympatric over broad expanses of sub-Saharan Africa and differ in their ethology, yet pellet analyses reveal very similar feeding niches. The discussion below begins with a review of the two species emphasizing studies based in Africa. From there I discuss taphonomic implications of the results presented above.

4.4.1 Barn Owls, *Tyto alba affinis* Blyth

Tyto alba (Scopoli) is a cosmopolitan species present on every continent save Antarctica, generally at lower latitudes but inhabiting the temperate areas of North America and Europe (Mikkola 1983). Several subspecies are described across its range. The nominate subspecies, *Tyto alba alba* (Scopoli) occurs in southern-central Europe including the UK (Mikkola 1983). The African subspecies, *T. a. affinis* Blyth occurs in sub-Saharan Africa, Bioko, Zanzibar and Pemba. It is roughly the same size or perhaps slightly larger as shown by measurements summarized from the literature and listed in Table 4.4.

Roosting Habits Long term studies on barn owls reveal they are capable of exploiting a wide variety of places as roosts, including: barns and sheds, tree cavities, chimneys, hay bales, wells, Hamerkop nests, church towers, agricultural silos and cliff cavities relatively (Bunn et al. 1982; Taylor 1994; Zimmerman et al. 1996; Kolbe 1946; Wilson 1988a). Barn owls are reported also to roost on the ground and in dense tree canopies (Bunn et al. 1982; Colvin 1984). The common

Table 4.2: Taxonomic representation as proportion MNI with single classification ANOVA.

	closed					open				
	3	4	13	24	44	12	18	23	F(1,6)	p>F(1,6)
Acomys	0.004	0.000	0.009	0.000	0.012	0.038	0.008	0.000	1.281482345	0.300828
Aethomys	0.000	0.000	0.000	0.003	0.061	0.000	0.000	0.000	0.642937067	0.453227
Arvicanthis	0.020	0.076	0.013	0.003	0.207	0.000	0.031	0.132	0.027544817	0.873635
Crocidura	0.411	0.324	0.283	0.248	0.329	0.346	0.310	0.047	1.177455338	0.319538
Dasysmys	0.000	0.000	0.000	0.000	0.049	0.000	0.000	0.000	0.5625	0.481618
Dendromus	0.095	0.120	0.117	0.058	0.049	0.077	0.070	0.038	1.475683134	0.270084
Elephantulus	0.000	0.000	0.004	0.000	0.000	0.000	0.008	0.019	3.652362423	0.104546
Gerbillus	0.012	0.004	0.067	0.099	0.000	0.000	0.023	0.000	1.118224926	0.331006
Lemniscomys	0.016	0.011	0.009	0.014	0.012	0.038	0.039	0.057	48.34213669	0.000439
Mastomys	0.036	0.127	0.018	0.014	0.122	0.038	0.016	0.198	0.148629648	0.713146
Microchiroptera	0.016	0.000	0.000	0.000	0.000	0.000	0.023	0.009	1.421058525	0.278235
Mus cf. musculoides	0.083	0.051	0.049	0.017	0.000	0.077	0.070	0.066	2.52373137	0.163245
Mus cf. triton	0.079	0.047	0.058	0.003	0.012	0.000	0.163	0.028	0.328616974	0.5873
Praomys	0.004	0.000	0.000	0.000	0.012	0.000	0.016	0.000	0.15515866	0.707271
Saccostomus	0.024	0.025	0.009	0.000	0.000	0.038	0.054	0.104	11.11670295	0.015725
Steatomys	0.126	0.160	0.287	0.316	0.085	0.154	0.109	0.019	2.282725129	0.18157
Suncus	0.032	0.000	0.018	0.000	0.000	0.000	0.008	0.000	0.693935508	0.436726
Tatera	0.004	0.025	0.018	0.224	0.037	0.000	0.023	0.028	0.652279623	0.450123
Thallomys	0.028	0.007	0.018	0.000	0.000	0.192	0.023	0.245	8.377907809	0.027533
Zelotomys	0.012	0.022	0.022	0.000	0.012	0.000	0.008	0.009	1.832962368	0.224549
Totals	1	1	1	1	1	1	1	1		

Table 4.3: Taxonomic representation as arcsine transformed proportion MNI with Single classification ANOVA.

	closed					open				
	3	4	13	24	44	12	18	23	F(1,6)	p>F(1,6)
Acomys	0.063	0.000	0.095	0.000	0.111	0.197	0.088	0.000	0.638555879	0.454695
Aethomys	0.000	0.000	0.000	0.058	0.250	0.000	0.000	0.000	0.913211379	0.376165
Arvicanthis	0.141	0.280	0.116	0.058	0.473	0.000	0.177	0.372	0.058989133	0.816191
Crocidura	0.696	0.605	0.560	0.522	0.611	0.629	0.591	0.219	1.33935872	0.291134
Dasysmys	0.000	0.000	0.000	0.000	0.223	0.000	0.000	0.000	0.5625	0.481618
Dendromus	0.313	0.354	0.348	0.243	0.223	0.281	0.267	0.196	1.391581676	0.282788
Elephantulus	0.000	0.000	0.067	0.000	0.000	0.000	0.088	0.138	3.234363951	0.122217
Gerbillus	0.109	0.060	0.262	0.319	0.000	0.000	0.153	0.000	1.241955445	0.307734
Lemniscomys	0.126	0.105	0.095	0.117	0.111	0.197	0.198	0.240	65.45474695	0.000191
Mastomys	0.190	0.365	0.134	0.117	0.357	0.197	0.125	0.461	0.076770479	0.791021
Microchiroptera	0.126	0.000	0.000	0.000	0.000	0.000	0.153	0.097	1.543818837	0.260407
Mus cf. musculoides	0.292	0.228	0.224	0.131	0.000	0.281	0.267	0.260	1.942275011	0.212854
Mus cf. triton	0.285	0.219	0.244	0.058	0.111	0.000	0.415	0.169	0.011789941	0.917075
Praomys	0.063	0.000	0.000	0.000	0.111	0.000	0.125	0.000	0.026035941	0.877109
Saccostomus	0.155	0.160	0.095	0.000	0.000	0.197	0.235	0.328	9.727197622	0.020615
Steatomys	0.364	0.412	0.565	0.597	0.296	0.403	0.336	0.138	2.551324307	0.161316
Suncus	0.179	0.000	0.134	0.000	0.000	0.000	0.088	0.000	0.349252723	0.576106
Tatera	0.063	0.160	0.134	0.494	0.192	0.000	0.153	0.169	0.902515001	0.378789
Thallomys	0.167	0.085	0.134	0.000	0.000	0.454	0.153	0.518	10.04056897	0.019351
Zelotomys	0.109	0.148	0.150	0.000	0.111	0.000	0.088	0.097	0.949090224	0.367575

Table 4.4: Descriptive Measurements of the Barn Owl, *Tyto alba*

	European Barn Owl *Tyto alba alba*	African Barn Owl *Tyto alba affinis*
Body Mass	Combined Average 350 g	Combined Average 342 g
males	280-365g (mean 312g N=17)	mean 329g N = 11
females	290-450g (mean 362g N=55)	mean 363g N=7
Wing Length	Combined Average 334 mm	Combined Average 293 mm
males	259-309mm (286 mm N=174)	283-307mm (293 N=11)
females	263-305mm (287 mm N=164)	285-306mm (294 N=7)

source: Baudvin (1975); Voous (1950); Fry et al. (1988)

qualities to these roosting sites is the need for a dark, and enclosed space, hence they are referred to as cavity roosters. Even when ground roosting or roosting in trees they will seek out circumstances that mimic a cavity. Of the three instances during the current study in which a barn owl was observed roosting in the open, one was in the branches of a short acacia growing on a hill slope in which the tree crown stretched to the ground, creating a dark pseudo-cavity. Similarly, another tree crown roost was in a stand of very dense-canopy acacia along a river bank. Only once, was a barn owl observed in a fairly open tree canopy.

In open areas devoid of artificial structures or caves a variety of roosting sites are still available to host barn owls. The two primary roosting sites observed during this study were small vertical fissures in granitic rock outcroppings and the hollowed interiors of living and dead trees. The study area is dotted with outcroppings of Cambrian basement rocks. Smaller outcroppings are called kopjes or tors while larger, steep-sided hills are called inselbergs. These geological features are commonly comprised of durable, crystaline rocks such as granites that are exposed by either horizontal or lateral erosion of the surrounding sedimentary surfaces (Gerrard 1988; Jager 1982). During formation and cooling, igneous rocks such as granite develop horizontal and vertical cracks called joints. The size and shape of rock outcrops such as inselbergs and tors are determined by subsurface chemical weathering and the joint spacing of the rock. Linton (1955) described a two stage process for tor develpment, in the first stage water percolating into the joints of buried rocks facilitates chemical weathering, and "rotting" of these rocks. When exposed by erosion (the second stage), the rotted rocks are eroded more quickly than large blocks, or corestones that form between widely spaced joints. Rocks with more, narrowly spaced joints erode faster leading to smaller boulder heaps (Gerrard 1988; Holmes 1965; Linton 1955). The terms tor and kopje are often

used interchangeably, but Thomas (1974) distinguishes tors, chemically weathered corestones, from kopjes – corestones that experience collapse along joints while exposed above ground. The rock joints often have a vertical orientation that form fissures in the kopjes. These fissures are preferred roosting places for owls. Smaller rocks lodged in the fissures provide perches. The areas beneath these perches accumulate concentrations of microvertebrate remains and the perches themselves were heavily whitewashed – both indications of extended use. Barn owls are noted to be animals of habit, using roosts, and even the same parts of a roost repeatedly (Bunn et al. 1982, personal observation).

The hollowed interiors of trees are another source of barn owl roosting sites. The trunks of dead trees may remain upright on the landscape after the tops of the tree have toppled. These tall columns become catchments for the ejected pellets of owls either roosting inside the hollowed trunk, or using the top rim as a perch. Alternatively, living trees may form hollow cores as they age. The baobab tree, *Adansonia digitata*, is particularly amenable to this phenomenon. Baobabs are soft wooded members of the *Bombacaceae*, the family including the kapok and balsa wood trees. Baobabs are very stout trees, with trunks up to 10 meters in diameter (Wickens 1982). The great size implies great age and indeed carbon dates from the heartwood of a tree 4.5 m in diameter returned an age of 1010 $\pm$100 (Swart 1963). As these trees mature the cores often become hollow. Water turgidity helps maintain the strength of boughs, and during drought, limbs may snap away or openings into the interior may be created by elephants browsing on the succulent bark (Barnes 1980). These openings provide an opportunity for owls to roost and nest inside the trees. Seven baobab roosting sites were observed in Tarangire National Park during the current survey. In larger trees the major boughs may hollow out as well such that the insides form a dendritic labyrinth. Pellets aggregate at the base of the hollowed interior where they remain protected from the elements for the life of the tree. Many also accumulate outside, just below the opening into the tree.

The baobab is widely distributed throughout the drier shrublands, treed grasslands and woodlands of the Sudano-Zambesian lowland biome (Wickens 1982). In the study area it is found in Tarangire National Park and north through the rift valley and areas bordering Lake Manyara National Park. However, it was not observed in the Ngorongoro highlands, nor anywhere in the Serengeti National Park.

Areas in the northern and western extent of Serengeti host woodlands under rainfall regimes comparable to Tarangire and Lake Manyara so this factor alone does not provide an answer. Elevation may be key as baobabs are reported to occur most frequently below 1000 meters but have been observed at 1500 m (Wickens 1982; Wilson 1988b). Most of the Serengeti lies higher than 1200 meters a.s.l. while Tarangire and Lake Manyara are at least 200 meters lower.

Activity patterns Most owls are nocturnal but some barn owl populations are partly crepuscular. It is evident from numerous observations of barn owls active during daylight hours that there is no strong intrinsic or physical limitation on their diurnal activity. Barn owls can fly, and hunt effectively in daylight, and often do in English and Scottish study sites (Bunn et al. 1982; Taylor 1994). However, diurnal activity has associated risks for owls, who are often mobbed by flocks of smaller birds during the day or may be threatened by diurnal raptors. In the Tanzania study area, barn owls were observed departing their roosts around 19:00-19:30 or 30-60 minutes after sunset (sample size 14 days of observation [approximately 60 hours] at 4 roosting sites.) Taylor (1994), based on personal observations of *Tyto* in Africa and from discussions with researchers in Malaysia, reports similar, strictly nocturnal behavior as do others for North America (Colvin 1984) and Australia (Dickman et al. 1991). Diurnal activity may be restricted to barn owls living in the extreme northern portion of the range. The presence of diurnal rodents such as *Arvicanthis* and *Lemniscomys* in the diet of the Tanzanian barn owl suggest that some daylight activity may occur, but it is equally likely that the rodents are active into the dusk and early evening. Diurnal hunting may be a balance between external threats and the activity patterns of preferred prey (Bunn et al. 1982). The strength of the diurnal threats; the diversity and abundance of nocturnal mammalian prey would all suggest that Tanzanian barn owls should be strictly nocturnal. Barn owls typically have two or three main bouts of hunting activity during the course of the night, one near or soon after dusk and one early in the morning, at approximately two or three AM (Taylor 1994). Irregularly owls may have a third bout in the middle of the night (Bunn et al. 1982).

Ranging Behavior Descriptions of habitat use by barn owls range from "strongly territorial" (Andrews 1990, p. 178), to "not territorial" (Fry et al. 1988, p. 109). The discrepancies likely arise from differences in the behavioral repertoire associ-

ated with emigration, mating and hunting. Barn owls are unanimously described as sedentary within a home range of several square kilometers that is occupied year-round (Bunn et al. 1982; Mikkola 1983; Taylor 1994). During the mating season, males call (or if one is generous, "sing") as they depart the roost, and engage in confrontational intercept flight with other males. While these behaviors have been interpreted as active defense of mating territories (Bunn et al. 1982) it seems that once mates have paired little active effort is made to defend a hunting territory though the nest itself is vigorously protected (personal observation). While studying the Barn Owl in Scotland, Taylor (1994) observed,

> five of the pairs tracked [by radio telemetry] in 1984 were nearest neighbors to each other and their ranges overlapped considerably, with no indication of defense of hunting areas (Fig. 7.3). Neighboring males were sometimes seen foraging, with no apparent aggression, within about 150-200 m of each other in these overlap areas in circumstances which suggested they were aware of each other's presence. Birds returning to the nest with prey sometimes flew directly over their foraging neighbours without eliciting attacks or threats. Attacks were seen on only three occasions when intruders actually entered occupied nest sites" pp. 101-102.

Similar observations were made during telemetry studies of Barn Owls in New Jersey (Colvin 1984), nor is it uncommon to observe several pairs nesting in close proximity under conditions approximating a colony (Smith et al. 1974). Avery suggests that hunting areas may be partitioned (Avery 2001, p. 128), though no empirical evidence is presented. Bunn et al. (1982) report occasional territory defense between five pairs of barn owls in north-west England but the distinction between defense of mating territories and hunting territories is not very clear. The sedentary nature of the barn owl explains why bone densities are very high at their roosts. Evidence for colonial roosting implies that roosting sites, as opposed to prey availability may be the most important ecological factor limiting barn owl abundance and thus good roosting sites are likely to be reused by successive generations of owls.

Studies employing radio telemetry on barn owls provide the best estimate of home range use, though these studies have only been conducted in temperate

regions. Colvin (1984), during his study of the barn owl in New Jersey, reports mean home ranges of 953.3 ha for males and 652.1 ha for females but observes that the majority of time was spent between 0.4 km and 1.6 km from the nest. A study by Taylor (1994) on Scottish barn owls found that most sightings (89.5 % in the summer months) of plumage marked members of the barn owl study population were within one kilometer of the nest. Radio telemetry used during the same study revealed an average home range size of 318 ha for males and 308.2 for females. These areas correspond to a circle with a radius of approximately one kilometer. Results from two other North American barn owls studies summarized by Taylor indicate mean range sizes of 308 ha for males/294 ha for females and 418 ha for males/369 ha for females respectively (Byrd 1982). Pooling these results, the best available approximation of barn owl home range is approximately 680 ha. Similar studies on the African subspecies are needed to confirm its sampling radius and would also provide an interesting ecological comparison between temperate and tropical members of the same species.

Diet and Prey Selectivity A bewildering set of claims have been made about prey abundance in pellets relative to prey abundance in the source community. Mikkola (1983), in an oft cited book, claims,

> it has been well documented that the Barn Owl *does not prey selectively* on small mammals but takes all species according to their availability (e.g. Schmidt 1970, Vernon 1972). This suggests that the study of the Barn Owl's diet is suitable for determining the presence of nocturnal small mammals species within its hunting territory. (p. 47 emphasis added)

Offering a different opinion, Dodson and Wexlar (1979) claim,

> owls may be *extremely selective* in their choice of food species. Pellets of barn owls from northeastern Ohio (Dexter 1978) revealed 14 of 28 species of small mammals living in the region, and 97% consisted of the remains of but three species. (p. 281 emphasis added)

A careful review of the source literature justifies a more conservative interpretation of barn owl prey sampling. For example, Vernon (1972) is cited in support of the

owl as unselective predator by Mikkola above, most likely based on the following words from his summary,

> Both [Barn and Grass] owls were found to be non-selective, and to take the most accessible prey within a certain size range (Vernon 1972, p. 121)

However in the discussion, Vernon elaborates more fully,

> The prey items in the diets of *Tyto alba* and *T. capensis* show that most small vertebrates are vulnerable to predation. The two owls appear to be specially well adapted to preying upon rodents and shrews which are nocturnal or crepuscular, while arthropods are also regularly taken. In areas where these two groups are exceeded in number by other faunal groups, *Tyto alba* will readily switch to preying upon birds, lizards, scorpions or golden moles. Groups such as bats, frogs and elephant-shrews appear to be taken in lesser numbers in relation to their actual abundances, possibly because thy are not readily accessible to the owl, or because they are not preferred (Hanney, 1962a [sic]). (p. 120)

From the discussion it is clear that Vernon thinks barn owls are non-selective, but within the ecological constraints of their adaptation. Similarly, the results of a comparison between trapping and pellet analysis lead Hanney (1963) to conclude,

> that the numbers of certain species of secondary importance in the owl's diet were generally inversely proportional to the numbers of the primary prey taken. In view of this and of the unknown factors which must influence the prevalence of any one species component of the owl's diet, pellets cannot be used in any quantitative population studies of rodents. (p. 313)

What then can be said regarding the prey selectivity of barn owls? A reasonable summary is given by Andrews (1990), who is careful to reveal some of the caveats underlying claims to barn owls as non-selective predators. More fully the literature reveals:

Barn owls are capable of taking a very wide variety of prey, of which mammals are the most common. Throughout their range barn owls consume prey from all five vertebrate Classes, Aves (Bonnot 1928; Laurie 1971), Reptilia and Amphibia (Lenton 1984), Pisces (Bent 1938) and Mammalia (Taylor 1994, and references therein). Many invertebrate prey, such as insects are also taken, especially when they occur in concentrated abundance. Invertebrates, however form a small percentage of overall prey biomass and their remains are poorly preserved in pellets (Mikkola 1983; Taylor 1994). In the majority of dietary studies, mammals are the dominant prey group. In a sample of 52 barn owl dietary studies, Taylor (1994) found micromammals made up between 74-100% of the remains recovered in pellets. Very often the dominant micromammal species recovered in pellets is also the most abundant in the micromammal community sampled by the owl, suggesting that barn owls, within the constraints of activity pattern and prey size, randomly sample the microvertebrate community, however this is unlikely due to evidence of differential prey vulnerability as is discussed below.

The maximum prey size for barn owls is at least 371 g. The maximum sized prey for a barn owl is roughly that of a medium rat. Juvenile rabbits (e.g. *Oryctolagus cuniculus*, *Sylvilagus floridanus*), opossum (*Didelphis virginiana*) and muskrat (*Ondatra zibethicus*) are taken as well as small mustelids (*Mustela nivalis*)(Glue 1974; Marti 1988; Colvin 1986). The most explicit estimation for maximum prey size is 371 g based on skeletal measurements of *Rattus norvegicus* recovered in pellets (Colvin 1986).

Barn owls hunt preferably over open habitat and are thus expected to be biased toward open habitat micromammals. Barn owls exhibit several anatomical specializations for hunting terrestrial prey in open habitats. These include wings designed for slow, buoyant flight[2], feathers specialized for silent flight[3], long legs for catching prey in tall vegetation, and an exceptional acoustical sensory and positioning system for finding prey (Payne 1971). Import-

[2]Owls have a large wing area, and with an estimated body weight of 500g the approximate wing loading is only 0.29 g/cm^2. Very light even for an owl. The tawny owl by comparison has a wing loading of approximately 0.40 g/cm^2 (Mikkola 1983).

[3]A comb like leading edge to the flight feathers improves laminar air flow, soft hairs on the trailing edge of feathers may reduce air turbulence, and the surfaces of the wings have downy hairs that reduce noise created by relative movement of feathers over one another (Taylor 1994).

antly, these adaptations are not optimal for pursuit predation of volant prey, nor for hunting in densely wooded vegetation where a more agile form of flight and better visual perception are required (Mikkola 1983). Long term visual sighting and radio telemetry confirm their preferential use of open grasslands, and margin habitats between grasslands and more closed vegetation (Bunn et al. 1982; Colvin 1984; Glue 1967, 1971; Taylor 1994). The preference for margin habitats is important for mitigating the open habitat bias in the prey assemblage.

Despite broad selectivity barn owl assemblages do exhibit biases and evidence of differential predation Though the potential prey spectra is quite large, and many species interchangeable, this should not be taken to mean that the barn owl samples the fauna randomly. In a controlled experiment where prey abundances could be artificially manipulated, Fast and Ambrose (1976) observed that their single barn owl study subject captured voles (*Microtus pennsylvanicus*) significantly more often than white-footed mice (*Peromyscus leucopus*). The potential explanations for the bias are numerous, but chief among them is the issue of relative vulnerability. *Microtus* is a larger, less agile prey item and may be easier to capture. Another possibility is that the owl can distinguish between the two prey and prefers the larger species because it offers greater energetic returns. Both hypotheses presume that the observations are not simply unique to the one study bird. A study by Dickman et al. (1991) examined the first hypothesis and found differential predation on mice with juvenile females taken at greater frequency than other groups, a result they argue stems from differential habitat use and competition between mice for cover. They conclude, "our observation of differential predation of small mice are unlikely to be the result of active selection by owls" (p. 74). While their results provide strong evidence that differential habitat use by prey effects their risk of capture, it fails to dismiss a coincident factor of active selection. Furthermore, the study relies on trapping data as a baseline for establishing the relative abundance of prey in the environment which has been shown to suffer its own biases (Wingate and Meester 1977). Dickman et al. (1991) attempt to mitigate trapping bias by using pitfall traps in conjunction with standard live traps, but any trapping scheme has associated biases. The issue can only be settled through more thorough study under controlled manipulation of prey species and abundances. The studies conducted so far indicate an important

distinction, that between *predator selectivity* of prey and *differential vulnerability* of the prey. The evidence for differential vulnerability (especially of juvenile and small individuals) is compelling but may be offset by predator selection for larger individuals that offer a higher energetic return. The strength and prevalence of prey selection remains uncertain and depends on assessing the sensory capabilities of the predator, which is difficult to measure.

Barn owl prey assemblages differ from one habitat to the next and from season to season. Though prey abundance in pellets may not be a direct reflection of abundance at large, many authors have remarked on the consistent patterns of change in prey abundance (including presence and absence of species) across different habitats. Glue (1967) observed changes in the relative abundance of species across five different general habitat types in England and Wales. A broader area study also found regional changes across Britain and Ireland (Glue 1974). A similar study in France demonstrated changes in prey community composition across ecogeographic regions (Libois et al. 1983). From a taphonomic standpoint these studies illustrate that barn owls readily switch to new prey as they become available from one region to the next (i.e. they are not strongly dependent on a small set of prey species) and one habitat to the next. It is from these observations that one can claim the barn owl is, to an extent, non-selective. More detailed live-dead comparisons are needed to determine the degree of bias. For example, while species abundances may be biased or differ slightly from trapping or other metrics, rank order abundance may be maintained; and as Andrews (1990) has pointed out, it is not at all clear which is really the most accurate metric of abundance, trapping or the thanatocoenosis. The time averaged nature of most thanatocoenoses may provide a better long-term picture of micromammal community composition than short-term trapping.

Summary Barn owls exhibit a suite of adaptations developed for nocturnal ambush of ground dwelling prey amidst herbaceous vegetation by using silent, buoyant flight to quarter a territory. The telemetry studies of Colvin (1984) and Taylor (1994) indicate a biased use of open grassland habitats and forest margin habitats. Given these adaptations, it appears the birds are opportunistic, acoustic, nocturnal predators (crepuscular in some areas) adapted to hunting terrestrial prey, generally in the body size range of 20-100 g but with a maximum size limit no less

Table 4.5: Descriptive Measurements of the Spotted Eagle Owl, *Bubo africanus*

	African Spotted Eagle Owl *Bubo africanus africanus*
Body Mass	Combined 487-850 g (mean 666; N=45)
males	males 550-620 g
females	females 640-730 g
Wing Length	Combined Average 336; N=30
males	males 323-348 mm (333; N=15)
females	females 314-360 mm (339; N=15)

source: Fry et al. (1988)

than 371 g Colvin (1986). Within these constraints (small, nocturnal, terrestrial, herbaceous dwelling) the relative abundance of the prey in pellets approximates their abundance in the described niche. The organisms most abundant in the barn owl's preferred hunting niche include smaller, nocturnal rodents and most shrews. The relative abundance for these groups in pellets may be a good, if biased estimator of their abundance in the faunal community, but this hypothesis requires additional experimental testing. Additionally, barn owls will sample prey outside their preferred niche but at lower frequency.

4.4.2 Eagle Owls

Compared to barn owls, far less is known about the Spotted Eagle Owl, *Bubo africanus (Temminick)* . Three subspecies of spotted eagle owl occur in East Africa, *B. a. cinerascens* and *B. a. tanae* occur in Kenya, and only *B. a. africanus*. is known to extend into Tanzania (Zimmerman et al. 1996). Size measurement for the spotted eagle owl (Fry et al. 1988) indicate a mean body weight nearly double that for the barn owl, however the spotted eagle owls occurring in Serengeti appeared only slightly larger than *Tyto alba affinis* though no measurements specific to that subpopulation are available. The two species are sympatric and common throughout the study area.

Roosting Habits Spotted eagle owls are reported to prefer rocky areas and to roost either in trees or on the ground (Fry et al. 1988). Brain (1981) describes a

spotted eagle owl roosting in a dolomitic cave, the roost occurring at the base of a 9 m deep shaft. Similarly, Demeter (1982) report a spotted eagle owl roost along the edge of a lava bubble. In the Serengeti, spotted eagle owls were observed roosting in open settings such as the sparse canopy of acacia trees, or in the open, atop rock outcroppings. Spotted eagle owls rely on crypsis to avoid detection during the day. They have more elaborate camouflage than barn owls, including "ear" tufts that help them blend in against tree trunks. When approached on foot spotted eagle owls are hesitant to flush and will slit their eyes and sit immobile, hoping to avoid detection (personal observation). If forced to move during daylight they risk being mobbed by smaller birds.

Activity Pattern and Ranging Behavior Eagle owls are sedentary and nocturnal (Fry et al. 1988) though diurnal prey such as *Arvicanthis* does appear in pellets (Demeter 1982). No detailed observational data are available on the activity pattern or ranging behavior of this species.

Diet and Prey Selectivity Like the barn owls, spotted eagle owls may take a wide variety of prey items, including all types of vertebrates (Demeter 1982). Although fish have yet to be reported in their diet. Insect and invertebrates may also be eaten, but they form a rather small components of prey biomass (Demeter 1982). As in barn owls, terrestrial mammals are the most common prey, but the dominant species vary from one location to the next – indicating flexibility in prey preference to suit availability (Brain 1981; Demeter 1982; Dickman et al. 1991). When certain species are ubiquitous, spotted eagle owls, like barn owls may concentrate on them to the exclusion of others, giving the temporary illusion of prey selectivity. For example Siegried (1964) reports on 74 spotted eagle owl pellets collected between October and November 1964 in the Sandveld area of south-western Cape province, South Africa. This assemblage was heavily dominated by gerbils of the genus *Tatera* (81 out of 94 prey items or 86%).

Summary Very little information is available regarding the ecological proclivities of spotted eagle owls. What is available indicates a great deal of overlap with barn owls. Both species are sedentary and prey on a wide range of animals. Eagle owls are more prone to roosting in trees and thus may be more common in woodland habitats. Eagle owls are also described as a "perch and pounce" predator in contrast

with barn owls, which hunt more from the wing over open areas (Fry et al. 1988; Taylor 1994).

4.5 Taphonomic Implications

Microfaunal accumulations, if analyzed correctly, contain a great deal of information that is otherwise difficult to gather. Owl roosts may aggregate tens of thousands of specimens in dense mats several inches thick below a roosting or nesting place (personal observation). Guerin (1928) reports that one barn owl captured over 1100 prey items in the span of 90 days. By comparison, in areas with high densities of small mammals, trapping seldom yields greater than 10% success; at that rate it would take 100 days of continuous trapping with 100 traps to match what a barn owl collects over roughly the same period. Analysis of fossil and modern microvertebrate assemblages requires that we have a good taphonomic model for the processes at work and an understanding of how taphonomic processes influence analytical findings. Actualistic research dedicated to diagnosing different accumulating agents has focused on breakage (Andrews and Nesbit-Evans 1983; Andrews 1990; Dodson and Wexlar 1979; Hoffman 1988; Kusmar 1990; Saavedra and Simonetti 1998), surface modification (Andrews 1990; Denys et al. 1995; Fernandez-Jalvo and Andrews 1992; Fernandez-Jalvo et al. 1998) and chemical composition (Dauphin et al. 1997), with generally good results. Ecology of the accumulating agents also provide criteria for inferring taphonomic mode and should not be overlooked (Avery 2002). Here I discuss the taphonomic implications of roosting behavior and trophic ecology at sites outside caves and rock shelters.

4.5.1 Taphonomic mode and site formation

Dense micromammal accumulations are typically associated with caves and rock shelters, leading some to predict that "although large numbers of remains are deposited by owls in open areas, these pellets are usually subject to diverse environmental process and few bones survive" (Kusmar 1990, p. 629). While it is well demonstrated that bones exposed on a land surface may be quickly destroyed (Andrews and Cook 1985; Behrensmeyer 1978; Behrensmeyer and Hill 1980; Shipman and Walker 1980), the results of this survey clearly show that dense bone concentrations can form under conditions favorable to fossilization in areas outside large

caves and rockshelters. In the course of this survey, small rock fissures in kopjes, dead tree cavities and the hollowed interiors of living trees all provide conditions conducive to the formation of dense microfaunal accumulations. Both fissures and tree stumps have been proposed previously as taphonomic modes for various fossil accumulations (Behrensmeyer and Hook 1992; Denys et al. 1997), and the results of the current survey support the idea that this taphonomic mode is perhaps more common than previously thought.

When considering the impact of different taphonomic agents, Tchernov (1992) argued that bone assemblages were the result of a guild of owls. He argues that,

> As guilds of owls are not only universal and widespread, but also exist for very long periods and hence display purified stereotyped behavior, these scenarios were constant over time; guilds of strigiforms always consisted of several species of different sizes, in which *Tyto alba* was generally represented. Thus, in spite of certain distortions reflected in the accumulated assemblages as compared with the biocoenosis in the vicinity of the site these biases are constant over time and hence samples are comparable. (p. 155)

Tchernov was focused on cave settings for which there is better evidence for the involvement of multiple accumulating agents. In comparing open-air sites it is reasonable to question whether they can be considered similar to concentrations occurring in caves. It appears barn owls are capable of exploiting, and reusing small, natural cavities in open areas just as they exploit caves. However, the partitioning of roosts between different species in open-air sites may be stronger than in caves. Both barn owls and spotted eagle owls are reported to use caves (Brain 1981), but the results of the current study indicate spotted eagle owls are less likely to exploit very small cavities, preferring instead to roost in the open and camouflage themselves against rocks or in the crowns of trees. As a result fissure fillings and tree stump roosts may be more homogeneous as regards accumulating agent than large caves or rock shelters. Open roosts on the other hand are expected to suffer the co-occurring and compound effects of increased digestion and breakage resulting from the physiology of the predator as well as increased trampling and weathering as a result of prolonged surface exposure.

Cavity roosts occurring in open-air settings may differ from cave roosts in the duration of the sampling interval. Baobabs, though long lived, sample a relatively

short interval compared to kopjes and caves. The exact duration over which these sites accrue bones is unknown, but can be tested by radiocarbon dating on modern assemblages. In collecting pellets and bone detritus from inside a particularly large baobab in Tarangire, I noticed subsurface concentrations of bone. Careful excavation of such sites may provide effective measures of Holocene climate change.

4.5.2 Trophic overlap and comparative taphonomy

Davis (1959) early on recognized the important role barn owls play in accumulating fossil assemblages, but others soon suggested that mammalian predators could produce similar assemblages (Andrews 1983; Mellet 1974) presenting a problem of taphonomic equifinality. Early efforts to resolve the problem focused on breakage patterns. Since many mammalian predators masticate their prey, bone breakage is expected to be much higher in mammalian predator assemblages (Andrews 1983, 1989; Mellet 1974). However several practical problems confront studies of bone breakage in microvertebrate assemblages. The most entrenched problem is separating predator breakage from breakage due to trampling, diagenesis, recovery and curation. For this reasons, the study of breakage pattens to discern taphonomic agency is not likely to be helpful when used alone except when the assemblage is very well preserved (Andrews 1990). As with many aspects of historical science, taphonomic agency is best studied through a conjunction of methods including analysis of mechanical damage (Andrews and Nesbit-Evans 1983; Andrews 1990; Denys et al. 1995; Dodson and Wexlar 1979; Hoffman 1988; Kusmar 1990; Mayhew 1977; Saavedra and Simonetti 1998), chemical modification (Denys et al. 1997; Dauphin et al. 1997) and ecological considerations (Avery 2002).

The analysis of prey assemblages from cavity and open roosts in the current study suggests that the barn owl, and spotted eagle owls exhibit only subtle differences in the relative abundance of species under each taphonomic mode.

Regardless of how the analysis is conducted (proportions or arcsine transformed proportions) three taxa exhibit an increased prevalence in open roosts associated with spotted eagle owls; *Lemniscomys*, *Thallomys*, and *Saccostomus*. A summary of their abundances under open and closed roosting regimes is shown in Table 4.6.

The exact species designation of the *Lemniscomys* morphotype is unclear, but the possible species are similar in their ecology. All are semi-diurnal, grazing rodents, with an approximate adult weight of 90 g. Why this taxon should be more

Table 4.6: Summary of taxa percent abundance for three species across open and closed roost types

	Open			Closed		
	Mean	Range	Std Dev.	mean	Range	Std Dev.
*L*emniscomys	1.23	0.90-1.58	0.26	4.46	3.85-5.66	1.04
*S*accostomus	1.16	0.0-2.55	1.24	6.55	3.85-10.38	3.41
*T*hallomys	1.06	0.0-2.77	1.21	15.36	2.33-24.53	11.60

abundant in open roosts is a mystery. The prey size is well within the range of both owls and if anything, it is the barn owl that would be expected to catch a prey item that favors open grasslands. The difference in proportional representation is not strong but is consistent at 1.23% in cavity roosts and 4.46% in open roosts.

Thallomys appears in greater relative abundance in open roosts than in cavity roosts. *Thallomys* is an arboreal rodent that forages and nests in trees, favoring *Acacia* and *Brachystigia* open woodlands. It's higher relative abundance in open roosts may be the result of opportunistic predation on this species by spotted eagle owls roosting in the crowns of trees.

Saccostomus shows a slight bias toward open roosts. This larger rat is slow moving and more strictly terrestrial than other rodents. With a body size ranging between 40-85 g it is well within the size limits of both predators. Its bias remains a mystery as well.

Overall, the biases present between cavity roosts and open roosts is small compared to the variability between roosts in different habitats, or even in roughly the same habitat. The lack of a strong difference between open roosts and cavity roosts suggests that these taphonomic modes may be considered isotaphonomic with regards to prey composition, with the possible exception of *Lemniscomys sp./Arvicanthis nairobae*. This result is similar to the conclusions reached by Brain (1981) from a similar comparison of barn owl and spotted eagle owl pellets, though it should be considered a preliminary hypothesis until a more thorough investigation of mechanic damage and analysis of fresh pellets from known predators is completed.

If the hypothesis of isotaphonomy between cavity and open roosting taphonomic modes is not corroborated one may still wonder how great the impact is on the analysis of these assemblages. Clearly the impact will depend on the type of analysis being conducted and the methods employed. Phylogeographic analysis,

by definition, is the study of the geographical distribution of species and must be affected by taphonomic modes that alter species composition. Similarly, the taphonomic analysis of bone chemistry has shown association with the digestive physiology of different species and will be influenced (Dauphin et al. 1997; Denys et al. 1997). Less clear is the impact on diversity studies, taxonomic habitat indices (THI), and ecological structure analysis (ESA) (Andrews 1996; Behrensmeyer et al. 1992; Damuth 1982; Nesbit-Evans et al. 1981; Reed 1998; van Couvering 1980). Of these, diversity studies are probably most susceptible, especially when small samples are used because multiple predators will sample a broader range of activity patterns, prey sizes, hunting ranges etc. and thus increase simple species richness relative to sample size (Fernandez-Jalvo et al. 1998). The effect of taphonomic agency on THI and ESA are less clear as these methods are designed to emphasize ecological community structure more than taxonomic community structure (Andrews 1990; Reed 1998). The robusticity of these analysis should be tested using random sampling experiments in order to better understand their response to taphonomic variability.

4.6 Conclusions

Field observations reveal ecological conditions relevant to the taphonomic interpretation of micromammal accumulations. First of these is that in open areas, i.e. outside large caves and rockshelters, spotted eagle owls and barn owls use different roosting locations, largely to the exclusion of each other. The exclusion may be due to active defense of specific, small roosting niches by barn owls, but it also appears that eagle owls have adaptations for roosting in more exposed and open locations, including more cryptic plumage and the presence of "ear" tufts (Fry et al. 1988). The results from this survey coincide with reports in the literature proposing a fairly strict partitioning in roosting behavior between these two species of owls. Barn owls are associated with cavity roosts such as the fissures in kopjes or the hollowed interiors of trees dead and living. Spotted eagle owls are associated with open roosts such as the crowns of trees, cliff faces and rock outcroppings. Despite the strong differentiation there is overlap with spotted eagle owls and barn owls sharing caves and rock shelters as well as very dense canopy trees (Brain 1981; Demeter 1982).

Faunal composition between open and cavity roosts were found to be very similar though minor but significant differences were noted in three taxa: *Lemniscomys, Thallomys* and *Saccostomus*. The similarity presents the convenient possibility that cavity and open roosting modes may be considered isotaphonomic with respect to faunal composition. Additional taphonomic studies are needed to determine whether the faunal similarities between open and cavity taphonomic modes is corroborated and what effects changes in species composition has on the paleoecological analysis of microvertebrate assemblages.

Chapter 5

Paleoenvironmental Analysis

5.1 Introduction

The predators that accumulate fossil micromammal assemblages employ different strategies for hunting prey and have adaptations specific to those strategies. For example, the barn owl is an open-habitat specialist. Its hunting preference will influence what prey species are taken and thus the structure of the resulting taphocoenosis. At one theoretical extreme it is possible that predator bias leads to homogeneous assemblages despite very different source communities or biocoenoses. The owls may simply ignore prey species in difficult habitats, or prey with different activity patterns. The goal of this chapter is to determine whether owls hunting in areas with different land cover produce recognizable assemblages. The strategy adopted here is to analyze micromammal assemblages from modern Serengeti owl accumulations and use these as the basis for studying the spatial ecology of micromammals as seen through the taphonomic filter of predation. Conveniently, the same tack addresses a second challenge, that of verifying and calibrating analytical methodologies of paleoenvironmental reconstruction. As analytical techniques evolve it is necessary to recalibrate them against modern data. With these aims in mind, the following questions guide the analysis:

1. Do hunting ranges incorporating different habitats induce shifts in the representation of prey taxa?

2. If differences exist, does the fauna accurately reflect the habitats surrounding the roosts?

3. Do any of the prey violate or appear outside their published niche descriptions?

4. Are the differences between assemblages sufficient to detect various types of "savanna" habitats?

A review of the materials and data collection methods is given in Section 5.2. The basic issue of differences in faunal abundances between roosts, raised by the first question above, is addressed in Section 5.3. The second and third questions are fundamental to the use of indicator species in paleoecological analysis and are considered in concert with this method in Section 5.4. Compound indicators, in the form of taxonomic ratios, are considered here as well. Next the taxonomic habitat index is explored as a method for combining the individual indications of several species. This method provides a means of systematically comparing different assemblages and so is considered along with the fourth question above.

The study area lies just to the north of Olduvai Gorge. Plio-Pleistocene deposits at Olduvai have yielded substantial micro- and mega-faunal remains. A recent study by Fernandez-Jalvo et al. (1998) suggests that predators played an important role in the accumulation of the Olduvai microfauna and concluded that taphonomic bias induced by the predators distorted the representation of the fauna leading to inaccurate paleoenvironmental reconstructions. Given the proximity of Olduvai to the Serengeti along with the large degree of faunal overlap between the Olduvai fossil micromammals and the extant Serengeti fauna, this chapter concludes with an analysis of the fossil rodent assemblages from Middle and Upper Bed I at Olduvai Gorge using data reported in the literature.

5.1.1 Fundamental Assumptions

Any discussion of paleoenvironmental analysis first requires a treatment of the assumptions underpinning the analysis. The assumption of taxonomic uniformitariansim recurs in many paleoenvironmental analyses of fossil microfauna. Under taxonomic uniformitarianism one assumes that a fossil representative of a taxon shared the ecological proclivities of its extant kin. This method is obviously more applicable to recent fossil faunas for which there are representatives still living, and for African rodent faunas it is best applied to assemblages from the Middle

Miocene and younger. The Miocene saw a rapid radiation of muroid rodents and the origin of many modern genera (Jacobs 1987).

Taxonomic uniformitarianism (AKA principle of transferred ecology) at first seems like an egregious assumption especially in the context of hominin evolution. Here we are trying to understand the ecological implications for dramatic changes in the hominoid lineage by employing the assumption that rodents, one of the most rapidly speciating lineages of mammals, have remained ecologically stagnant. Defense of this assumption rests in part on the numerical abundance of micromammal species. We assume that some micromammals may have changed but most of them have not, and that sufficient similarities remain to make a meaningful interpretation (Wesselman 1984). Transferred ecology has also been defended on the grounds of necessity; without it there was simply no way to proceed (Avery 1982, p. 238). The assumption of transferred ecology cannot be tested with modern ecological data, but rather must be confronted with resort to first principles and anatomical comparisons; this is ecomorphology.

Ecomorphology seeks to link anatomical form with function so that autecology may be interpreted independent from an organisms phylogenetic history and without recourse to the assumption of transfered ecology. The method has been applied to megafauna with good results (Kappelman 1988, 1991; Plummer and Bishop 1994). Ecomorphology should be applicable to micromammals as well, but here the necessary research into comparative morphology and function has lagged behind that of large mammals. Ecomorphological methods are sometimes referred to as "taxon-free" approaches. However, it has been noted that they rely on a taxonomic diagnosis to limit the analysis to a certain group (e.g. antelopes) and should properly be called "phylogeny-free" methods. Most important is that they are nearly free from the assumption of transferred ecology.

There is an important overlap between species diagnosis and ecomorphology that has not yet been addressed in paleontological literature, and which helps mitigate the severity of the assumption by transferred ecology. The overlap results from using the same criterion as the basis for taxonomic assignment and ecomorphological analysis. Consider the case in which an analyst examines an isolated fossil molar. Based on the morphology the analyst assigns it to some taxonomic group. The very same criteria (molar morphology) may be used to designate an ecomorphological character such as dietary class, thus it is no surprise that taxo-

nomic grouping and ecomorphological grouping coincide. The overlap isn't total however. One may presume that a gerbil is arid adapted because modern gerbils have specialized physiology for water retention, low frequency hearing and ricochetal locomotion critical for survival in the open. Some, but not all of these traits may be inferred from a skeleton and used for ecomorphic designation. The benefit to the ecomorphic approach is that we are forced to define a more explicit causal relationship, say between locomotor habit and ecology, than is required by transferred ecology, which relies more on correlation than causal explanation. The point worth making, however is that ecomorphic information is tacitly considered in the taxonomic diagnosis of fossil specimens. The assumptions used to gather ecological information from the individual specimens overlap to a degree not before appreciated, and as a result transferred ecology and ecomorphology are likely to coincide. Ecomorphology, however, becomes the only viable method for taxa lacking clear associations to living forms. Whichever method is used, ecological assignments are ascribed to individual specimens and from there the data must be integrated into a more complete picture. The subsequent sections describe methodologies for integrating these data. For the remainder of the discussion I'll refer to "taxa" or "taxon" as a shorthand term for the unit of analysis, in application this may be a species, genus, tribe, or ecomorph.

5.2 Materials and Methods

Chapter 2 gave an overview of the vegetation patterns and ecological trends in the study area. The distribution of roosting sites is reproduced here in Figure 5.1 . We observed that precipitation increases from its lowest value of 527 mm at roost 24 in the southern grasslands up to 886 mm at roost 44 in the northern extension. Rainfall influences erosion and the rate at which land surfaces become dissected by drainages and valleys, thus there is a general trend toward topographic heterogeneity as measured by slope and the standard deviation of slope, with lower values in the south and larger values in the north. The same prevailing winds that influence rainfall patterns also distributed ash fall from volcanic eruptions along a similar gradient. Stemming from the interaction of these factors is a general vegetation gradient with the southern most roost (24) situated in a grassland, a cluster of roosts near Seronera that grade from bushed grassland to treed grassland

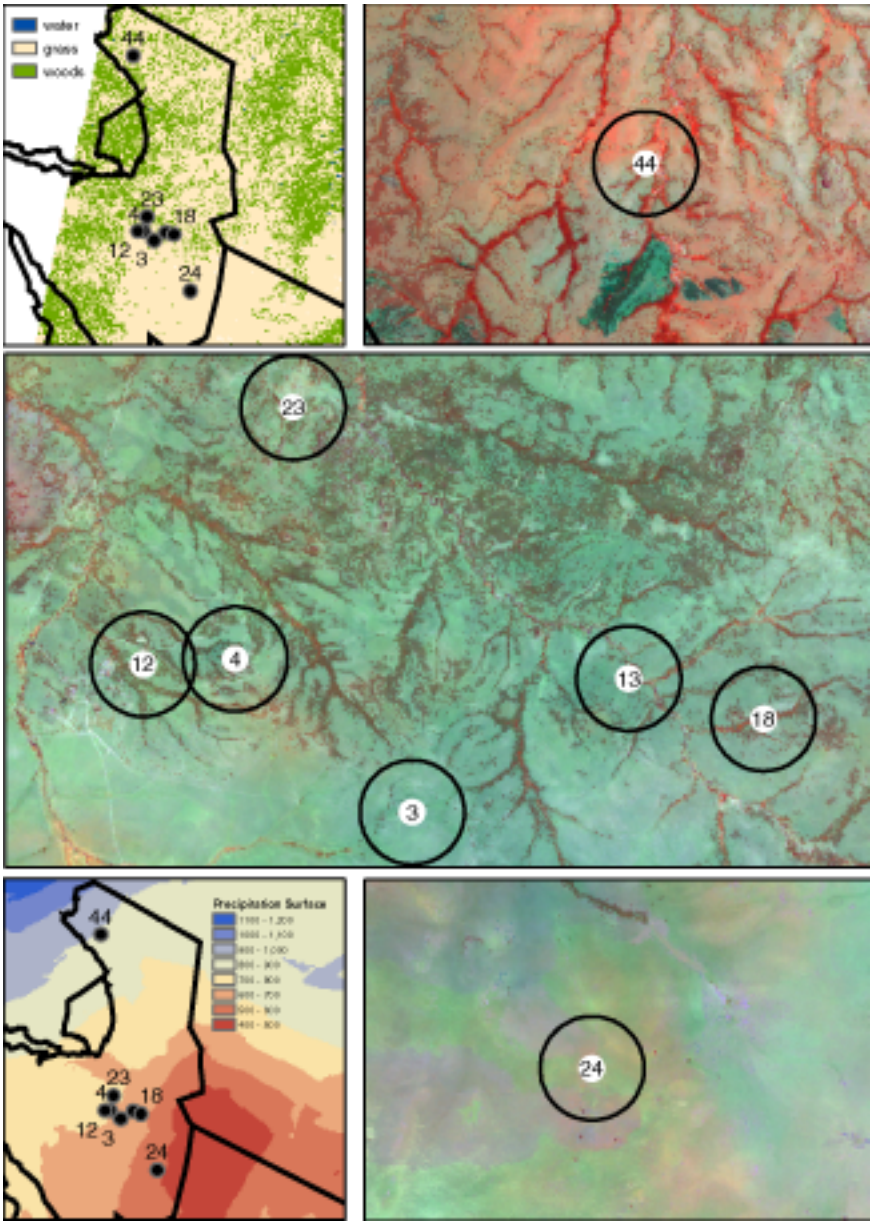


Figure 5.1: Distribution of analyzed roost sites. The upper left pane shows the roosts against a background map of woody vegetation, and against precipitation in the lower left. Remaining panes show close-ups of roosts outlined by 1.5 km buffer against a landsat background. The background includes a semi-transparent overlay of the vegetation classification to highlight woody vegetation.

into more dense woodland and finally roost 44 in the northern extension along small patches of dense gallery forest surrounded by tall wooded grasslands. Table 5.1 summarizes climatic and land cover attributes for the different roosts.

Taphocoenoses from eight roosts in the Serengeti National Park were analyzed as discussed in Chapter 3 in conjunction with habitat mapping based on supervised classification of Landsat 7 ETM+ satellite imagery. Classification results were integrated into a GIS of the study area with coverages detailing hydrology, elevation and topography, soils, and precipitation as described in Chapter 2. Roost locations were recorded with a GPS receiver and mapped into the GIS. 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 yet been conducted on ranging behavior of these animals in Africa. Prey specimens in the taphocoenoses were curated, identified and cataloged following methods described in Chapter 3. The results of Chapter 3 indicated a faunal community that is consistent, overall with a tropical mosaic of grassland and woodland, "savanna, " albeit one in which the larger, more diurnal taxa are under-represented. Within the general category of semi-arid woody grasslands, is it possible to distinguish more subtle habitat categories, such as grasslands vs. wooded grasslands, or wooded grasslands vs. relic forest?

In Chapter 4 we paused to consider the influences of different accumulating agents. Two owls were directly observed during the course of the study and their roosting behavior was found to differ significantly with the barn owls inhabiting closed roosts such as fissures, caves and the interiors of trees, while spotted eagle owls roost in the open, on the ground, against rocks at kopjes or in the crowns of threes. In an analysis of diet three species were found to differ significantly in their representation at open and closed roosts, *Thallomys*, *Saccostomus* and *Lemniscomys*. This grouping recurs in subsequent analyses implying that accumulating agent may explain the association between these taxa. This is examined more carefully in the following sections, starting with an analysis of correlations between taxa and between taxa and various ecological characteristics of the roosts.

Table 5.1: Summary of ecological and land cover characteristics at the roosts. Elevation values are given in meters, precipitation in millimeters, slope as percent ranging between 0 and 200. Land cover is given in percent pixels for an equal area around each roost. Dashes indicate an absence of that land cover, pluses indicate the land cover is present at less than 0.5 percent. The final column shows the average across all roosts. Land cover densities are coded as s = sparse, o = open, d = dense and c = closed.

		Roost ID								
		24	3	18	13	4	12	23	44	Avg.
Vegetation Summary	Codes									
Mean Elevation	ELEV	1759	1583	1607	1562	1536	1509	1472	1465	1533
Elevation Std. Dev.	SELE	10	6	11	11	13	8	23	18	13
Mean Annual Precipitation	MAP	527	679	635	655	702	708	709	886	711
Mean Percent Slope	MPS	1.5	1.1	2.5	2.8	2.5	2.1	4.6	4.9	2.9
Percent Slope Std. Dev.	PSD	0.6	0.4	1.0	1.3	1.1	0.8	3.5	2.2	1.5
Percent Woody Veg. Cover	PWV	0	2	26	20	33	35	28	28	25
Percent Land Cover										
sparse-open Grassland	soG	13	+	1	1	3	8	7	1	4
dense-closed Grassland	dcG	75	20	40	12	13	9	15	19	25
s-o Bushed Grassland	soBG	+	21	29	38	41	39	26	43	30
d-c Bushed Grassland	dcBG	13	58	4	29	9	9	23	10	19
o-d Grassed Bushland	odGB	+	2	23	19	31	27	23	26	19
d-c Grassed Bushland	dcGB	—	—	3	1	2	8	5	2	3
d-c Forest	F	—	—	—	—	—	—	—	+	+

5.3 Correlation Analysis

The distribution of points in the correspondence analysis of fauna conducted in 3 indicates that some taxa do not vary independently from one roost to another, but instead are associated. These taxa fall near each other in ordination plots. Conversely there are species that seem to dissociate by roost. They appear far apart on the correspondence analysis and have significant but negative partial chi-square values. The tables of partial chi-square values indicate which taxa are significantly associated or dissociated with a given roost, but in this format it is difficult to interpret co-occurrences of taxa.

Spearman rank correlation tests were performed on all pairwise combinations of taxa in the assemblage in order to determine relationships between them. Each test compares the pattern of rank abundance between two taxa across seven roosts. Roost 12 is excluded due to its small sample size. Tables 5.2 and 5.3 lists the Spearman rank correlation coefficients between each pair of taxa. Four taxa pairs were found to be highly significant and twenty were significant at a level of 0.1. The most significant results were negative correlations between *Gerbillus* and two other taxa, *Mastomys* and *Arvicanthis*. *Gerbillus* has a significant positive correlation with *Steatomys*. *Lemniscomys* is also found to have highly significant correlations with *Thallomys* and *Saccostomus*. *Arvicanthis* and *Mastomys* are correlated with each other and both are inversely correlated with *Gerbillus* and *Steatomys*. *Saccostomus* and *Thallomys* are correlated as are *Dasymys* and *Aethomys* but more weakly.

For comparison the CA of the fauna is reproduced in Figure 5.2, this time excluding roost 12. Comparing the differences to Figure 3.10 shows a slight rearrangement of points but the same overall pattern. Similarly, the partial chi-square table shown in Table 5.4 is only slightly altered by the exclusion of roost 12. In the new partial chi-square table entries for *Mus cf. triton* at roost 3, *Praomys* at roost 18 and *Crocidura* at roost 24 are slightly less significant.

Overall the patterns of correlation follow the distribution of points in the correspondence analysis. *Gerbillus* and *Steatomys* are correlated with each other and both are strongly associated with roost 24. *Tatera* is also associated with roost 24, but it does not follow the same pattern of distribution as *Gerbillus* or *Steatomys*. At the other end of the first axis of variation, *Arvicanthis* and *Mastomys* are correlated with each other and are associated with both roosts 44 and 23. *Saccostomus*,

Table 5.2: Spearman rank correlation coefficients between species. Rank abundance determined by %NISPn. Roost 12 was excluded due to small sample size. Each comparison has N=7 values.

	ELEP	ACOM	AETH	ARVI	DASY
ELEP	1.000				
ACOM	0.020	1.000			
AETH	-0.516	0.277	1.000		
ARVI	0.158	0.259	0.134	1.000	
DASY	-0.338	0.635	0.764*	0.612	1.000
LEMN	0.709	-0.296	-0.802*	0.143	-0.612
MAST	0.197	-0.185	-0.223	0.857*	0.204
MUSM	0.355	-0.148	-0.802*	-0.071	-0.612
MUST	0.433	0.371	-0.757*	-0.143	-0.408
PRAO	0.000	0.797	0.172	0.315	0.450
THAL	0.815	-0.093	-0.787*	0.144	-0.515
ZELO	-0.256	0.000	-0.401	0.179	0.000
SACC	0.716	-0.280	-0.787*	0.324	-0.515
DEND	-0.335	-0.074	-0.490	-0.393	-0.408
STEA	-0.473	-0.296	0.045	-0.857*	-0.408
GERB	-0.249	-0.168	-0.045	-0.991**	-0.515
TATE	0.079	0.037	0.757*	0.071	0.408

* Spearman rank correlation test significant at alpha = 0.1. (two-tailed test)
** Spearman rank correlation test significant at alpha = 0.02.
Crititcal values taken from Siegel (1956) Table P. This table applies for samples where $N < 10$.

Table 5.3: (cont'd) Spearman rank correlation coefficients between species. Rank abundance determined by %NISPn. Roost 12 was excluded due to small sample size. Each comparison has N=7 values.

	LEMN	MAST	MUSM	MUST	PRAO	THAL
LEMN	1.000					
MAST	0.429	1.000				
MUSM	0.857*	0.214	1.000			
MUST	0.500	-0.107	0.643	1.000		
PRAO	0.039	-0.039	0.236	0.355	1.000	
THAL	0.955**	0.360	0.811*	0.595	0.109	1.000
ZELO	-0.071	0.357	0.071	0.321	-0.256	-0.054
SACC	0.955**	0.577	0.739*	0.487	0.010	0.891*
DEND	-0.071	-0.214	0.214	0.536	-0.177	-0.126
STEA	-0.464	-0.750*	-0.250	-0.036	-0.453	-0.523
GERB	-0.252	-0.901**	0.000	0.126	-0.249	-0.245
TATE	-0.393	-0.214	-0.679	-0.679	-0.020	-0.378

	ZELO	SACC	DEND	STEA	GERB	TATE
THAL						
ZELO	1.000					
SACC	0.054	1.000				
DEND	0.714*	-0.018	1.000			
STEA	0.107	-0.523	0.607	1.000		
GERB	-0.162	-0.427	0.414	0.883*	1.000	
TATE	-0.750*	-0.378	-0.750*	-0.071	-0.054	1.000

* Spearman rank correlation test significant at alpha = 0.1. (two-tailed test)
** Spearman rank correlation test significant at alpha = 0.02.
Crititcal values taken from Siegel (1956) Table P. This table applies for samples where $N < 10$.

Figure 5.2: Correspondence analysis of %MNI values. The first two axes explain 64% of the inertia. Red diamonds indicate roosts and blue circles indicate taxa. Taxa codes are from the first four letters of the taxon name.

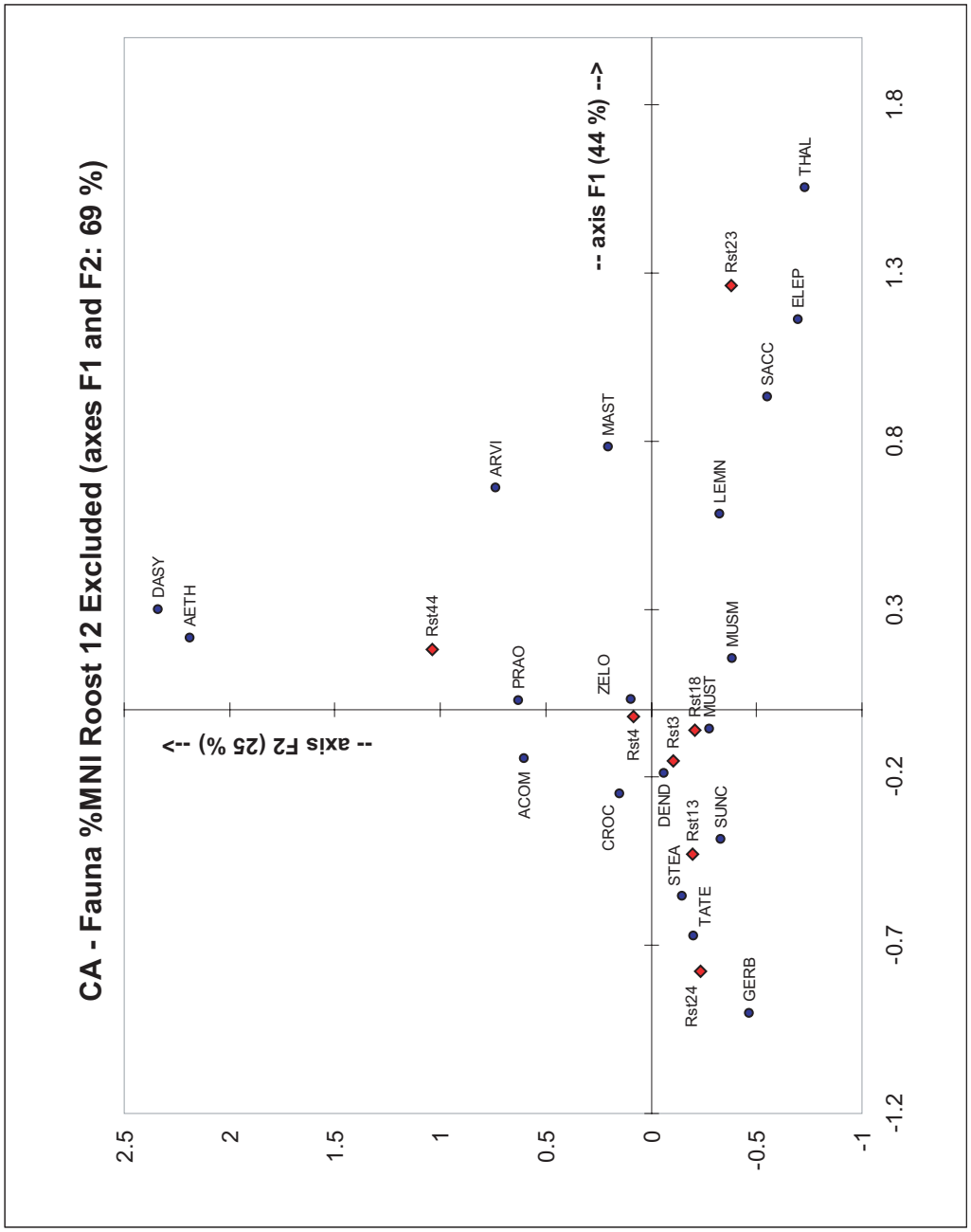


Table 5.4: Table of partial chi-squares for faunal MNI with roost 12 excluded. Cell values indicate the result of a chi-square test of independence between the taxa and the roost. (+) indicate associations and (-) dissociations. Significance levels are given at the bottom of the table. Those taxa marked by "!" were not found to vary significantly accross roosting sites and were not tested by partial chi-squares, though the direction of their associations is given.

	Rst3	Rst4	Rst13	Rst18	Rst23	Rst24	Rst44
CROC	(+) ***	(+) NS	(-) NS	(+) NS	(-) ***	(-) *	(+) NS
SUNC	(+) ***	(-) NS	(+) NS	(-) NS	(-) NS	(-) NS	(-) NS
ELEP!	(-) NS	(-) NS	(+) NS	(+) NS	(+) NS	(-) NS	(-) NS
ACOM!	(+) NS	(-) NS	(+) NS	(+) NS	(-) NS	(-) NS	(+) NS
AETH	(-) NS	(-) NS	(-) NS	(-) NS	(-) NS	(-) NS	(+) ***
ARVI	(-) **	(+) **	(-) **	(-) NS	(+) ***	(-) ***	(+) ***
DASY	(-) NS	(-) NS	(-) NS	(-) NS	(-) NS	(-) NS	(+) ***
LEMN!	(-) NS	(-) NS	(-) NS	(+) NS	(+) NS	(-) NS	(-) NS
MAST	(-) *	(+) ***	(-) ***	(-) **	(+) ***	(-) ***	(+) **
MUSM!	(+) NS	(+) NS	(-) NS	(+) NS	(+) NS	(-) NS	(-) NS
MUST	(+) *	(-) NS	(+) NS	(+) ***	(-) NS	(-) ***	(-) NS
PRAO!	(+) NS	(-) NS	(-) NS	(+) NS	(-) NS	(-) NS	(+) NS
THAL	(-) NS	(-) **	(-) NS	(-) NS	(+) ***	(-) ***	(-) NS
ZELO!	(-) NS	(+) NS	(+) NS	(-) NS	(-) NS	(-) NS	(-) NS
SACC	(-) NS	(+) NS	(-) NS	(+) **	(+) ***	(-) ***	(-) NS
DEND!	(+) NS	(+) NS	(+) NS	(-) NS	(-) NS	(-) NS	(-) NS
STEA	(-) ***	(-) NS	(+) ***	(-) **	(-) ***	(+) ***	(-) **
GERB	(-) **	(-) ***	(+) **	(-) NS	(-) *	(+) ***	(-) NS
TATE	(-) ***	(-) ***	(-) ***	(-) *	(-) NS	(+) ***	(-) NS

!: taxa not significant in test across all roosts.
(+): observed frequency > expected frequency
(-): observed frequency < expected frequency
NS: Chi-square by cell test non significant at the level of significance alpha=0.100
*: Chi-square by cell test significant at the level of significance alpha=0.100
**: Chi-square by cell test significant at the level of significance alpha=0.050
***: Chi-square by cell test significant at the level of significance alpha=0.010

Thallomys and *Elephantulus* are all correlated with each other and significantly associated with roost 23.

Gerbillus and to a lesser extent *Steatomys* are open habitat, grassland species and their presence at roost 24 is in agreement the habitat at this roost. Likewise *Elephantulus, Thallomys* and *Saccostomus* all prefer more closed bush-woodland habitats. In order to better interpret the axes of the ordination plots, rank correlation tests were conducted on each species in relation to six ecological variables measured at the roosting sites: elevation (ELEV), the standard deviation of elevation (ELEV SD), mean annual precipitation (MAP), percent slope and its standard deviation (SLOPE, SLOPE SD), and proportion of pixels in the Level A classification that were classed as woody vegetation (trees and shrubs) (PWV). The results of the correlation analysis are presented in Table 5.5. Only one result is highly significant, the positive correlation between *Arvicanthis* and mean annual precipitation. However there are trends to the other significant results. Generally, *Arvicanthis* is found to positively correlate with the factors that increase along the precipitation gradient, such as variability in elevation and density of woody vegetation cover. The correlations with slope and slope variation are not significant but they are large and positive. There is also a negative correlation with elevation since elevation values decrease to the north and west as one approaches Lake Victoria. Thus elevation trends negatively along the same gradient as increasing precipitation. *Mastomys*, which correlates in rank abundance with *Arvicanthis*, shows the same trend in relation to the ecological variables, though all results are slightly less significant. Conversely, *Steatomys* and *Gerbillus* show exactly the opposite trend. These taxa are more abundant at the higher elevation, in the southern portion of the park, where MAP, and PWV are both much lower. These correlations were calculated without roost 12 to avoid the effects of sample size on abundance that was detected earlier.

These results are in agreement with those from the ordination and partial chi-square analysis. Since many of the ecological variables co-vary it is not possible to declare which of these ecological factors has the strongest causal effect, but that is beyond the intent of the analysis and beyond the expectations for taphonomic assemblages. What these results demonstrate is that there are significant differences between roosting sites collected by owls and that these differences have interpretations relevant to land cover and other ecological parameters. In other

Table 5.5: Spearman rank correlation coefficients of comparisons between species and ecological variables. Rank abundance determined by %NISPn. Roost 12 was excluded due to small sample size. Each comparison has N=7 values.

	ELEP	ACOM	AETH	ARVI	DASY	LEMN
ELEV	-0.079	-0.185	-0.134	-0.857*	-0.612	0.071
ELEV SD	0.418	0.019	0.090	0.829*	0.412	0.126
MAP	-0.020	0.148	0.134	0.893**	0.612	0.000
SLOPE	0.388	0.374	0.270	0.703	0.618	-0.144
SLOPE SD	0.493	0.111	0.089	0.679	0.408	0.036
PWV	0.169	0.019	-0.135	0.847*	0.309	0.180

	MAST	MUSM	MUST	PRAO	THAL	ZELO
ELEV	-0.786*	0.286	0.214	0.039	0.000	-0.464
ELEV SD	0.739*	-0.306	-0.234	-0.109	0.145	0.108
MAP	0.857*	-0.143	-0.250	0.059	0.036	0.429
SLOPE	0.450	-0.505	-0.162	0.030	0.000	0.090
SLOPE SD	0.571	-0.393	-0.179	-0.197	0.144	0.143
PWV	0.829*	-0.072	0.018	0.010	0.118	0.450

	SACC	DEND	STEA	GERB	TATE
ELEV	-0.108	0.250	0.643	0.847*	0.000
ELEV SD	0.345	-0.432	-0.667	-0.855*	0.306
MAP	0.144	-0.286	-0.714*	-0.883*	-0.071
SLOPE	0.036	-0.450	-0.577	-0.691	0.396
SLOPE SD	0.216	-0.429	-0.571	-0.703	0.321
PWV	0.445	0.018	-0.559	-0.855*	-0.126

* Spearman rank correlation test significant at alpha = 0.1. (two-tailed test)
** Spearman rank correlation test significant at alpha = 0.02.
Crititcal values taken from Siegel (1956) Table P. This table applies for samples where $N < 10$.

words, these data support the proposition that there is an environmental signal in the taphonomic assemblages, and one that is capable of tracking very subtle shifts in land cover, climate, precipitation or topography. More detailed study of the autecology of East African micromammals along with continued sampling of taphonomic assemblages from known habitats is needed to refine the causal relationships underlying species distributions.

5.4 Niche representation and indicator species

Few studies detail the microhabitat use of East African micromammals, but the general habitat preferences are known for most species (Kingdon 1974; Avery 1982; Vesey-Fitzgerald 1966; Hubbard 1972; Delany 1972, 1986; Andrews et al. 1975). As a general check the species composition at every roost was compared against the known habitat preferences of the species occurring there and two questions posed:

1. For each species is there at least one land cover class that falls within the niche parameters for that species?

2. For each land cover class, is there a species that represents it?

Confronting these questions with the modern roost data essentially poses a test of basic indicator species approach to paleoenvironmental analysis. The indicator species method is the most direct means of interpreting a faunal assemblage. Faunal lists are examined and the analysis focuses on key taxa that are known to be diagnostic of particular environments. This method is commonly employed for smaller assemblages or when relative abundances are considered unreliable perhaps due to taphonomic changes (e.g. Denys 1987; Wesselman 1984, 1995).

A critique of the indicator species method is that results are generally subjective depending on what taxa the analyst chooses to emphasize or ignore. The interpretation may be very good depending on the experience of the analyst, but it is not easily reproduced by other researchers. Variations on the indicator species approach utilize the entire fauna and explicitly indicate the habitat proclivities of each species by comparison with modern forms or by morphological analysis. In this case a niche model is generated for each species, as was demonstrated in section 3.4.2, and the niches are synthesized by the analyst into some composite interpretation. Many of Avery's papers make use of this approach (Avery 1992b,

1993), and later papers employ a variation in which the niche models are based on vegetation biomes or combinations of biomes and microhabitats (Avery 1995, 2001).

Large data sets typically include many species and perhaps a long time sequence in which speciation and extinction are factors. In these cases multivariate methods may be employed to reduce the dimensionality of the data. Avery (1982) used factor analysis to examine species co-occurrence in Quaternary faunas of South Africa while Van der Meulen and Daams (1992) employed clustering with principal components analysis to analyze a large database of Early-Middle Miocene rodent faunas from Europe. In both cases the effect is to reduce the number of taxa by searching for those that covary and combining them into a composite variable. The last analysis is noteworthy as well for employing reproductive strategy (whether species were r or K selected) as a niche parameter. Their operating assumption is that rapidly reproducing lineages are favored during periods of climatic variability. Though not identical, reproductive strategy is a component of adaptive versatility which is in turn a key to the variability selection hypothesis of Potts (1996). Micromammals may prove useful in tracking climatic variability as well as paleoenvironment.

The indicator species approach has been validated as a method of analysis against modern faunas in several ways. Very generally, many students of avian trophic ecology have noted changes in species composition and relative abundance corresponding with habitat changes (Glue 1967; Avery 1992a; Avery et al. 2002; Libois et al. 1983). Avery (1982) in her analysis of Quaternary South African sites included analysis of modern assemblages following the lead of Chaline (1972) who also tested his methods against three modern assemblages. One might conclude the point proven, but in fact these types of calibration analyses are conducted far too infrequently. Niche models are constantly revised as new data on micromammal ecology and systematics becomes available. Methods of analysis change as well and new methods are introduced. In each of these circumstances the first activity should be to calibrate the analysis against a broad array of well documented modern comparative samples. Preferably the reference samples themselves would improve. Their sample sizes would increase with continued sampling and their habitat and ecological calibrations should be revised as well. Furthermore, calibration sites should be standardized across researchers, providing a common basis for com-

parison of results and a greater standardization in methodology. The Serengeti, by virtue of the extensive ecological research conducted in the park and the broadly published results, serves as a widely used modern analogue for paleontological and archeological studies. However, small mammals in the ecosystem are not very well documented. A small study by Laurie (1971) was the only previous attempt to study owl accumulations in the ecosystem.

In applying basic indicator species methods to the modern Serengeti data we can explore two types of questions. First are all the habitats present in the 1.5 km analysis radius accounted for by the species that appear in the owl assemblage? Reversing this question, we can examine whether any species are present that cannot be accounted for by the habitat. For example the Link Rat, *Deomys*, is a true forest endemic and its occurrence on the short grass plains would be in contradiction to the niche model for that species. Likewise, the appearance of *Gerbillus* in the riparian forests and wet grasslands of the northern extension would force reexamination of the *Gerbillus* niche model. We will see though, that the majority of species have broad habitat tolerances in accord with the full range of biomes present in Serengeti. As a result the indicator species approach, based solely on the presence or absence of species, has limited power to resolve subtle habitat changes in the ecosystem. Relative abundances provide the necessary missing information, and requires different methods as are addressed in the next section.

Figure 5.3 gives a graphical representation of niche use. Along the left margin, each block represents a roost, with five potential land cover classes making up the rows for each roost. Those land cover types that were observed at the roost are in black while those not present are grayed out. A column is given to every taxa. If the taxa is present at a roost, its niche space is blocked off. For example, *Acomys* occurs at roosts, 3, 18 13, 12 and 44, where it may occupy forest, bushland, or grassland land cover types. Shrews of the genus *Crocidura* and *Suncus* are excluded from the analysis. *Crocidura* because the genus has many species and would fill every niche. *Suncus* because too little is known about its microhabitat use to build a niche model. Figure 5.3 demonstrates overlap between the land cover classes that are present around each roost and the niches proposed for each of the taxa. In so doing the figure also provides a quick reference to the presence/absence distribution of the taxa and habitats across roosts. The method provides at least a first order validation of the niche models proposed for each species. None of the species occur

Figure 5.3: Niche association between taxa and habitats at each roost. Roost IDs and land cover classes appear down the left side. Land cover classes in bold are present at the roost. Red squares with then number 1 indicate the niche association of each species. Squares appear only if the taxa is present at the roost. Each bold land cover type should intersect the niche space of at least one species indicating that the land cover type is represented in the fauna. Conversely each species niche space should intersect at least one land cover type.

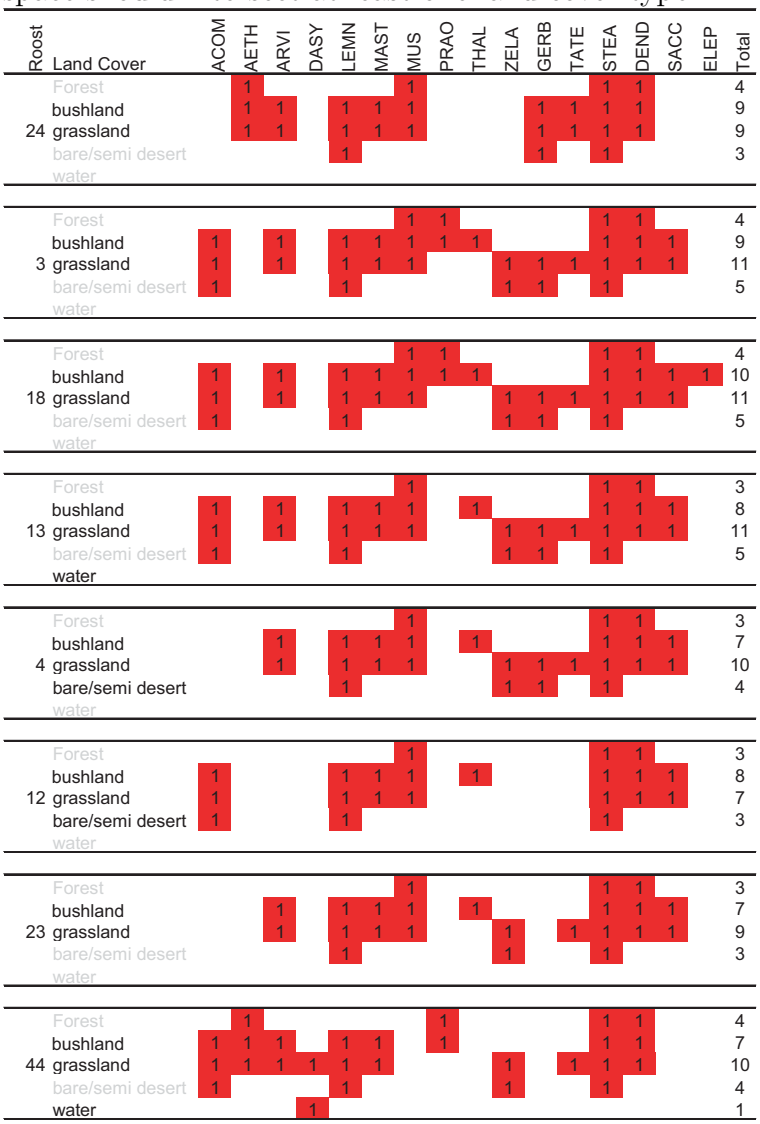


Table 5.6: Spearman rank correlation coefficients for comparisons between taxonomic ratios (rows) and ecological variables (columns). Correlations based on N = 7 roost sites. Roost 12 omitted due to small sample size.

	ELEV	ELEV SD	MAP	SLOPE	SLOPE SD	PWV
GM	0.571	-0.393	-0.714*	-0.179	-0.286	-0.523
DM	0.857*	-0.786*	-0.893**	-0.714*	-0.679	-0.847*
SM	0.857*	-0.929**	-0.821*	-0.821*	-0.857*	-0.883*

* Spearman rank correlation test significant at alpha = 0.1 (two-tailed test)
** Spearman rank correlation test significant at alpha = 0.02

unexpectedly at any roosts.

There is, however, one instance of a land cover type that is not represented by a niche model. Roost 13 thoroughly overlaps the wet, riparian habitats of the Ngare Nanyuki River. This is a perennial water source near roost 13 but there are no water loving species such as *Dasymys* or *Pelomys* associated with this roost. The river is rather small and rocky in the area near roost 13 and does not support extensive, marshes or riparian grasslands that would provide ideal habitat for these species.

5.4.1 Taxonomic Ratios

By focusing on taxa that have strong ecological affinities, one can concisely summarize the habitat characteristics of an assemblage. For example, Vrba (1985) found the summed proportion of Alcelaphini and Antelopini bovid tribes to be a good indicator of open habitats. Similarly the ratio of Gerbillinae to Murinae has been proposed as a rodent indicator of open habitats (Jaeger 1979; Dauphin et al. 1994; Fernandez-Jalvo et al. 1998). Spearman rank correlation tests between the ratio of Gerbillinae to Murinae and the six ecological variables fails to result in any significant correlations. However, the same tests conducted with the Dendromurinae:Murinae and Soricids:Murinae show very significant correlations, these are summarized in Table 5.6. The GM ratio is undermined by the abundance of *Tatera*. As was noted in the previous section, there is a strong correlation between *Gerbillus* and many of the ecological variables. However, *Tatera* does not follow this trend as strongly so the ratio is not quite significant. The highly significant correlations for Dendromurines are somewhat surprising, especially given the niche

models of the species. The five category niche model proposed by Fernandez-Jalvo et al. (1998) divides its mass evenly into all five categories (i.e. 0.2 for each habitat class), however Kingdon (1974) associates the genus with grasslands and dry savanna. Soft substrate is clearly a critical habitat factor for this burrowing species but it does not appear to occupy true forest based on the biogeographical distribution, which follows the Sahelian zone surrounding the lowland forests of Africa. The niche model should probably be revised to reflect a more open habitat preference. Similarly *Dendromus* is closely associated with a mid to tall grass understory. This species nests in grass and is adapted to climbing call grass stems and bushy understories using its prehensile tail. That these species should correlate with more open grasslands is thus consistent with what is known of their autecology. Still, the strongest correlations were found with the soricid:murid ratio. Too little is known about the proclivities of crociduran shrews to address this trend in depth, but it appears they may have an association for open habitats. That all three ratios have the same pattern, points to an even more parsimonious explanation, that the Murinae are more closely associated with dense vegetation than all the other groups.

5.4.2 Taxonomic Habitat Index

Moving beyond indicator species, habitat spectra analysis was developed by van Couvering (1980) as a way to systematically incorporate the entire fauna into the analysis. Derived from the faunal resemblance indices of Simpson (1960), habitat spectra allow taxa to be divided among multiple habitats. This system better reflects the flexibility that most mammals exhibit in the habitats they use. The taxonomic habitat index (THI) of Nesbit-Evans et al. (1981) is a further refinement that improves the hierarchical weighting structure for analysis at different taxonomic levels.

Fundamentally THI is a method of aggregating the information from each taxa into a composite interpretation of paleoenvironment. The analysis works from a contingency table of niche models with taxa as row headings and the different environments or habitats as column headings. The niche model proportions each species across habitats as is shown in Table 5.7. 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

Table 5.7: Niche models for Serengeti rodents.

		Land Cover				
		Forest	Woodland	Bushland	Grassland	Semi-Arid
Arvicanthis	ARVI	0	0	0.25	0.75	0
Aethomys	AETH	0.18	0.25	0.4	0.18	0
Mastomys	MAST	0	0.33	0.33	0.33	0
Mus	MUS	0.35	0.19	0.26	0.2	0
Oenomys	OENO	0.5	0.5	0	0	0
Pelomys	PELO	0	0	0.5	0.5	0
Thallomys	THAL	0	0.5	0.5	0	0
Grammomys	GRAM	0.4	0.35	0.2	0	0.05
Zelotomys	ZELA	0	0	0.2	0.7	0.1
Gerbillus	GERB	0	0	0.2	0.2	0.6
Tatera	TATE	0	0	0.4	0.6	0
Steatomys	STEA	0.2	0.2	0.2	0.2	0.2
Dendromus	DEND	0.05	0.27	0.4	0.28	0
Saccostomus	SACC	0	0.33	0.33	0.33	0
Otomys	OTOM	0	0.25	0.5	0.25	0
Xerus	XERU	0	0.33	0.66	0	0
Heterocephalus	HETE	0	0.2	0.3	0.4	0.1
*Acomys**	ACOM	0	0.17	0.17	0.17	0.5
*Dasysmys**	DASY	0	0	0.2	0.8	0
*Lemniscomys**	LEMN	0	0.1	0.1	0.5	0.3
*Praomys**	PRAO	0.8	0.2	0	0	0

* new niche models not included by Fernandez-Jalvo (1998)

spectrum. The results indicate the habitats that are most strongly represented by the species in the assemblages (Andrews 1990; Nesbit-Evans et al. 1981).

THI is sensitive to the habitat weightings given to each taxa, i.e. their niche models, and this aspect of the method remains subjective. The methodology is explicit about how to combine species niche models into models for higher taxa, and it is clear about how results are calculated; but it remains vague on the issue of how the niche models of individual species are constructed. However, THI ranks as an advancement over the indicator species approach because it requires the analysts to explicate a niche model for each taxa. Even if the niche models are subjective, clearly enumerating them leads to greater transparency and reproducibility in the analysis.

Nesbit-Evans et al. (1981) provide taxonomic habitat spectra for eleven modern faunas (mega- and micro-) including the Serengeti, but do not provide the individual niche models used to construct the spectra. However, in their ana-

Table 5.8: Numerical results of THI analysis. Table values indicate expected percentages of each habitat class for each roost.

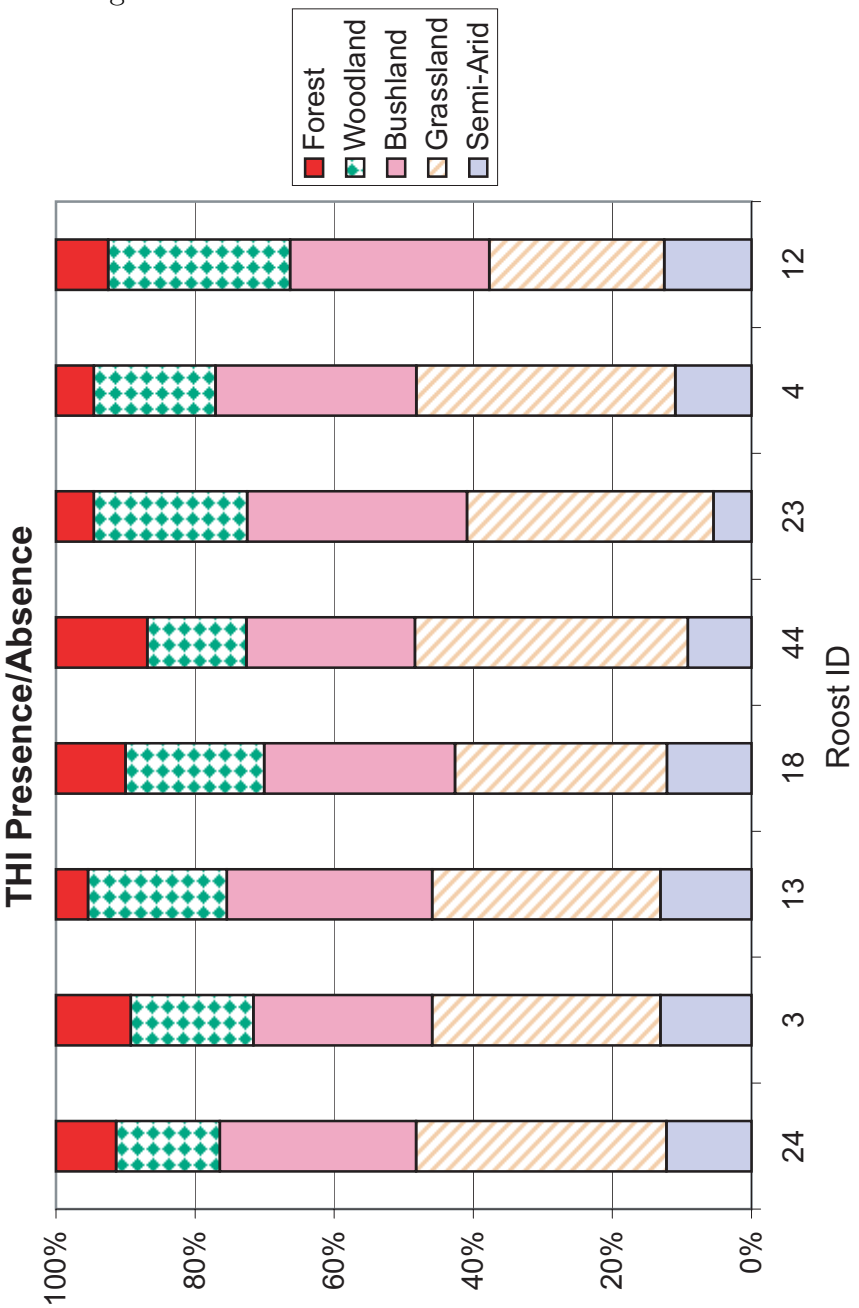
	Roost ID							
	24	**3**	**13**	**18**	**44**	**23**	**4**	**12**
Forest	8.67	10.77	4.62	10.00	13.17	5.45	5.45	7.50
Woodland	14.89	17.62	19.92	19.93	14.25	22.00	17.45	26.13
Bushland	28.22	25.69	29.54	27.43	24.25	31.55	28.82	28.63
Grassland	36.00	32.77	32.77	30.43	39.25	35.36	37.18	25.13
Semi-Arid	12.22	13.08	13.08	12.14	9.17	5.45	10.91	12.50

lysis of the Olduvai microfauna, Fernandez-Jalvo et al. (1998) provide individual niche models for the fossil faunas. These are reproduced in Table 5.7, and added to these are four new models for rodent taxa encountered during this study: *Acomys*, *Dasymys*, *Lemniscomys* and *Praomys*. Habitat spectra for the Serengeti taphonomic assemblages are shown in Figure 5.4. The numerical results from the analysis are given in Table 5.8.

Given the broad niche breadth of most rodents THI 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 even though they are absent or present in very small quantities at that roost. THI should at least return the habitat classes in their proper rank order. Roost 24 returns grassland, bushland, woodland, semi-arid and forest in that order. This agrees with the habitat classes measured around that roost, which were 88 % grasslands, and 13 % 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 in which the habitat classes are ranked: bushland, woodland, grassland, semi-arid, forest. From the perspective of accuracy this is appropriate as grassland is the dominant land cover category at all roosts, so the only inaccurate result would be at roost 12 where woody vegetation is over-represented in the analysis. Furthermore, evaluating the rank order of woodland and bushland is difficult with

Figure 5.4: THI Habitat spectra based on Serengeti taphonomic assemblages. Roosts are arranged in ascending order of percent woody vegetation cover from left to right.



the current data set because shrubs were not reliably distinguished from woodland in the imagery. A more basic test of woody vegetation versus non-woody vegetation is more appropriate. Recoding figure 5.4 produces Figure 5.5 where the roosts are divided simply into wooded and non-wooded categories. This approach does not appear very fruitful. Wooded categories are consistently over-represented. The figure does illustrate a weak trend in the relative height of the open categories. The combined values of grassland and semi-arid is high at roost 24 and declines along with increases in the measured percent woody vegetation cover at the roosts, with two notable exceptions roost 44 and 4. A rank correlation test of the open THI categories (combined) against the percent woody vegetation (PWV) index, however, is non-significant. Overall, the differences between roosts is not very great. Based just on species presence or absence, THI may have a difficult time discerning similar types of habitats especially where taphonomic agency is not strictly the same.

One possibility for amplifying the ecological signal presented by the fauna is to apply an additional weighting according to the relative abundances of taxa. Figure 5.6 shows habitat spectra base on THI values using the same vegetation categories and niche models but with values weighted acording to the relative abundance (based on NISPn) of the taxa. The general pattern is the same, but differences are exagerated bewteen the roosts. Roost 24 and 44, which were very similar before now show a greater abundance of grassland habitat at roost 44. This difference is largely driven by *Arvicanthis*.

The same rank order of habitat classes holds at roost 3 which is appropriate, as again this roost is mostly grassland and bushed grassland, where the woody component is again low shrubs interspersed within the herb layer. Dense shrubs occur along river drainages where there is also proper woodlands. These riverine shrubs and woodlands contribute to roughly 2% of the land cover.

A THI analysis of the Serengeti taphonomic assemblages yields results that are consistent in rank order of the habitat spectra across roosts with two exceptions. There is commonly some misrepresentation of habitats in a THI spectra brought about by the flexibility of small mammal species, so it is unsurprising for instance to observe some woodland and forest component in the roost 24 spectrum where these habitats do not exist. The spectra serve better to demonstrate relative influences of the different habitats. Roost 24 has the highest value for grasslands of all the

Figure 5.5: THI spectra with dichotomous representation of woody vegetation versus herbaceous vegetation.

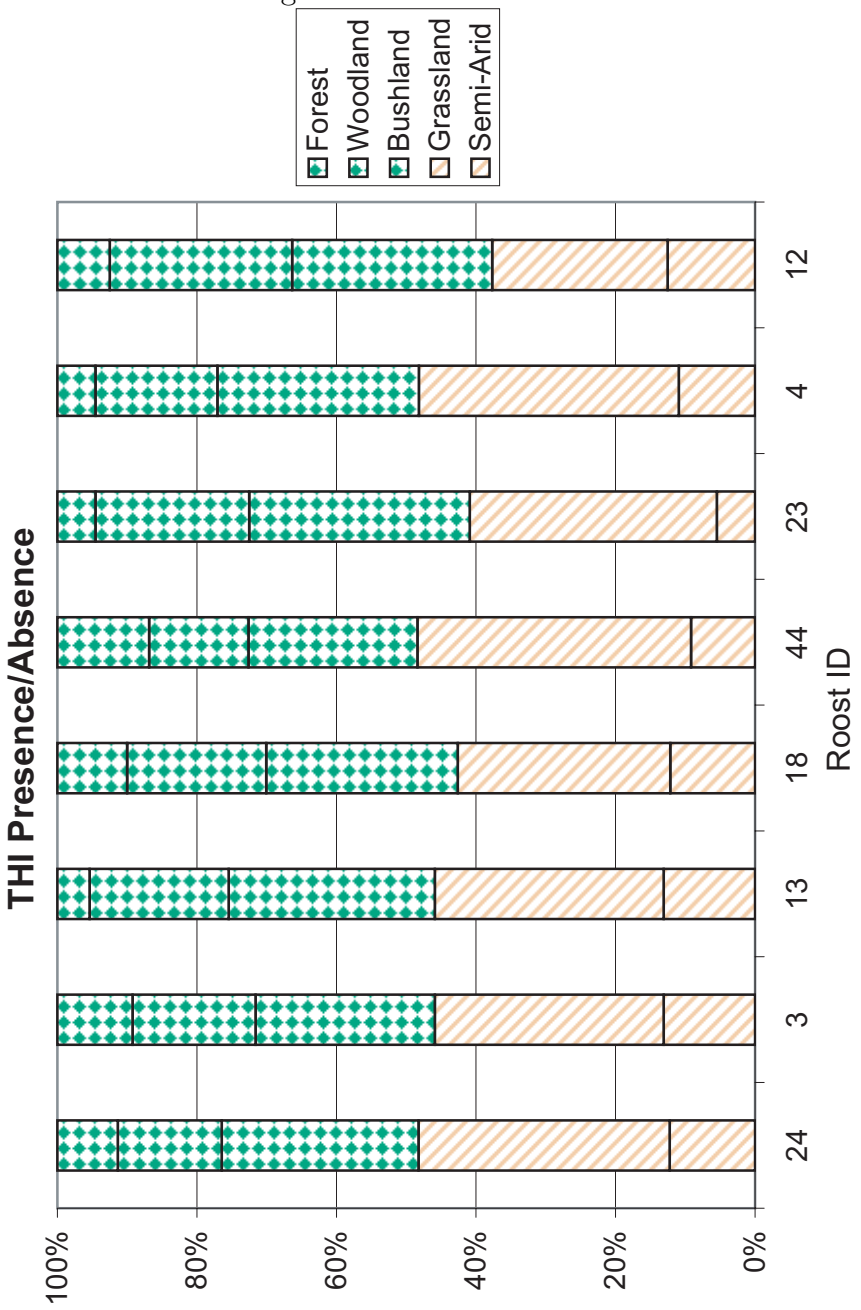
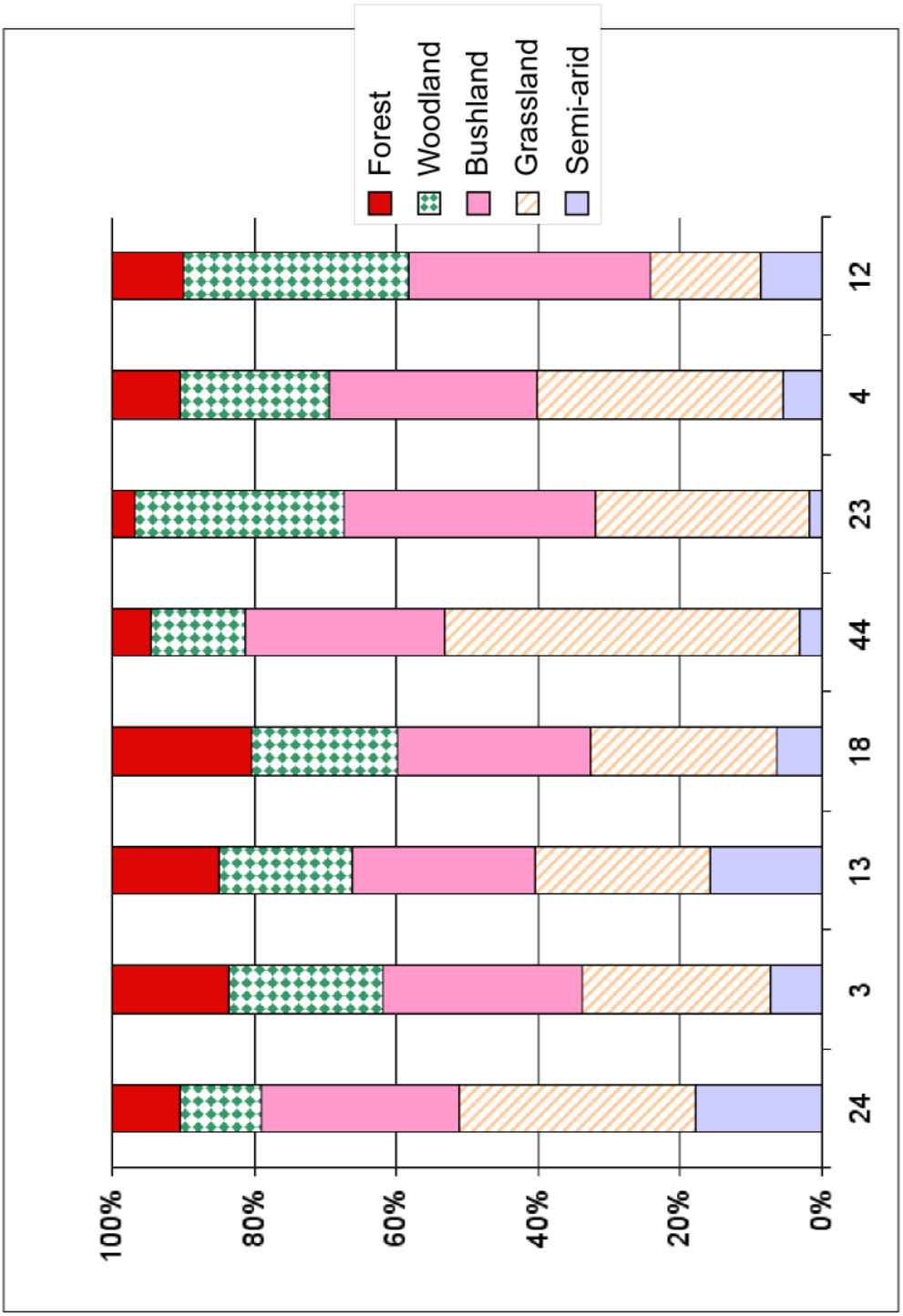


Figure 5.6: Habitat spectra based on taxonomic habitat indices weighted by NISPn. Roosts are given in ascending order of woody vegetation starting with the least wooded roost on the left.



roosts, though it is followed very closely by roost 44. Part of the similarity between roost 24 and 44 derives from the presence of *Dasymys* which is a marsh/grassland specialist. Under the current scheme this genus is weighted heavily on grasslands. Including a marsh/wetlands category as was done by van Couvering (1980) would probably improve the interpretation, but the five classes are maintained here for consistency with Fernandez-Jalvo et al. (1998).

THI can be improved most efficiently by developing better niche models. The niche models ask what is the probability of Habitat 1 given Taxa A, $p(H_1|T_A)$. This probability could be ascertained first by systematic survey of museum collection records, a task that will only become practical as collection 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 Taxa 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 $p(H_1|T_A) = 0.99$, but because it occurs in low abundance the probability of finding that species in Habitat 1, may be quite low, i.e. $p(T_A|H_1) = 0.001$. Cataloging museum specimens provides a first approximation of habitat indications, but due to taphonomic biases it would be better to calculate the niche model from taphonomic assemblages, such as those presented here.

As mentioned before, the efficacy of THI depends in large part on the quality of the individual niche models that form the basis of the analysis. Part of the error found in the current analysis may be attributed to the influence of *Steatomys*. This is the most abundant taxa at roost 24, and the partial chi-square scores from the contingency tables show significant positive associations with roosts 24 and 13, two of the drier and more open roosts along with a significant negative weighting on roost 23 and roost 3. The negative association at roost 3 is peculiar. But the weight of the evidence suggests that the niche model for *Steatomys* may need adjustment, with a greater weight given to drier, more open habitats.

5.4.3 Species diversity

Taxonomic habitat indices, and habitat spectra are reductionist. The interpretation is built up from the autecological signal of the individual species. Another approach is to examine the structure of the community as a whole. The diversity of species in a community may be informative, though taphonomic assemblages must again contend with predator overprinting. It is further a challenge to interpret the meaning of changes in species diversity between assemblages, as numerous factors are known to influence it.

5.4.3.1 Defining species diversity

Species diversity has two components; richness is the number of species in a community, evenness (also called equitability) is a quality of the relative abundances of species in the community. Diversity increases when there are more species and each is similar in abundance (high evenness). Diversity may be enumerated in several ways. Simple species richness is a very direct measure of diversity. It is also very sensitive to sample size. Two common diversity measures attempt to normalize diversity by sample size; the Margalef diversity index,

$$D_{MG} = \frac{(S-1)}{ln\, N} \tag{5.1}$$

and the Menhinick diversity index,

$$D_{MN} = \frac{S}{\sqrt{N}} \tag{5.2}$$

where S is the number of species and N is the total number of individuals (Magurran 1988). The fullest description of species diversity comes from a species abundance model.

5.4.3.2 Sample size effects on species diversity

Perhaps the earliest observation made about species diversity is that the number of species increases with the area that is surveyed (Rosenzweig 1995). Based on empirical data, Preston (1962a,b) proposed a power function to model the relationship, $S = cA^z$. The number of species, S is proportional to the area, A raised to the power of a constant, z. A similar relationship applies to sampling; species

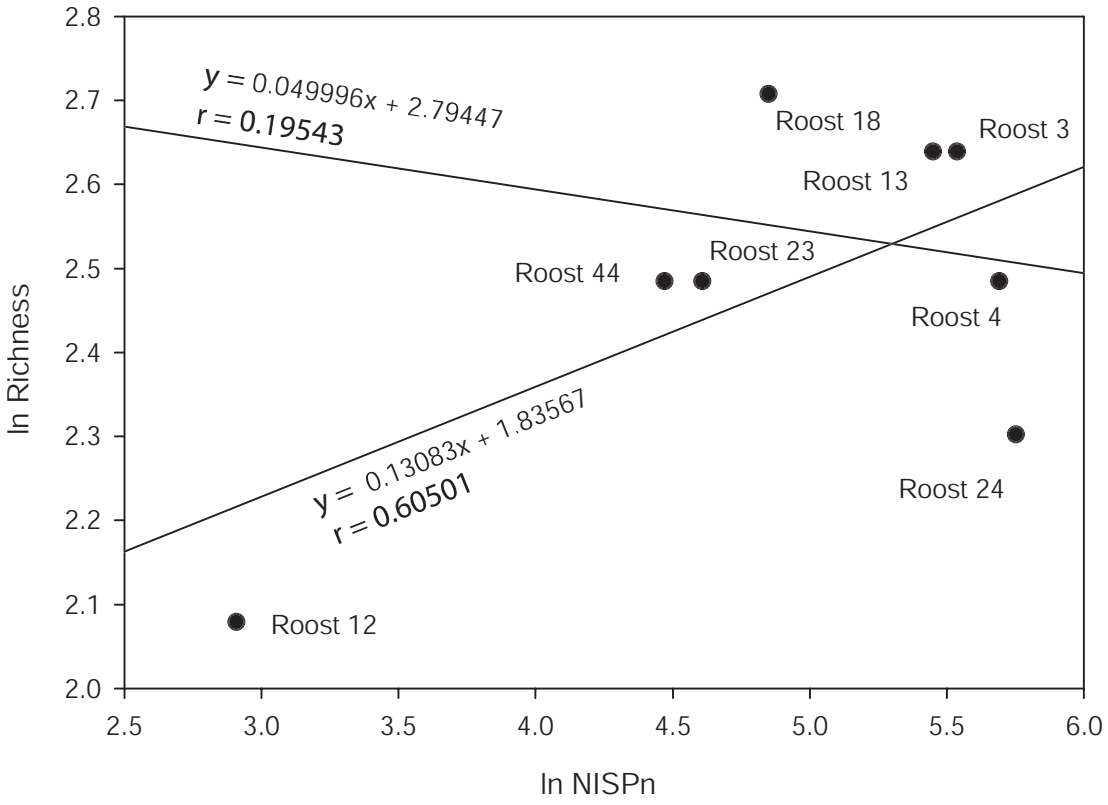


Figure 5.7: Log-log plot of taxonomic richness against sample size. Solid lines show least squares regression curves. The lower curve includes all roosts while the upper curve excludes the smallest sample at roost 12.

richness increases with sampling effort (Cruz-Uribe 1988; Grayson 1984; Hayek and Buzas 1997; Kintigh 1984; Magurran 1988). The Serengeti ossuaries vary in sample size from NISPn of 18 at roost 12 to 315 at roost 24. Species richness in the taphonomic assemblages ranges between 9 species at roost 12 up to 17 species at roosts 18. A total of 19 species were observed across all roosts. A regression of species richness on NISPn, Figure 5.7 indicates that richness correlates with sample size when all roosts are considered, however the curve is heavily influenced by the smallest roost. Eliminating roost 12 also removes the trend. This is not to say that sample size is not an issue with the remaining roosts. A comparison of rarefaction curves provides a more detailed picture.

5.4.3.3 Rarefaction

Rarefaction is a method that estimates species richness at cumulatively greater sample sizes (Krebs 1999). The expected number of species, $E(S)$ at different sample sizes is given by the equation,

$$E(S_n) = \Sigma_{i=1}^{S} \left[1 - \frac{\begin{pmatrix} N - N_i \\ n \end{pmatrix}}{\begin{pmatrix} N \\ n \end{pmatrix}} \right]$$

where n is the standardized sample size, N is the total number of individuals observed, N_i the number of individuals in the ith species. The curves shown in Figure 5.8 where generated using the PAST software. Outer curves display 95% confidence intervals. Species richness increases rapidly at first then begins to taper off as rare species are encountered less frequently and the curve asymptotically approaches the true richness. Rarefaction curves are useful for comparing samples of different sizes, however they are, strictly speaking, not appropriate when specimens represent more than one individual or when there is habitat heterogeneity (Tipper 1979; Grayson 1984). The number of individuals per specimen is relatively well constrained between MNI and NISPn, and since these values are very similar in the Serengeti assemblages, this assumption is reasonable. The rarefaction curves are most useful for revealing the general patterns in the assemblages. From these curves one see immediately that roost 24 is the largest assemblage yet the curve is rather flat, because the richness at the roost is low. Three other roosts have relatively large samples, roosts 3, 13 and 4. Roosts 18 and 23 and 44 have yet to level off and thus species richness in these assemblages is under represented.

5.4.4 Patterns of species richness between Serengeti taphocoenoses

Some patterns are evident even between samples of unequal size. Table 5.9 summarizes species richness by roost. The southern grassland roost (24) is the least diverse. It is the largest sample, yet it has the second lowest richness, and it ranks lowest on both adjusted richness measures. Roost 18 is clearly very rich, having one of the smaller sample sizes yet the greatest number of species. This roost

Figure 5.8: Rarefactions curves of taxonomic richness against MNI for eight roosts along with 95% confidence intervals around the curve.

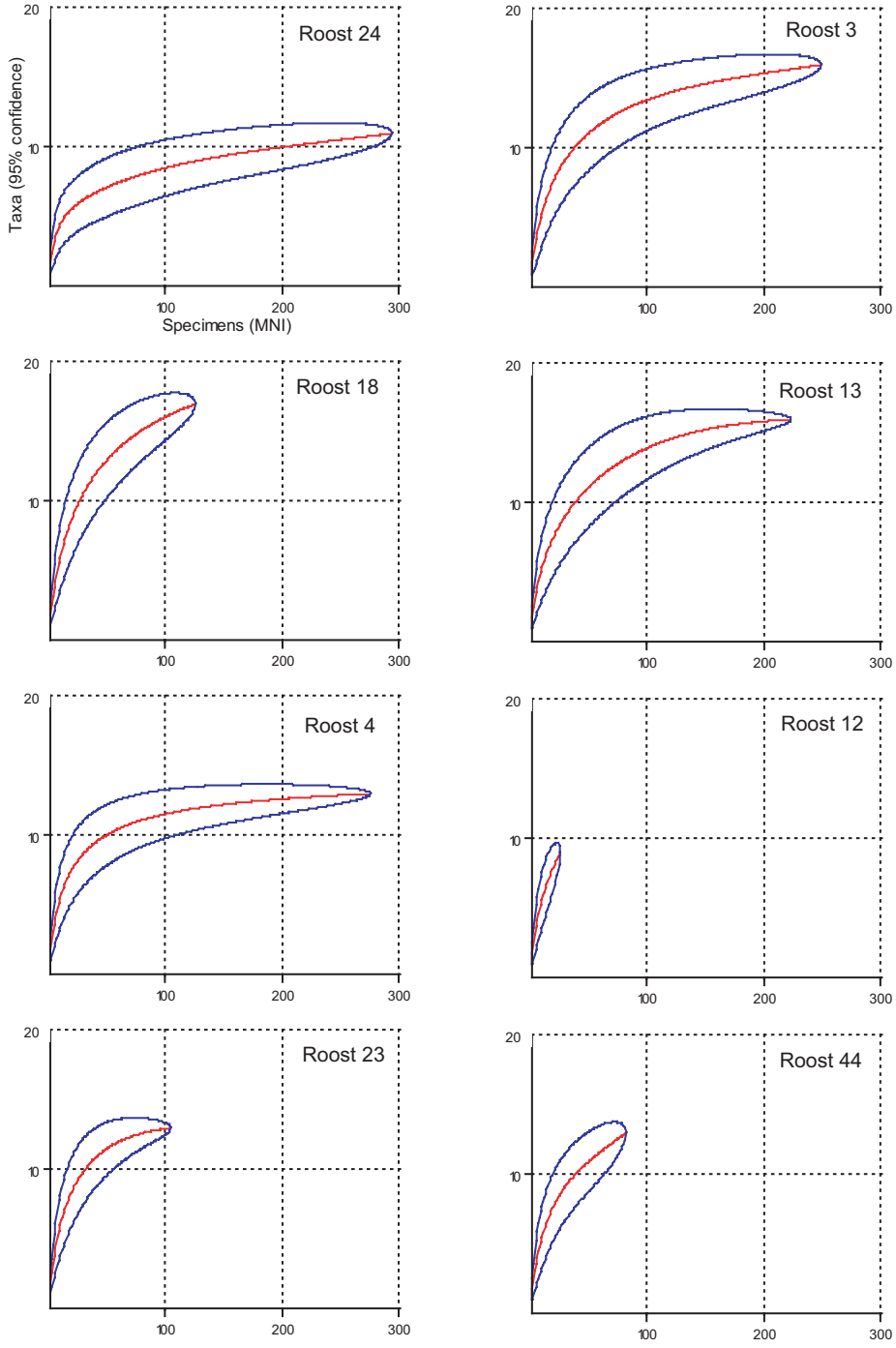


Table 5.9: Species diversity at Serengeti taphocoenoses.

	Rst24	Rst4	Rst3	Rst13	Rst23	Rst44	Rst18	Rst12
Richness	11	13	16	16	13	13	17	9
NISPn								
Individuals	316	297	252	232	99	85	127	17
Menhinick	0.6188	0.7543	1.008	1.05	1.307	1.41	1.509	2.183
Margalef	1.737	2.108	2.713	2.754	2.611	2.701	3.303	2.824
MNI								
Individuals	294	275	249	223	105	82	126	26
Menhinick	0.6415	0.7839	1.014	1.071	1.269	1.436	1.514	1.765
Margalef	1.759	2.136	2.719	2.774	2.578	2.723	3.308	2.455

ranks high by both indices. Roost 12 is also clearly diverse though it is difficult to establish its true position given the small sample size. Roost 44 and 23 share the same number of species but the smaller sample size of roost 44 causes it to rank higher; the same applies to roosts 3 and 13. Roost 4 always ranks low given its large sample size but comparably low richness. The middle roosts (3, 13, 23, 44) are all very close in richness as evidenced by the shift in rankings brought about by changing from MNI to NISPn.

5.4.4.1 Species abundance models

Almost all natural communities are characterized by unequal abundances, with a few species being very abundant and many being much less abundant. Species abundance models have been developed to mathematically define patterns of species diversity. Four models are common: the geometric series, log series, the log normal and the broken stick (Magurran 1988; May 1975). These four models are related, and when plotted on a rank/abundance graph, "can be seen to represent a progression ranging from the geometric series where a few species are dominant..., through the log series and log normal distributions where species of intermediate abundance become more common and ending in the conditions represented by the broken stick model in which species are as equally abundant as is ever observed in the real world" (Magurran 1988, p. 12). The models are taken to reflect differences in the way resources are partitioned in the community. The geometric distribu-

tion follows from a niche preemption model in which species sequentially occupy an ecosystem, each taking a uniform fraction of the resources that remain after the previous species. The log series is similar but with a non-uniform sequential partitioning of resources. These two models are presumed common under circumstances where abundances are regulated by one or a few limiting resources, such as arid or "harsh" environments. The broken stick model simply assumes a random division of resources. The log normal distribution is the most widely encountered in nature. While the geometric series results from competition for a few limiting resources the log normal distribution may result when there are many interacting factors controlling abundance (May 1975).

Recently a general model has been proposed. Hubbell (2001) argues that the four models described above are special cases of a zero-sum multinomial distribution (ZSM). An appealing characteristic of the ZSM is that species abundances are derived from population models based on individual birth and death rates (including speciation, immigration and emigration). The model is neutral in treating all species as having equal per capita probability of birth and death. Tests of the model against empirical data show that is fits as well or better than the log normal distribution (Volkov et al. 2003; McGill 2003).

Species abundance models provide the most complete description of the community, but it is not clear how species abundance patterns are affected by predator selection. Predator assemblages are necessarily subsets of the biocoenosis, but relationship between species abundance patterns in the biocoenosis and the taphocoenosis have not been determined for owl accumulated micromammal assemblages.

5.4.4.2 Patterns in species abundance and diversity

Figure 5.9 shows rank abundance plots for the eight roosts and diversity indices are summarized in Table 5.10 . The Shannon-Wiener diversity index is the sum of the proportions of each species in the assemblage,

$$H' = -\Sigma p_i \, ln \, p_i$$

where p_i is the proportion of the ith species in the assemblage. The maximum likelihood estimator for this value is simply the taxon sample abundance divided by the sample size, n_i/N. Observed values of the Shannon-Wiener index in the

Figure 5.9: Rank abundance plots for Serengeti taphocoenoses.

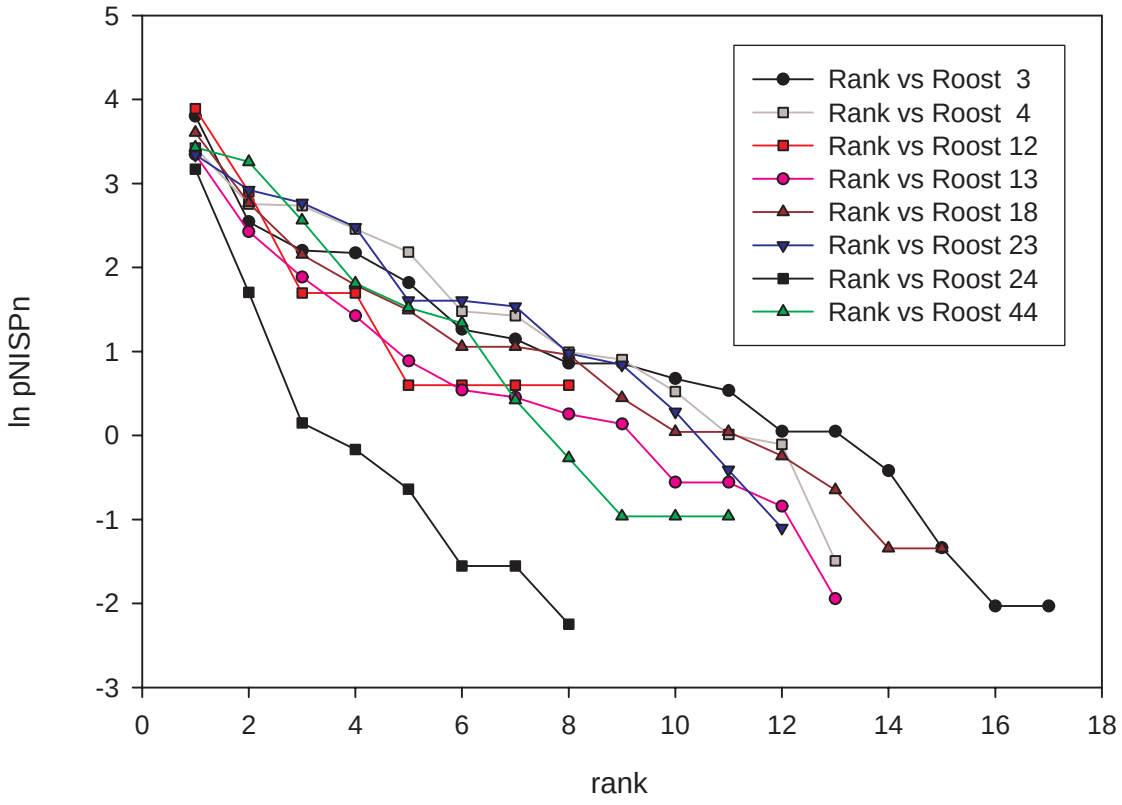


Table 5.10: Species diversity summary. Species diversity indices are given for both MNI and NISPn values. Abundances at each roost were tested against four species abundance models. The table indicates whether a chi-square test indicates the data fit the model (i.e. could not be rejected) at the $P < 0.05$ level. Tests were performed on both MNI and NISPn values. Results were the same for all roosts except roost 3, where MNI was not quite significant from the log series.

	Roost ID							
	Rst24	**Rst4**	**Rst3**	**Rst13**	**Rst23**	**Rst44**	**Rst18**	**Rst12**
Richness	11	13	16	16	13	13	17	9
NISPn								
Individuals	315	296	252	233	99	87	127	18
Shannon indx	1.606	2.036	1.912	1.964	2.066	1.937	2.06	1.588
Fisher alpha	2.214	2.777	3.801	3.9	4.003	4.279	5.277	7.753
Simpson indx	0.7661	0.8309	0.7545	0.7971	0.8323	0.7932	0.8076	0.6482
Equitability	0.6696	0.7936	0.6896	0.7085	0.8055	0.7551	0.7271	0.7229
Berger-Parker	0.3259	0.3064	0.4524	0.3103	0.2828	0.3176	0.3701	0.5294
MNI								
Individuals	294	275	249	223	105	82	126	26
Shannon indx	1.683	2.043	2.003	2.044	2.184	2.014	2.234	1.868
Fisher alpha	2.255	2.835	3.815	3.95	3.906	4.351	5.295	4.877
Simpson indx	0.7741	0.8264	0.7815	0.8116	0.8561	0.8159	0.8408	0.8018
Equitability	0.7018	0.7966	0.7226	0.7373	0.8517	0.7851	0.7886	0.8502
Berger-Parker	0.3163	0.3236	0.4177	0.287	0.2476	0.3293	0.3175	0.3462
Fit to:								
Geometric	no	yes	no	no	yes	yes	yes	yes
Log Series	no	no	no/yes	yes	yes	yes	yes	yes
Log Normal	N/A	yes	yes	yes	yes	yes	yes	N/A
Broken Stick	no	yes	yes	no	yes	yes	yes	yes

Serengeti samples range from 1.588 to 2.066 when calculated using NISPn; and between 1.683 and 2.044 when calculated on MNI. The rank order of the Shannon-Wiener index is similar using either MNI or NISPn except that roost 12 and roost 24 change rank. The Shannon-Wiener index is sensitive to very small samples (Cruz-Uribe 1988), which may explain the difference in positioning of roost 12 between the Shannon-Wiener and the richness measures. Roost 18 once again ranks high, and it is joined by roost 23.

The Shannon-Wiener index was also used to test for statistically significant differences between roosts using the relationship,

$$t = \frac{H'_1 - H'_2}{(Var\, H'_1 + Var\, H'_2)^{1/2}}$$

pairwise tests were conducted for all roost except roost 12. All comparisons were not significant at the P = 0.05 level except for those involving roost 24. All comparisons between roost 24 and another roost were highly significant. The least improbable comparison was between roost 24 and roost 44 ($t = -2.3269$, $p = 0.021675$). The overall similarity in diversity structure is evident in the rank abundance curves, where roost 24 appears an outlier. Goodness of fit tests to four common abundance models show that most roosts could be accommodated by at least one except roost 24. The tests also reveal that there is no single abundance model that adequately describes them all. The log-series model describes all but roost 24 and roost 4. The parameter of the log series, α is also a measure of diversity. For those assemblages that can be fit to a log-series distribution, Fisher's α is purported to be more robust to differences in sample size than the Shannon-Wiener index (Magurran 1988). Values for α are listed in Table 5.10. Once again roost 18 ranks high both for counts by MNI and NISPn. Roost 12 also exhibits a high value of alpha, though it changes depending on whether MNI or NISPn is used. A surprising difference is seen in the position of roost 4. This roost is rated as more diverse by the Shannon-Wiener index but much lower using α. This discrepancy arises from the equitability seen in roost 4, a factor that also explains why roost 4 does not fit a log-series distribution.

The Simpson index is defined as the opposite of dominance,

$$1 - D = 1 - \Sigma \left(\frac{n_i}{n}\right)^2$$

where n_i is the number of individuals in the ith taxon. Values of Simpson's index range from 0 to 1 with larger values indicating greater evenness in the assemblages. Similar to evenness, the equitability index, E is defined in relation to the Shannon diversity index,

$$E = H'/ln\, S$$

where S is the number of taxa. The denominator represents the maximum attainable value of H' and thus equitability is the ratio of the observed diversity to the maximum possible diversity. The Berger-Parker index is also included as a measure of dominance. This index is simply the ratio of the most abundant taxa to the whole. It's simplicity help make it one of the more robust indicators in relation to sample size (May 1975).

The evenness at roost 12 shifts depending on whether counts are made with MNI or NISPn but generally toward low evenness. Roost 24 is uniformly low in evenness and equitability across indices and counting metrics. This roost is heavily dominated by three taxa, *Steatomys*, *Tatera* and *Gerbillus*. Roost 3 also shows low evenness as it is dominated by *Crocidura*. Roost 23 consistently exhibits the greatest evenness and the lowest dominance.

In summary, roost 24 is characterized by relative and absolutely low species richness, and high dominance of three taxa. This roost does not fit any of the species abundance models. Roost 23 shows relatively high richness and diversity and is the most equitable. Roost 18 also has high absolute richness along with high relative diversity, but it is slightly less even than roost 23. Roost 12 is highly variable as a result of the small sample size. The remaining four roosts are very similar though roost 4 stands out slightly as having relatively low richness but higher evenness.

5.4.4.3 Patterns of species diversity in the Serengeti assemblages

Species diversity does not lend itself to simple interpretation. Avery (1982) in her interpretation of micromammal taxonomic diversity proposed that, "low indices would be expected in a desert other harsh environment," (p. 309). She reached a similar conclusion for evenness, that it would be greater in more favorable environments. Thus she chose to us the Shannon index as a way of combining both inputs while dampening the effects of sample size. Since that time numerous patterns

have emerged from studies of species diversity in modern ecosystems.

One of the most prevalent is the relationship between species richness and productivity. In general, as productivity increases so does the number of species. However the relationship is most often unimodal. Species richness rises quickly in low productivity environments but then tapers off and declines in high productivity environments (Diamond 1988; Owen 1988; Ricklefs and Schluter 1993; Rosenzweig 1995; Tilman 1993). The phenomenon has been observed across a broad range of habitats and ecosystems (Rosenzweig and Abramsky 1993). Among rodents, the unimodal relationship between species richness and diversity has been reported from studies in the U.S. (Brown 1973; Owen 1988) and Israel (Abramsky and Rosenzweig 1984). The unimodal relationship complicates simple comparisons of species diversity. For example, in their study of desert rodent diversity Abramsky and Rosenzweig (1984) noted a peak in the number of rodent species at 80 mm mean annual rainfall in rocky habitats and at 120 mm mean annual rainfall in sandy habitats. These peaks are followed by declines in the number of species with the lowest species richness occurring at 300 mm and 660 mm for rocky and sandy habitats respectively. Given two assemblages with differing diversity it is not possible to know which represents the more productive environment, arid environments may host *greater* rodent species richness than more mesic environments (Dauphin et al. 1994).

Furthermore, mammals species diversity may be indirectly related to productivity through plant species diversity. Figure 5.10 plots species richness in relation to mean annual precipitation for all roosts except 12. Roosts 24, 13, 3 and 4 all have samples larger than 200 MNI and make for the fairest direct comparison. Roost 4 shows surprisingly low diversity given both its position on the precipitation gradient and large sample size. Given the large sample size of roost 24, a monotonic trend for decreasing species richness in relation to mean annual precipitation is not supported by these data. One could argue for a unimodal pattern cresting at roost 18, but it is difficult to distinguish that pattern from a simple monotonic increase in diversity.

Species richness also depends on habitat heterogeneity. Generally, heterogeneity increases the number of microhabitats, thereby increasing the diversity of species adaptations and the overall number of species in a community. If a region incorporates more than one habitat type, such as forest margins along grasslands,

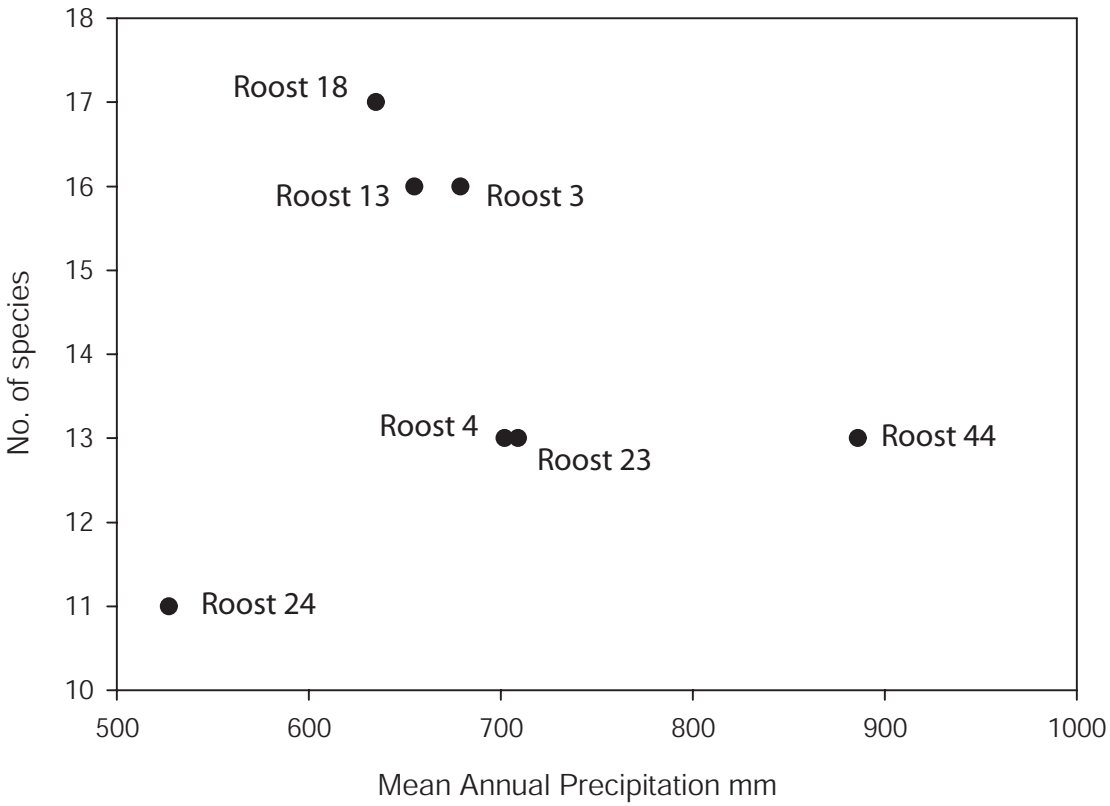


Figure 5.10: The relationship between species richness and precipitation for those roosts with samples greater than 100 MNI.

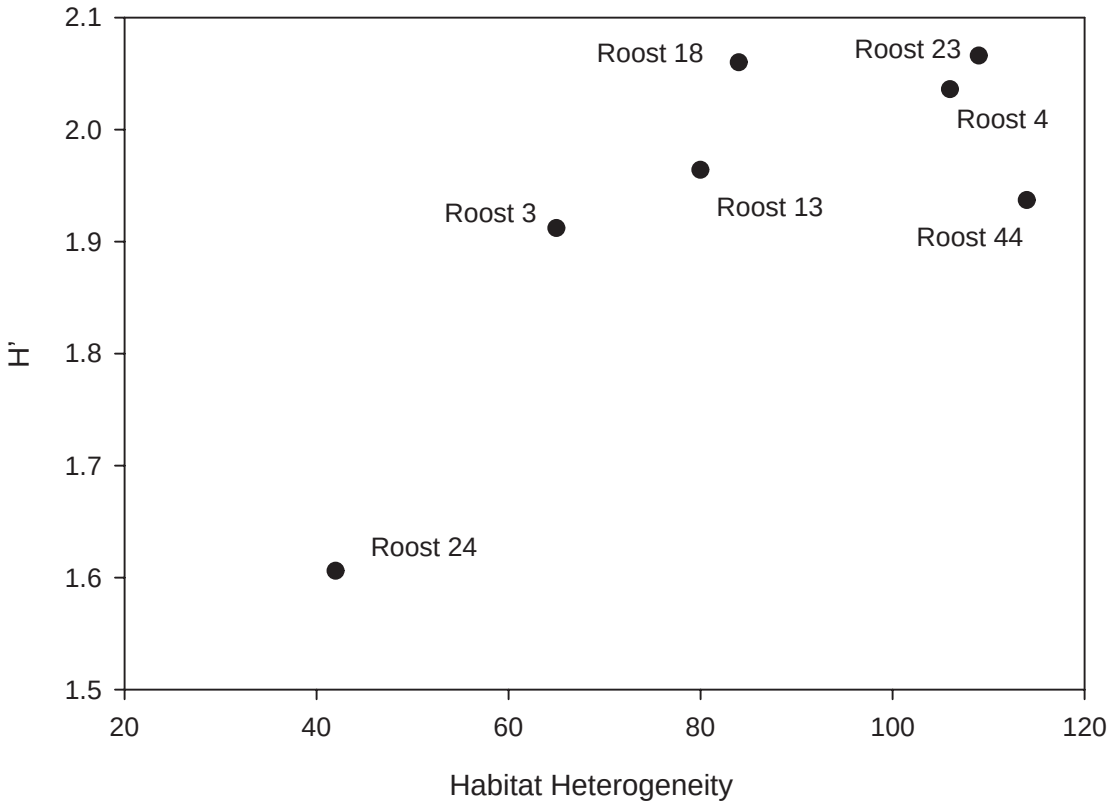


Figure 5.11: Scatterplot of species diversity (H') against habitat heterogeneity. Heterogeneity was measured from variance the first principal component of the satellite image mosaic. Higher values indicate greater heterogeneity in the pixels. The Pearson's product moment correlation coefficient is significant for this relationship ($r = 0.783$, $P < 0.05$)

riparian woodlands along river courses, swamps within woodland etc, then diversity will be increased. Whittaker (1972) referred to point measures of diversity as alpha diversity. Furthermore, he noted that as one moves away from a given point, or if one increases the area sampled new habitats are encountered and along with them new taxa. The diversity added through the addition of habitat heterogeneity he referred to as beta diversity. The combination of the two is the total regional diversity. Figure 5.11 shows diversity plotted against a summary measure of habitat heterogeneity around each roost. Heterogeneity was measured from the variance of pixels values in the first principal component of the satellite image. The Shannon index of diversity is shown to correlate with habitat heterogeneity around the

roost. It is possible that both habitat heterogeneity and productivity are contributing to species diversity at the roosts, but of the two heterogeneity seems to have the stronger influence. This is not unexpected given the close relationship between small mammals and vegetation. Andrews and O'Brien (2000) surveyed mammal diversity in conjunction with climatic variables and plant species diversity. Small mammals were not observed to correlate with mean annual precipitation, though they do correlate with other water variables, especially those associated with seasonality. Small mammals were also found to correlatve very strongly with plant species diversity. The Serengeti data may also indicate close associations to plant diversity, however the relationships are on a different spatial scale, and this may affect species diversity.

Recently, Chase and Leibold (2003) reported that the productivity-diversity relationship is scale dependent. Comparing diversity at the local level, they observed a unimodal productivity-diversity relationship. However in comparing diversity between different watersheds they observed a monotonic rise in diversity. Their results indicate that alpha diversity may decrease in high productivity areas at the same time that total diversity is increasing. This is accomplished by reducing the number of taxa found in any one habitat but reducing the number of taxa shared between habitats.

5.4.4.4 Conclusions

Differences in species diversity are evident between roosting sites, and the pattern of diversity between roosts does not contradict predictions of increased diversity associated with both productivity and heterogeneity. However, it is not possible to separate the effects of productivity from those of habitat heterogeneity. Predator bias may be reflected in the high dominance at roost 24. This roost fit none of the common abundance models.

5.5 Olduvai Paleoenvironments

The hominid paleontological site at Olduvai Gorge lies just to the south of the study area. Paleolithic archeological sites at FLK have yielded rich Plio-Pleistocene faunas including both large and small mammals (Gentry 1978a,b; Jaeger 1976; Butler and Greenwood 1976). The FLK sites occur in Middle and Upper Bed I

Table 5.11: Stratigraphic summary of the Middle and Upper Bed I deposits including taphonomic interpretation for the microfauna.

Level	Age (Ma)	Screening	Accumulator	Modification
Tuff IF	1.749			
FLKN1		Yes	B. leakeyae	Intermediate
FLKN2		Dry	Bubo lacteus	low
FLKN3		Yes	Bubo lacteus	low
FLKN4		Yes	mammal + B. lacteus	extreme + low
FLKN5		Yes	mammalian carnivore	extreme
FLKN6		Yes	unknown	unknown
Tuff ID	1.764			
Tuff IC	1.761			
FLKNN1		No		
FLK-Zinj		Yes	Bubo?	intermediate
FLKNN2		Yes	Tyto alba	very low
FLKNN3		Yes	owl	low
Tuff IB	1.798			

Modified from Fernandez-Jalvo et al. (1998)

deposits and span a time interval of approximately 50,000 years between Tuff IB at 1.798 ± 0.014 Ma and Tuff IF at 1.749 ± 0.007Ma (Walter et al. 1991). Table 5.11 presents a summary of the stratigraphic levels during this time period at Olduvai Gorge. Lavocat (1965) gave a brief description of the microfauna, and more detailed taxonomic treatments followed for the elephant shrews (Butler and Greenwood 1976) and rodents (Jaeger 1976; Denys 1990, 1992, 1998). Of the 17 rodent genera known from Olduvai, all but two, *Heterocephalus* and *Otomys*, have been noted in the modern Serengeti ecosystem and twelve overlap with genera in the taphonomic assemblages. The biogeographic stability over the past 1.8 Ma invites direct comparison with modern faunas and their habitats.

Earlier analyses of the Olduvai microfauna concluded, that the faunas associated with Upper Bed I represented a more xeric adapted community than those associated with Middle Bed I and proposed climatic change as the cause. Butler and Greenwood (1976) note that xeric adapted Macroscelideans, such as *Elephantulus* become increasingly more abundant through Upper Bed I times. They observe, "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).

A similar interpretation follows from analysis of the rodent faunas (Jaeger 1976; Denys 1998). Jaeger (1976) notes that the Upper Bed I deposits from FLKN6 have a greater proportion of *Gerbillinae* than do the Middle Bed I deposits from FLKNN and FLK-Zinj indicating a transition to drier conditions toward Upper Bed I, but overall more humid than the current environment at Olduvai. True forest genera such as *Hybomys* and *Lophuromys* are absent, but open woodland is indicated at several levels by the presence of *Thallomys*. The genera *Oenomys* and *Grammomys* from levels FLK-Zinj and FLKNN1 in Middle Bed I he takes to indicate the presence of riparian or lake margin forest.

The micromammal interpretations fit well with those of the megafauna and pollen which again indicate a drying transition between Middle and Upper Bed I (Bonnefille 1984; Kappelman 1984; Plummer and Bishop 1994). However, Andrews (1983) pointed out that taphonomic differences between levels at FLK may influence faunal diversity and affect paleoenvironmental interpretation of the microfauna. He proposed that abundance of *Gerbillinae* in the Upper Bed I deposits may be an artifact of predator preference for gerbils. Accounting for the bias led him 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 north western part of the Serengeti ecosystem rather than to any of the habitats in the immediate vicinity of Olduvai Gorge today" (p. 84).

Since then, improvements in micromammal taphonomy allow better diagnosis of accumulating agents. Fernandez-Jalvo et al. (1998) revisited the issue of taphonomic bias at Olduvai Gorge with a detailed analysis of surface modification and breakage, the results of which are summarized in the right hand columns of Table 5.11. In addition to the taphonomic analysis Fernandez-Jalvo et al. (1998) include a paleoenvironmental analysis that attempts to account for taphonomic sampling bias. They concur with the general pattern of a more open, arid environment for the uppermost part of Upper Bed I but place the transition later in time. They propose that the greatest change in environment occurred between the lower part of Upper Bed I (FLKN4-6) and the upper part of Upper Bed I (FLKN1-3). The previous hypothesis for a transition between Middle Bed I as represented by FLKNN2,3 and FLK-Zinj and the lower part of Upper Bed I (FLKN4-6) they attribute to a shift from owl predation to a mammalian carnivore. Finally they conclude that even the most arid and open environments at the top of Upper Bed

I were likely a form of woodland and that, "none of the environments were open grassland such as that present in the modern Serengeti ecosystem." (p. 169).

Given the emphasis on the impact that predation plays in the abundance of species present in fossil micromammal assemblages, comparing the fossil faunas to modern owl-accumulated assemblages may provide some insight into the faunal patterns at Olduvai. Among all studies there appears to be a consensus as to the general trend of paleoenvironmental change during Middle and Upper Bed I. The disagreement revolves around timing of the change and the interpretations of the fauna in terms of habitat reconstructions.

5.5.1 Timing of environmental change.

Fernandez-Jalvo et al. (1998) argue that predator selectivity "may produce changes in species composition ... between FLKNN and FLKN." (p. 166) as opposed to environmental change. Middle Bed I is argued to have been the work of a non-destructive accumulator such as the barn owl, *Tyto alba*, that "may favour murines against gerbils, as seen in modern assemblages (Andrews, 1990; Laurie, 1971)" (p. 166).

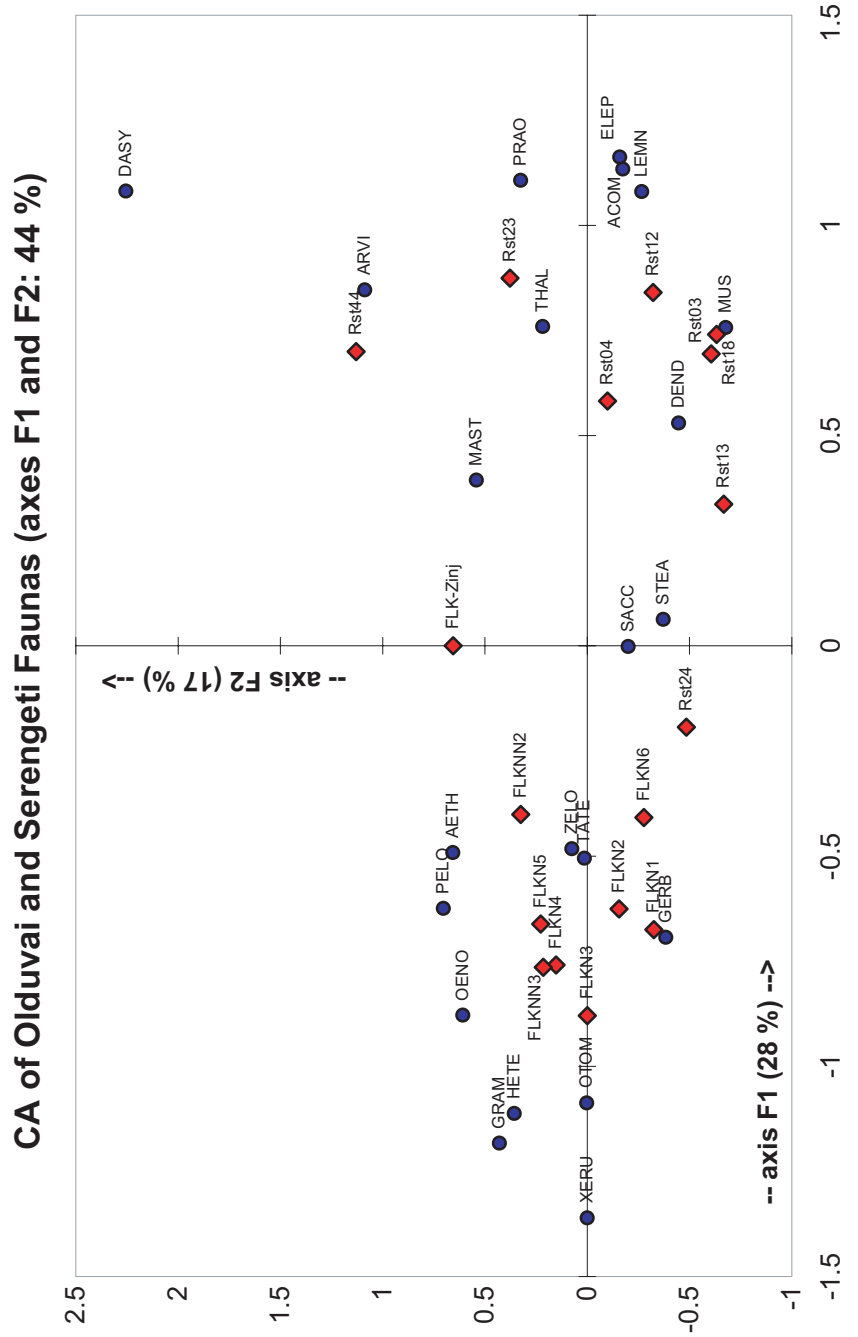
However the modern taphonomic data from Serengeti owl roosts do not support this proposition. Roost 24 in the mid-grass plains has an abundance of *Gerbillinae* including *Gerbillus* and *Tatera*. The Gerbillinae/Murinae ratio at roost 24 is 5.94 – higher than for any of the Olduvai assemblages – and it is most likely the work of barn owls entirely. A barn owl was in residence when the roost was collected, fresh barn owl pellets were observed and it is a cavity roost in a kopje fissure, which is the roosting environment favored by barn owls. Furthermore the pattern of faunal turnover observed between FLKNN 2-3 and FLKN4-6 includes the introduction of *Gerbillus*, but *Tatera* is present in similar abundance on both sides of this transition. If the murine abundance in FLKN4-6 is the result of predator preference of murines to the exclusion of gerbils it is unclear why *Tatera* – a gerbil – would be unaffected. Given the modern data, predator selection is not a sufficient explanation for the faunal shift between FLKNN4-6 and FLKN2-3. The purported faunal change within Upper Bed I between FLKN4-6 and FLKN1-3 appears part of the trend beginning from Middle Bed I.

5.5.2 Paleoenvironment

Overall the environment at Olduvai appears to have been more mesic than the current environment at Olduvai. However the Upper Bed I layers have more xeric and open adapted fauna. FLKN1 especially resembles, in faunal composition and abundance, the more open roosts in the modern taphonomic assemblages. Figure 5.12 shows the plot from a correspondence analysis including both the modern taphonomic assemblages from Serengeti along with the Olduvai assemblages. The first axis of variation separates the Olduvai assemblages on the left from the modern taphonomic assemblages on the right. Taxa unique to the Olduvai assemblages, such as *Xerus*, *Heterocephalus*, *Grammomys*, and *Pelomys* appear to the far left as does *Aethomys*, which though present in the taphonomic assemblages is far more abundant in the fossil deposits. Likewise fauna unique to the modern assemblages such as *Dasymys, Praomys* and *Lemniscomys* appear to the far right. Taxa in common between modern and fossil assemblages appear near the middle of the first axis. The second axis disperses the modern assemblages roughly according to precipitation and vegetation cover. The most open roost, roost 24, is at the bottom of the plot and the more closed and moist roosts such as 12, 44, and 23 appear higher up as do their associated taxa such as *Praomys, Thallomys*, *Dasymys, Arvicanthis* and *Mastomys*. Similarly, the Middle Bed I assemblages, FLK-Zinj, FLKNN3 and FLKNN2 all appear higher on the second axis, these grade into FLKN3-5 along the middle of Axis 2. The lowest fossil point on the second axis is FLKN1. It appears that the more dry, and open assemblages share common taxa, especially the gerbils. Interestingly, as they become more mesic the modern and fossil assemblages incorporate different species. In northern Serengeti, under higher precipitation one finds more *Praomys*, *Thallomys*, *Dasymys* and *Arvicanthis*. At Olduvai, mesic environments incorporated *Grammomys*, *Oenomys*, *Otomys*. The CA plot suggests that the more arid environments of Plio-Pleistocene Olduvai shared similar taxa with the drier portions of the modern Serengeti, but that there are perhaps more diverse ways to build mesic communities.

In its position along the second axis, FLKN1 appears to be intermediate in its degree of openness, supporting the contention that it does not represent a grassland plain in the sense of the modern Serengeti. FLKN1 differs from roost 24 in the presence of *Otomys*. Modern representatives of this genera prefer mesic grasslands, either at altitude or in association with surface water. The habitat surrounding

Figure 5.12: CA of Olduvai and Serengeti Microfauna combined. First two axes account for 44% of the inertia. The first axis separates fossil from modern assemblages. The second axis positions dry open habitats at the bottom and more mesic and closed habitats toward the top.



modern Lake Ndutu, to the west of Olduvai, may present a good modern analogue.

5.6 Conclusions

This chapter examined the pattern of mammal distribution in taphocoenoses across eight roosting sites in Serengeti ranging from the southern grassland plains to the Mara River in the northern extension. The results clearly show that these roosts differ despite the hunting preferences of the accumulating agent. Open grasslands are easily distinguished from more closed woodland mosaics by a relatively high abundance of gerbils, especially *Gerbillus*; by relatively low species richness coupled with high dominance of a few taxa. Within the woodlands, there is a good deal of variability between roosts. The structure of the variability as evidenced in the correspondence analysis suggests that there may be a signal that distinguishes different types of woodland roosts, but that these faunal assemblages may form many unique arrangements of species. This study observed at least three faunal patterns among the woodland roosts. Several analytical methods were tested with the taphocoenosis. Indicator species revealed that all species were found within their expected niche parameters, however the more detailed niche models required for accurate use of the taxonomic habitat index are in need of development and refinement.

Chapter 6

Summary and Conclusions

The general aim of this dissertation is to improve the precision and accuracy of paleoenvironmental interpretations made from fossil micromammal assemblages. The approach taken here is to examine modern taphonomic assemblages and compare their faunal composition against the land cover and habitats that lie within 1.5 km around owl roosting sites. Owl roost were examined because other research has shown them to be important accumulators of densely concentrated fossil micromammal assemblages (Davis 1959; Andrews 1990). The distance of 1.5 km represents our best current estimate of hunting ranges used by barn owls based on telemetry studies in temperate regions (Colvin 1984; Taylor 1994). No data on ranging are available for spotted eagle owls so the same value is used for both. This assumption will clearly need testing in the future.

To meet the stated aim it was necessary to develop a thorough understanding of the land cover and habitat surrounding the roosts as well as the fauna that appear at each. Chapters 2 and 3 addressed the basic issues of quantifying land cover and tallying the relative abundances of taxa that make up the eight analyzed ossuaries.

Numerous ground surveys conducted during the field work were used to develop models, called signatures, of the spectral reflectance properties of each type of land cover in the ecosystem. Using these signatures, I trained a computer algorithm to classify pixels in two landsat extended thematic mapper images. The resulting vegetation map showed the distribution of land cover types in the ecosystem. Additional digital maps were developed for hydrology, topography, soils and precipitation, and all were compiled into a geographical information system

for analysis.

Analysis of the patterns of physiognomic vegetation reveal that vegetation responds to several interdependent factors that can be organized into three hierarchical groups: climate, topography and disturbance. Climatic factors such as temperature, precipitation, and wind patterns operate at the broadest spatial scale (over tens or hundreds of kilometers or more) and have the most general effect on vegetation (Andrews and O'Brien 2000; O'Brien 1993; Pratt et al. 1966). Prevailing wind patterns contribute to the formation of a complex gradient that extends across the ecosystem in a north by northwesterly direction. Precipitation follows this gradient, with the lowest mean annual precipitation (ca 400 mm) and a more unimodal pattern of 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).

The same wind pattern distributed and size sorted natrocarbonatitic ash from eruptions of volcanos in the Ngorongoro highlands at the southern portion of the ecosystem (Dawson 1964; Hay 1976). Thus the complex, north by northwest gradient in precipitation extends to topographic heterogeneity, soil mineral composition and soil depth. Augmenting this gradient, are the local topographical or caternary gradients. These also influence soil texture, mineral composition and hence soil moisture availability (de Wit 1978; Jager 1982). The caternary gradients are linked in part to the precipitation gradient as the topography becomes more dissected in areas with higher rainfall. Disturbance factors such as fire, grazing, browsing and burrowing have important local influence on plant species composition and community structure as is seen in the abrupt ecotonal boundaries between grassland and riverine forest in the northern portions of the ecosystem. In the north fire and browsing play important roles in determining the location, size and patterning of tree stands, and open grassland patches. It has also been proposed that disturbance factors, especially fire and grazing are the dominant factors maintaining the Serengeti plains (Bell 1982; McNaughton 1985), however works by Belsky (1983, 1984, 1990) and others (Coughenour and Ellis 1993) point to edaphic factors such as soil alkalinity, salinity and depth as more important for excluding trees and maintaining the grasslands as such. Yet these studies are relatively short term. The harsh edaphic conditions are the result of fairly recent volcanic eruptions. As the landscape evolves, weathering will alter soil chemistry, and faulting will

fracture shallow calcretes perhaps allowing woody vegetation to encroach on the plains. The presence of woody vegetation inside Olduvai Gorge, on the kopjes and around Lake Ndutu indicate that factors other than climate limit woody vegetation growth.

Ossuaries from eight roosting sites were selected for detailed faunal analysis. The roosts were selected based on several factors. Sample size was an important criteria, as was distribution along the complex gradient. The faunal analysis returned a total of 20 taxa all of which are common to tropical "savanna" environments in Africa, and all are in accord with what has previously been reported for the Serengeti region. While this study found no new species, the analysis shows that owl accumulated assemblages (this study and that of Laurie [1971]) detect nocturnal micromammals as well as, or better than does trapping. Scansorial animals such as *Graphiurus*, and *Paraxerus* were missed, but many diurnal and fossorial animals that would not be expected in owl pellets because of the differences in activity patterns and locomotor habits were still collected by the owls. It is revealing that none of the published faunal lists for Serengeti is complete. Table 3.11 provides the most thorough listing of micromammal genera for the ecosystem that is currently available.

Investigations of micromammal taphonomy have focused, in large part, on cave and rock shelters. However, dense micromammal concentrations are also known from open-air sites for which the taphonomy has not been thoroughly investigated. Chapter 4 explored micromammal site formation processes outside of caves and rock shelters. This chapter also addressed questions of differential prey selection between owl species and prey size limitations raised in the preceding faunal chapter.

Observations on roosting preferences made in the field, show that barn owls and spotted eagle owls occupy very different roost types, what I've called cavity roosts and open roosts respectively. Barn owls prefer to spend daylight hours sequestered in the twilight regions of small fissures or in the hollowed interiors of tree trunks. Vertical fissures in kopjes – boulder heaps typically from granite basement rocks – were found to be favored roosting sites for barn owls and this made locating roosts easier. Where they are present and old enough to have hollowed cores, baobab trees also make suitable roosts for barn owls. In contrast, spotted eagle owls were found to prefer roosting in open situations such as tree crowns or against rocks. The difference in roost types was very significant statistically, as well as taphonomically

and ecologically. Tree crown roosting by spotted eagle owls may explain in part the higher abundance of *Thallomys*, an arboreal rodent that lives and feeds in *Acacia* trees, at their roosts. Preservation may also be better in cavity roosts where surface assemblages are protected from weathering, though this benefit may be offset in part by slow depositional rates inside fissures and tree cores.

Subsurface assemblages were noted inside tree hollows. Careful excavation could produce a detailed record of local climate change and perhaps address issues of vegetation dynamics during the Holocene. These changes may detect differences in land use patterns in the Tanzania national parks resulting from the presence and subsequent removal of pastoralists from the ecosystem.

The behavioral difference between owl species also implies that in open-air settings assemblages are more likely to be homogenous with regard to accumulating agent. Caves attract a broad suite of inhabitants including both barn owls and spotted eagle owls. In open areas however, these species clearly exploit different roost types and thus the assemblages that form are more likely the result of a single species. Kopjes provide both types of roosts. Water cached in the boulders along with the better drained soils around kopjes promote woody vegetation growth where spotted eagle owls roost, while vertical fissures that form along joints in the rock are preferred by barn owls. Yet, the assemblages are spatially discrete at the kopjes and would be expected to remain so in the fossil record unless there is tremendous turbation.

Faunal composition between open and cavity roosts were found to be very similar, especially in regards to the presence or absence of taxa. Of the twenty taxa recorded during the faunal analysis only two are unique to a single roost type. *Dasymys* and *Aethomys* are only recorded in closed roosts, but both are rare overall so this result cannot be distinguished from chance. Minor but significant differences were noted in the relative abundances of three taxa: *Lemniscomys, Thallomys* and *Saccostomus*. The overall similarity between eagle owls and barn owls may mean that cavity and open roosting modes are effectively isotaphonomic with respect to faunal composition. Additional taphonomic studies are needed to determine whether the faunal similarities between open and cavity taphonomic modes is corroborated and what effects changes in species composition has on the paleoecological analysis of microvertebrate assemblages.

Results from Chapters 3 and 5 demonstrate the pattern of mammal distribution

in taphocoenoses across eight roosting sites in Serengeti ranging from the southern grassland plains to the Mara River in the northern extension. These results show that roosts differ despite the hunting preferences of the accumulating agent. Barn owls prefer to hunt in open habitats yet still capture prey species indicative of other niches. Arboreal species such as *Thallomys*, rocky habitat species such as *Acomys,* and thicket loving taxa such as *Aethomys*, *Dendromus*, *Elephantulus* were captured as were diurnal taxa such as *Lemniscomys* and *Arvicanthis*. Subtle biases may influence the relative abundances of taxa in the owl accumulations relative to their abundance in the biocoenosis. Small mammal populations fluctuate dramatically over short time spans in response to fire and other disturbance factors. This short term variability confounds somewhat the notion of an equilibrium relative abundance of taxa. In this regard, the time averaged assemblages produced by owls provide a better overall picture of relative abundances of taxa in different habitats. Variability between ossuaries in similar habitats may be estimated by comparing the cluster of roosts around Seronera. Roosts 4, 12, 13, 18 are all similar in vegetation patterns and also cluster together based on faunal composition.

Roost 3 also falls into this cluster despite being a more open, grassland roost as measured by the woody vegetation map. Roost 3 is geographically close to the other roosts and is situated just at the boundary between woodland and grassland. It is mostly surrounded by grassland but its proximity to the woodland zone may indicate that the vegetation surrounding roost three has been more wooded in the past and thus it shares some taxa with the other neighboring roosts.

Dry, open grasslands as found at roost 24 are distinguished from more closed woodland mosaics by a relatively high abundance of gerbils, especially *Gerbillus*; and by relatively low species richness coupled with high dominance of a few taxa. Within the woodland zone, the more mesic roosts (23 and 44) are most distinct. Roost 23 is characterized by a significantly high abundance of *Thallomys*. The prevalence of this arboreal rodent at roost 23 is in accord with the known habitat proclivities of this taxa, however the abundance of *Thallomys* is variable across woodland roosts and across owl species. The wetlands around roost 44 are reflected in the presence of *Dasymys.* Both roosts share significantly high abundances of *Mastomys*, *Arvicanthis*. These taxa may be reliable indicators of more mesic environments.

Thus gerbils, such as *Gerbillus*, tend to be associated with the more xeric,

open roosts, while murines and especially *Mastomys* and *Arvicanthis* and *Dasymys* are associated with more mesic, closed habitats. The ratio of gerbils to murines appears to provides a good indication of habitat openness/aridity but the ratio was not significantly correlated with woody plant cover or any of the other ecological and climatic variables. Rank correlations with mean annual precipitation were strongly negative and the result may become significant if the power of the test is increased through additional sampling and analysis of ossuaries.

Habitat can also be inferred by pooling together data on the habitat proclivities of each taxon. Niche models are a means of explicating the habitat preferences of a taxon and the taxonomic habitat index is a system for additively combining niche models in order to estimate the relative significance of habitat classes (Nesbit-Evans et al. 1981). Habitat spectra are graphical plots of the importance of each habitat as indicated by the pooled habitat proclivities of the fauna in an assemblages. Using just the presence or absence of taxa gave results that accorded to the habitats surrounding the roosts. The grassland category was generally most abundant and the combination of semi-arid and grassland classes ranked roosts in approximately the correct order of woody vegetation as measured from the vegetation map. However, differences between the roosts were very subtle. Weighting the THI values by the taxon relative abundances amplified the differences between roosts. THI appears to be very sensitive to differences in the niche model. The procedure is a direct linear summation of habitat proclivities, thus a weak or incorrect niche model for an abundant taxon will lead to inaccurate results.

The Serengeti fauna overlaps substantially with the taxa present at Olduvai and a comparison was made between fossil faunas and the Serengeti taphocoenoses. The fossil microfaunas at Olduvai were recently treated to a detailed taphonomic study (Fernandez-Jalvo et al. 1998). Their work indicates that owls were active in accumulating the micromammal assemblages at the FLK sites spanning the interval between 1.75 and 1.80 Ma. Numerous changes in faunal abundance are recorded in the three levels at FLKNN-I (including the Zinjanthropus site, which is synchronous with FLKNN-I level 1 and abbreviated FLKNN1-3,Zinj) and the six levels at FLKN-I (abbreviated FLKN1-6). Fernandez-Jalvo et al. (1998) argue that predator selectivity was the primary cause for faunal shifts between FLKNN and the lower levels of FLKN based on the proposition that barn owls preferentially prey on murines to the exclusion of gerbils. Data from the Serengeti taphocoenoses do

not support this conclusions and suggest that if gerbils were present in the FLKNN levels they would have been taken, as they are in modern barn owl assemblages in areas where gerbils are abundant.

The Olduvai fauna were tabulated in approximately the same manner as the MNI values used for the current study, thus relative abundances based on MNI should be comparable. Both data sets were plotted in a common correspondence analysis. The plot separates modern and fossil assemblages along the first axis of variability. The second axis orders the modern roosts roughly by woody vegetation density and precipitation. Roosts 23, 44 and 4 are highest on the second axis while 3, 13 and 24 are lowest. Of the Olduvai assemblages, the FLKNN levels are highest on the second axis, agreeing with the interpretation that these represent a more mesic and closed environment. FLKN1, 2 are low on the second axis, consistent with a more xeric environment for these levels. Of the modern roosts, roost 24 shares the greatest similarity with the Olduvai assemblages (it is furthest to the left on the first axis) and the similarity with FLKN1-2 is based on the prevalence of *Gerbillus* at these roosts. *Gerbillus*, as has been discussed, appears to be a reliable indicator of arid and open habitats and this association may be more stable through time. Mesic habitats at paleo-Olduvai incorporated different taxa than are commonly found in mesic habitats of modern Serengeti. The difference may be due to greater flexibility of niche assembly in mesic habitats than in xeric habitats.

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Appendix A

Signature Listings Training Data

A.1 Signature Zonation

Table A.1: The following table indicates which signatures were active in the classification of grassland, woodland, riverine and lake zones. Zeros indicate the signature was excluded from the zone labeled at the column heading. Plus signs indicate the signature was included.See text for further details.

		Zone			
Value	Signature Name	grassland	woodland	riverine	lakes
1	157 cGS	0	+	+	0
2	170 oGW	0	+	+	0
3	178 dSG	+	+	+	0
4	217 cTS	+	+	+	0
5	220 dTG	+	+	+	0
6	226 dG	+	+	+	0
7	262 oG	+	+	+	0
8	273 oTG	+	+	+	0
9	276 oTG	+	+	+	0
10	281 dG	+	+	+	0
11	286 dG	+	+	+	0
12	293 dGS mix	+	+	+	0

13	294 oG	+	+	+	0
14	296 WcG	+	+	+	0
15	319 oTG	+	+	+	0
16	325 oGW	+	+	+	0
17	326 oTG	+	+	+	0
18	329 DoGW	0	+	+	0
19	330 cG	+	+	+	0
20	331 dG	+	+	+	0
21	332 oSG	+	+	+	0
22	337 dSF	+	+	+	0
23	343 WcSG	+	+	+	0
24	345 oG	+	+	+	0
25	347 oG	+	+	+	0
26	353 dTG	+	+	+	0
27	360 oGS	0	+	+	0
28	374 oG	+	+	+	0
29	381 dG	+	+	+	0
30	382 dG	+	+	+	0
31	403 dTG	0	+	+	0
32	408 dTG	+	+	+	0
33	441 cG	+	+	+	0
34	442 cG	+	+	+	0
35	443 cG	+	+	+	0
36	445 cG	+	+	+	0
37	446 cSG	+	+	+	0
38	447 cG	+	+	+	0
39	448 cG	+	+	+	0
40	450 cG	+	+	+	0
41	463 cG	+	+	+	0
42	464 cG	+	+	+	0
43	481 dG	+	+	+	0
44	487 cSG	+	+	+	0
45	490 cG	+	+	+	0
46	493 dSG	+	+	+	0

47	498 cG	+	+	+	0
48	504 cG	+	+	+	0
49	506 cSG	+	+	+	0
50	507 cG	+	+	+	0
51	508 cG	+	+	+	0
52	524 cSG	+	+	+	0
53	530 dG	+	+	+	0
54	532 dG	+	+	+	0
55	545 dG	+	+	+	0
56	547 sG	+	+	+	0
57	567 cSG	+	+	+	0
58	573 oG	+	+	+	0
59	608 oG	+	+	+	0
60	662 dG	+	+	+	0
61	669 cG	+	+	+	0
62	671 cG	+	+	+	0
63	676 dTG	+	+	+	0
64	683 dG	+	+	+	0
65	694 cSG	+	+	+	0
66	702 cG	+	+	+	0
67	707 cG	+	+	+	0
68	722 dGS	+	+	+	0
69	724 oTG	+	+	+	0
70	726 cTG	+	+	+	0
71	734 dGS	+	+	+	0
72	754 dTG	0	+	+	0
73	755 oGW	0	+	+	0
74	756 dG	+	+	+	0
75	m 171 175 257 303 oGW	+	+	+	0
76	m 2019 2020 bare	+	+	+	0
77	m 282 614 616 dG - 3	+	+	+	0
78	m 292 725 oTG - 2	+	+	+	0
79	m 295 728 oTG - 2	+	+	+	0
80	m 298 299 oG - 2	+	+	+	0

81	m 333 528 674 1189 dG - 4	+	+	+	0
82	m 380 682 cG - 2	+	+	+	0
83	m 478 589 dSG - 2	+	+	+	0
84	m 534 542 537 oG - 3	+	+	+	0
85	m 543 551 dG - 2	+	+	+	0
86	m 844 850 dG - 2	+	+	+	0
87	u 2001 water Ngorongoro L. Magadi	+	+	+	+
88	u 2002 water L. Empakai	+	+	+	+
89	u 2007 cloud	+	+	+	+
90	u 2009 water Lagarja	0	+	+	0
91	u 2010 water Ndutu deep	+	+	+	+
92	u 2011 water Ndutu med	+	+	+	+
93	u 2012 water Ndutu shallow	+	+	+	+
94	u 2013 water L. Natron	+	+	+	+
95	u 2014 dG	+	+	+	0
96	u 2015 dSF kopje	+	+	+	0
97	u 2016 water Eyasi	+	+	+	+
98	u 2017 water Manyara	+	+	+	+
99	u 2018 water L. Masek	+	+	+	+
100	u 2025 water Karatu resevoir	+	+	+	+
101	u 2025 water resevoir	0	+	+	+
102	u 2028 dG	+	+	+	0
103	u 2029 dG	+	+	+	0
104	u 2032 dG	+	+	+	0
105	u 2033 dG	+	+	+	0
106	u 2035 dG	+	+	+	0
107	u 2036 bare wet ground Natron	+	+	+	+
108	u 2040 oSW	+	+	+	0
109	u 2053 cG	+	+	+	0
110	u 2054 sG or bare	+	+	+	0
111	u 2055 RsG or bare	+	+	+	0
112	u 2056 dTG cf 708 709 710	0	+	+	0
112	Count of signatures per zone	102	112	112	13

Appendix B

Mathematical Topics

B.1 Nonparametric correlation statistics

B.1.1 Spearman's rank correlation, ρ

The general form of the Spearman rank correlation coefficient given by Siegel (1956) as,

$$r_s = \rho = \frac{\Sigma x^2 + \Sigma y^2 - \Sigma d^2}{2\sqrt{\Sigma x^2 \Sigma y^2}} \tag{B.1}$$

where: x^2 and y^2 are the integer ranks of the observations $(1, 2, \ldots N)$ and d^2 is the squared distance of rank values of paired observations, $(x - y)^2$. Tied values are given an average rank, for example if observations of rank 6 and 7 are tied, they each are given the rank 6.5. Ties reduce the sum of squares, Σx^2, and a correction factor must be applied if there are many ties. Substituting terms into B.1 and applying a correction factor for ties yields the general calculation given by Siegel (1956),

$$r_s = \rho = \frac{\frac{N^3-N}{12} - \Sigma T_x + \frac{N^3-N}{12} - \Sigma T_y - \Sigma(x-y)^2}{2\sqrt{\left(\frac{N^3-N}{12} - \Sigma T_x\right)\left(\frac{N^3-N}{12} - \Sigma T_y\right)}} \tag{B.2}$$

where: N is the number of observations, T is the correction value for ties, $T = \frac{t^3-t}{12}$, and where t is the number of observations tied at a given rank. Simplifying equation B.2 gives the computational form used by Mathematica (Wolfram 1999),

$$r_s = \rho = \frac{\frac{N^3-N}{6} - \Sigma T_x - \Sigma T_y - \Sigma(x-y)^2}{\sqrt{\left(\frac{N^3-N}{6} - 2\Sigma T_x\right)\left(\frac{N^3-N}{6} - 2\Sigma T_y\right)}}$$

If there are no ties, or few ties, a simplified form may be used,

$$r_s = \rho = 1 - \frac{6\Sigma d^2}{(N^3 - N)} \tag{B.3}$$

where notation follows that of Equation B.1.

Compared to Pearson's parametric correlation coefficient, r, the efficiency of rho, is about 91% Siegel (1956). However, it is equally as powerful as Kendall's tau, another rank correlation statistic (Siegel 1956). Values of Kendall's tau and Spearman's rho are not directly comparable however, because they use different underlying scales. Sokal and Rohlf (1995) note that Spearman's rho differs from Kendall's tau by giving greater weight to "pairs of ranks that are further apart" (p. 600). Despite this difference the two tests are equally capable of detecting correlations. Siegel (1956) notes that, "both coefficients utilize the same amount of information in the data, and thus both have the same power to detect the existence of association in the population" (p. 219). The significance of rho is tested against a Student's t distribution with df=N-2 when sample sizes are greater than 10. For smaller samples critical values are determined by exact methods. A table of critical values for small samples can be found in Siegel (1956), Table P, on page 284.

B.1.2 Kendall's coefficient of rank correlation, τ

The general form of the Kendall rank correlation statistic, tau, is given by Siegel (1956) as,

$$\tau = \frac{S}{\frac{1}{2}N(N-1)} \tag{B.4}$$

where S is the count of ranks and N is the sample size. Methods for calculating S, are given in Siegel (1956, pp. 214-216) and Sokal and Rohlf (1995, pp. 594-597). Tied observations are given averaged rank. A more general equation for tau is provided by Wolfram (1999),

$$\tau = \frac{N_c - N_d}{\sqrt{(N_c + N_d + N_x)\,(N_c + N_d + N_y)}}$$

where: $N_c$is the number of concordant observations, that is agreement in rank of pairwise observations; $N_d$is the number of discordant observations; N_x is the number of ties in the first list and N_y is the number of ties in the second list.

B.1.3 Kendall's coefficient of concordance, W

Tests for agreement among more than two variables.

$$W = \frac{\left[\frac{12}{ab(a+1)}\Sigma^a\left(\Sigma^b R_{ij}\right)^2\right] - 3b(a+1)}{b(a-1)}$$

where: a is the number of samples or blocks, b is the number of treatments. Values of W can range between 0 and 1 Sokal and Rohlf (1995).

B.1.4 Gamma Distributions

Gamma distributions are a family of probability density functions that have a skewed shape. The are based on the gamma function,

$$\Gamma(\alpha) = \int_0^\infty x^{\alpha-1}e^{-x}dx \tag{B.5}$$

According to Devore (1991) some important properties of the gamma function include:

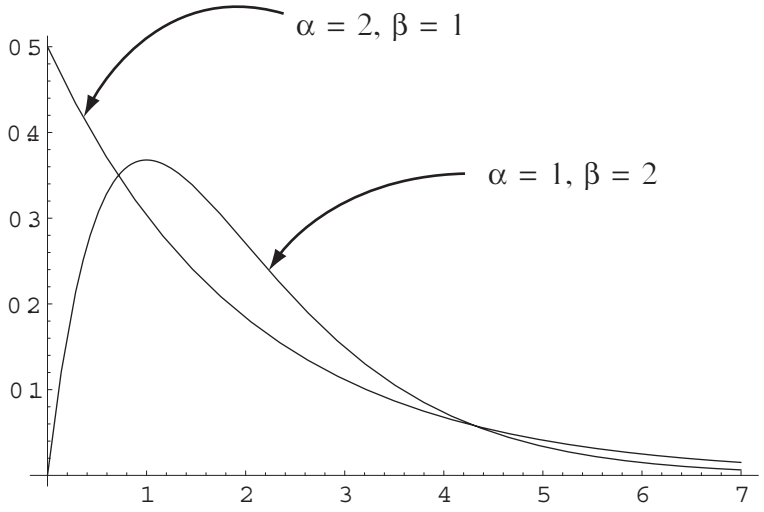
1. For any $\alpha > 1$, $\Gamma(\alpha) = (\alpha-1)\cdot\Gamma(\alpha-1)$
2. For any positive integer n, $\Gamma(n) = (n-1)!$
3. $\Gamma(\frac{1}{2}) = \sqrt{\pi}$

A continuous random variable, x is said to follow a gamma distribution if the probability density function of x is,

$$f(x;\alpha,\beta) \quad = \begin{cases} \frac{1}{\beta^\alpha\Gamma(\alpha)}x^{\alpha-1}e^{-x/\beta} & x \geq 0 \\ 0 & \text{otherwise} \end{cases} \tag{B.6}$$

where $\alpha > 0$, and $\beta > 0$. The standard gamma distribution has $\beta = 1$, thus the standard gamma distribution is given by the equation,

Figure B.1: Gamma probability density functions. Plots illustrate the gamma distribution with two values for alpha and beta.



$$f(x;\alpha) = \begin{cases} \frac{x^{\alpha-1}e^{-x}}{\Gamma(\alpha)} & x \geq 0 \\ 0 & \text{otherwise} \end{cases} \tag{B.7}$$

Plots of two gamma distributions are shown in Figure B.1. When $\alpha \leq 1$, $f(x;\alpha)$ continuously decreases over the range of x. When $\alpha > 1$, $f(x;\alpha)$ shows a single interior mode. The parameter α is called the *shape factor* and β the *scale factor*.

B.1.5 The Chi-square, χ^2, Distribution

The chi-square distribution, symbolized as χ^2, is a special case of the gamma distribution. If $\nu = d.f.$ = degrees of freedom , the chi-square distribution is given by the gamma probability density function with $\alpha = \nu/2$, *and* $\beta = 2$. The general formula for the chi-square probability density function is thus,

$$f(x;\nu) = \begin{cases} \frac{1}{2^{\nu/2}\Gamma(\nu/2)} x^{(\nu/2)-1}e^{-x/2} & x \geq 0 \\ 0 & \text{otherwise} \end{cases}$$

The chi-square distribution arises frequently in scientific investigations as the distribution of normal deviates. For example let $(x_1, x_2, x_3, \ldots, x_n)$ be a random

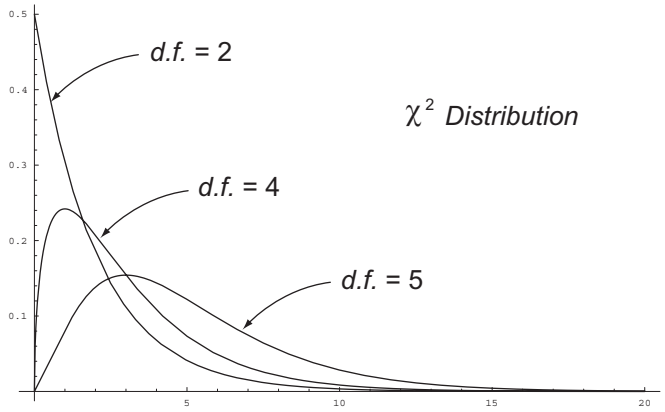


Figure B.2: Plots of the chi-square probability density functions for several values of ν= d.f. When ν is small the curve is uniformly decreasing with greater chi-square values (x axis). Greater values of ν reveal a single maximum.

sample from a normal distribution, $N(\mu, \sigma)$. The normal deviates of this sample equal $(x_i - \mu)/\sigma$. Replacing the parametric mean with the sample mean we find that the sum of squares divided by the variance, $\Sigma\frac{(x_i-\overline{x})^2}{\sigma^2}$, is chi-square distributed. Another perspective is gained from the equality,

$$\frac{\Sigma(x_i - \overline{x})^2}{\sigma^2} = \frac{(n-1)}{\sigma^2} \cdot \frac{\Sigma(x_i - \overline{x})^2}{n-1} = s^2\frac{(n-1)}{\sigma^2}$$

From the last term we get the chi-square distribution as a result of multiplying sample variance by a constant. Thus the chi-square distribution describes the expected spread of the variance when calculated from multiple independent samples. It is used in calculating the confidence interval for this parameter. In addition to sample variances, many other phenomena follow chi-square distributions. Statistical distance values resulting from a classification are chi-square distributed , as is the G statistics and Pearson's test for goodness of fit (commonly called the chi-square statistic). Figure B.2 shows plots of the chi-square density function for varying degrees of freedom.

B.2 Runs Test

A runs test examines whether seriated events occur at random. A practical application is the analysis of residuals around a regression line. If there is a linear

relationship between the variables, then points are expected to alternately fall above and below the regression line. However, a non-linear relationship such as a power function will result in more values falling above or below the line depending on the power of the power function. Grayson (1984) applies this test to an analysis of MNI vs. NISP values conducted by Gifford et al. (1980). Further examples appear in Sokal and Rohlf (1995).

B.3 Raster Imagery and Basic Definitions

A raster image is a matrix of R x C pixels (picture elements) each containing a discrete or continuous greyscale value, $f(r, c)$at each location (r, c)(Looney 2000). Color composites of multiple raster layers are generated by loading greyscale values $f(r, r)$into a three dimensional color cube with red, green, and blue dimensions.

B.4 Classification Theory

"A classifiers function can be formulated in terms of a mapping of its input variables to its (given) output conditions. We can write:

$$\Re^p \xrightarrow{\Gamma(n,p)} \prod$$

where p is the number of attributes, q is the number of classes and n is the number of samples" German (1999, p. 1) .

One limitation of maximum-likelihood classifiers MLC is that they require a minimum of p+1 input vectors for the covariance matrix to be non-singular. That is, the training sample size (number of pixels in the training sample) must be at least equal to the number of bands in the image plus one. And generally it is recommended to have at least 10p to 100p vectors .

B.5 Distance Measures

Euclidean Spectral Distance

Spectral or Euclidean distance, is the straight line distance between a measurement vector, x_i and the class mean vector $\overline{x}_c$.

$$D_{(a,b)} \equiv \left[\Sigma^n (x_i - \overline{x}_c)^2\right]^{1/2} \tag{B.8}$$

where:

n is the number of bands,

i is a particular band (ERDAS 1999).

Statistical Distance

Statistical distance normalized the euclidean distance according to a classes standard deviation. The distance between two points P and Q with bivariate coordinates x and y is given by the equation,

$$\begin{aligned} D(P,Q) \equiv a_{11}(x_1 - y_1)^2 + a_{22}(x_2 - y_2)^2 + \ldots + a_{pp}(x_p - y_p)^2 + \\ 2a_{12}(x_1 - y_1)(x_2 - y_2) + 2a_{13}(x_1 - y_1)(x_3 - y_3) + \ldots + \\ 2a_{p-1,p}(x_{p-1} - y_{p-1})(x_p - y_p) \end{aligned}$$

This algebraic expression is known as the positive definite quadrat form and can be written more tersely in matrix form,

$$[d_{11}, d_{22} \cdots d_{pp}] \begin{bmatrix} a_{11} & a_{21} & \cdots & a_{p1} \\ a_{12} & a_{22} & & \\ & & \ddots & \\ a_{12} & & & a_{pp} \end{bmatrix} \begin{bmatrix} d_{11} \\ d_{22} \\ \vdots \\ d_{pp} \end{bmatrix} \tag{B.9}$$

Where $d = (x - y)$ and $a \geq 0$. Recall that quadratic forms such as $x'Ax$, are called *positive definite* if

$$0 < x'Ax \tag{B.10}$$

for all vectors $x \neq 0$ (Johnson and Wichern 2002).

Mahalanobis Distance

$$D^2_{(c,x)} \equiv (x - \overline{x}_c)^T \left(Cov_c^{-1}\right)(x - \overline{x}_c) \tag{B.11}$$

Where x is the measurement vector (pixel value across all bands) and $\overline{x}_c$is the class mean vector, $Cov_c$is class the covariance matrix (ERDAS 1999). Note that the Mahalanobis distance is simply the quadratic form of the squared statistical distance. There is some inconsistency in application of the terms and symbols for Mahalanobis distance. At times it is symbolized as D^2as above, other times it is simply referred to as D though in both cases it is usually the square of the statistical distance.

B.6 Maximum-Likelihood Classification

Maximum Likelihood

Likelihood is a means for selecting among several available hypotheses. The maximum-likelihood method as applied to remote sensing data seeks to find the class that is most likely given a particular measurement vector, x,

$$L(c|x) \equiv \frac{a_c p(x|c)}{\Sigma^m a_r p(x|r)} \tag{B.12}$$

where $p(x|c)$is the probability of observing § given the class probability model c(Jensen 1996). The denominator is a normalization term based on the sum of all class probabilities. Thus the decision to classify measurement vector §into class $c$is determined by calculating the probability of §given $c$and assigning it to the class that return the highest probability. The probability of belonging to class c, p_c is calculated as,

$$p_c \equiv ln(a_c) - [0.5\, ln\, (|Cov_c|)]\, e^{-\left[0.5(x-\overline{x}_c)^T \left(Cov_c^{-1}\right)(x-\overline{x}_c)\right]} \tag{B.13}$$

where $c$represent a given class, $a$is the *a priori* probability that a pixel belongs to that class, $Cov_c$is the covariance matrix of class c, §is the measurement vector, and $\overline{x}_c$ is the class mean vector(ERDAS 1999).

The first term is the *a priori* probability of the class value. In a standard MLC the *a priori* class values are all equal (=1), but one may choose to weight certain classes if their proportions are known before hand from independent data. Application of a priori weighting is termed Bayesian classification(Jensen 1996).

B.7 Fuzzy Classification

Fuzzy set theory works by attributing member sets to elements in proportion to their suitability to the different sets. Thus any element may belong to multiple sets with different degrees of certainty.

Let Xbe a universe whose elements are denoted x.

$$X = \{x\}. \tag{B.14}$$

Classical set theory holds that membership in a class Ain $X$is a binary decision, x either belongs in A or not

$$P(x \in A) = \{1, 0\} \tag{B.15}$$

However for a fuzzy set B in X, membership is determined by a membership function such that x is associated with the set B by some real number (typically between 0 and 1) called a membership grade (Wang 1991).

$$f_B(x) \in \mathbb{R}\{0 \rightarrow 1) \tag{B.16}$$

In practice fuzzy classification is performed much like standard maximum likelihood-classification. Training samples are collected, models developed and class values assigned by maximum-likelihood. However, unlike MLC more than one class value is attributed to each measurement vector (Jensen 1996).

Fuzzy Mean

$$\overline{x}_c^* \equiv \frac{\Sigma^n f_c(x_i) x_i}{\Sigma^n f_c(x_i)} \tag{B.17}$$

where n is the total number of sample pixel measurement vectors, $f_c$is the membership function of class c, and $x_i$is a sample sample measurement vector(Wang 1991). Note that the fuzzy mean has the form of a weighted average,

$$\overline{\mathcal{Y}}_w \equiv \frac{\Sigma^n w_i Y_i}{\Sigma^n w_i} \tag{B.18}$$

Where the membership grades $f_c(x_i)$ serve as the weighting factors w_i(Sokal and Rohlf 1995).

Fuzzy Variance_Covariance

$$Cov_c^* \equiv \frac{\Sigma^n f_c(x_i)(x_i - \overline{x}_c^*)(x_i - \overline{x}_c^*)^T}{\Sigma^n f_c(x_i)} \tag{B.19}$$

where n is the total number of sample pixel measurement vectors, f_c is the membership function of class c, and x_i is a sample sample measurement vector(Wang 1991). Note that the fuzzy covariance is similar to the standard multivariate covariance but weighted by the membership function. Thus, the membership function acts like a marginal probability.

Fuzzy Convolution

Image convolution is a method of applying contextual or neighborhood information to an image pixel (picture element). A symmetrical NxN matrix of elements defines a "window" whose center passes over every pixel. The fuzzy convolution algorithm returns,

$$T_k \equiv \Sigma\Sigma\Sigma_{i,j,b}^{s,s,n} \frac{w_{ij}}{D_{ijb[k]}} \tag{B.20}$$

where, s is the dimension of the window, n is the number of bands, w_{ij} is the weighted spatial distance of neighboring pixels in the search window, D weighted spectral distance to the class.