Micromammal Paleoecology:

Theory, Methods, and Application to Modern and Fossil Assemblages in The Cradle
of Humankind World Heritage Site, South Africa

by

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Thesis directed by Associate Professor Matt Sponheimer

Many Plio-Pleistocene hominin-bearing sites in Africa contain large samples of small mammalian fauna. Micromammals, relative to larger fauna, are a useful proxy for reconstructing local habitat. Due to their ubiquity, their small home ranges, their close affinity with certain microhabitats, and their diversity, micromammals may contribute to more precise and fine-scale reconstruction of local paleoenvironments relevant to hominin evolution. These reconstructions are inherently dependent upon modern ecological knowledge and accurate niche modeling. This thesis focuses in greater detail on the community composition of modern micromammals in specific habitat types as well as the ecology of the predators that accumulate their remains. Particular emphasis is placed on the ecosystems surrounding several South African hominin-bearing caves where the African Barn Owl (*Tyto alba affinis*) has been identified as a primary contributor to fossil assemblages. The preliminary results of a pilot study on micromammal and owl ecology conducted in the Cradle of Humankind World Heritage Site are illustrate the stark differences between modern and Plio-Pleistocene micromammal communities in this area.

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Introduction

The Plio-Pleistocene has been characterized as a temporal period in which significant global climatic change took place (Peters and Maguire, 1981; Vrba, 1985, 1995; Cerling, 1992; Shackelton, 1995; deMenocal, 1995, 2004; Trauth et al., 2005; Maslin and Christensen, 2007). Concurrent with broad scale climatic shifts, were significant evolutionary changes in a wide variety of animal taxa, including hominin lineages (Klein, 1999; Tattersal, 2009). Extinctions, adaptive radiations, and dramatic ecosystemic shifts are evidenced during this time (Wessleman, 1984, 1995; Vrba, 1985; Cerling, 1992; Sikes, 1994; Denys, 1999). Pertinent to the hominin Plio-Pleistocene narrative is the disappearance of the gracile australopiths, the emergence of the robust hominin lineages, and ultimately the genesis of our own genus, *Homo* (Klein, 1999; Tattersal, 2009). Multiple lines of evidence; isotopic, geological, palynological, climatological, and paleontological all serve to corroborate global climatic shifts as well as to support regional and local paleoecological reconstructions (Vrba, 1980, 1985; 1995; Cerling, 1992; deMenocal, 1995, 2004; Denys, 1999; de Wit et al., 2000; Lee-Thorp et al., 2007; Trauth et al., 2005; Maslin and Christensen, 2007). Indeed, accurate paleoecological interpretation inherently relies on the concurrence of data from numerous disciplines to strengthen reconstructive techniques (Kingston, 2007; Maslin and Christensen, 2007). Disagreement between methods provides an excellent way to identify discrepancies and biases in methodology and to elucidate instances in which paleoecosystems

may have been decoupled from global climatic change, thus responding differently at regional and local scales (Kingston, 2007).

Micromammal paleoecological reconstruction provides a useful avenue by which all three scales relevant to hominin evolution, global, regional, and local might be investigated, but its true potency lies in elucidating paleoecosystems at a local scale (Cartmill, 1967; Wesselman, 1984; Denys, 1985, 1999; Avery, 1995a, 1995b 1998, 2001, 2005, 2010; Matthews, 2000, 2005; Reed, 2003, 2007, 2011; Avery et al., 2010; Reed and Denys, 2011) In the context of this paper, micromammals include rodents and shrews with a body mass of less than 300 grams (Andrews,, 1990; Reed, 2007). Micromammals are particularly auspicious paleoenvironmental proxies because they are highly endemic, ubiquitous, and prolific in both modern ecosystems and fossil assemblages. It has been argued that they are closely tied to specific microhabitats (Wesselman, 1984, 1995; Reed, 2007). Therefore, they offer uniquely fine scale spatial and temporal resolution for paleoenvironmental reconstruction (De Graafff 1981; Hafnar and Hafnar 1988; Skinner and Chimimba, 2005). Furthermore, they respond strongly and rapidly to habitat heterogeneity and plant species diversity, so the composition of micromammal communities is intrinsically linked to the habitats in which they reside (Batzli 1991; Barett and Peles 1999; Andrews and O'Brien 2000; Avenant 2005, 2007; Denno et al., 2005). Paleoecological reconstruction based upon micromammals has become more popular and widely utilized in both Eastern and Southern Africa, though thorough analyses are still lacking for several important Plio-Pleistocene hominin-bearing localities (Cartmill 1967; Wesselman 1984; Denys 1985; Pocock 1985, 1987; Avery,

1995, 1998, 2001, 2005, 2010; Matthews 2000, 2005; Reed, 2003, 2005, 2011; Reed

and Denys, 2011).

As promising as micromammal paleoecology appears, all reconstructive

methodologies that utilize fossil data must be thoroughly interrogated for biases

and firmly rooted in established ecological paradigms. Such interrogation is

particularly pertinent to micromammalian studies because current methodology for

micromammalian paleoecological reconstruction is heavily reliant upon accurate

niche modeling (Fernandez-Jalvo, 1998; Reed, 2003, 2007).

Recent micromammalian paleoecological analyses highlight the necessity of

two important methodological calibrations. The first of these includes establishing

concrete ecological baselines and niche models from which to work. Implicit in

creating these niche models is both a better understanding of the general ecology of

micromammals and the ecological processes, frequently predation, which contribute

to the accumulation of their remains at fossil localities. At this general theoretical

level the relationships between habitat, prey species, and predator species and the

ways in which these relationships translate to predator selectivity and differential

susceptibility of prey, require attention (Andrews, 1990; Reed, 2005). Additionally,

better and more thorough information regarding the autoecology of all prey and

predatory species is of the utmost importance because these data are used to create

the species specific niche models from which paleoecologists work to build their

reconstructions. If autoecological information is inaccurate, reconstructions based

upon them will be as well. The second methodological improvement involves

calibrating interpretations of paleoenvironment to the dynamics of the ecosystems local to fossil sites (Avery, 2001; Reed, 2003, 2007). Granted, modern environments are sure to differ from those which prevailed during the Plio-Pleistocene, but regional analogs frequently exist and it is nonetheless important determine the exact nature of extant ecological relationships between extant predator and prey species (Andrews, 1990; Avery, 2001; Reed, 2007).

In many fossil sites throughout Africa, particularly those in Southern Africa, micromammalian assemblages are frequently the result of accumulation by owls (Davis 1959; De Graaff, 1960; Wesselman, 1984; Pocock, 1985, 1987; Andrews, 1990; Avery, 1998, 2001, 2010; Reed, 2003, 2005). This has been determined to be the primary mode of micromammal deposition in the Plio-Pleistocene hominin-bearing cave sites of South Africa (Avery, 2001, 2010). More specifically *Tyto alba affinis*, the African Barn Owl has been demonstrated to have a distinct affinity for habitually roosting in caves and amassing large collections of regurgitated pellets, or coprocoenoses (Davis 1959; Glue 1971; Vernon, 1972; Bunn et al., , 1982; Taylor, 1994; Reed, 2003, 2005). The African Barn Owl is thought to have contributed largely to the micromammalian collections at Makapansgat, Sterkfontein, Swartkrans, and Gladysvale (Glue, 1971; Vernon, 1972; Pocock, 1985, 1987; Avery, 1995, 2001, 2010; Reed, 2003, 2005). Evidence suggests that, given appropriate niche models for the owl accumulators and the micromammalian species accumulated, as well as calibration to local environments, coprocoenoses are valid proxies for determining the composition of small mammal communities local to the roost site (Talyor, 1994; Avery, 2001; Matthews 2000, 2005; Reed, 2003, 2005,

2007). Small mammal community composition, in turn, may serve as a proxy for local habitat composition near important hominin sites during the Plio-Pleistocene (Avenant, 2005, 2007; Reed, 2003, 2007).

The first aim of this paper is to discuss the relevancy of the niche concept and niche models to micromammalian paleoecological reconstruction. Appropriate niche models are reliant upon neoecological research and can only be constructed through the incorporation of general niche concepts for both predator and prey guilds, as well as detailed autoecological data for every species involved in the model. It is the second aim of this paper to discuss some ecological factors salient to determining both the niche of owls and micromammals and the ways in which these considerations might bias or alter coprocoenoses and thus affect the taphonomy of fossil assemblages.

Once due consideration has been given to the modern ecological interplay between habitat, micromammalian community structure, and owls, the current status of micromammal paleoecology will be discussed. Brief summaries of micromammalian paleoecological reconstructions throughout East Africa will be included, but this paper seeks to focus particularly on the reconstructions of Swartkrans and Sterkfontein (Avery, 2001) as well as other Plio-Pleistocene sites in South Africa (De Graaff 1961; Pocock 1985, 1987; Avery, 1995, 1998, 2001, 2010).

Finally, preliminary analysis of vegetative sampling, small mammal diversity and owl-accumulated assemblages collected in the Cradle of Humankind World Heritage Site, South Africa (in which the Sterkfontein Valley is located), are

presented. These data represent the first results from a pilot study, the larger goal

of which is to better attune micromammalian niche models and investigate the

nature of the predator-prey relationship characterizing owls and micromammals in

the Sterkfontein Valley. Information from the modern ecosystem is compared to

fossil samples from the important hominin-bearing sites Sterkfontein Member 4

(~2.8 Mya) and Swartkrans Member 1 Hanging Remnant (~1.8 Mya). The inclusion

of this study serves the dual purpose of both better illustrating some of the specific

calibrations and reconstructive techniques utilized by paleoecologists and described

in the text, as well as generate new ecological and paleoecological data for the

region. (To provide the reader with suitable reference for this analysis, Chapter Five

provides a brief summary of both the climate and micromammal species local to the

Cradle of Humankind).

      With a proper understanding of owl and small mammal niche ecology and

their interplay with environmental variables such as local climate and habitat type,

the reliability of micromammalian paleoecological reconstructions can be improved.

These reconstructions supplement other lines of paleoecological evidence and

provide useful information regarding the dynamic environment that prevailed

during Plio-Pleistocene times. This environment likely facilitated hominin radiation,

speciation, and extinction events. Between 2-1 Mya, at least three if not more

species of hominin coexisted in South Africa (Klein 1999; Berger et al., 2010).

Improved understanding of fine scale vegetation and landscape patterns

characterizing the environments local to important hominin-bearing cave sites may

lead to better understanding of the ecological relationships and factors contributing

to hominin niche separation and the coexistence of South African hominins in the

Cradle of Humankind.

Chapter Two

Niche Theory

This chapter seeks to discuss the origin, evolution, and current usage of niche

theory as well as discuss its pertinence to paleoecology. Different generations and

subdisciplines of ecology have variously defined niche, alternately embracing and

spurning the theory. Most definitions of the niche concept recognize its inherent

duality, alluding to both the biological requirements of an organism as well as its

relationships, direct or indirect, with other species in a shared ecological community.

It is at the nexus of these two interacting dynamics that the ecological niche of a

species lies (Hutchinson 1957; Whittaker and Levin 1975; Griesemer, 1992, Cowell,

1992; Chase and Leibold, 2003). The weight afforded either of these factors has

caused a fundamental bifurcation in the lineage of the term (Griesemer, 1992,

Cowell, 1992). Nonetheless, niche, in all of its various permutations, has been a

central tenant of ecological and evolutionary theory for the last century, with

considerably deeper conceptual roots stretching back even to Aristotle (Aristotle

350 B.C.E.). In a process characterizing scientific paradigms, niche theory has

progressed through several dialectic stages (Kuhn 1962; Chase and Leibold, 2003).

Some would argue that niche theory is currently entering a stage of revision and

synthesis (Hubbell 2001; Chase and Leibold, 2003). Recently (see Hubbell 2001)

the analytical utility of niche theory to questions of ecological import has been

debated. After a long and not particularly pretty history within ecological theory, the

principles and practicality of contemporary ecological work within a niche-based

framework remain unresolved. With niche theory suspended in such an inchoate form in contemporary ecology, where it is most directly applicable, how can it be of use to those who wish to develop hypotheses about ecosystems that existed millions of years ago? What is niche theory's pertinence to paleoanthropology and the study of hominins?

The reality is that paleoecology lacks the extensive datasets to which modern ecology has access. The paleobiological record, while by no means poor, only expands via the discovery of more and novel fossilized specimens. Fossilization is rare and does not result in equal preservation of all life forms, meaning that paleoecologists will never be able to account for all pertinent ecological variables. Meanwhile, the contemporary ecologist has the luxury of designing hypotheses that can be directly tested either through experimental research or the collection of field data. This being the case, those working to understand the deep past are highly dependent upon modern ecological research to illuminate broad scale biological and ecological patterns, which can in turn be applied to paleoecological problems.

Drawing on contemporary datasets and analytical formulations, paleoecologists are able to appropriate tools for estimating community characteristics such as species diversity, relative abundance, niche overlap, niche breadth, and discern patterns of niche shift and displacement (Tilman, 1980; Nesbit-Evans et al., 1981; Pianka 1981; Andrews, 1990; Krebs, 1999; Odling Smee et al., 2003). While tenuous in some ways, these tools nonetheless lend scientific validity to paleoecological interpretations.

Modern ecology and niche theory are integral to understanding whether or not reconstructing paleoenvironment via micromammals is an effective methodology for accurately representing local habitats. Niche theory is of relevance to the paleoenvironmental reconstructions addressed herein because paleoecologists rely upon niche modeling for micromammal species and utilize community structure and composition estimates to make inferences about local habitats at important Plio-Pleistocene hominin-bearing sites. Niche theory is useful in assessing the overall fidelity of small mammal species to specific microhabitats as well as determining the degree to which barn owls accurately and comprehensively sample small-mammal communities. Niche theory therefore informs the degree to which both the niche assemblage of small mammal communities and their interactions with owls inherently bias fossil assemblage composition and ultimately local paleoecological and paleoenvironmental reconstruction based upon these presumed relationships.

More insight into niche theory can be gained from a thorough understanding of the evolution of the theory itself. In ecology, the word niche has a convoluted etymology and a turbulent history (Whittaker and Levin, 1975; Griesemer, 1992, Cowell, 1992; Hubbell 2001; Chase and Leibold, 2003). Any genuine understanding of niche necessitates familiarity with its scientific roots and evolution, which is why it so often defies simple definition. As the prominent ecologist R.B. Root declared in 1967, "The niche concept remains one of the most confusing, and yet important topics in ecology". From its historical roots in the tradition of natural science, to its inception as an ecological term, to the multitudinous mathematical models

developed in attempts to validate and quantify it, niche still remains an elusive but theoretically valuable ecological concept (Whittaker and Levin, 1975; Chase and Leibold, 2003). Naturally, the literature and history on niche theory is extensive. I have chosen here to distill some salient components of classical niche theory and use them to frame discussion in later chapters.

The concept of niche inevitably has its roots in the work of early naturalists, such as Linneaus, and Darwin, who noted differences in the traits, roles, and habits of each creature on earth. The classificatory systems of Linneaus (1758) implicitly acknowledge ecological diversity and the fact that different species possess unique traits. Darwin (1859, 1872) referred to a species as having specific "lines of life'.

However, the term niche did not formally appear in the ecological literature until Joseph Grinnell published a paper in 1917 entitled, "The Niche Relationships of the California Thrasher". Grinnell's conception of niche was closely tied to habitat and the functional requirements of a species within that habitat, thus stressing a spatial concept of niche. Grinnell's niche concept has been interpreted as the ultimate distributional unit (Pianka, 1981). While it is true that Grinnell emphasized species distribution and their environmental requirements heavily, he also recognized that the availability of those resources depended upon a number of factors including the distribution and requirements of sympatric species. In fact, Grinnell's concise treatment of niche, just a short paragraph at the end of his 1917 paper, is among the simplest and most direct description of the theory one will find in the literature.

> These various circumstances, which emphasize dependence upon cover, and adaptation in physical structure and temperament thereto, go to demonstrate the nature of the ultimate associational niche occupied by the California Thrasher. This is one of the minor niches which *with their occupants all together* make up the chaparral association. It is, of course, axiomatic that no two species regularly established in a single fauna have precisely the same niche relationships. (Grinnell 1917:433).

In the above passage, Grinnell succinctly acknowledges species physical (biological) requirements, goes on to describe species niche as a role in a biological community, *and* anticipates the Principle of Competitive Exclusion (Gause, 1934). The fact that Grinnell's work has been effectively distilled into the parochial interpretation that species niche equals its habitat requirements and distribution does a disservice to this innovative ecologist. In the end Grinnell's seminal work effectively captures the nucleus of the niche concept.

A mere ten years later, in 1927, Charles Elton published *Animal Ecology*. In it, Elton famously analogizes the 'role' of a badger in its ecological community to the 'role' of a vicar in a human community, and writes that it is "therefore convenient to have some term to describe the status of an animal in its community, to indicate what it is *doing* and not merely what it looks like, and the term used is "niche" (Elton, 1927). With the publication of *Animal Ecology*, Elton established an important dimension of niche theory, that of an organism's relationships with other species and its position within an ecological community. Furthermore, (and of notable importance to interpretation of paleoecological communities) Elton recognized similarities between the organizational qualities of ecological communities globally.

> These examples illustrate the tendency which exists for animals in widely separated parts of the world to drift into similar occupations, and it is seen also that it is convenient sometimes to include other factors than food alone when describing the niche of any animal (Elton, 1927: 65).

In other words, there is often a remarkable degree of evolutionary convergence of species towards niche similarity in different ecological communities, where different species use similar resources in similar ways (Whittaker and Levin, 1975).

Elton's emphasis on community role has earned his theory of niche the moniker, 'population niche concept' to contrast Grinnell's 'environmental niche concept'. However, as with Grinnell, the implication that Elton's definition of niche was so narrow that it neglected to emphasize the role of environmental or habitat requirements is false. Species requirements formed the foundation upon which Elton constructed his definition of niche, which simply recognizes inter- and intra-species relationships more explicitly. A false bifurcation of the niche concept, dating back to these two ecologists, has plagued the field since (Griesemer, 1992, Cowell, 1992; Chase and Leibold, 2003). The reality is that species niche lies at some nexus point incorporating both species requirements and species interactions. Furthermore, the dynamic interaction of these requirements and relationships (and thereby the relative importance of either) is unique in every case.

With his brilliant synthesis, the zoologist G.E. Hutchinson crystalized this inherent duality in his now famous *Concluding Remarks* at the Cold Spring Harbor Symposium, 1957. In the first workable analytical model pertinent to the theory, Hutchinson suggested that niche be envisioned as an n-dimensional (multi-dimensional) hyperspace in which species might be located. The hyperspace is delineated by axes, which are based on some quantifiable aspect of species niche

and are organized along a gradient. Two axes are recognized; habitat and niche. Habitat axes utilize extensive variables, or those factors imposed upon a species by virtue of its environment and requirements. These variables are also referred to as intercommunity, for they affect numerous species and/or communities depending upon scale of reference.

Naturally, hyperspace models based using habitat axes exclusively were the first to be studied, as habitat variables tend to be concrete, easy to measure, and generally geometric in character (Grinnell and Storer, 1924; Whittaker and Levin, 1975). Things like elevation, ambient temperature, moisture, and so forth are reasonable axes upon which species tolerances, ranges, and distributions can be plotted (in a process known as ordination) (Whittaker and Levin, 1975). Important ecological patterns have and continue to be discerned using habitat hyperspace modeling, but it becomes clear that habitat hyperspace insufficiently captures all elements of niche differentiation (Levin, 1970).

Niche axes are based upon intensive or intra-community variables. Niche variables incorporate biological parameters and pertain to relationships both within and between species (Hutchinson, 1957). Compared to habitat axes these axes are more difficult to quantify for they are often less clear, less geometric, and essentially innumerable. Moreover, multiple important niche variables are sometimes collapsed into a single niche axis, which can result in the loss of relevant information. The fundamental problem with niche axes, and the root of much frustration regarding the theory itself, lies in quantifying relationship variables. Theory

certainly supports the notion that species evolve toward differences in niche, but quantifying niche parameters and interpreting the predictions of current analytical models remain an elusive task (Whittaker and Levin, 1975; Chase and Leibold, 2003; Holt, 2009).

Hutchinson (1957) further conjectured that within this n-dimensional hyperspace, any given species has a range of variables (habitat and otherwise) that it can tolerate, termed the "functional niche" or "virtual niche". However, some of this range is pre-empted by competing species, thereby relegating the species of interest to a narrower proportion of the n-dimensional hyperspace referred to as the "realized niche". These niche types are traditionally conceptualized as where a species can *potentially* exist and where a species *actually* exists.

The theoretical gestalt of Hutchinson's n-dimensional hyperspace incorporates infinite numbers of habitat and niche axes to define and delineate the realized niches of all species residing in an ecological community. Or at the very least it offers a tool to isolate those axes of greatest importance in predicting niche diversity in a given community. In a biological system, however, many aspects of this goal prove difficult for reasons both pragmatic and theoretical (Levin, 1970). Not only is the sufficiently detailed data required by this approach time consuming and difficult to obtain, feedback and non-linearity – processes that amplify and confuse direct interpretation of ecological data - mean that every ecological community and system is uniquely complex and nuanced (Levin, 1970; Holt, 2009; Soberon and Nakamura, 2009).

The three ecologists discussed above were primary progenitors of an instrumental ecological theory. Hutchinson in particular served as the harbinger of an era of hypothesis generation, experimental testing, and field verification utilizing niche theory and n-dimensional hyperspace as an analytical model. The Hutchinsonian conception of niche, with its Grinnelian 'habitat' and Eltonian 'niche role' components, is still the dominant paradigm in niche theory and will serve to inform my ecological discussions of owls and micromammals.

It would be wrong to exclude one final ecologist, Georgii Gause, whose observations of marine terns provided a theoretical mechanism for niche differentiation that could be mathematically expressed and tested. Gause's "Principle of Competitive Exclusion" states that two species competing for the same resource cannot coexist if all other ecological factors are held constant and therefore must exhibit niche differentiation to coexist in a given community (Gause ,1934). A number of mathematical models were developed based upon competitive exclusion, of which the Lotka-Volterra (Lotka, 1924; Voltera, 1926) is perhaps the most notable. Competitive exclusion affirmed two fundamental components of niche theory. First, the principle cemented the notion that many species survive together because they differ in resource utilization or other requirements. Second, competitive exclusion made the coexistence of species mathematically plausible and set up a mechanistic framework for the evolution of species diversity.

Later models improved upon the Lotka-Volterra models, attempting to incorporate different types of competition and designed to explore the concepts of

niche overlap, breadth, partitioning, and assembly within ecological communities (Pianka, 1981; MacArthur, 1972; Tillman, 1980). These models, however, should ultimately be regarded as variations on the theme of competitive exclusion. While competitive exclusion provided much fodder for testing ecological hypotheses, ecologists and critics grew dissatisfied with its inability to accurately quantify niche.

Two shifts then occurred in ecology regarding niche theory. The first of these was increased concern amongst professional ecologists (concurrently occurring in all sciences) over the lack of statistical rigor and valid null hypotheses evident in research generated by niche theory (Popper, 1963; Strong et al., 1979). Additionally, data amassed by field ecologists suggested that the tacit assumption that competition was the only factor driving niche differentiation was flawed. These observations of discrepancy led to more pluralistic incorporation of other niche differentiation mechanisms. Variables such as access to resources, seasonal and successional factors, population structure and dynamics, and, importantly, predation must also be considered (Paine, 1966; Whittaker and Levins, 1975).

Expanding upon MacArthur's (1972) attempts to create better analytical models for niche theory, Levin (1970) addressed the debate over the singular importance of competitive exclusion directly, in a paper entitled *Community Equilibria and Stability, and an Extension of the Competitive Exclusion Principle*. In it Levin writes,

> The purpose of this paper is to show that there are instead certain dimensions of paramount importance [to a species]. Which dimensions those are is determined by which factors are limiting those species, be those factors resources, predators, or others. Two species cannot

coexist unless their *limiting factors* differ and are independent; that is the only criterion one need examine at a given time and place (Levin 1970).

In addition to acknowledging that multiple factors contribute to species niche, Levin emphasized the potential for periodic rather than constant states of equilibrium. Levin's limiting factors permit the persistence of several species in a fluctuating balance so long as the limiting factor for each species differs to a significant enough degree.

An example of this occurs in ecosystems in which a predator species concentrates upon a prey species, which is above some critical population threshold until such a point as that prey resource is depleted. The predator then switches to an alternate prey base. In this way several species can coexist in the same ecological community in an alternating boom and bust pattern. Owls are an excellent example of this pattern. In South African barn owls, for example, pellet analyses have revealed that owls prey heavily and alternately upon *Mastomys, Mus,* and *Otomys* during periods of rodent population explosion and diversify their diet when these species populations are in decline (Vernon, 1972; Taylor, 1994; Avery, 2005).

While Levin's expansion of the competitive exclusion principle provided theoretical justification for the existence of other regulatory mechanisms relating to niche determination, the problem of determining precisely what and how many of these limiting factors influence species niche remains to be addressed. Explicitly quantitative measures of niche are terribly difficult to generate and likely enumerable. The most that can be done is to look for the axes that suggest the distinct niche patterns. Some obvious factors have already been indicated: resource

availability, competitor interactions, and predator interactions. However it is necessary to keep in mind less obvious variables such as seasonality, genetic variation, spatial variation, and intraspecific interactions.

Predation, with specific regard to predator-prey dynamics is of the utmost relevance to issues of taphonomy, particularly when assemblages are thought to have been accumulated by predator activity. Knowing the biases inherent in a given assemblage as a result of the behavioral and niche characteristics of the accumulator *and* the accumulated are essential for interpretation. Therefore it is prudent to spend a little time considering this particular niche-delimiting factor.

Predators and prey strongly and directly influence one another's behavior, morphology, and population dynamics and, in essence, they shape one another's niches. In a number of now classic studies by Gause (1934) utilizing protozoans, the Russian biologist was able to demonstrate out-of-phase oscillations in interacting predator-prey populations later validated by MacLulich (1937) in populations of snowshoe hare and lynx. These studies showed that predator population levels grew or declined in relatively symmetrical proportion to prey populations, albeit with a certain lag time from change in prey population to response in that of the predator.

In a 1966 study, R. T. Paine was the first to explicitly demonstrate that the top-level predators play a critical role in regulating the species composition of a given community. Paine found that the carnivorous starfish *Pisaster ochraceus* reduced the numbers of the mussel *Mytilus californianus*, a dominant competitor for intertidal space, thereby creating ecological space for other species to cohabit a the

tide-pool and increasing the biotic diversity. Integral to Paine's conclusion is the notion of spatiotemporal heterogeneity, a recurrent theme in studies of biodiversity and niche proliferation. Micromammals are no exception to this theme, increasing in diversity with increasing habitat heterogeneity in both space and time and responding to multiple forces of predation (Ylonen and Brown, 2007).

Still, even pluralistic models, including predation have been dissatisfactory in fully explaining the niche of various species and some ecologists, fed up with the mathematical difficulties and overly reductionist nature of the theory, have sought to abandon niche entirely.

Recently, Hubbell (2001) proposed a unified neutral theory of biodiversity and biogeography. In effect, the theory and models he has developed require no consideration of species niche; species are in essence identical in their ecological niche and neutral to one another. Owing to its remarkable success at explaining patterns in certain ecosystems Hubbell suggests that ecologists, ought to "re-think completely the classical niche-assembly paradigm" (2001:320). Hubbell's theory has since been both validated and refuted, with studies evidencing notable weaknesses in his models (Chase and Leibold, 2003). While Hubbell's contributions certainly revitalized discussion about niche theory, most ecologists are quite reluctant to jettison the idea entirely (Chase and Leibold, 2003). His contentions, however, are pertinent. In many ways niche models are cumbersome and overly reductionist, but their theoretical value remains, particularly for paleoecology, which seeks to answer somewhat broader questions than much of modern ecology.

The pertinent question remains, if niche theory is still suspended in rudimentary form in the field of modern ecology, how then can it be of use to paleoecology? It is true that at the present time, the full dynamics of any ecosystem, to say nothing of paleoecosystems, cannot be interpreted utilizing niche theory alone. Nonetheless it is useful to have at least some guiding parameters, initial hypotheses, and relevant ecological paradigms from which to work. Chase and Leibold (2003) concede to the limitations of working within a niche framework but they also argue quite pragmatically that,

> Niche provides a currency that can incorporate and synthesize many seemingly disparate ideas ranging from the individual to the ecosystems level. Niche concept allows us to describe and evaluate the consequences of trade-offs in the ways in which species respond to and affect aspects of their environment. Such trade-offs are important in generating variability among communities and explaining relative abundances and distributions of species (2003:175, 178).

Paleoecologists will never be able to assess a fossil assemblage and infer with perfect accuracy the structure of the paleocommunity they seek to reconstruct. This is true because the fossil record is a function of the processes and circumstances by which it was preserved as well as the difficulties conferred by assumptions of uniformitarianism. Still, understanding modern ecological concepts such as niche theory, and refinement of autoecological knowledge important in defining the niche models for particular species serves to illuminate potential biases of niche-based models and refine techniques used in paleoecological interpretations.

In micromammalian paleoecological reconstruction, niche-based models are drawn upon heavily. A few key models regularly employed by paleontologists will

be discussed briefly in the following, including ecomorphological or "taxon-free" models, taxonomic ratios, taxonomic habitat indices, and species diversity indices.

Ecomorphological models seek to relate anatomical morphology, functionality, and locomotor adaptation to specific habitat types, thereby sidestepping the difficulties of uniformitarian assumptions (Plummer and Bishop 1994; Andrews and Humphrey 1999; Reed, 1997). While theoretically well suited to paleoecological assemblages and fruitful in assessment of larger fauna, ecomorphological models for small mammals remain underdeveloped and regularly excluded from anthropologically relevant studies of this nature (Reed, 1997). Given proper methodological development 'taxon free' approaches may be useful additions to the toolkit of micromammalian paleoecologists.

Taxonomic ratios tally and compare the abundance of taxa with strong niche affinities and ecological tendencies (Vrba 1980, 1985, 1995). In microfaunal analyses, akin to the Alcelaphine:Antelopine bovid index (or AAC) which assesses the relative proportions of bovids adapted to closed versus open environments, the Gerbillinae:Murinae index has been used as an indicator of aridity (Vrba, 1980, 1985; Fernandez-Jalvo et al., 1998). Gerbils, largely arid adapted species, are compared to Murines traditionally been ascribed to wetter, more mesic environments. However, Reed (2003, 2007) was unable to find strong correlations between aridity and the G:M in his research on small mammal communities in the East African Serengeti. According to Reed (2003) Dendromurinae:Murinae (Climbing Mice: Murines) and Soricids:Murinae (Shrews: Murines) ratios were

better indicators of aridity and density of vegetative cover. This finding may be due to the generalist tendencies of many Murine species, and the affinities of Dendromurines and Soricids for dense cover and wetter habitats, respectively (Skinner and Chimimba, 2005).

Taxonomic habitat indices (THI) and species diversity indices remain the most specific measures of micromammalian habitat reconstruction (Nesbit-Evans et al., 1981). Taxonomic habitat indices incorporate all species in an assemblage thereby returning a composite interpretation of local habitat. Essentially, each species, based upon its niche profiles and microhabitat affinities is assigned a THI score. Fernandez-Jalvo (1998) suggest five primary habitat types into which species might be sorted including, forest, woodland, bushland, grassland, and semi-arid categories. Species then receive weighted scores depending on their affinity for a particular habitat type as ascribed by the modern ecological literature. Scores are summed to 1.

There are many ways that THI can be manipulated, though most frequently researchers choose to apply additional weighting to account for the relative abundance of species. This returns a more accurate picture of local habitat as it draws upon both autoecological profiles and the degree to which certain species are represented in a given environment. Naturally, THI has its biases and proves weakest when niche models for particular species are insufficient. Hence ongoing research regarding the autoecology of species ought to be considered and

incorporated in THI analyses. Reed (2003, 2007) explicitly states the need for revision in some small mammal species such as *Dendromys* and *Steatomys*.

Finally, species diversity estimates are used to examine overall community structure. The relative abundance of species varies between ecological communities, but greater diversity has generally been acknowledged as indicative of equable environments while lower diversity generally means that fewer species are able to successfully coexist (McKinney and Drake 1998). The Shannon-Weiner diversity index (Shannon 1948), which assesses both species abundance (number of species in a given community) and species evenness (number of individuals belonging to each species in a given community), is frequently employed in conjunction with THI analyses. This measure is sensitive to both diversity and species dominance. Having either additional, unique species, or greater evenness in the species represented thus increases the index. Unfortunately the index, which predicts higher diversity in more equable climes, may contrast with biases introduced by predatory accumulators. As Taylor (1994) and others have demonstrated, in less equable climes (such as deserts and higher latitudes) and under seasonal conditions in which prey are scarce, barn owls tend to take a greater diversity of prey. Conversely, when environments are productive and prey species abundant, barn owls are able to specialize on the most abundant species, which would lead to lower diversity values based on coprocoenoses and confusingly suggest less equable conditions.

These paleoecological approaches are highly dependent upon accurate niche models, meaning that niche theory and neoecological work are of the utmost

importance to accurate paleoecological reconstruction. Cross-fertilization between the two fields is not just useful, it is essential. Indeed, the Hutchinsonian niche model provides a useful framework within which to assess the basic requirements and niche characteristics of modern species and from which to build appropriate niche models for micromammalian reconstructions. It also provides paleoecologists with a way to explain the patterns and diversity observed in paleoecosystems.

Chapter Three

Barn Owl Ecology

The common barn owl, the subject of scrutiny in this chapter, is a nocturnal avian predator and member of Tytonidae. The oldest recorded owl fossils occur in the middle Paleogene with the first members of Tytoninae appearing during the late Eocene in a 'savannah-like' habitat (Mlikovsky, 1998). Fossils from the Quaternary period include only modern species, the earliest of which is a *Tyto alba* specimen from Olduvai Gorge, Tanzania (Brodkorp and Mourer-Chauvire, 1984; Mlikovsky, 1998). Unfortunately, there is a paucity of fossilized avian remains from which to interpret evolutionary patterns and dispersal, as the osteological structure and softness of bird bones are not conducive to preservation. Still, it can be said with certainty that barn owls were present in their modern aspect by the early Pleistocene and probably long before this (Mlikovsky, 1998).

Taphonomic investigations of numerous fossil-bearing localities dated to the Plio-Pleistocene in South Africa implicate barn owls as primary accumulators of micromammalian remains (Avery, 1998, 2001). Indeed, caves are very frequently used as roosts in natural African populations. This suggests that the relationship between *Tyto alba* and micromammalian communities has persisted for the last 4 million years and likely far longer. This temporally consistent relationship between avian predator and mammalian prey may serve to shed light not only on the species composition of paleocommunities local to key hominin bearing sites, but may also offer some insight as to the nature of major climatological and ecological shifts occurring during the Plio-Pleistocene and relevant to hominin evolution.

Distribution, Anatomy, and Physiology

Tyto alba likely attained something akin to it's modern global distribution

approximately 1 Mya and represents one of the most ubiquitous and well-studied of

all modern avian predators (Taylor, 1994). The African subspecies*, Tyto alba affinis*,

is less well represented in the literature than subspecies in either Europe or North

America. This is unfortunate, given its demonstrable contemporaneity with

hominins during the Plio-Pleistocene. The African variant differs from some of its

conspecifics in a few significant ways. The bird is generally smaller than other

subspecies, with an average mass of about 300 to 330 grams. It also tends to have

paler plumage on its undersides, longer wings despite its small body size, and long

legs (Fry et al., 1988; Taylor, 1994). Each of these characteristic traits has been

hypothesized as adaptive to forage in open savannah-like habitats (Taylor, 1994).

More generally, anatomical and physiological traits make barn owls well

suited to their nocturnal foraging habits. Soft, downy feathers reduce the noise of

flight, while a stiff comb-like fringe on the leading edge of their primaries also

contributes to their airborne stealth (Bunn et al., 1982; Taylor, 1994). Vision is less

important to these animals than might be inferred from their large eyes, and

acoustic cues actually serve as their primary means of prey location and navigation

for capture. The characteristic heart-shaped plumage of the face, in addition to

asymmetrically placed ears facilitate sound capture and assessment of multi-tonal

frequencies at very finite levels (Payne 1971). In fact, the birds are so sensitive to

tonal frequencies, it is suspected that they can differentiate one prey species from

another, and even isolate intra-specific variables such as sex and age class (Payne

1971; Taylor, 1994). Upon successful capture, barn owls generally swallow their

prey whole though large prey items can require more processing (Kusmer 1990).

This behavior, coupled with the characteristically high pH of the barn owl's stomach,

results in remarkable preservation in compact pellets of all prey items and skeletal

elements consumed making pellet assemblages ideal ecological proxies (Smith and

Richmond 1972; Dodson and Wexlar 1979; Andrews, 1990).

Diet

    While micromammals comprise the vast majority of what a barn owl

consumes, bats, birds, reptiles, amphibians, and often insects are known to

supplement their diet, sometimes sustaining them in times of prey scarcity (Taylor,

1994; Granjon and Traore, 2007). Indeed, our observations in the Sterkfontein

Valley revealed high proportions of insects in the dry season. Some common themes

characterize all barn owl prey, with subtle variation occurring between biomes and

global regions. According to Taylor's (1994) thorough study of owl dietary

composition, more than three quarters of all diets consist of 90% small mammals.

Numbers of available prey taxa in any given geographic locality range from 2-25

species, evidencing significant foraging niche width in the barn owl. In most cases,

one, two, or three species make-up 80% of an owl's diet. Diversity in the diet of

African subspecies appears to be higher with an average of five or six species

dominating (Vernon, 1972; Perrin 1982; Taylor, 1994). Owls respond to

spatiotemporal differences in prey abundance and diversity, which are

environmentally significant variables because they reflect fluctuation in resources and climate. They specialize on abundant prey species when food resources are ample and are more generalist in their feeding behavior food is scarce (Taylor, 1994).

Reproduction is also timed with seasonal availability of prey (Taylor, 1994). Breeding in all varieties of barn owl begins just before seasonal increases in primary productivity and subsequent increases in small mammal population densities. Interestingly, African barn owls do not breed relative to peak population densities, but instead lay eggs in the dry season, their young hatching and maturing when prey densities are declining significantly. It has been postulated that the prolific vegetative growth brought on by heavy seasonal rainfall impedes the owls hunting efficiency (Fry et al., 1988; Taylor, 1994;). Vegetative die-back and fire disturbance regimes may prove beneficial in facilitating prey capture. In this scenario, *density* of resource becomes less important than the parameters controlling *access* to that resource.

Often, the dominant micromammalian taxa in an owl's diet at any given time reflect those species' dominance in the greater ecological community (Avery, 1998; Avenant 2005, 2007; Terry 2010). However, direct correlations between coprocoenoses, micromammal community structure, and species diversity must be cautiously drawn. Activity patterns, intraspecific dynamics of prey populations, and predator bias for specific sizes, ages, and sexes of prey must all be considered. Generally, these considerations are dependent upon both the individual owl and the

small mammal species. It is also important to remember that, because owls are nocturnal, diurnal prey species tend to be highly under-represented (Andrews, 1990). In many South African coprocoenoses, and indeed in preliminary sampling of micromammalian diversity in the Sterkfontein Valley presented in Chapter Seven, the ubiquitous but diurnal omnivore *Rhabdomys pumilio* is rarely represented because of its circadian tendencies (Perrin 1982; Andrews, 1990; Taylor, 1994).

It is frequently noted that owls prey upon juvenile individuals, seldom take prey items in excess of 20% of their body mass, and are biased in prey sex ratios (Derting and Cranford 1989; Wallick and Berrett 1976; Andrews, 1990; Taylor, 1994). Vezina (1985) has demonstrated a common correlation between prey and predator body weights with average prey mass intake roughly equal to 10% of predator body mass. On the South African subcontinent the barn owl has a slightly higher average of 14% prey to predator body mass, commonly taking prey in the 8.2-19.0% mass range (Perrin 1982; Vernon, 1972; Taylor, 1994). In most of southern Africa, generalists such as *Mastomys* (the prolific multimammate mouse) dominate assemblages, followed closely by other widely distributed genera such as *Otomys, Aethomys*, and *Michaelamys* (Avenant 2005). Shrews are consistently the most numerous non-rodent prey and, as noted in Chapter Seven, were *the* dominant micromammal in all pellet collections from the Cradle of Humankind.

Habitat Selection

In terrestrial ecosystems, it is often plants that set the stage upon which natural enemies interact (Denno et al., 2005), thus habitat, particularly vegetation,

plays an important role in governing the dynamics of predator and prey. Structure, composition, complexity, and the seasonal patterning of the vegetative landscape determine where an owl will hunt and delimit productive prey patches (Taylor, 1994; Tarboton and Erasmus 1998).

Though characterized as a non-selective opportunist (Mikkola 1983) and quite widespread throughout various habitats across the world, *Tyto alba* has a demonstrable affinity for open habitats (Colvin 1984; Rosenburg 1986; Taylor, 1994; Leech et al., 2009). The bird's body size, it's hunting strategy, and its morphological adaptations to flight are less suited to maneuvering through closed environs. It has been shown both experimentally and through field observations, that owls do, in fact, disproportionally utilize open areas (Marti 1974; Fast and Ambrose 1976; Colvin, 1984; Rosenburg 1986; Torre et al., 2004; Leech et al., 2009). In a study of owl populations in North America, the grassland component of the research area was quantified at 16% of total available habitat and yet radio-telemetry demonstrated that 48% of foraging time was spent in the grassland component (Rosenburg 1986). However, this bias is actually not that severe, particularly when compared to the stricter adherence by other owls to very specific habitats (Tarboton and Erasmus, 1998).

Trapping programs have been used in conjunction with pellet analyses in an attempt to identify and quantify discrepancies between species diversity in the local habitat and that reflected in owl pellets. Trapping, of course, is not without its own set of problematic biases. Prey species are subject to differential trappability. Some

traps and bait types are more effective than others, certain genera are "trap-shy",

while still others live in micro-habitats not amenable to trap-based sampling

methods (such as arboreal and fossorial species) (Derting and Cranford 1989;

Taylor, 1994; Avenant, 2005). To mitigate this, researchers combine trap types and

proxies. A comparative study by Torre et al. (2004) tested three proxies for

estimating micromammal community structure in the Mediterranean. Owl pellets,

trap data, and scat from a mammalian carnivore (*Genetta genetta*) were all found to

differ significantly in the degree to which they reflected species diversity and

composition. Though the barn owl was, overall, the most effective in sampling a

broad diversity of species (89.5% of total), some species associated with more

forested habitats were notably absent in the pellets but found in genet scat. Ideally

numerous proxies should be used to ascertain species composition in a given

ecological community, an approach that has been seldom attempted. In this respect,

the time-averaged nature and potential for multiple accumulators in fossil-bearing

sites thus might actually improve the robusticity of assemblages derived from caves.

It is therefore an ecological certainty that owls prefer to hunt in relatively

open areas. This naturally has the potential to bias micromammal community

structure as reconstructed from pellets, skewing species diversity and relative

abundance towards prey species residing in open habitats and altering fundamental

interpretations of local habitat. The question of greatest pertinence here is, to what

degree does this tendency obscure the actual micromammal taxonomic composition

at a given locality and can useful and accurate inferences about local habitat be

made regardless?

Fortunately, though preference for open habitats in barn owls is evident, the bias is somewhat mitigated by both their sensitivity to the relative abundance of local species and their propensity for hunting in ecotonal habitats. While biases towards open areas must be noted in paleoecological reconstruction and interpretation, they are probably not crippling to its methodology.

A recent study by Terry (2010) presents compelling evidence that barn owls sample from all habitats in their range and demonstrate high ecological fidelity at the local landscape scale, particularly for habitat types closest to their roost site. Taylor (1994), in a long-term study of Scottish barn owls, also demonstrated that the birds are quite responsive to fine-scale variation in habitat types. His study area included a mosaic of differing habitats, ranging from conifer plantations, to rough grassland, to low altitude pastoral farmland, each with a resident mating pair. Taylor observed significant relationships between the owls' habitat composition and diet, as well as correlation between taxa represented and their microhabitat associations. Using coprocoenoces and vegetative sampling from roost sites in Tanzania, Reed (2003, 2007) also found that shifts in relative species abundance correlated well with local habit characteristics. Finally, studies conducted by Vernon (1972) found the dominance of gerbils in arid Namibia and murine species associated with mesic habitats in the Cape region. These studies suggest that barn owls are responsive to local micromammal community composition.

Also noted in by Taylor, was a preference in the Scottish owls for forage in woodland edge habitats, particularly those with moist, tall, grassland components.

This preference was marked and similar edge foraging phenomena are observed in North American barn owls (Byrd 1982). It has been well demonstrated that ecotones are often characteristically rich in species diversity and resources and that they facilitate predator-prey interaction (Fagan et al., 1999). Hunting ranges for the average barn owl incorporate several patches of both used and unused habitat (Taylor, 1994). Areas of heavy cover are not frequented by owls for foraging, but may serve as reservoirs, refuge, and dispersal corridors for prey species, effectively provisioning edge habitats with a greater density of prey (Denno et al., 2005). It is speculated that both predators and prey move in parallel to these edge habitats, utilizing resources unavailable in the focal habitat (Denno et al., 2005).

Prey Selection

Species diversity, species composition, relative abundance of taxa, mean prey size, age-class, and sex vary on local, seasonal, inter-annual, and long-term scales (De Graaff 1981; Taylor, 1994; Lidicker 1999, 2000; Avery, 2005; Skinner and Chimimba, 2005). Rodents are responsive to fluctuations in microhabitat, habitat, and landscape level processes driven by both abiotic and biotic factors contribute to this variation (Ernst et al., 2000). While seasonal and inter-annual cycles are interesting, and can be assessed via regular collection of pellets, effective techniques for discerning these types of variation are rare in the paleo-record. Isotopic analyses may eventually prove useful in isolating some of these finer scale trends. The slow, accumulative processes characterizing most fossil-bearing cave sites in South Africa effectively time-average samples to such a degree that a species composition proxy

for seasonal and inter-annual change is often lost. Inferences about local micromammal community structure (albeit over a relatively long period of time) and long-term shifts in owl dietary habits, however, are far more within reach (Taylor, 1994; Avery, 2001; Reed, 2007).

An example of one such long-term dietary shift can be found in the Cradle of Humankind, where fossil-assemblages from Sterkfontein and Swartkrans have both yielded very different species composition patterns when compared to modern data. The rodent species *Mystromys albicaudatus* dominates the micromammals derived from these Plio/Pleistocene localities (Avery, 2001, 2010). A similar pattern of species dominance, presented in Chapter Seven was evidenced in our samples from Sterkfontein and Swartkrans. Though still extant in South Africa, *M. albicaudatus* is now very rare and has been relegated to endangered species status (Skinner and Chimimba, 2005). Accumulation of micromammals at these fossil sites have been attributed to barn owls and the dominance of *Mystromys* is far beyond the scope of biases inherent in barn owl prey selectivity. Therefore it is likely that the overwhelming presence of *Mystromys* is otherwise explained.

Predator-prey dynamics, such as those characterizing owls and micromammals, are inherently complex and dependent upon maximizing energy return, minimizing energy spent and, for prey, maximizing predator avoidance (Barbosa and Catellanos, 2005). Conflation of predator selectivity and the differential susceptibility of prey are frequent and thus there is much disagreement in the ecological literature regarding how selective barn owls are (Marti 1974; Fast

and Ambrose 1976; Derting and Cranford 1989; Yom-Tov and Wool 1997; Torre et al., 2004; Terry 2010). Lack of consensus on this matter and failure to examine habitats of barn owls in the regions local to fossil sites can lead to taphonomic confusion and thus inaccurate paleoecological interpretation.

For instance, owls have certain prey size constraints due to body size and researchers do not agree on how selective owls are in this regard (Yom-Tov and Wool 1997). Obviously, in smaller species adults provide greater energetic return for cost of capture. Conversely large-bodied rodent species may be underrepresented, or their representation in coprocoenoses may be skewed towards juveniles. Juveniles may be less fit and experienced in predator evasion, may be of the appropriate size class for consumption, and may be forced by adults into more dangerous areas for forage (Derting and Cranford 1989). It is readily apparent that these biases are specific to prey species and depend upon the unique behaviors of each taxon, not merely the selectivity of the owls. Modern ecological data specific to local and regional environments must be established in order to avoid this difficult conflation in paleoecological studies.

One potent example of a misinterpretation that influenced a paleoecological reconstruction elucidates the matter. An initial reconstruction using micromammals at Olduvai by Fernandez-Jalvo (1998) concluded that shifts in micromammal faunal composition (an increase in gerbil abundance) resulted from a change in predatory accumulator. Thus micromammal species differences were attributed to taphonomic shift and considered insignificant. This conclusion was

based upon the belief that barn owls do not frequently take gerbils, which can be large-bodied. However, via modern ecological calibration, Reed (2003, 2005, 2007) demonstrated that barn owls in the Serengeti frequently eat gerbils. Gerbils are important indicators of aridity and thus more accurate niche modeling for Serengeti owls revealed significant environmental shifts at Olduvai that may otherwise have gone overlooked.

It seems reasonable, given the above discussion regarding owl ecology, that shifts in micromammalian community structure can be taken to reflect shifts in climate and that predatory biases introduced by owls are not especially problematic to paleoenvironmental reconstruction. The climatic shifts that these micromammals reveal presumably also influenced hominin evolution and therefore warrant further inquiry. However, more must be known regarding micromammalian niche before inferences regarding climate-driven habitat change are attempted.

Taphonomic Considerations

As a final note before moving into a discussion of micromammalian ecology the information presented above regarding the autoecology of *Tyto alba* must be assimilated into a theoretical and analytical taphonomic approach. Unfortunately, the relationship between fossil assemblages and ecology is not simple or straightforward. Multiple accumulators, predatory and otherwise, contribute to fossil assemblages over long periods of time (Andrews, 1990). The preservation process itself, from deposition to mineralization, subjects remains to the deleterious effects of weather, trampling, transport, and differential sorting (Andrews, 1990).

Under good preservation conditions, the relative contribution of barn owls compared to that of other predators such as mammalian carnivores, raptorial birds, and other owl species, can be determined. Different predatory species exhibit different digestive processes, which can be discerned using a few key variables. Bone loss, bone breakage, and bone digestion have been quantified for different predatory species in a number of controlled experimental studies (Dodson and Wexlar 1979; Hoffman 1988; Andrews, 1990; Kusmer 1990; Simons et al., 1991; Terry 2010), and when the relative degree of each of these factors is combined reasonable inferences about accumulator identity can be made.

Bone loss occurs when some skeletal elements are either completely destroyed or digested. High loss of skeletal elements is characteristic of predatory species that process their foods heavily, both in a mechanical and a chemical sense. Bone loss is measured by comparing the relative proportion of any given skeletal element to the total number of elements expected based on minimum number of individuals (MNI). There is a distinct 'owl' pattern in bone loss, as the owls unique digestion preserve high proportions of both cranial and post-cranial elements (Andrews, 1990). In diurnal raptors, five of the more robust skeletal elements are generally preserved, while in mammalian carnivores bone loss is quite high (Dodson and Wexlar 1979; Hoffman 1988; Kusmer 1990). Bone breakage is another useful proxy. Both the location of the break and the frequency of breakage provide clues to predatory accumulators. Breakage in barn owl coprocoenoses is minimal, followed by other raptorial birds, and finally small mammalian carnivores (Kusmer 1990). Unfortunately, fossil assemblages subject to the ravages of time are often broken via

other processes, so this must be taken into account. Bone digestion also follows a pattern similar to that of breakage, with owl digestion being the least destructive, followed by raptorial birds and carnivores (Andrews, 1990).

Once the relative contributions of different accumulating agents have been taken into account, one can begin to assess the micromammals themselves (Andrews, 1990). Most significantly, one can begin to reconstruct overall community structure. Generally these reconstructions incorporate known habitat preferences and relative abundances of individual species represented in a fossil assemblage to infer paleohabitat (Fernandez-Jalvo 1998; Denys 1998; Reed, 2007).

As a final note, the study and reconstruction of paleoecosystems must recognize a fundamental assumption, that of taxonomic uniformitarianism (otherwise known as transferred ecology). It is an unavoidable reality that no species extant today can be expected, *a priori*, to occupy precisely the same niche as did its distant predecessors. Nor can the niche role of extinct species be fully known. Species often inhabit specific microhabitats, which might be present in a variety of 'larger' habitats thus making habitat reconstructions "far from straightforward" (Andrews, 1990). The difficulties presented by taxonomic uniformitarianism, while significant, are inherent to any field studying ancient life. This does not necessarily condemn all research that seeks to understand past ecosystems using contemporary analogy and in any case it is difficult to see a way forward without doing so.

Chapter Four

Micromammalian Ecology

As with owls, the Hutchinsonian niche concept provides a useful framework within which to discuss micromammalian ecology. This chapter serves to explore both the habitat 'requirement' and niche 'relationship' components of micromammalian ecological niche in a broad sense. Its aim is to highlight the ways in which currently established niche models for many South African micromammal species may be problematic and to discuss the ways in which the discrepancies in these niche models, so frequently drawn upon by paleoecologists, can be improved upon or mediated.

While barn owls feed on a variety of animals, two groups of mammals, shrews and rodents, make up the greatest proportion of their diet worldwide (Brown et al., 1988; Taylor, 1994; Tarboton and Erasumus 1998). The general requirements of these small mammals, particularly their dietary habits, habitat preferences, and morphological adaptations, determine their relative distribution on the landscape and thus their availability for predation (De Graaff 1981; Skinner and Chimimba, 2005).

Distribution of habitat and availability of resources are governed on a broader scale by prevailing abiotic conditions, most notably, geology, elevation, and climate including, rainfall, seasonality and temperature (Ernst, 2000). Thus the

dynamic link between predators and prey is inextricably linked to climate and landscape.

Furthermore, the relationship between micromammals and other community members, including interspecific interactions with other micromammal species, predators, and larger animals sharing an ecosystem can have profound impacts upon micromammal ecology and habitat affiliation (Brown et al., 1988; Derting and Cranford 1989; Kotler 1991; Keesing 2000; Perrin and Kotler 2005; Kinahan and Pillay 2008; Hagenah 2009). The different contexts of foraging, predator avoidance, and intraspecific interaction may necessitate the exploitation of multiple microhabitat types in a single species or function to delimit a species use of habitat types (Sih, 2005; Wolff and Sherman, 2007; Ylonen and Brown, 2007).

Classification and Generalized Anatomy

Rodents represent a major branch of the mammalian tree of life and, unlike other lineages, have experienced few extinctions of major families since their first radiation roughly 55-65 Mya (De Graff, 1981; Skinner and Chimimb 2005; Wolff and Sherman 2007: Honeycutt et al., 2007). Their persistence and diversity, about 2,000 species to date, or 39% of all recognized species of mammals, imply an impressively stable evolutionary strategy, responsive and well adapted to prevailing ecological and environmental conditions (Haffner and Haffener, 1988; Wilson and Reeder, 1993). They are represented on every continent excluding Antarctica and a few oceanic islands (Honeycutt et al., 2007). Convergent evolution also characterizes the order, with fossorial and arid adapted species arising independently on many

continents. Of the 29 extant families of rodents, eight are found on the South African subcontinent (De Graff, 1981; Skinner and Chimimba, 2005; Honeycutt et al., 2007).

Of notable importance to paleoecological studies is the speciose Muridae family, which represents 66% of all rodent taxa and contributes greatly to mammalian diversity on most continents (Honeycutt et al., 2007). This family includes the subfamilies Gerbillinae and Murinae. A ratio derivative of these two subfamilies has been used as an ecological proxy to infer the relative aridity of a local habitat in any given time and/or place (Fernandez-Jalvo et al., 1998).

Despite the enormous species diversity and impressive array of body plans and morphological variation, the members of the order Rodentia are remarkably uniform in certain aspects of their jaw and tooth morphology (De Graff, 1981; Skinner and Chimimba, 2005). Rodents, as their moniker implies (*rodre* or to gnaw), are all in possession of a set of ever-growing incisors, powerful jaw musculature, and lack canines and premolars, which results in a distinctive diastema between the incisors and cheek teeth. Morphology of the cheek teeth is distinctive at the genus and frequently at the species level and is used to identify specimens found in owl pellets.

Shrews, which are classified in the order Eulipotyphla and family Soricidae, are also relatively speciose and widely distributed on the South African subcontinent, with 17 of 266 species represented (Churchfield 1990; Skinner and Chimimba, 2005). The family Soricidae itself dates back to the Oligocene, but shrews possess what is believed to be one of the most primitive of all mammalian body

plans (Findley and Yates, 1991). The high-cusped, thickly enameled teeth of these creatures are well adapted to their insectivorous habits and they are sympatric with other micromammal species in almost all regions (Churchfield 1990; Findley and Yates 1991).

Diet

Rodents fall vaguely into three main dietary categories, herbivory, granivory, omnivory, while shrews are strictly insectivorous. The relative energy required to sustain metabolic functions and engage in necessary reproductive behaviors differs from species to species in micromammals, as does the energy content of various foods (De Graff, 1981; Churchfield 1990; Findley and Yates 1991; Skinner and Chimimba, 2005; Kinahan and Pillay 2008). Micromammals, in accord with optimal foraging strategies, respond to the quality, availability, and distribution of these resources in such a way that they maximize energy returns and minimize energy costs (MacArthur and Pianka 1966; Brown et al., 1994) The degree to which any given species of rodent can be strictly categorized into one of the above dietary guilds is debatable and highly dependent upon both the spatial and temporal availability of a given food type. A species that is described as omnivorous may easily feed strictly on foliage during times of increased primary productivity and adjust its diet during periods of plant food scarcity to include greater proportions of insects, seeds, and so forth. Indeed, many African rodents including a number of those species represented in and around the hominin-bearing cave sites of Sterkfontein and Swartkrans, exhibit remarkable dietary flexibility and habitat

tolerance, enjoying widespread distributions (De Graff, 1981; Avenant 2007; Skinner and Chimimba, 2005).

The four-striped mouse, *Rhabdomys* and the multimammate mouse *Mastomys* are ubiquitous across all of South Africa. Both have been collected both from the very edges of the arid Namib desert, to the highlands of Lesotho, to the frosty grasslands of the eastern Highveld, showing little more than subtle variation in size from region to region (Skinner and Chimimba, 2005). These genera are widespread and catholic in both their habitat and dietary affinities. *Mus* and *Mastomys* are thoroughly ubiquitous and undergo significant population booms and busts frequently, primarily due to their efficient exploitation of available resources. These species appear to consume any available food source, even turning aggressively carnivorous during bouts of population explosion (Coetzee, 1975; Skinner and Chimimba, 2005). Quantifying the diets of these species is entirely dependent upon local resource availability and thus they remain problematic for paleoecology (Avery, 2001; Reed, 2003)

The aforementioned species are, however, all notable generalists, so it is perhaps useful to turn our attention to seemingly more specialized species. Interestingly, even specialists prove difficult to catalog dietarily. The widespread *Otomys*, commonly described as a grazer and selective herbivore (Skinner and Chimimba, 2005), evidences significant dietary flexibility and appears to consume plant matter rather indiscriminately (Davis 1973). Dietary flexibility in *Otomys* even holds over broader temporal scales. Hopley et al. (2006) conducted carbon isotope

analyses on both modern and fossilized *Otomys gracilis* and found that, despite identical dental morphology, presumably adapted for grazing, fossilized specimens from the Holocene ate considerably higher proportions of C_3 relative to extant *Otomys* species. This would imply that *O. gracilis* consumed a more mixed diet than the C_4 dominated diet characteristic of modern *Otomys sp*.

Kinahan and Pillay (2008) found that differential exploitation of folivory promoted co-existence in a community of six sympatric and ecologically similar granivorous African rodents. Differences in gut morphology and food preferences suggested that the six species occupied a dietary spectrum ranging from heavier reliance on foliage to primarily grains and seeds. The authors suggest that species tending towards folivory, which in this study included *Steatomys pratensis* and the virile *Mastomys*, may have a lower ability to compete for granivorous resources but are subsequently better adapted to a wider diet. Kinahan and Pillay go on to point out that Perrin and Curtis (1980) and Kerley (1992) both obtained similar foliage dominated results in their studies of *Steatomys* gut content and yet deferred to earlier dietary classification schemes which categorized *Steatomys* as a granivore.

Certain individuals, often juveniles, are forced by intraspecific interference and displacement, to forage in sub-optimal areas. Derting and Cranford (1989) found that juvenile female mice were the most frequently taken rodent age and sex class by barn owls. Via observation and florescent dye marking, these researchers determined that this bias in the owl diet likely had a great deal more to do with the interference and dominance behavior of adult females and larger male mice than

with owl preference. This suggests that the juvenile females were effectively forced into situations with sub-optimal resource and refuge availability. Fortunately, while it is important to consider all relevant ecological concerns before delving into the paleontological record, such subtle niche structure is unlikely to bias paleoecological reconstructions.

These studies highlight the necessity of ongoing modern ecological work, particularly those research projects utilizing multiple lines of evidence and many regions to refine understanding of dietary ecology. Such approaches ensure that reference texts and literature regarding species frequently used by paleoecologists as modern analogs are accurate. It is possible that catholic dietary tendencies characterize many rodent species commonly perceived as specialists, or semi-specialists, but such hypotheses require further testing and field data across multiple habitats and temporal scales. Research corroborating stomach contents and isotopic data may provide useful means for obtaining accurate dietary spectra for rodent species. Determination of dietary flexibility in rodent species is essential to making valid inferences about the composition of the environments they inhabit and the resources they utilize.

Habitat Selection

While food resources must surely be present and in sufficient quantity to sustain the energetic requirements of a given species, so too must other important habitat elements. Dietary resources are certainly the primary determinants of species habitat selection, but other considerations of rodent ecology must be taken

into account. These considerations include but are not limited to requirements for refuge, appropriate breeding and nesting locations, access to water, and so forth (De Graff, 1981; Churchfield 1990; Skinner and Chimimba, 2005).

For some species, other habitat considerations may tell us as much about local habitat composition and structure as diet itself. Species requirements and/or preferences for specific types of refuge can at times preclude a species from inhabiting a given habitat despite the availability of sufficient food resources (De Graff, 1981; Skinner and Chimimba, 2005).

Numerous studies have assessed the role of vegetation in micromammal habitat preference (Kotler 1991; Barrett and Peles 1999; Lidicker 1999; Ernst et al., 2000; Keesing 2000; Blaum et al., 2006; Krystufek et al., 2007; Hagenah 2009). Regardless of scale, rodents respond to spatial heterogeneity by biasing their activities towards safer areas, which generally correspond strongly with vegetative cover (Ylonen and Brown, 2007). Rodents inhabiting open agricultural fields use fence lines where grasses are longer and vegetation denser, rodents in England and Scotland have been shown to forage primarily in or near hedgerows and near woodland edges, while rodents in experimental studies, will, if given the choice and faced with the threat of predation, always choose enclosure areas with more cover even if food quality is poorer in these areas (Ylonen and Brown 2001; Brown and Kotler 2004). In fact, many studies have demonstrated that giving up densities (GUD's) – a quantified measure of the food an organism leaves untouched under manipulated conditions - are higher in riskier food patches. Kotler et al. (1991)

found that desert rodents express significantly higher GUD's in open areas than in those with even moderate scrub cover. Therefore, despite owl preference for hunting in open areas, habitat heterogeneity is sure to present in any ecosystem in which it hunts.

The nature and structure of vegetation used is also important to various species. Multiple species of *Dendromus*, the climbing mouse, are able to coexist in similar habitats by foraging primarily at different heights in tall grasses. *D. melanotis* utilizes lower portions of grass stalks, while *D. mysticalis* forages higher on the grass stalks for smaller insects and the seeds at the top of the stalks (Skinner and Chimimba, 2005). *Thallomys* (Acacia Rats) are strongly associated with Acacia trees and are dependent upon them for both food and cover (Skinner and Chimimba, 2005).

Krystufek et al. (2007) looked for nested hierarchies of rodent species in thicket-valley vegetation of varying height classes and found no correlation between any of the rodents, but a significant correlation between specific taxa and specific height classes of vegetation. For burrowing rodents, substrate type may be far more significant than vegetation and sandy or alluvial substrates are generally preferred (Skinner and Chimimba,, 2005). The effect of substrate type is evidenced particularly in gerbils and mole rats. Thus, given the appropriate substrate, even members of the notably arid adapted gerbil subfamily are common in less arid regions. *Tatera,* the gerbil genus most frequently encountered in the Sterkfontein Valley, is apparently independent of a specific vegetation association and have been

taken in habitat types ranging from open grassland to savannah woodland (Skinner and Chimimba, 2005).

Pronounced seasonality, rainfall, and moisture levels impact both vegetation and small mammals. For shrews, moisture appears to be the most important determinant of distribution and habitat preference. This is probably because of their dependence upon invertebrate prey, for many of which moisture is key to certain life cycle stages. Vegetation itself is therefore far less important than prey base, but prey is highly dependent upon moisture (Churchfield 1990).

Community Interaction

The foregoing discussions of dietary ecology and habitat affinity have focused upon species requirements, but if niche theory teaches us anything, it is that species and populations are defined not only by the food they eat and the habitats in which they reside, but also upon the relationships they have with other species in an ecological community (Elton 1927; Hutchinson 1957). Species characteristics and population dynamics are governed as much by sympatric context as by environmental constraint. The ways in which interspecific interactions play out within a given ecological community can strongly influence resource and habitat utilization for many small mammal species (Kinahan and Pillay 2008; Wolff and Sherman 2007). These interspecific interactions take place between other small animal species with which rodents and shrews directly compete for resources, they occur between small mammal species and large animals, (particularly large mammalian herbivores which alter and shape micromammal microhabitat), and

they encompass interactions with numerous species of predators (Keesing 2000; Ylonen and Brown 2007; Kinahan and Pillay 2008; Hagenah 2009). These variables must be considered in paleoecology too.

Intraspecific interactions within a population, territoriality, mating, competitive interference and brood rearing behaviors, all influence small mammal habitat associations and alter individual susceptibility to predation by owls (Taylor, 1994; Ylonene and Brown 2007). Social interactions, so nicely illustrated by the bias towards juvenile female rodents in owl predation revealed by Derting and Cranford (1989), can strongly influence predation rates. For instance, species that engage in noisy territorial altercations, mating rituals, or opt for the production of many precocial yet expendable young, are generally easier targets for owls (Ylonen and Brown 2007).

Rodents and shrews interact most directly with one another, often utilizing the same microhabitats and overlapping resource bases. Shrews seem remarkably well adapted to sympatry both with rodents and other shrew species (Churchfield 1990, 1991). In the tropical regions of Zaire, up to 25 species of shrews have been reported coexisting in a single region. Churchfield (1990) states that shrews comprise only 8% of fauna in South Africa and that owls are their main predators. In the widely distributed genus *Crocidura*, up to three and four species occur sypmatrically in some habitats. The grassy pathways constructed by *Otomys* as it grazes grassy stalks and reeds are frequently used by these shrew species as well as other rodent species, notably *Rhabdomys pumilio* (Skinner and Chimimba, 2005).

As is evident throughout this chapter, small mammals respond to both spatial and temporal heterogeneity in habitat. Large mammals, particularly medium to large sized herbivores both contribute to spatial heterogeneity by changing vegetative structure and impacting resource availability. Controlled studies by Keesing (2000) in East African and Hagenah et al. (2009) in South African savannas, do not agree on whether vegetative structure or resource availability have a greater impact on small mammal community structure. Keesing (2000) determined direct competition for resources between large and small herbivores to be the primary determinant of micromammal diversity and relative abundance in controlled experimentation with ungulate exclusion. It was determined that survival rates of small mice in ungulate-free enclosures did not differ significantly from those with ungulates, and yet rodent community composition changed rapidly and dramatically.

Conversely, Hagenah et al. (2009) found that while the exclusion of medium-sized herbivores (warthogs, impalas, and nyalas) increased the abundance of high-quality grass resources, this had little effect on small mammal community composition, whereas the exclusion of large herbivores and bulk feeders (i.e. zebra, buffalo, and rhino) led to an increase in overall vegetation height, promoting greater rodent abundance and species diversity, while altering rodent species composition. This observation led the researchers to conclude that reduction of vegetation cover and increased predation risk had the greatest effect on murid rodents. This contrasts strongly with Keesling's (2000) conclusions that resource competition was of greatest import. Shrews, on the other hand, do not do well at all in areas frequented by large herbivores (Churchfield 1990). It is probable that both factors,

alteration of cover and resource competition, influence micromammal community composition. However, the relevant lesson for paleoecological interpretation is that taxonomic habitat analyses, while at times necessarily narrow in scope, must not be so myopic as to exclude consideration of other species coexisting within a given ecological community.

Located at the nexus of many food webs, rodents are preyed upon by a great variety of predators. Shrews, with their pungent odor and foul flavor are not as heavily preyed upon. Owls are their primary predation threat but nonetheless, shrews only consistently make up 5-13% of owl diets. (An interesting contrast to their dominance in owl diets in the Cradle of Humankind). Predators range from small carnivores, to diurnal raptors, to snakes and reptiles, to nocturnal owls (De Graff, 1981; Skinners and Chimimba 2005; Ylonen and Brown 2007). Predation risk varies spatially and temporally and small mammals must mitigate this risk while carrying out necessary foraging and reproductive activities (Ylonen and Brown 2007). As discussed earlier, small mammals minimize predation risk and optimize foraging activity by adhering to specific microhabitats and avoiding others (De Graff, 1981; Skinner and Chimimba, 2005; Ylonden and Brown 2007). The necessity of sufficient refuge has already been addressed, but additional circadian behaviors are employed by small mammals to further mitigate predation risk. Rodents can be nocturnal, diurnal, crepuscular and poplyphasic, as well as responsive to seasonal change, moonphase, and substrate type (Ylonden and Brown 2007). Nocturnal rodents often prefer denser vegetation and forage in solitude and silence under the cover of darkness. Diurnal rodents, however, are frequently found in open habitats

where they are better able to spot threatening prey. They are also usually colonial, with advanced alarm calls and communicative systems (Ylonden and Brown 2007). All but two of the rodent species found in South Africa are nocturnal, with the notable exceptions being *Rhabdomys* and *Otomys* (De Graff, 1981; Skinner and Chimimba, 2005).

The foregoing discussion gives one a sense of the larger ecological paradigms governing micromammals and considerations for constructing appropriate niche models. However, these niche models require detailed knowledge of the habitats and species local to the regions in which paleoecological research is to be conducted thereby providing local calibration for reconstructions. The following chapter will address the climate, vegetation and micromammal species characterizing the Cradle of Humankind pertinent to discussions found in Chapter Six and Seven.

Chapter Five

Climate, Vegetation, and Micromammal Diversity in the Cradle of Humankind, WHS

Having established some general tenants of owl and micromammalian ecology, and before launching into paleoecological interpretation, it is necessary to gain familiarity with the nature of the extant flora and microfauna characterizing the Cradle of Humankind region of South Africa. Naturally, the climate has changed a great deal over the approximately five million years that have elapsed since the beginning of the Pliocene. However, many micromammalian species have persisted for that time, albeit in differing relative abundances, making them *excellent* subjects for paleoecological research. In fact, only a single confirmed extinct rodent species, *Proodontomys cookei,* is represented at fossil assemblages in the Sterkfontein Valley.

South Africa exhibits an extremely varied climate, but broader intercontinental interpretations generally characterize the subcontinent as 'semi-arid'. Less than 5% of the region currently receives an annual rainfall in excess of 800mm annually (Schultze, 1997). Furthermore there is a high degree of variability in inter-annual primary production – a measure of biomass directly related to rainfall – generally greater than 50%. The South African subcontinent becomes increasingly more arid, with less predictable seasonality as one moves east to west. Mean annual temperature (MAT) in the Highveld region in which the Cradle of Humankind is located is about 14-16 degrees Celsius. The Highveld is located at an altitude that ranges from 1450-1750m and is characterized by the occurrence of

frost, the onset of which occurs most often between mid-April to late May. Finally, mean annual precipitation (MAP) for the region falls between 650-750 mm per annum, with predictable seasonal rainfall patterns. This rainfall is largely concentrated during the early summer months (Schultze 1997).

The combined interactions of these climatic variables, in conjunction with the natural template of the landscape, produce relatively homogeneous environments characterized by specific plant types organized into biomes. South Africa is divided into seven distinct biomes, desert, succulent karoo, Nama-karoo, savanna, forest, grassland, and fynbos, which themselves are further subdivided. The Cradle of Humankind falls within the grassland biome, specifically the northern grasslands referred to by Acocks (1975) as the "Bankenveld" or 'false grassland' (O'Connor and Brendenkamp 1997).

Grasslands represent the third largest biome in South Africa (13.1%) and are differentiated from savannas by water-balance, vegetative composition, and temperature variables. Savannahs experience higher temperatures in the non-growing season than do grasslands. They are characterized by the co-dominance of woody plants and grasses, and in reality their vegetative proportions occupy a spectrum with anywhere from 5-90% vegetative cover. In South Africa savanna is the dominant biome type (53.7%) and is further subdivided into a nutrient poor and moist 'Broad-Leaved' savanna as well as a nutrient rich but arid 'Fine-Leaved' savanna (Scholes 1997). The Sterkfontein Valley lies very near the Grassland-Savanna border as well as near the confluence of moist and arid savanna types.

Their close proximity means that the interaction between these biomes and sub-biomes is important. It is believed that this region has been quite dynamic in the past, changing as the Grassland and Savanna biomes contracted and expanded in response to global and regional climatic change, particularly during the Plio-Pleistocene (Avery, 2001). Thus the Cradle of Humankind is an excellent research site for those interested in the interactions of savannas and grasslands and their influence on native flora and fauna.

The Bankenveld grassland in which the Sterkfontein Valley is located, is transitional between the grasslands of the high inland plateau and the savanna of the low inland plateau. The area is underlain largely by dolomite (particularly in the Western Transvaal) and is frequently called the 'Klipveld' because of its abundant surface rock. The variation in topography, soil depth, and rainfall gradients have resulted in vegetative mosaics with many co-dominant species and high diversity (O'Connor and Brendenkamp, 1997). Micromammalian community diversity is strongly influenced by this habitat heterogeneity and plant species diversity, so the Bankenveld grasslands possess a wealth of microhabitat types and much micromammal diversity (Andrews and O'Brien 2000).

Only those species found within the Cradle of Humankind and surrounding Highveld regions will be included in the following species list. As stated earlier, most of the species identified in the important fossil-bearing localities in and near the Cradle of Humankind are still extant today. Their ecological habits and strong association with particular microhabitats form the basis of paleoecological

interpretations for the key Plio-Pleistocene sites located in the area. Species descriptions are taken from De Graaff (1981) and Skinner and Chimimba, (2005) unless otherwise noted. Some of the subfamilies important to these interpretations have been emphasized in bold.

Cryptomys hottentotus – African Mole-Rat

This species is the only representative of the Hystricognathi suborder found in the Highveld region, and is one of three genera of mole-rats. Neither a mole, nor a rat, these creatures are fossorial, using their large, thickened incisors for excavation. They have reduced eyes and pinnae, a highly developed sensory perception for life below the surface, are thermolabile, and are excellent metabolizers of vitamin D and other minerals. Sandy soils and river alluviums are frequently home to *Cryptomys*, though they do not reside in clays. They are strictly herbivorous, a characteristic shared only with *Otomys* (the Vlei Rat), eating the succulent underground parts of plants, fleshy roots, bulbs, and tubers that are often toxic to other animals. Interestingly, they are not uncommon in the pellets of barn owls so it is suspected that they venture aboveground during the night either for forage or to collect den-lining materials.

Graphiurus murinus – Woodland Mouse

This species has a bushy tail and is commonly mistaken for a small squirrel. It is infrequently taken by barn owls despite its wide distribution perhaps because of its arboreal tendencies. This Dormouse prefers woodland or rocky areas with

woody vegetation. It is solitary and nocturnal, foraging mainly for insects, seeds, and termites.

Acomys spinosissimus – Spiny Mouse

This mouse is uncommon the Highveld given its narrow thermoneutral zone and poor ability to tolerate temperature extremes, but it has been noted from areas near Makapansgat (Pocock 1985, 1987). It is nocturnal and terrestrial, prefers rocky outcroppings but can live in dry woods and thickets, and eats mostly grass seeds.

Subfamily: Murinae

An important subfamily from a paleoecological perspective; the murines are a diverse group with a total of 281 genera and about 1,300 species to date. At least 14 representatives of this subfamily are present in and around the Cradle of Humankind and are useful for their specific association with habitats (some being more specialized than others).

Lemnisomys rosalia – Single-Striped Mouse

This species, while also unlikely to be found in the Highveld, inhabits a wide variety of vegetation, apparently preferring long grassland or ecotonal areas like vleis and woodlands. It consumes at least 50% foliage including grass, herbs, and weeds.

Rhabdomys pumilio – Four-Striped Mouse

An ubiquitous generalist, *Rhabdomys* exhibits noticeable variation in size from region to region, tending to be smaller in arid western regions. It is notably one of only two *diurnal*/crepuscular species (the other being *Otomys* –the Vlei Rat), with activity peaks in the morning and afternoon. It cannot thermoregulate at temperatures below 5 degrees Celsius, which may be a primary explanation for its diurnal habits. It is a quintessential grassland species, occurring in a wide variety of habitats with grass cover. An opportunistic omnivore, it eats seeds, fruits, herbs, grasses, and insects, with a diet that varies by season and geographic location.

Dasymys incomptus – African Marsh Rat

This species tends to have a more northerly distribution, but it is sympatric with *Otomys* (Vlei Rat) and shares its preference for wet habitats, reed beds, and vleis.

Mus – Neave's Pygmy Mouse, Desert Pygmy Mouse, Pygmy Mouse

M. neavi has not been widely observed in the area, but Pocock (1974) did note its occurrence in owl pellets collected at Makapansgat. It is found in rocky montane grassland with bracken fern and also in *Protea* (a flowering plant often referred to as sugarbush) woodland.

Current distribution maps suggest that *M. indutus* would be common in the Highveld region. The species had a very wide habitat tolerance, is terrestrial and nocturnal and often lives in areas with dead wood. Considerable oscillations in its

population density have been documented and it is a primary prey item for Suricates (*Suricata suricata*). Grass seeds, and *Acacia* seeds are its primary food at low densities, but it becomes highly carnivorous at high densities.

Tolerant of a wide variety of habitats, the pygmy mouse (*M. minutoides*) lives in rocky areas, vleis, riverine associations, grasslands, and seems particularly prominent as a successional species in burnt grasslands, where its small size makes it somewhat less conspicuous than larger species. It is nocturnal, terrestrial, and feeds on grass seeds, herbage, and insects.

Mastomys– Natal Multimammate Mouse, Southern Multimammate Mouse

It is now recognized that *M. coucha* is likely the predominant species of multimammate mouse in the Highveld and it is associated with higher altitudes - up to 2400m (Avenant, 1996) – and drier habitats (it is rarely found in areas with >700mm rainfall). (*M. natalensis* appears to be associated with slightly wetter habitats with >500mm annual rainfall). As their name implies, all members of the genus are prolific breeders, quick to colonize disturbed areas and slowly replaced by more specialized species. They are nocturnal, terrestrial, and have home ranges of approximately 600-700m^2. They are omnivorous and cannibalistic during population explosions. They are well suited to exploiting any favorable habitat, particularly during periods of high productivity.

Thallomys – Acacia Rat and Black-Tailed Tree Rat

As their name implies, these rats are arboreal and strongly associated with *Acacia* trees, feeding mostly on the tree's leaflets and seeds.

Aethomys ineptus – Tete Veld Rat

This rat is yet another generalist, quite catholic in its habitat requirements. It is partial to grasslands with some scrub, savannah woodland, rocky areas with debris or scrub, and is often found at higher altitudes. It eats insects, vegetation and seeds.

Michaelamys namaquensis – Namaqua Rock Rat

Though also catholic in its habitat requirements, and well adapted to arid habitats, this rat is common in rocky hillsides with low total foliage cover. It is nocturnal, communal and terrestrial, with omnivorous feeding habits.

Otomys – Angoni Vlei Rat, Vlei Rat

Vlei rats are stocky and hairy with grooved incisors and laminate teeth. They are one of two strictly herbivorous South African rodents. They have digestive adaptations which include long fermenting large intestines that are well-suited to their herbivorous dietary habits. An ancestral species, *Otomys gracilis,* has been recorded in the fossil record from the Late Pliocene (3-2 Mya).

Terrestrial and predominantly diurnal, *O. angoniensis* also shows some propensity for crepuscular and even nocturnal activity. They reside in the mesic

parts of grasslands and woodlands and are associated very closely with reed beds and semi-acquatic grasses along vleis and riverbeds. Their well-defined runs are used by a number of coexisting rodents such as *R. pumilio*. They feed on succulent stems and rhizomes of grasses and fine reeds.

Widely distributed, *O. irroratus* may be more tolerant of non-vlei habitats than *O. angoniensis*. In addition to the habitat types listed above, it has been identified in montane areas and on grassy hillsides. It is crepuscular, terrestrial, and semi-aquatic. They eat nearly all plant species that occur in their habitat, though grass is preferentially eaten. This species is often taken by both *Tyto alba* and by *Tyto capensis*, which shares the rodent's habitat preferences.

Subfamily: Gerbillinae

The gerbils are notable in their association with more arid habitat types. They share a characteristic morphology, with tawny coloration, well-developed hind legs, big eyes, and a tendency to saltatory movement.

Tatera– Bushveld Gerbil, Highveld Gerbil

Nocturnal, terrestrial, omnivorous and quite common, the Bushveld Gerbil (*T. leucogaster*) prefers sandy soils and alluvium for its burrows. It is apparently independent of a particular vegetation type as long as burrowing substrate is suitable and can occur in areas with as little as 250mm of rainfall. Believed to tolerate drier conditions than the Bushveld Gerbil, even the Highveld Gerbil (*T. brantsii)* is often found in areas with less than 200mm rainfall. Both are omnivorous.

Subfamily: Mystomyinae

Mystromys albicaudatus – White-Tailed Mouse

This genus contains only one species currently, though *Proodontomys cookei* is considered to have been very closely related to *Mystromys* and is certainly a member of Mystromyinae. *Mystromys* dominate fossil assemblages at both Sterkfontein and Swartkrans, but is now listed as endangered. Current distributional patterns follow the grassland biome very closely, particularly in the eastern regions of South Africa. It appears to favor rocky areas with good grass cover, especially those composed of dolerite and basalt. It is associated with grasses such as *Aristida* and the shrub *Diospyros afromontana*. It is nocturnal, terrestrial, and is cold adapted. It is an omnivore with a specialized stomach designed to improve its generally poor ability to digest fiber. It consumes insects, seeds, and green plants.

Saccostomys campestris – Pouched Mouse

A catholic species, the pouched mouse prefers sandy substrates with brush or cover of woodland. It is nocturnal, terrestrial, solitary . It is an opportunistic omnivore and hoarder, with a strong affinity for seeds.

Subfamily: Dendromurinae

Malacothrix typical – Gerbil Mouse

So named because of its outwardly similar appearance to gerbils, this mouse is nocturnal and terrestrial, uses short-grass habitats, is often found in areas with 100-150mm of rainfall, and consumes mainly vegetative matter.

Dendromus– Grey Climbing Mouse

Despite the implication of their name, the 'tree mice' spend the majority of their time no more than two meters above the ground in grass and brush. Their tails are used for grasping and they are almost exclusively insectivorous. *D. mesomelas* is fonder of taller grasses and woodier plants, while *D. mysticalis* is also characterized as granivorous, eating the tops of grass stems in addition to insects.

Steatomys– Fat Mouse, Kreb's Fat Mouse

All fat mice utilize torpor during colder seasons, relying upon their thick layer of fatty insulation. The Fat Mouse (*S. pratensis)* inhabits loose, sandy substrates and the fringes of rivers and swamps in arid areas, while Kreb's Fat Mouse *(S. krebsii*) utilizes dry sandy grasslands to a greater degree. Both species are nocturnal, terrestrial, omnivorous gramnivores.

Shrews

Myosorex varius – Forest Shrew

The name 'forest shrew' is somewhat of a misnomer, as this species is frequently found in grassland or savannah given sufficient wet habitat, particularly under dense grass along the banks of streams. It is primarily nocturnal in warmer seasons, but switches to diurnal activity during colder periods, and is an opportunistic insectivore.

Crocidurinae

Suncus– Greater Dwarf Shrew, Lesser Dwarf Shrew, Least Dwarf Shrew

All of these shrews are insectivorous and all are associated with a wide variety of habitats including moist riverine, savannah woodland, open grassland, and mixed bushveld. *S. varilla* is often associated with termite mounds, which it uses for cover.

Crocidura– Swamp Musk Shrew, Reddish-Grey Musk Shrew, Lesser Red Musk Shrew

Crocidura are very adaptable to a wide variety of habitats and often, three or four species will be found living sympatrically. *C. mariquensis* is found only in very damp habitats, whereas *C. cyanea* appears to have quite a wide tolerance, occurring in moist, dense grassy habitats, bordering reed beds, and in drier bushveld habitats. *C. hirta* is fonder of wetter, marshy areas, though all of these species are commonly associated with riverine and vlei-like areas.

Macroselidae – Elephant Shrews

Elephantulus myurus – Eastern Rock Elephant-Shrew

Currently *E. myurus* is the only elephant-shrew expected to occur in the region, though Makapansgat and Sterkfontein have yielded extinct members of both the *Macroscelides* and *Elephantulus* genera. *E. myurus* is strictly associated with rocky koppies where it can take cover from predators. It is predominantly diurnal, but activity peaks at dawn, and they are also active at night. This species is extremely agile and quite fast, communicates with foot thumps, and enters torpor in cold temperatures. Diets generally consist of 90% invertebrate prey.

Chapter Six

Micromammal Paleoecology in Plio-Pleistocene Africa

Until Cartmill (1967) pioneered techniques for micromammalian paleoecological interpretation in the 1960's, data gathered regarding micromammalian fauna largely consisted of species lists, vague descriptions of potentially new species, and relatively small datasets. Few interpretive or quantitative analyses were conducted (De Graff, 1961; Pocock 1985, 1987; Denys 1990; Avery, 1998).

Furthermore, inadequate description, poor communication between researchers studying different fossil-bearing sites at different times, and poor systematic resolution for many micromammalian taxa, have resulted in much taxonomic confusion with regards to Plio-Pleistocene microfauna. Avery (1998) points out that this confusion is probably related to the historical assumption made by early collectors that Plio-Pliestocene micromammals differed from modern species. Ongoing taxonomic revision reveals that, in fact, most species are indistinguishable morphologically from related extant species and may safely be assumed to be similar in their habits to their modern counterparts. This is not, of course, sufficient evidence to warrant assumptions of taxonomic uniformitarianism between any fossilized specimen and currently existing species. However, it does serve to significantly reduce the conflation of ecological and niche variables concomitant with using modern analogs to describe the tendencies of completely unrelated extinct species.

Cartmill (1967) recognized the potential utility of micromammals and began to implement taxonomic habitat analysis techniques using fauna from Pleistocene sites throughout sub-Saharan Africa (Cartmill, 1967; Avery, 1998). Little ecological work had been done until the 1990s, though the last decade has seen more coordinated and sophisticated efforts in this vein of research (Avery, 1998, 2001, 2010; Denys, 1985; Matthews, 2005; Reed, 2003, 2005, 2007, 2011; Reed and Denys, 2011; Winkler et al., 2009). Of particular import are those studies that explicitly correlate modern ecological data with paleoassemblages (see Avery, 2001; Reed, 2003, 2005, 2007). These efforts attempt to incorporate the numerous ecological variables associated with both predator selectivity and the differential vulnerability of prey species (as discussed in greater detail in the preceding chapters) to calibrate local paleoecological interpretations. This type of research is pragmatic, drawing its theoretical underpinning from modern ecological research and extrapolating that methodology to paleoecology.

Micromammalian paleoecological analyses have been conducted at numerous East and South African sites (Cartmill, 1967; Wesselman, 1984; Pocock, 1985, 1987; Denys, 1985, 1990, 1999; Avery, 1998, 2001, 2010; Fernandez-Jalvo, 1998; Reed, 2003, 2007; Matthews, 2005). These researchers have utilized variations of the reconstructive techniques and niche representation models delineated at the end of Chapter Two. Briefly, these techniques include comparison of taxonomic ratios, the construction of taxonomic habitat indices (THI), and species diversity measures.

The following will focus primarily on current paleoecological interpretations in South African localities with particular attention paid to the Plio-Pleistocene sites including Makapansgat, Sterkfontein, Taung, Swartkrans, Gladysvale, and Kroomdraai. Numerous other South African sites in the Western Cape region have received considerable analyses thanks to the work of Avery (1982, 1987), Matthews (2005), and Matthews et al. (2007) but these sites are either relatively older or younger than the australopithecine and early *Homo* producing sites that are the object of inquiry here. Moreover, these sites are located in quite different vegetational and climatological biomes both presently and historically and as such possess different small mammal community patterns.

Before delving into the details of South African micromammal paleoecology, it is necessary to provide the reader with a quick summary of similar reconstructions conducted in East Africa. Much foundational work in micromammal paleoecology was developed at Omo and Olduvai Bed-I and subsequent researchers have followed in the methodological footsteps of these first efforts (Cartmill, 1967; Denys, 1985; Fernandez-Jalvo, 1998; Reed, 2003, 2007). Generalized similarity in ecological patterns observed in both Eastern and Southern African fossil localities corroborate hypotheses suggesting a global cooling and drying with increased seasonality, while differences between the two regions are suggestive of the more regional and local effects of such large-scale climatic change (Peters and Maguire, 1981; Vrba, 1985, 1995; Cerling, 1992, 1999; Shackelton, 1995; deMenocal 1995, 2004; Trauth et al., 2005; Kingston, 2007; Maslin and Christensen, 2007).

East Africa

  East Africa has featured prominently in the narrative of hominin evolution. Dotted with sites aligned in a roughly north-south orientation along the East African Rift Valley, this region of Africa has proved an excellent repository of fossilized material. Many of these sites have produced a large quantity of micromammals, though deposition in most cases and at most localities is more ambiguous than some of the South African sites. Taphonomic analyses suggests that, while the barn owl *Tyto alba* was a significant contributor to microfaunal assemblages throughout the region, the process of alluvial deposition characterizing many East African sites probably incorporates coprocoenoses of multiple avian and small mammal predators (Korth, 1979; Wesselman, 1984, 1995; Fernandez-Jalvo et al., 1997; Reed, 2003, 2005). Furthermore, the movement of water and deposition of alluvial sediments means that microfaunal assemblages accumulated in this way demonstrate relatively less fidelity to specific microhabitats representing instead a mosaic of relatively local habitats than those assemblages found in South Africa caves (Andrews, 1990).

  Microfaunal assemblages from the Pliocene (~ 5-2.6 Ma) are well represented by the East African localities of Hadar, Laetoli and Omo Members B and C, the Pleistocene (~2.5-1 Ma) sites of Olduvai Beds I and II, the Koobi Fora formation, and Omo F and G, finally Late Pleistocene to Holocene (~1-0 Ma) are represented by Olduvai Bed IV and the Laetoli Ngaloba beds (Denys, 1999). While other localities with micromammalian fauna exist, I will focus here on Hadar, Laetoli,

Omo, and Olduvai because these sites have yielded large assemblages of rodent faunal material, can be ordered and assessed chronologically, and are each associated with important hominin specimens.

Denys (1985) employed correspondence analysis, cluster analysis and utilized a similarity index to compare the microfauna communities represented at Laetoli to those from Hadar, Omo, and Olduvai. Significantly, the micromammalian faunal assemblages characterizing each East African site, even those believed to be contemporaneous, are more distinct in taxonomic composition (and by inference habitat composition) from one another, than are most modern localities. For example, paleoenvironmental reconstructions at Hadar and Shungura Omo Formation Members B and C, both dated to ~ 3.4 Mya and younger, suggest similar habitat composition and yet are dramatically distinct in their respective faunal compositions (Denys, 1999; Klein, 1999). This suggests a high degree of endemism at each locality, hence the notable distinctness in rodent community structure at Hadar, Omo, Laeotoli, and Olduvai. Denys (1985) postulates that these areas served to isolate populations but that the presence of rivers and paleo-lakes throughout the rift system offered rich intermediate/transitional ecotonal environments, facilitating diversification of rodent species into specific ecological niches.

Hadar

Hadar, located on the southern edge of the Afar Triangle in Ethiopia represents the northernmost East African site to be discussed here. The site itself is a sedimentary formation, dated to 3.4 Mya and younger and has famously yielded

the *Australopithicus afarensis* specimens "Lucy" and the "Dikika baby" (Klein, 1999;

Tattersal, 2009). The majority of paleoenvironmental reconstructions emerging

from analysis of Hadar materials implicate a more humid and closed environment

than is observed at other, younger East African localities. The micromammalian data

support this interpretation, with the presence of *Tachyoryctes* (Mole Rat) and

Praomys (Swamp Rat or Soft-Furred Mouse) suggesting a wooded/mesic landscape

(Denys, 1999).

Laetoli

Laetoli has yielded assemblages dating back to the Pliocene (~3.4 Mya) as

well as the Middle and Late Pleistocene to Holocene (1-0 Mya), these are the Laetoli

and Upper Ndolanya beds and the Laetoli Ngaloba beds respectively (Denys, 1985,

1990, 1999). Laetoli is perhaps best known for its remarkably well preserved

hominin footprints as well as 13 hominin fossil specimens attributed to

Australopithicus afarensis (Klein, 1999). Additionally, the site boasts a wealth of

vertebrate mammalian remains including approximately 500 rodent specimens. The

taphonomy of the site has been attributed to three processes, coprocoenosis,

dispersal by rains, and the preservation of larger species trapped within their

burrows (Denys, 1985).

These specimens dating to the Early and Middle Pliocene derive from two

distinct levels, the Laetoli beds ca. 3.4– 2.6 Mya and the Upper Ndolanya Beds ca. 3-

2.5 Mya, contributing 22 fossil bearing localities in total (Denys, 1985).

Micromammalian evidence suggests subtle differences between the two periods,

with the older Laetoli beds reflecting relatively drier conditions than the later occurring Upper Ndolanya Beds, the microfaunal communities of which suggest association with more covered, humid grassland or riverine environments. The later occurring Laetoli Ngaloba beds, however, corroborate the aridification trends observed elsewhere, but analyses of micromammalian remains have not been conducted (Denys, 1985; Reed and Denys, 2011).

Omo

This area, in South-West Ethiopia, is stratigraphically divided and represents two significant temporal periods ranging from the Late Pliocene to the Early Pleistocene and have produced specimens attributed to *Australopithecus afarensis*, *Paranthropus aethiopicus*, and arguably various permutations of early *Homo* (Klein, 1999). Omo evidences a shift in small mammal community composition from those adapted to climatic stability and more tropical vegetation types to those better able to cope with decreased climatic stability, landscape heterogeneity, and more arid conditions (Wesselman, 1984).

Members b through E reflect a period of roughly 3.4 to 2.4 Mya and are associated with *A. afarensis* and *P. aethiopithecus* (Klein, 1999)*.* Generally, paleoecological interpretation of micromammalian remains is indicative of a wooded environment 3 Mya, even reflecting micromammalian species communities adapted to tropical forest settings (Wessleman, 1984, 1995). Members C through E evidence a decline in the relative proportion of tropical adapted species and the notable emergence of more xeric adapted ones.

Omo Members F and G, dated at the earliest to 2.34 Mya and associated most notably with early Homo specimens reflect a drastic shift to arid conditions with preponderance of gerbils (esp. the very arid adapted *Jerboa*) and, by Member G, the complete disappearance of any forest-adapted species (Wesselman, 1984, 1995). This evidence is cooroborated by similar micromammalian indications of aridity in the 1.6 Mya old Koobi Fora Formation (Wesselman, 1995).

Olduvai

Olduvai Gorge, situated on the edge of the Serengeti, has yielded the greatest wealth of fossilized micromammalian faunal remains in East Africa (Fernandez-Jalvo, 1998; Reed, 2003, 2007). As at Laetoli, different temporal levels are present at Olduvai, but the focus will remain on sediments dated to the Plio/Pleistocene boundary. The Late Pliocene to Early Pleistocene (~2.5-1 Ma) is represented by Olduvai Beds I and II, while Middle and Late Pleistocene to Holocene (~1-0 Ma) is represented by Olduvai Bed IV (Denys, 1999).

Olduvai Bed I (specifically the FLK Bed I sequences ca. 1.7 Mya) lies at the confluence of the Main and Side gorge and is particularly important for micromammals (Klein, 1999; Reed, 2003, 2007). Several rodent taxa present in the FLK Bed sequences overlap with species extant in the area today (Reed, 2003, 2007). The presence of contemporaneous species in the fossil assemblage at Olduvai corroborates well with Reed's (2003, 2005) interpretation of a "relatively stable metacommunity structure for East African Rodents through the Pleistocene".

Analysis of the Olduvai microfauna have been broken down into two

significant intervals, Middle Bed I and Upper Bed I (Fernandez-Jalvo, 1998; Reed,

2003, 2007). Analyses of microfauna imply a shift from a more mesic environment

in Middle Bed I, to a more xeric environment in Upper Bed I. More specifically,

Middle Bed I has been characterized as more mesic than the later beds due to

presence of *Aethomys* (Bush/Rock Rat) and *Thallomys* (Acacia Rat), both of which

prefer shrubby woodland, lake margins, and woodlands with a grassland understory.

Upper Bed I, meanwhile, has been reconstructed as a more xeric/dry environ due to

the presence of *Gerbillus* (Gerbils) and *Steatomys* (Fat Mouse) (Reed, 2007).

Interesting, and in contrast to what is seen evidenced in any modern small

mammal assemblages, is the presence *Otomys*. The genus *Otomys* has been

traditionally characterized as a grazer. Hence its presence in the Upper Bed I

assemblage would seem to be indicative of stable moist grassland or marsh. Oddly

there are no other faunal indicators for this habitat type specifically, which leave

two possible explanations for the presence of this taxa within Upper Bed I. Either

the more xeric environment implicated by the presence of other taxa like *Gerbillus*

and *Steatomys* also included a moist grassland component (perhaps in limited areas

bounding the paleo-lake), or *Otomys* is more catholic in its dietary tolerance and

hence capable of subsisting in a broader range of habitats, a distinct possibility given

preceding discussions of the autoecology of this genus (Reed, 2007).

In correlating recent analyses of the Olduvai micromammalian assemblages

with other paleoecological data, some discrepancies arise. For instance, the AAC

(Alcelaphine:Antelopine bovid index) (Vrba, 1980, 1985) ratio indicates a more intermediate, grassland environment in the Middle Bed I sequence contrasting starkly with the mesic reconstruction indicated by the micromammals. It is plausible, however, that this discrepancy has more to do with a scaling issue than anything significant climatically – large mammals are capable of wider dispersion than smaller mammals, which are also inherently more sensitive to local conditions (Reed, 2007). There is modern precedent for African lakes that include both a dry and moist grassland component. It is possible that this type of environment characterized paleo-lake Olduvai during the Pleistocene (Fernandez-Jalvo, 1998; Reed, 2003, 2007).

The apparent decrease in micromammalian taxonomic diversity throughout all sites in East Africa correlates well with a pattern of general climatic drying, changes in the dynamics and structure of the East African Rift system itself (opening), and the spread of a more uniform savannah-like environment throughout this region of Africa (Peters and Maguire, 1981; Vrba, 1985, 1995; Cerling, 1992, 1999; Shackelton, 1995; deMenocal 1995, 2004; Trauth et al., 2005; Kingston, 2007; Maslin and Christensen, 2007). However, it is important to note that despite these broader patterns (which are indeed corroborated to great extent by micromammals), micromammalian assemblages at each site differ significantly, thereby reflecting paleoenvironment on a much finer scale than indicated by larger fauna and other measures.

South Africa

The karst geology predominating at most South African faunal and hominin

bearing localities produces excellent fossil assemblages characterized by a

remarkable degree of preservation (Klein, 1999; Tattersal, 2009). Additionally,

hominin-bearing sites are often found in caves, a setting particularly conducive to

owl-accumulated coprocoenoses, especially those of *Tyto alba* with its marked

affinity for utilizing caves as roost sites (Taylor,, 1994; Reed, 2003, 2005). The South

African landscape was an important theater for hominin evolution. *Australopithecus*

africanus, *Paranthropus robustus*, and *Homo* have been described from the north-

central and north-eastern areas (Klein, 1999; Tattersal, 2009). With the exception of

Taung and Makapansgat, nearly all hominin remains have been recovered in and

around the Sterkfontein Valley in the Cradle of Humankind, World Heritage Site (see

Figure 6.1). It is notable that recently yet another species, *Australopithecus sediba,*

was discovered here and thus joins the pantheon of hominin species known to have

inhabited to the region (Berger et al., 2010).

Today the region is located quite near the confluence of several vegetation

biomes and it has been postulated that the composition of the dominant vegetation

types in the Sterkfontein Valley have fluctuated significantly as these biomes have

expanded and contracted in response to geological uplift, climatic shifts, and other

abiotic processes (du Toit, 1933; deMenocal, 1995; Partridge et al., 1995; Avery,

2001). It is apparent from multiple datasets including pollen records, lacaustrine

and marine sediments, macrofaunal assemblages, isotopic analyses and indeed

possibly even the hominin fossil record itself that a significant climatic period occurred during the Plio-Pleistocene (Peters and Maguire, 1981; Vrba, 1985, 1995; Cerling, 1992, 1999; Shackelton, 1995; deMenocal 1995, 2004; Trauth et al., 2005; Kingston, 2007; Maslin and Christensen, 2007). The following micromammalian paleoecological analyses reflect these Plio-Pleistocene changes to differing degrees. Hominin fossil-bearing localities from this time period include Makapansgat, Sterkfontein, Taung, Swartkrans, Gladsyvale, and Kroomdrai. Temporally the sites range from the oldest estimates of over 3 Mya at Sterkfontein and Makapansgat (though Sterkfontein is likely no older than 3 Mya - see Berger et al., 2002; Conroy, 2005) to approximately 1.0 Mya at Swartkrans (Klein, 1999).

Swartkrans and Sterkfontein remain the only sites for which full micromammalian paleoecological reconstructions utilizing relative species abundances, taxonomic habitat analyses, and species diversity indices have been attempted (Avery, 2001). However, preliminary assessments for micromammals do exist for the other sites (De Graaff, 1960; Pocock, 1985, 1987; Avery, 1998). Makapansgat, Gladysvale, and Kromdraai all exhibit the same overwhelming dominance of *Mystromys* seen at Sterkfontein and Swartkrans. Broom (1937, 1939) was able to describe some of the fossil rodent species derived from the Limeworks at Taung, though they are excluded here. It is unfortunate that better samples do not exist, for Taung represents the southernmost australopithecine-bearing locality yet known and as such local paleoenvironmental reconstructions would serve to broaden understanding of australopithecine distribution and habitat-type association.
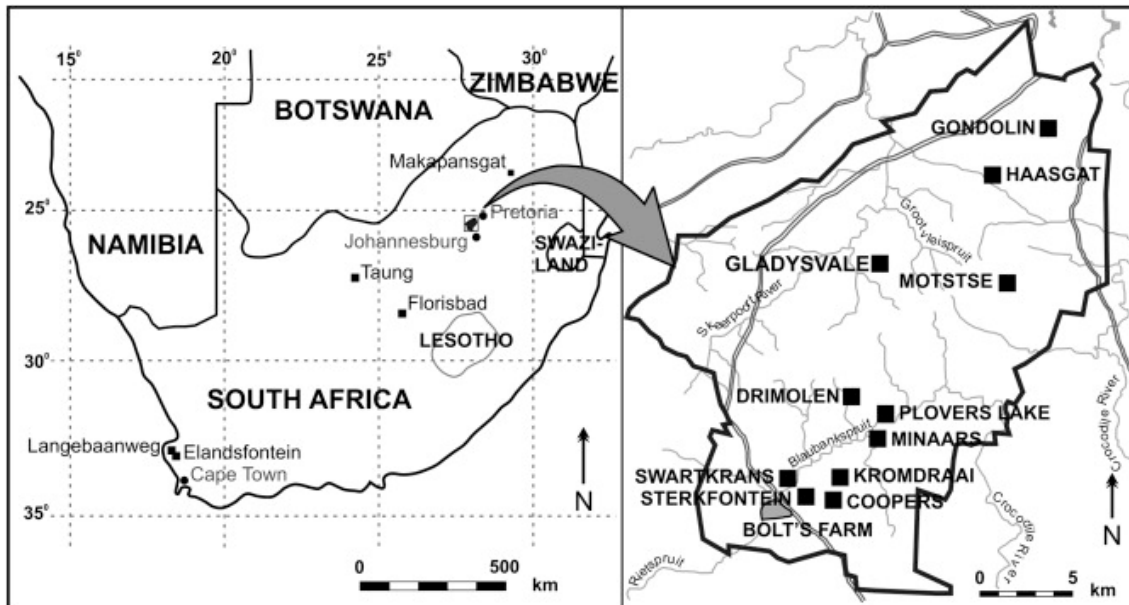
Fig. 6.1. Map of southern Africa with locations of important Plio-Pleistocene sites. The Cradle of Humankind World Heritage Site is shown in the insert, with the location of Gladysvale Cave and the other hominin-bearing caves in the vicinity. (Figure after Pickering et al., 2007)

Makapansgat

Micromammalian remains at the Makapansgat Limeworks have been recovered from australopithecine-bearing Members 3 and 4 as well as the Makapansgat Rodent Corner In Situ pink Breccia (MRCIS) and the Exit Quarry basal Red Mud (EXQRM). Though dating is problematic in a number of South African sites, broad estimates utilizing faunal and paleomagnetic techniques suggest an age a little older than 3 Mya to 2 Mya (Klein, 1999). The Rodent Corner and Exit Quarry, have tentatively been included with Member 4, which appears to be slightly younger than Member 3. Hence, Makapansgat represents what is arguably (Sterkfontein being the notable contender) the oldest hominin-bearing South African site (Klein, 1999).

Previous paleoenvironmental reconstructions (Reed, 1998, Sponheimer et al., 1999) imply a bush and woodland environment with a Highveld summer rainfall regime and mixed C_3/C_4 vegetation. Isotopic research conducted by Hopley et al. (2006) on the three most common rodent species represented at the site provides support for the previous reconstructions. Rodent sotopic values indicative of mixed C_3, C_4 feeding provide additional evidence for a more mixed woodland-savanna environment with a greater proportion of woodland during the mid-Pliocene than that which exists at Makapansgat today. Denys (1999) interprets the Makapansgat paleoenvironment indicated by these micromammals similarly, arguing that it does not correspond to modern Transvaal Highveld habitats but likely reflects a mixed and mosaic habitat with savannas-like affinities.

A comprehensive study assessing relative species abundance and rodent community structure at Makapansgat remains to be undertaken, but preliminary assessment by Pocock (1985) revealed the presence of *Otomys* and *Proodontomys cookie*, and *Mystromys.* Gerbils are rare but closely resemble *Tatera*. Shrews including Myosorex are common, akin to what was observed in modern collections (see Chapter Seven) but unlike Sterkfontein and Swartkrans.

Just as at Sterkfontein and Swartkrans *Mystromys* dominates the assemblage in Member 3 but, Pocock (1985) notes with interest, *Mystromys* is completely absent from the Exit Quarry and Rodent Corner blocks. Pocock (1985) infers that Member 3 is therefore older than the other sediments and that *Mystromys* catastrophically declined to regional extinction in the interim. Today *Mystromys*, is not found near

Makapansgat at all and is rare in the Sterkfontein Valley (Skinner and Chimimba,,

205). The absence of *Mystromys* from all but Member 3, as well as the fact that

Makapansgat is located a significant distance north of the Sterkfontein Valley, may

corroborate Avery's hypotheses that savanna and grassland biomes fluctuated

widely in the region (Avery, 2001).

Gladysvale

In a preliminary assessment of the micromammalian remains from

Gladysvale Cave, South Africa, which is located 13 km northeast of Swartkrans and

Sterkfontein, Avery (1995) identified 29 rodent species, all extant with the sole

exception of *Proodontomys cookei*. Chronological control at the site remains

indeterminate as the samples were drawn largely from the dumps of material

discarded when the site was mined for calcite. Recent flowstone analyses of the site

estimate a younger than original faunal associations (~650 – 7Kya) (Pickering et al.,

2007). The apparent stability of the rodent community suggests an environment

comparable to the bush underlain by relatively extensive dense grass, which exists

at the site presently. Once again, *Mystromys* dominates the taxonomic composition

of the site though, interestingly, to a lesser degree than at any other sites in the area

(i.e. Not over 50% of MNI). The presence of more riverine adapted species such as

Dasymys may also implicate a less seasonal rainfall regime than the modern pattern

(Avery, 1998).

Kromdraai A & B

Of the two members Kromdraai A and B, only Kromdraai B has yielded hominin remains to date, though both A and B have produced a wealth of fossil fauna (Klein, 1999). De Graaff (1961) and Pocock (1985) both report fauna dominated by Mystromys and Otomys and note the decline of the former to replacement by true murids. De Graaff (1961) concludes that the Kromdraai B deposit was formed under conditions wetter than those today, an assumption drawn from the presence of *Myosorex*, *Grammomys* and *Maystomys*. *Myosorex* is known to favor wet, riverine, and vlei regions, while *Grammomys* is frequently associated with trees. *Mastomys*, however, is a generalist and its presence may not suggest any conclusive habitat (Skinner and Chimimba,, 2005).

Sterkfontein and Swartkrans

Pocock (1985, 1987) was the first to assess the micromammalian fauna at Sterkfontein and Swartkrans and he quickly noted the preponderance of *Mystromys* and *Otomys* observed in subsequent analyses when micromammalian assemblages were expanded and revisited by Avery (2001).

Avery's study utilized micromammalian remains from both Sterkfontein and Swartkrans. She uses three discrete samples, the oldest of which derives from Sterkfontein Member 4 (2.8-2.6 Mya), followed by both Sterkfontein Members 5E and Swartkrans Members 1-3 (2-1 Mya), lastly Sterkfontein Member 5 infill is included for comparison (100 Kya). Assemblages were confidently attributed to *Tyto alba* on the basis of taphonomic assessment of digestion in *in situ* lower molars from rodent specimens. For the purpose of environmental reconstruction, climate

correlates (including mean annual precipitation, mean monthly rainfall, minimum

and maximum temperature ranges, percent winter rainfall, and summer aridity

indices) with modern micromammalian species derived from roost sites in the

Sterkfontein Valley were established. Modern rodent distributions were compared

with vegetational patterns from biome and sub-biome maps. However, unlike Reed's

(2005) study conducted on the East African Serengeti, information on local

vegetational patterns near roost sites were not collected from the field. Using

taxonomic habitat analyses and notably excluding generalist species, Avery

concluded that proportional representation of small mammal species from the fossil

assemblages generally correlated well with the current proportions of vegetation in

the Sterkfontein Valley landscape. However, proportional representation of riverine

grassland was extremely large and species diversity low. Avery contributes this to

the extraordinary preponderance of *Mystromys albicaudatus* which has been

construed as a species that favors riverine grasslands. Further assessment of the

Sterkfontein Name Chamber (probably a component of M5) also reveals an

assemblage dominated by *Mystromys* and *Otomys* (Avery, 2010).

The resultant reconstructions suggest that both Sterkfontein and Swartkrans

represent interglacial deposits as well as transitional ecotones between savanna and

grassland of both moist and arid varieties. In addition, Avery concludes that the area

experienced overall lower mean annual precipitation (500mm opposed to current

approximations of 750mm) (Acocks, 1975; O'Connor and Brendenkamp, 1997;

Schultz, 1997), higher seasonality, warmer mean annual temperatures, and

narrower temperature ranges. More specifically, Sterkfontein M4 suggests open

woodland with bush and thicket, while the younger deposits suggest wooded

grassland (moist savanna) or plains. Swartkrans appears to have had a lower mean

annual precipitation during accumulation than Sterkfontein (310mm) and

microfauna implicates medium density woodland or bush and greater proportions

of edaphic grassland along a river. Avery suggests that the valley may have

represented a modern day catena, in which broad and fine-leaved savannas

intergrade continuously, with the fine-leaved variety concentrated towards valley

bottoms and drainages and the more broad-leaved savanna occurring on hillsides

and plateaus. Avery specifically describes the locality as follows, "a succession from

riverine grassland, sometimes *Acacia* trees, hillsides with bush, grass and some

trees, to plains with open savanna woodland" (2001:113). Avery concludes that at

the landscape level, vegetation was not homogeneous, but varied with time and

climate flux. This reconstruction agrees rather generally with reconstructions based

on macrofauna by Reed (1997) and Brain (1995) though her suggestions place

rainfall estimates as rather lower than other attempts.

There are a number of factors to consider in this reconstruction. The first of

these has to do with the potential for predator bias. Avery alludes to *Tyto alba's*

preference for open, riverine, and ecotonal environments, and concludes, akin to

Denys (1990), that both grassy steppe and riverine microhabitats were present. The

preponderance of *Otomys* alongside *Mystromys* corroborates this interpretation.

However, it would seem problematic that generalists were excluded. Given the

dominance of *Mystromys*, habitat signals would not be obscured by including

generalists and the presence of generalist may indicate the existence of

microhabitats otherwise excluded or underrepresented. It has been demonstrated owing to their broad physiological tolerances, generalist species frequently colonize under-populated areas and exploit a wider range of dietary resources when interspecific competition is high (Skinner and Chimimba,, 2005; Krystufek et al., 2007; Kinahan and Pillay, 2008).

Clearly, the ecological role and the corollary habitat and environmental propensities of *Mystromys* are of utmost importance here given the species overwhelming dominance during the Plio-Pleistocene and its "catastrophic" decline in subsequent millennia. The autoecology of modern *Mystromys* species remains somewhat unresolved. According to Skinner and Chimimba (2005), The species follows the grassland biome very closely in the eastern parts of the subcontinent and yet its dietary, behavioral, and physiological adaptations are remarkably generalist. *Mystromys* is omnivorous, nocturnal, terrestrial, and is in possession of a low and broad thermoneutral zone, so it is cold adapted (Skinner and Chimimba, 2005). Though Skinner and Chimimba (2005) note that the species prefers good grass cover and has been found on rocky slopes, cliffs, and in areas with short, sparse grasses, they do not explicitly acknowledge an affinity for *riverine* grasslands. Hence the strict categorization of *Mystromys* in all taxonomic habitat analyses as a riverine grassland species may require revision. As noted in Chapter Two, taxonomic habitat analyses are heavily reliant upon appropriate and accurate niche models. Several scenarios provide potential explanation. Firstly, it is likely that current niche models for *Mystromys* are insufficient in scope and depth, or that the modern *Mystromys* upon which these models are based is more derived in its habits

(if not its morphology) than its Plio-Pleistocene predecessor. Second, it is clear that some local ecological, environmental and/or climatic changes, however slight, affected this species more dramatically than others, nearly all of which (including *Otomys*), remain well represented in the area nearly two million years later. A notable exception to this is now extinct *Proodontomys cookei*, the only other known genus in the Mystromyinae subfamily. In fact, the species was originally classified as *Mystromys* and only later transferred to its present genus status by Pocock (1987) on very slight morphological evidence. It is possible that these species, given their close phylogenetic relationship, shared general habitat and niche proclivities that lead to their decline.

Many of the described micromammalian paleoecological studies highlight the necessity of better autoecological data to supplement existing niche models for micromammalian species and patently demonstrate the need for calibration to local ecosystemic processes. The next chapter will present the very preliminary findings of a pilot study whose aim is to achieve such calibration for the Cradle of Humankind in South Africa.

Chapter Seven

Pilot Study in the Cradle of Humankind, South Africa

Introduction

Utilizing methodology and research design similar to that conducted in Serengeti habitats near Olduvai and Laetoli (Reed, 2003, 2007, 2011), and expanding upon analyses conducted by Avery (2001) this preliminary study addresses the composition of small mammal ecological communities and their associated habitat complexes in The Cradle of Humankind, World Heritage Site, South Africa. These modern ecological data will ultimately be compared to micromammal fossil samples derived from the hominin-bearing localities of Sterkfontein and Swartkrans. It is the larger goal of this study to provide an ecological baseline for micromammalian paleoecological reconstruction by determining whether coprocoenoses accumulated by owls are indicative of the local habitat diversity, structure, and composition in this area. These baseline calibrations may then be used to facilitate more accurate interpretation of fossilized assemblages.

It should be noted that this attempt represents a preliminary analysis only and will serve to summarize raw data regarding the species composition, diversity, and habitat indications of each modern and fossil site. Future research and full development of this project will entail thorough examination of the hydrology, elevation, topography, precipitation, soil type, and vegetative composition and

structure prevailing at each site. Naturally, advanced statistical analyses and various permutations of taxonomic ratios and taxonomic habitat indices will be employed as these analyses developed. Nonetheless, cursory information regarding species composition and relative abundance reveals some interesting trends in the modern data as well as striking differences between modern and fossilized micromammalian communities.

Methods

Modern roost data derives primarily from three roost sites, Malapa, Kimberly, and Gladysvale all located within the Cradle of Humankind approximately 10km from Sterkfontein and Swartkrans. Coprocoenoses were also collected from two sites located in The Cradle Nature Reserve, but have been excluded from the current analyses owing to their small sample size and the present uncertainty regarding the identity of the predatory accumulator. Each modern site was selected for its location in a unique habitat type. Coprocoenoses in Malapa and Kimberly have been collected for both dry and wet seasons, while the Gladysvale specimens represent a collection of decayed and likely seasonally averaged pellets. Wet and dry season samples from both Malapa and Kimberly roosts, respectively, have been combined for better comparison with the Gladysvale samples.

The Sterkfontein and Swartkrans fossil collections are from the Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria. Sterkfontein material derives from Member 4, dated to ~2.8 Mya and is associated with *Australopithecus africanus* (Klein 1999). Remains from Swartkrans derive from

Member 1, Hanging Remnant. Member 1 has been dated to ~ 1.8 Mya and is associated primarily with *Paranthropus robustus* but notably also produced *Homo* specimens (Klein 1999).

Samples were collected over the course of two field seasons, the first taking place during the dry season, May 2010 and the second during the wet, rainy months of the austral summer, January, 2011. Identification of both roost and fossil specimens were made by O. C. C. Paine and myself with the aid of comparative collections housed in the Ditsong Museum, Pretoria and the Iziko Museum of Natural History, Capetown. Material processing and identification took place in Capetown under the tutelage of Thalassa Matthews, a paleontologist and rodent specialist at the Iziko Museum, as well as on the University of Colorado, Boulder campus following the second field season.

Species identifications for both modern and fossil micromammals were made on the basis of distinctive tooth morphology with the aid of a microscope. Certain species are more readily identified to the genus versus the species level. Generalist species including *Mastomys, Rhabdomys*, *Aethomys*, and *Micaelamys*, all proved difficult in some instances, as distinguishing features are either located on maxillary or mandibular portions that were missing. Generally, all specimens have been identified at least to the level of genus, which provides relatively reliable ecological data regarding habitat preference (Reed, 2003). Fortunately, the tooth morphology of the dominant species, *Mystromys* and *Otomys*, are easily differentiated - *Mystromys* on the basis of its uniquely 'zipper-like' pattern of molar invaginations

and *Otomys* for its prominent laminae. No extinct species were identified in preliminary assessment. The Soricidae *Crocidura*, *Myosorex*, and *Suncus* have been collectively categorized as 'insectivores' or alternately 'shrews' given the difficulties of discerning species on the basis of tooth morphology alone (Matthews, personal communication).

Vegetation was sampled in point transects by members of the field team. Plant type and percent vegetative cover have been determined thus far with species identification pending.

Species composition, relative abundance, and species diversity are all assessed using minimum number of individuals (MNI) for modern roosts, and number of identified specimens (NISP) (mandibular and maxillary material only) for the fossil specimens. The Shannon-Weiner Index (Shannon, 1948) (see Chapter Two) was calculated for each site to assess relative diversity.

$$H = - \Sigma \, p_i \, ln \, (\, p_i \,)$$

Results

Roosts and Vegetation

The Malapa roost is positioned very near the *Australopithecus sediba* bearing cave Malapa (Berger et al., 2010). The roost is located in a rocky crag and preliminary taphonomic observations support the argument that the accumulator is a young barn owl (personal observation; Berger, personal communication). The surrounding landscape is varied in its topography with outcroppings of dolomitic

rock, as well as a mixture of trees, bushes and grasses. Preliminary assessment of vegetation near the roost site suggest a ground cover composition of 85% grasses, 10% forbs, and 5% short trees (<1 m in height).

The Kimberly roost site is located in a lone dilapidated building and one of very few human-made structures in the reserve. It is situated in the midst of a wide expanse of grasslands. Preliminary ground cover analyses suggest a ground cover composition of 95% grasses, 5% forbs, and 5% short trees.

Gladysvale, a site which has yielded two hominin teeth, has long been occupied by a mating pair of barn owls (Berger, personal communication). The cave is located in the side of a sharply incised valley, characterized by a spectrum of vegetative cover ranging from densely wooded riparian areas on the valley floor, hillsides with mixed vegetation and numerous rocky koppies, and elevated grassy plateaus. A point transect survey of vegetative cover has tentatively described 10% rock, 65% grasses, 5% forbs, and 20% trees.

Micromammalian Community Composition: Modern Roosts

Species dominance at the modern roosts is as follows. At the Malapa roost, like all other roosts, shrews dominate the assemblage, followed by *Mastomys*, *Mus*, *Steatomys*, *Tatera*, *Michaelamys*, and finally *Otomys*. The Kimberly roost, following shrew dominance, is characterized by *Mastomys*, *Otomys*, and *Steatomys*. Gladysvale had the highest proportion of shrews, but this is followed notably by *Dendromus*, *Michaelamys*, *Mastomys*, and *Otomys*.

At Sterkfontein and Swartkrans, similar to Avery's 2001 analyses, *Mystromys* dominates followed by *Otomys*. *Mystromys* is slightly more dominant at Sterkfontein and *Otomys*, slightly less when compared to Swartkrans. However, these higher proportions may simply be due to the presence of five *Elephantulus* specimens at Sterkfontein.

When data for modern roosts are averaged, Shrews, *Mastomys*, and *Otomys* dominate with 59% of total species represented. Shrews and six rodent species make up 80% of the total assemblage. At the subfamily level, Insectivores[1] and Murinae are relatively evenly represented, while Dendromurinae follow with gerbils and mole rats each representing 5% respectively. The fossil samples, when combined are dominated by Mystromyinae, with the Murinae representing 27% of all taxa.

Table 7.1 lists raw data based upon MNI for each site, while Table 7.2 lists raw data for each of the fossil sites utilizing NISP based upon maxilla and mandibles only. Table 7.3 includes Shannon-Weiner Diversity values. Relative abundance data sorted by genus (excepting shrews), is illustrated in Figures 7.1 and 7.2, while relative abundance data sorted by genus *and* major subfamily for all mammalian taxa at both the modern roost sites and fossil sites are represented in figures 7.3 and 7.4.

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[1] Note that Insectivore is neither a subfamily, nor are shrews classified as Insectivora by Skinner and Chimimba (2005). Nonetheless, this categorization is used for easy reference as shrews are all insectivorous.

Taxa	Malapa	Kimberly	Gladysvale	Storage	Chateau	Total MNI
			Roost ID			**Total**
Insectivora						
(Shrews)	42	60	55	4	7	168
Macroscelidae						
Elephantulus myurus	0	0	0	0	0	0
Rodentia						
Deomyinae						
Acomys spinosissimus	2	2	0	0	0	4
Murinae						
Aethomys ineptus	2	1	2	0	0	5
Dasymys incomptus	0	0	0	0	0	0
Grammomys dolichurus	0	0	0	0	0	0
Lemniscomys rosalia	0	0	0	0	0	0
Mastomys coucha	15	31	10	4	8	68
Michaelamys namaquensis	7	3	10	0	1	21
Mus sp.	10	2	3	0	0	15
Mus cf. minutoides	0	2	0	0	0	2
Otomys sp.	5	15	9	2	5	36
Rhabdomys pumilio	1	6	3	0	0	10
Thallomys sp.	0	1	0	0	0	1
Subtotal Murinae	40	61	37	6	14	158
Dendromurinae						
Malacothrix typica	0	0	0	0	0	0
Dendromus sp.	4	7	16	2	0	29
Steatomys sp.	8	12	8	0	0	28
Subtotal Dendromurinae	12	19	24	2	0	57
Gerbillinae						
Gerbillurus paeba	0	0	0	0	0	0
Tatera sp.	6	6	7	0	0	19
Subtotal Gerbillinae	6	6	7	0	0	19
Bathyergidae						
Cryptomys hottentotus	1	9	0	0	0	10
Mystomyinae						
Mystomys albicaudatus	0	0	0	0	0	0
Subtotal Rodentia	61	97	68	8	14	248
Totals	103	157	123	12	21	416

Table 7.1. Taxonomic representation presented as the minimum number of individuals (MNI) for modern roost sites in the Cradle of Humankind World Heritage Site, South Africa.

Taxa	Site ID		Total
	Sterkfontein Mem 4	Swartkrans Mem 5-Hanging Remnant	NISP
Insectivora			
(Shrews)	0	0	0
Macroscelidae			
Elephantulus myurus	5	0	0
Rodentia			
Deomyinae			
Acomys spinosissimus	0	1	1
Murinae			
Aethomys	1	4	5
Dasymys	0	0	0
Grammomys	0	0	0
Lemniscomys	0	0	0
Mastomys coucha	1	1	2
Michaelamys namaquensis	0	3	3
Mus sp.	0	0	0
Mus cf. minutoides	0	0	0
Otomys sp.	14	38	52
Rhabdomys pumilio	1	1	2
Thallomys sp.	0	0	0
Subtotal Murinae	17	47	64
Dendromurinae			
Malacothrix typica	0	0	0
Dendromus sp.	3	2	5
Steatomys sp.	0	0	0
Subtotal Dendromurinae	3	2	5
Gerbillinae			
Gerbil sp.	1	0	1
Bathyergidae			
Cryptomys hottentotus	1	1	2
Mystomyinae			
Mystomys albicaudatus	61	107	168
Subtotal Rodentia	83	158	241
Totals	88	158	241

Table 7.1. Taxonomic representation presented as the number of identified specimens (NISP) for Sterkfontein and Swartkrans.
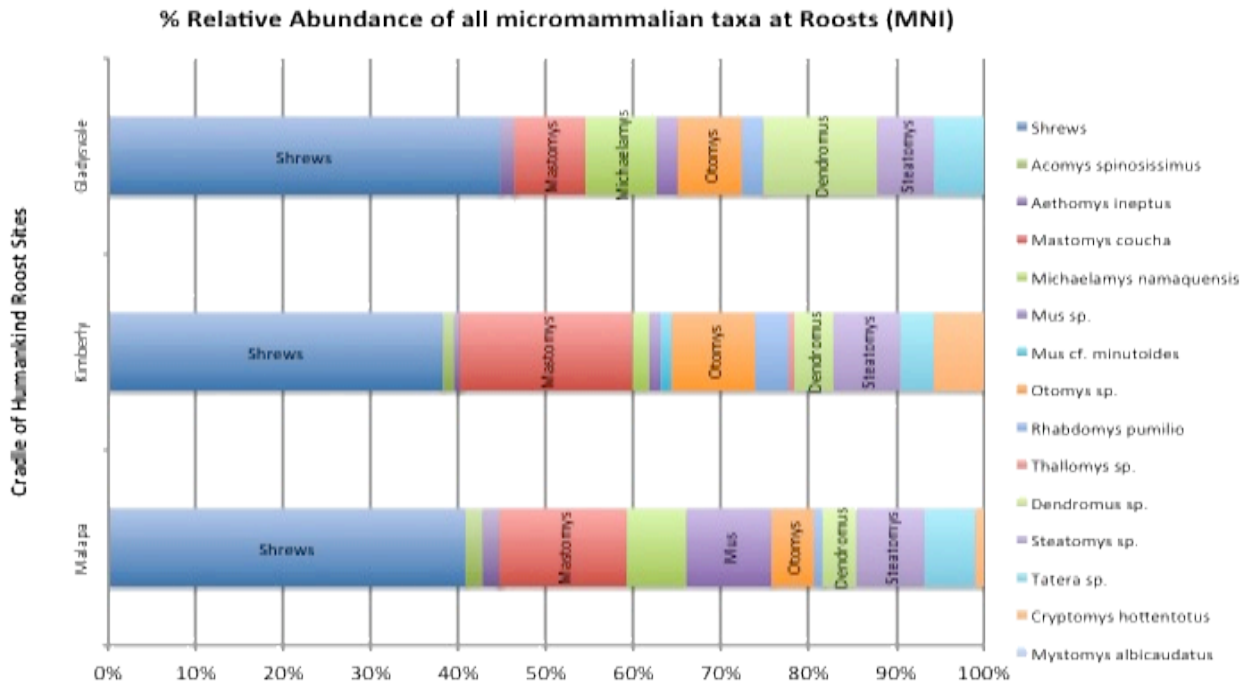
Figure 7.1: Relative abundances (%MNI) of all mammalian taxa at modern each roost site.
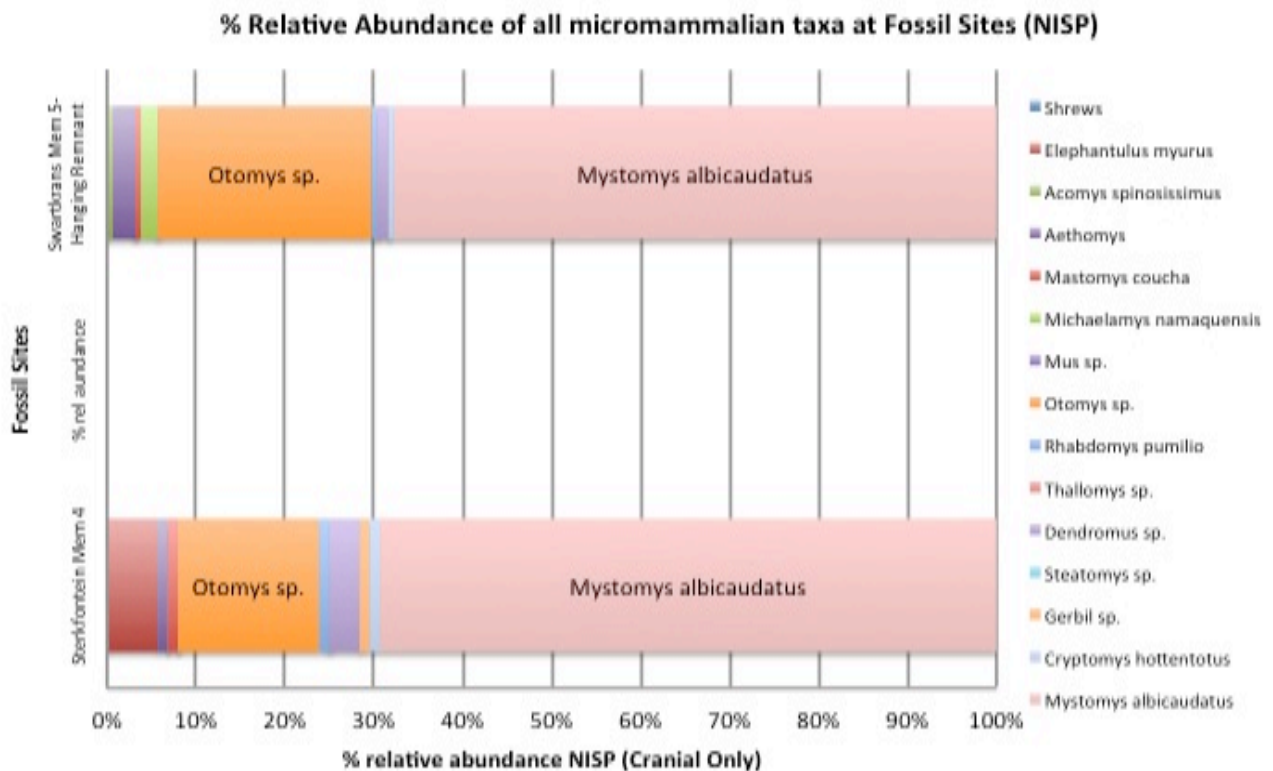

Figure 7.2: Relative abundances (%NISP) of all mammalian taxa for the fossil sites Sterkfontein and Swartkrans.
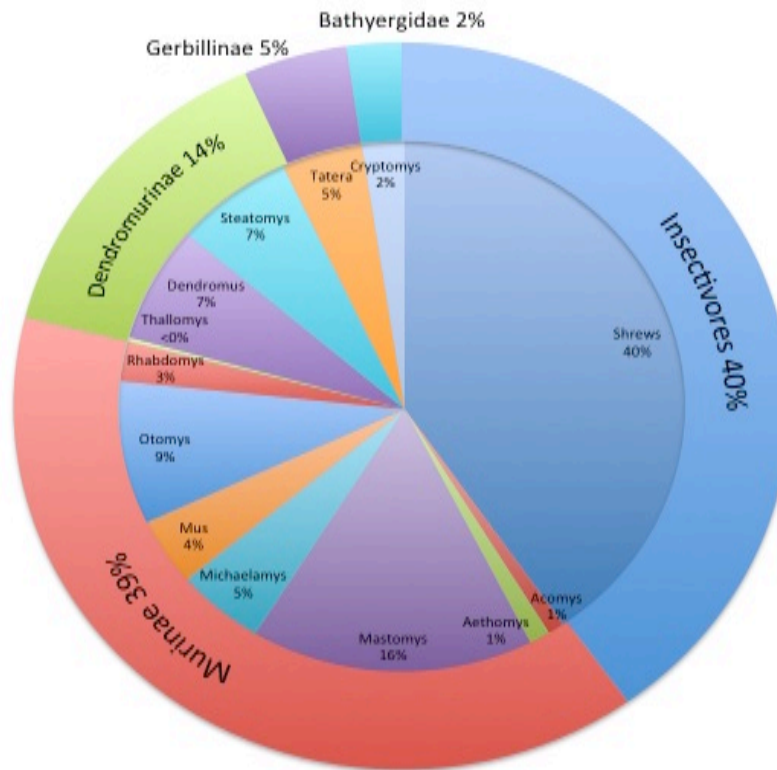
Figure 7.3: Relative abundances (%MNI) of all mammalian taxa and major subfamilies from all roosts combined.
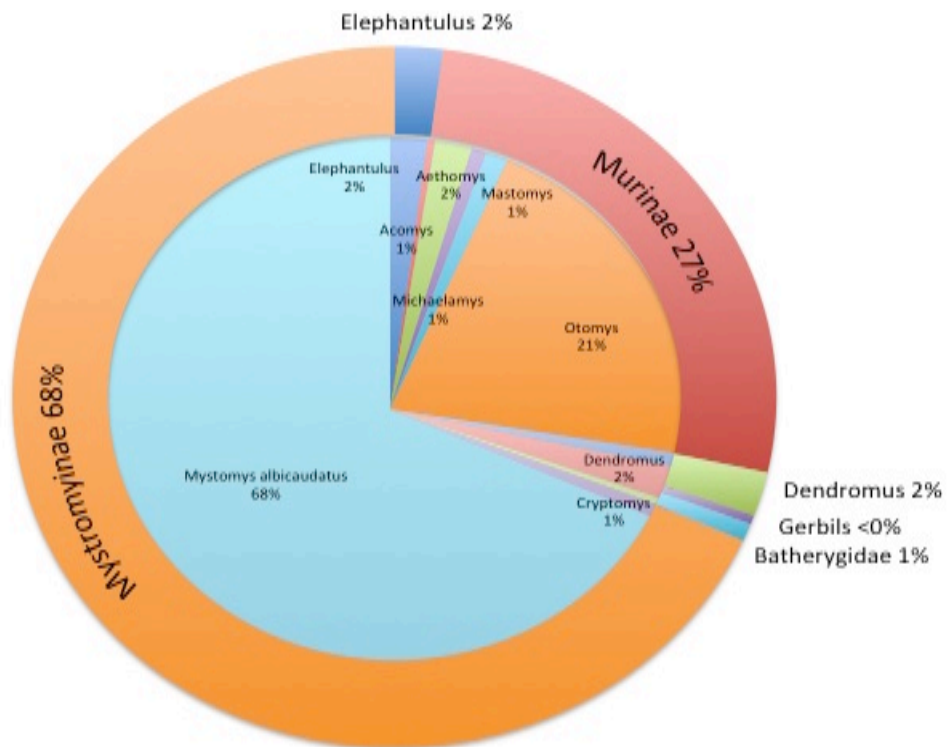

Figure 7.4: Relative abundances (%NISP) of all mammalian taxa and major subfamilies from Sterkfontein and Swartkrans combined.

	Malapa	Kimberly	Gladysvale	Sterkfontein Member 4	Swartkrans Member 1 Hanging Remnant
Shannon-Weiner Diversity Index	1.9356887	1.9676718	2.0023327	1.0790057	0.9584921
Species Richness	12.0	14.0	12.0	9.0	9.0
Total Abundance	103	157	135	88	158

Table 7.3: Summaries of Shannon Diversity Index calculations for each modern and fossil site.

Discussion and Conclusion

How well do modern taxa reflect local habitat?

It would appear that each modern roost exhibits unique species compositions and diversity. Though shrews featured prominently at all sites, and *Mastomys*, a well-known generalist species, follows at Kimberly and Malapa, the relative abundances of the various species do reveal different compositions. Kimberly has the greatest species richness, though Gladysvale actually exhibits the highest Shannon-Weiner value. This is likely because species are more even in the mixed terrain near the Gladysvale roost site than at Kimberly, where grassland and generalist species dominate. Both Sterkfontein and Swartkrans have low calculated diversity values owing to the dominance of *Mystromys* and *Otomys*. Avery (2001) did not assess Shannon-Weiner Diversity in her study of Sterkfontein and Swartkrans, but a later study of the Name Chamber at Sterkfontein (Avery, 2010) revealed very high diversity values (~2.4), which she hypothesized reflected mixing with other stratigraphic members. It is possible that mixing occurred in our Gladysvale collections and that the high species richness observed at the Kimberly roost may be a function of larger sample size.

The domination of shrews at all modern roost sites is most interesting. Shrews are widespread and multiple species are frequently found sympatrically (Churchfield, 1990, 1991). *Suncus* and *Myosorex* are generally associated with wetter habitats and riverine or vlei settings, while *Crocidura* tends to be more catholic in its habitat requirements and is found frequently throughout South Africa (Skinner and Chimimba 2005). Interestingly, Churchfield (1990) notes that shrews regularly make up only 5-13% of owl diets worldwide and yet our samples reveal the consumption of greater than 30% shrews. Shrews are clearly an important component of the diet of the barn owls in this region of South Africa. More information about shrews in this region, their patterning on the landscape, their ecological importance, and their habitat associations, including their climatic correlates, are needed to determine the full implication of their dominance in the owls diets. This is particularly true given the fact that shrews are completely absent from the fossil assemblages.

How do modern taxa and compare to the fossil assemblages from Sterkfontein and Swartkrans?

Generally, preliminary assessments of taxonomic composition agree with those described by Avery (2001). *Mystromys* and *Otomys* are, at both sites, the dominant species. *Mystromys* is completely absent from the modern coprocoenosis, and, though *Otomys* is relatively well represented at each modern roost, it is never more than the third most represented species. More detailed discussion of the

significance of the dominance of these fossil assemblages can be found in Chapter

Six, but early analyses do generally agree with the findings of other researchers.

Chapter Eight

Conclusion

One aim of this thesis was to examine the interplay between habitat type,

micromammal community composition, and owls to identify the main biases

inherent in coprocoenoses and to determine whether these biases are small enough

to allow accurate paleoecological interpretation based upon micromammals.

Though predator selectivity certainly contributes to biases in coprocoenoses, it

would appear that within the constraints of body size and activity pattern, the

ubiquity and semi-generalist nature of the barn owl, its proclivity for including

ecotonal and edge habitats in its foraging range, and its sensitivity to fluctuations in

relative abundance of its prey base, make it a more reliable sampler of small

mammal diversity and community composition than any other single measure

(Reed, 2003, 2005, 2007). This makes owl accumulated fossil assemblages ideal

proxies for reconstructing micromammalian paleocommunities and, by

extrapolation, local habitats.

In this assessment, it would seem that ambiguity in the details of

micromammalian ecology introduces as much bias as the owls themselves.

Autoecological knowledge of species varies greatly in its depth and detail depending

on the relevance of that species to human research interests (Reed, 2003). Species

thought to have specific habitat associations or dietary propensies may, in fact, be

more catholic in their requirements than traditionally ascribed (Hopley et al., 2006;

Kinahna and Pillay 2008). Furthermore, many micromammal species are highly

generalist, with broad diets and wide habitat tolerances (Skinner and Chimimba 2005). These species are problematic for current micromammal paleoecological methodologies, which rely on genus and species specific information regarding habitat preference.

Though biases certainly exist and better resolution is needed for the modern niche models and local environments upon which micromammal paleoecological reconstruction depends, these reconstructive techniques do appear to provide useful and valid paleoecological interpretations. Naturally, caveats must be acknowledged in interpretation and are best mitigated not only with accurate niche models but, importantly, by corroboration with and comparison to other lines of paleoecological evidence.

The results of preliminary assessments of modern coprocoenoses in the Cradle of Humankind, South Africa nonetheless demonstrate micromammalian community structure that is distinct to specific habitat types in the area. The fossil micromammal assemblages collected from Sterkfontein and Swartkrans agree broadly with the assessments made by Avery (2001) in their assessments of composition and dominance of species. However, micromammal paleoecological reconstructions in this area would benefit greatly from more detailed ecological assessment both in terms of the habitat affinities and dietary ecology of particular species, especially *Mystromys albicaudatus* and *Otomys*. Also, the near absence of shrews in the Pleistocene deposits of Sterkfontein and Swartkrans despite the

apparent importance of shrews in the diets of modern owls, necessitates better understanding of the shrew ecology in the region.

Ultimately research similar to that conducted by Reed (2003, 2005, 2007) and the preliminary research presented herein must be undertaken to improve the caliber of micromammalian paleoecological reconstructions. These fine scale reconstructions help paleoecologists and paleoanthropologists understand not only how the large-scale climatic shifts that occurred during the Plio-Pleistocene manifest regionally and locally, but they also may serve to elucidate the subtler nuances of landscape that created niche space for the coexistence of multiple hominin species.

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