1. INTRODUCTION

1.1 OVERVIEW OF PROJECT

This project will focus on the micromammal assemblage (under 400g) from Sibudu Cave. After species identification, I will attempt an environmental reconstruction based on micromammal species diversity and presence within the assemblage. An environmental profile will be drawn up for each level used in the analysis based on microhabitats, vegetational and climatic data associated with individual species. Comparisons will then be made with other proxy environmental data from macrofaunal (Plug 2004), seed (Wadley 2004) and charcoal (Allott 2004) studies in order to create a feasible environmental reconstruction of the immediate environment around Sibudu.

With studies of this nature, it is imperative that archaeologists are aware of the implications of taphonomic biases and realise the utility of combining mechanical, behavioural and ecological data to establish the possible agent responsible for bone accumulations. An indepth taphonomic study (Andrews 1990) is a prerequisite to an accurate analysis of a faunal assemblage. This study provides the basis of such a study with comparisons between the likely predators based on the five predator categories determined by Andrews (1990). This chapter provides an extensive summary of taphonomy, so as to identify the possible agents that may introduce a bias into a microfaunal assemblage. I also discuss the importance of recognizing these agents.

1.2 LITERATURE REVIEW

Since Cartmill (1967) pioneered ecological interpretations of micromammalian faunas from East and South Africa, few ecological studies focused on small mammals until Denys (1998) undertook further ecological comparisons between the two regions and Avery (1982, 1986, 1990, 1995, 2001) looked at South African assemblages. These studies showed that bones of small mammals can accumulate in very high frequencies, (Armitage 1985; Andrews 1990; Avery 1990, 1995; Denys 1998) and can provide evidence about the environments in the vicinity of the site over time (Avery 1990, 2001; Denys 1998).

1.3 ENVIRONMENTAL RECONSTRUCTION

The introduction of a small mammal sequence into an archaeological site is very useful as many micromammal species are habitat specific and there is much variability among faunas from different ecozones (Brain 1981; De Graaff 1981; Avery 1986). This variability makes it possible to define ecological zones by their associated small faunas (Avery 1982, 2001; Andrews 1990; Denys 1998), because small mammals are a group considered to be good climatic indicators (Denys 1998; Avery 2001).

Small mammal data can be compared to other proxy data in order to establish an accurate model of the past environment (Avery 1990, 2001; Denys 1998). With these palaeoenvironmental interpretations it is important to use all available lines of evidence to achieve as accurate an environmental reconstruction as possible. In recent years, various methods have been developed for interpreting micromammalian data in terms of past shifts in climate (Avery 1982, 1986, 1990, 1995, 2001; Denys 1998). These methods make use of population and community attributes, and ecological and biological information (Denys 1998; Avery 2001).

It is evident that there is a close correlation between the proportion of micromammal species and the composition of the vegetation types on the landscape (De Graaff 1981; Avery 1990). Much information on climatic change that can be drawn from micromammals comes from evidence for changes in the composition of vegetation in the neighbourhood of the site from which the sample is drawn (Avery 1990). This is because many small mammal species are relatively specific in their choice of habitat and food to which they are adapted (Avery 1990). Avery (1990) argues that during the Holocene, change tends to be represented in proportions of various species, either individual or grouped for similar habitats and food preferences, rather than the species represented. Avery (1990, 2001) suggests that these fluctuations in micromammal species provide an idea of fluctuations in proportions of vegetational types. These vegetational fluctuations, in turn, can be interpreted in terms of climatic change, such as rainfall, as climate may be the major factor influencing vegetational life forms (Avery 1990). Avery (1990) points out that it is, however, difficult to determine the

factor or factors involved because temperature and rainfall regimes all change independently and this may produce a variety of end results (Avery 1990, 2001).

Population structure in an area can also provide an indication of changes in environmental conditions as not all micromammal species are equally adapted to extreme conditions and environments (Avery 1990, 2001). Sudden changes or fluctuations in environmental conditions may result in a variable representation of species and populations. It should therefore be possible to distinguish the traits of those that are adapted to stable environments from those that are not (Avery 1990). Each species will have characteristic population structures under the conditions to which it is adapted, determined by extrinsic properties of the environment and intrinsic properties of the species (Dodd & Stanton 1981). It should be noted that the use of this kind of analysis has to assume that there are no changes in intrinsic properties and that there has been either no predator or accumulator bias, or no change in bias (Avery 1990).

Avery (1982, 1990) identifies four environmental factors that may act as regulators on species diversity, distribution and population structure in the environment. These factors are weather, food, shelter and other animals or pathogens (Avery 1990). Vegetation types form an integral part of at least three of these environmental factors, indicating that there is a strong connection between vegetation and micromammals that are exposed to the threats of predation (Avery 1982, 1990, 2001).

When analysing microfaunal assemblages, these factors can provide excellent data on the possible vegetational types that can be associated with small faunas in different ecozones. Another factor that is difficult to determine is the effect that predators have on reducing a population through over-predation (Avery 1990, 2001). The size and hunting range of predator species and their relationship to the size and range of prey species is almost impossible to establish, making it extremely difficult to determine the impact that predator numbers have on prey population densities.

In an archaeological context, the uses of micromammalian assemblages as environmental indicators have two main advantages (Avery 1982). Firstly, archaeological sites mostly comprise stratified units representing periods of time.

When the micromammal remains are excavated as discrete samples they are indicative of the conditions during the accumulation of that unit (Avery 1982, 1990). Secondly, in archaeological sites, micromammal remains were probably deposited independently of material collected by humans. Assemblages are therefore unlikely to be influenced or biased by individual human preferences (Avery 1982, 1990).

1.4.1 TAPHONOMY

It is evident that a number of agents may influence the makeup of a microfaunal assemblage at any stage through the introduction of various biases (Andrews 1990). It is important to recognise these agents as well as taphonomic and mechanical biases that may distort data and affect environmental interpretations (Avery 1990). Taphonomic studies have facilitated the basis for identifying the modification patterns found in microfaunal bone assemblages and the identification of possible contributors to these assemblages. These modification patterns allow archaeologists to assess the nature of the biases in an assemblage and they can consequently infer, with some degree of accuracy, what past environments and ecosystems were like. These environmental reconstructions are useful in our understanding of the effects that environmental pressures may have on species migrations and biological evolutionary trends (Avery 2001) in early hominids, during glacial and interglacial periods.

The study of past ecosystems can be complex, because the relationship between fossil assemblages and ecology during fossilization is not simple, due to taphonomic processes during site formation (Andrews 1990). Different sets of physical, chemical and biological agencies may produce modifications on the skeletal remains (Fernandez-Jalvo 1995; Fernandez-Jalvo *et al.* 1998). Bone modifications are the basic criteria for detecting taphonomic processes during site formation and these, in turn may have a direct influence on palaeoecological and biostratigraphical interpretations (Fernandez-Jalvo 1995).

Bone modification refers to any form of alteration to individual bones; for example cracking, surface marks, abrasion, polishing and breakage caused by different mechanisms (Behrensmeyer 1991). These mechanisms include mechanical damage patterns from predation, weathering, insect activity (Behrensmeyer 1978), trampling, transport by wind and water, topography and post- depositional agencies (Andrews

1990). These processes may change the composition of fauna at numerous stages of its preservation (Fernandez-Jalvo & Andrews 1992; Fernandez-Jalvo *et al.* 1998). It is important to identify the agent responsible for accumulating the material and to take into account any factors that may have influenced the sample, as these agents introduce biases that may affect any interpretations (Andrews 1990). According to Andrews (1990) these modification mechanisms fall into the following categories: modifications by cause of death, modifications shortly after death, modifications after burial and modifications by recovery.

It is essential to identify the predator responsible for accumulating a sample (Avery 1990) as predation is an important accumulator of small mammal bone. It is also the primary stage of bone modification that can be recognized in the fossil record as indicated by skeletal representation, breakage, digestion and tooth mark modifications (Fernandez-Jalvo 1995). Extensive research on small mammal taphonomy has shown that it is possible to determine which predator was the likely accumulator in small mammal assemblages (Andrews & Cook 1985; Andrews 1990). The results of these studies show that predators of small mammals can be divided into five categories (Table 1.1) that are distinguished by the surface modifications that they produce on their prey (Andrews 1990).

These categories were determined by the differing degrees of surface modification visible on bone. The surface modifications were found to be very characteristic indicators of predator species, as modifications were found to be consistent within a species and to, differ significantly between species (Andrews 1990). These classification categories are thus useful in palaeoenvironmental and palaeoecological studies, because they provide proxy means for the identification of a predator.

1.4.2 PREDATORS OF SMALL MAMMALS

Pedation is an important accumulator of small mammal bone and is the primary stage of bone modification that can be recognised in the fossil record (Fernandez-Jalvo 1995). Prey assemblages of this nature may arise from various activities, including: predators carrying their prey to a favoured roosting place, storing of excess food supplies in caches and outside dens and from the deposition of indigestible prey

remains in scats and pellets (Rautenbach 1982; Andrews 1990). Following Andrews (1990), small mammal predators have been divided into three categories: mammalian predators, diurnal birds of prey and nocturnal owls. Nocturnal owls have been identified as the likely contributors to the Sibudu micromammal assemblage and this category will therefore be discussed, according to their geographical distribution in southern Africa, habitat, habits and dietary preferences. Due to the scope of this project an in-depth discussion of the dietary preferences, habitat and geographic distribution of mammalian predators and diurnal birds of prey have been excluded. These two groups have been grouped into two broad categories: mammalian predators which include, canids, mustelids, felids and vivverids (Andrews 1990; Mills & Hes 1997) and diurnal birds of prey which include, falcons, buzzards, eagles and harriers (Andrews 1990).

1.4.3 AVIAN PREDATORS

Many birds of prey regurgitate pellets that contain the indigestible remains of their prey. These pellets may accumulate in large quantities if they are deposited around regular nesting and roosting sites. Extensive surveys done in Europe and southern Africa have shown that owls are major contributors of small mammal bone in fossil assemblages (Avery 1982; Andrews 1990).

1.4.4 NOCTURNAL OWLS

Fossil owls are known from the Eocene, and some living genera have been identified in Miocene and Oligocene deposits (Andrews 1990). As a group owls hunt by night although some species hunt by day as well, particularly in the early morning and late evening (Kemp & Calburn 1987; Andrews 1990). They usually swallow their prey whole, sometimes removing the head first, undigested remains, are later regurgitated as pellets (Kemp & Calburn 1987). The most prolific pellet producer is the Barn Owl *Tyto alba* (Andrews 1990).

BARN OWL (*Tyto alba)*

Tyto alba is a nocturnal species with a world wide distribution and is the best-studied owl in the world (Kemp & Calburn 1987). It is found on every continent except

Antarctica and includes many oceanic islands in its range (Kemp & Calburn 1987). The success of this owl species may be attributed to its great mobility and its ability to exploit the widest range of nocturnal conditions (Kemp & Calburn 1987).

The Barn Owl takes a wide range of prey species, due to its ability to hunt in more diverse terrain than other species (Steyn 1982; Kemp & Calburn 1987). It does, however, prefer more open habitats and are therefore more common in open savannah, adjacent to grassland or low scrub (Kemp & Calburn 1987). An estimated 42g of food a night is required to maintain a Barn Owl in southern Africa, rising to about 82g in winter (Kemp & Calburn 1987). Barn Owls are opportunists and due to their size are small mammal specialists, taking a wide range of prey species that range in size from young hares to crickets and termites. Rodents usually form about three-quarters of the prey consumed by this species, which is normally eaten at the individual owls roosting site (Kemp & Calburn 1987). The Barn Owl will roost in a variety of crevices found in trees, rocks, man-made structures and often in the twilight zone of caves or rock shelters (Levinson 1982; Kemp & Calburn 1987). *Tyto alba* is considered to be the likely contributor of the micromammal assemblage at Sibudu.

GRASS OWL (*Tyto capensis*)

The Grass Owl looks very similar to its close relative the Barn Owl, buts its biology is very different (Kemp & Calburn 1987). This species distribution extends from Cameroon and Ethiopia to South Africa and through Asia to eastern Australia (Kemp & Calburn 1987). It is restricted to the eastern third of southern Africa and is mostly found in the highveld and escarpment grasslands. *Tyto capensis* lives entirely on the ground and is virtually confined to open expanses of moist grassland, bracken and heath (Kemp & Calburn 1987).

Although both *Tyto capensis* and *Tyto alba* overlap in their ranges and prey, each concentrates on the prey to which it is most suited (Kemp & Calburn 1987). *Tyto capensis* is mostly nocturnal but has been known to hunt during daylight hours if it is overcast (Kemp & Calburn 1987). Little is known about their hunting methods at night but there is evidence that suggests that much searching is done on the wing (Kemp & Calburn 1987). This species eats mainly larger rodents, especially *Otomys* vlei rats with a few smaller rodent and insectivore species (Kemp & Calburn 1987).

SPOTTED EAGLE OWL (*Bubo africanus*)

The Spotted Eagle Owl is the large horned owl most familiar to people in southern Africa. It occurs throughout the subcontinent and nests in a wide variety of sites, often in and around farmyards and even in the window boxes of suburban houses (Kemp & Calburn 1987). This species is known to take a wide variety of prey that includes: snails, arachnids, insects, small mammals and birds (Kemp & Calburn 1987). The Spotted Eagle Owl is most common in rocky, broken terrain and roosts on cliff ledges, steep slopes, buildings or in trees (Kemp & Calburn 1987). This species is crepuscular and nocturnal, hunting from perches and at times by aerial pursuit (Kemp & Calburn 1987).

CAPE EAGLE OWL (*Bubo capensis capensis*)

The Cape Eagle Owl is one of the largest and most powerful owls in the world (Steyn 1982; Kemp & Calburn 1987). This species occupies mountain ranges from Ethiopia to the Cape of Good Hope extending down to the sea and into arid koppies in parts of the Karoo and Namibia (Kemp & Calburn 1987). The Cape Eagle Owl is crepuscular and nocturnal hunting mainly small primates (Steyn 1982), scrub hares, red hares and hyraxes from perches (Kemp & Calburn 1987). It nests in a scrape made in caves, among boulders or on a ledge. The actual nest site may be revealed by the prey remains that accumulate there. These remains consist of larger prey in particular the hind limbs of hares with the feet attached (Kemp & Calburn 1987). The presence of such large prey remains at a site confirms that the roost/nest does not belong to the smaller owl species (Spotted Eagle Owl, Barn Owl and Grass Owl) which have much weaker feet than the Cape Eagle Owl (Kemp & Calburn 1987) and therefore are unlikely to have the ability to take these prey species.

MILKY EAGLE OWL (*Bubo lacteus*)

The Milky Eagle Owl is considered one of the most powerful nocturnal predators and is most common in woodland and bushveld in southern Africa (Kemp & Calburn 1987). This species hunts mainly from perches, hunting medium sized mammals such as hedgehogs but has been known to take young monkeys, Secretarybirds and even some carrion (Kemp & Calburn 1987). The Milky Eagle Owl roosts mainly in trees (Steyn 1982; Kemp & Calburn 1987). This species preference for roosting in trees and

its preference for larger prey species (Steyn 1982; Kemp & Calburn 1987), suggest that it is an unlikely contributor to the bone assemblage at Sibudu.

1.4.5 DIURNAL BIRDS OF PREY

Little work has been done on the significance of diurnal birds of prey as accumulators of small mammal bone in fossil assemblages (Andrews 1990). Studies have shown that bone assemblages accumulated by kestrels *Falco tinnunculus* differ significantly from Barn Owl accumulations (Mayhew, cited in Andrews 1990) due to the fragmentary nature of the bone found in these species scats and pellets. For most diurnal raptors, it is difficult to obtain large enough samples, due to the small amount of bone found in their pellets (Andrews 1990). They eat all but the smallest prey by tearing the carcass apart before ingestion. Other diurnal raptors, such as peregrine falcons *Falco peregrinus*, have a preference for birds as opposed to small mammals and have not been intensively investigated (Andrews 1990). The larger eagle species in southern Africa target larger prey such as small primates and small bovids and are therefore unlikely contributors of micromammal assemblages.

Most mammalian species are effective hunters of small mammals and hunt mostly at night (Mills & Hes 1997). These predators produce the greatest modifications to the bones of their prey because of their shearing teeth (Andrews 1990).

There are certain secondary bone modifications that occur shortly after death that are not related to the cause of death (Fernandez-Jalvo & Andrews 1992). These modifications include mechanisms such as decay, scavenging, trampling, weathering and transport. Bones lying on the surface of the ground may be exposed to these mechanisms which play a significant role in the accumulation of small mammal bone (Fernandez-Jalvo 1995). This will determine the skeletal composition of a fossil assemblage (Andrews 1990).

Table 1.1 : A summary of modification caused by digestion on molars and incisors (Andrews 1990)**.**

Category	Degree of Modification	Predators
1	Light digestion with only slight penetration of the enamel, and where there is deeper penetration it is localized.	barn owls, snowy owls and great grey owls.
2	Little modification and a light degree of digestion, but enamel is completely removed from the tips of prey incisors.	long-eared owls and some African species of eagle owl.
3	A high degree of destruction and moderate/heavy digestion of the enamel over large parts of the crowns of prey teeth.	tawny owls and European eagle owls.
4	Extreme grades of enamel and dentine corrosion.	smaller sized owls as well as kestrels and peregrines and mammals like viverrid and some mustelids.
5	No modification visible because assemblage is highly fragmentary.	include the most destructive of the diurnal raptors as well as mammals like felids and canids and some mustelids.

1.4.6 SECONDARY BONE MODIFICATIONS

Many small mammals are eaten by scavengers and, due to their size, small mammal carcasses that are exposed on the surface are quickly disposed of. The modifications that are produced are very similar to those produced from the initial predation (Andrews 1990). Attempts have been made to distinguish modifications from initial predation and secondary scavenging (Binford 1981; Shipman 1986) but this work has been based on large mammals (Behrensmeyer 1978). The modifications caused by scavenging in a micromammal assemblage are thus difficult to distinguish from those modifications caused by primary predators (Fernandez-Jalvo & Andrews 1992).

Trampling is highly destructive to small mammal bones and causes dispersal soon after death. The effects of trampling on large mammal bones have been described in some detail (Andrews & Cook 1985; Behrensmeyer *et al*. 1986), but there are virtually no records of the effects of natural trampling on small mammal bones due to their extremely fragile nature (Andrews 1990). Studies in Wales on the effects of trampling on owl pellets showed that bones and pellets around owl nests are often exposed to trampling by roosting owls (Andrews 1990). Continuous exposure resulted in a highly damaged and broken assemblage (Andrews 1990).

Recent studies on bone modifications, suggest that striations and puncture marks, previously believed to be the result of scavenging activity,are superficial trampling marks produced from pressure against grains of sediment (Fernandez-Jalvo 1995). The significance of the results from the above studies indicates the complex variables that archaeologists are faced with when assessing the possible causes of bone modifications present in fossil assemblages. It is therefore imperative that all the mechanism involved in the accumulation of an assemblage be identified, as failure to do so may lead to a biased interpretation, and thus any information inferred from this bias may result in an inaccurate interpretation of data.

Weathering comprises all effects of weather on bone, namely physical affects (subaerial weathering) and/or chemical affects (corrosion) (Fernandez-Jalvo 1995) in both surface and subsurface contexts (Behrensmeyer 1978). The rate of weathering reflects how quickly a bone passes through the weathering stages and duration concerns the span of time that a bone is exposed to weathering agents (Lyman 1994). Exposure to weathering agents begins once soft tissues have been removed from bone and the way this tissue is removed determines when exposure begins (Lyman 1994).

The effects of weathering are distinguishable from other types of modification such as digestion through differences in the effects that weathering has on dentine and bone. Weathering can be identified through uniformity and lack of localisation of surface alteration on the bone (Fernandez-Jalvo & Andrews 1992). The different weathering phases identified by Behrensmeyer (1978) are useful in controlling for variation in the accumulation history of individual bones, by studying weathering patterns and spatial distribution in a deposit (Behrensmeyer 1978).

There is evidence for pre-depositional breakage in fossil assemblages (Brain 1981; Avery 2001) and the likely cause of these breakages was thought to be the transport of bone before burial (Andrews 1990). Experiments done by Dodson (1973) and Korth (1979) found that very low water velocities were sufficient to move small mammal bones (Dodson 1973). The earliest evidence of modification was seen to be the disarticulation of the skull bones and the loss of teeth from the mandibles. This was then followed by the perforation of the thin bone of the skull, the mandible, the pelvis

and the scapula but no breakage was evident (Korth 1979). It is therefore possible to distinguish between an assemblage that has accumulated through fluvial agencies and an assemblage from a predator accumulation (Andrews 1990). It is evident that fluvial agencies introduce a measurable bias to any fossil assemblage and it is therefore essential that any analysis of an assemblage of this nature should include a consideration of these biases (Voorhies 1969).

After burial, bones are subject to *in situ* modification through soil and sediment corrosion (Andrews 1990) in a biologically and chemically active environment (Fernandez-Jalvo & Andrews 1992). The type of soil matrix will determine the rate and type of etching visible on the bone surface (Andrews 1990). Root marks may form on the surfaces of bone and may cause corrosion through the action of organic acids (Fernandez-Jalvo 1995). All of these modification mechanisms produce surface modifications that affect the entire bone surface and are thus easily distinguishable from digestion, which is localised in its effects (Fernandez-Jalvo & Andrews 1992).

Collection methods can be an important source of modification, dependent on the sophistication of the technique used during recovery (Andrews 1990). Very often collection methods are not suitable for elements of such a small size, which can result in a skewed sample with smaller species being underrepresented (Avery 1990). Due to the nature of small mammal bone, some form of damage is always likely to occur (Andrews 1990) no matter how careful the technique. Another factor that influences the content of small mammal assemblages is selection bias on the part of the collector selecting for specific skeletal parts (cranial elements) and neglecting to include others (postcranial elements). Dry sieving has been found to be moderately destructive to assemblages of a small and fragmentary nature (Fernandez-Jalvo & Andrews 1992). This technique was found to scratch the surface of small mammal bones and the resulting striations were found to be similar to the patterns of some weathering stages (Fernandez-Jalvo & Andrews 1992). The action of dry sieving was further found to destroy a large percentage of cranial elements, it is therefore important when recovering microfaunal assemblages, to wet sieve the soil matrix in a 500 micron sieve which usually recovers all sizes of small mammal bone (Andrews 1990).

1.5 SUMMARY

Environmental reconstructions are useful in our understanding of climatic changes and the effects that environmental pressures may have on species migrations and biological evolutionary trends (Avery 2001) in early hominids and humans. It is, however, clear that taphonomic and mechanical biases may distort data (Avery 1990) and the effect that this may have on environmental interpretations must be recognised. A useful amount of information can be extrapolated from micromammal remains and it is vital when analysing assemblages that archaeologists realise the utility of combining mechanical, behavioural and ecological data to establish the possible agent responsible for bone accumulations.