The taphonomy of a micromammalian faunal assemblage from the Saldanha Bay Yacht Club: a contribution to the study of the South African west coast palaeoenvironments

Fredrick Kyalo Manthi

A thesis submitted in fulfilment of the requirements for the degree of Master of Philosophy in Archaeology

Department of Archaeology, University of Cape Town

September 2002

Abstract

This thesis provides a broad outline of the effect of taphonomic and ecological processes on the accumulation and transformation of micromammalian faunal assemblages, and the importance of the signatures left behind by these processes in the reconstruction of ancient ecosystems. Micromammalian remains recovered from a rich Terminal Pleistocene site near the Saldanha Bay Yacht Club (SBYC) along the South African west coast have been examined following Andrews' (1990a) procedures.

In the investigation of the effect of taphonomy on the SBYC faunal remains, murids (rodents) and soricids (shrews) have been examined separately and in as much detail as possible. The analyses have shown that the long bones of the soricids exhibit a relatively higher degree of completeness than those of the murids, suggesting preferential preservation of the former. Additionally, soricid jaws have yielded higher minimum number of individuals (MNIs) than long bone counts whereas for murids the opposite is the case. These observations have indicated the need for more taxonomically resolved analyses on the effect of taphonomic processes on micromammalian remains.

Three micromammalian species represented in the SBYC faunal samples (*Tatera afra, Myosorex varius* and *Suncus varilla*) yielded much higher MNI counts than did other species. This reflects the intermediate selective behaviour of the inferred accumulator of the fauna, the barn owl, although the spotted eagle owl has not been completely ruled out. The study of the SBYC micromammalian fauna has underscored the need to integrate both taphonomic and ecological factors in the attempts to infer potential predators that might have been responsible for the accumulation of microfaunal occurrences. This is also necessary for understanding the environmental contexts in which the fauna was accumulated and/or derived. The micromammalian species represented at SBYC have suggested that in the SBYC area some 15,000 years ago, there was a mosaic of microhabitats including well-vegetated and moist microhabitats, and an admixture of bush and sandveld. Overall, climatic

conditions in the SBYC area when the microfauna accumulated were moderate, and generally not different from the conditions prevailing today.

Acknowledgements

I would like to thank my supervisors Prof. John Parkington and Dr. Margaret Avery for their guidance, encouragement and their immeasurable patience especially in reading the many drafts that preceded this thesis. I am greatly indebted to Assoc. Prof. Andrew Smith of the Archaeology Department at the University of Cape Town (UCT), for his encouragement and support throughout my studies. I extend my gratitude to Cedric Poggenpoel of the Department of Archaeology, UCT, as well as Prof. Tim Dunne and Jaqui Sommerville of the UCT Department of Statistical Sciences, who helped me in various ways. I would like to thank Dr. Stephan Woodborne of QUADRU at the CSIR in Pretoria, for providing the radiocarbon date for the SBYC fauna. A word of thanks goes to my colleagues in both the UCT Archaeology Department and the Earth Sciences Division at the Iziko South African Museum, for their assistance and encouragement at different times. Special thanks are due to Dr. Dave Roberts and Thalassa Matthews for their kind assistance and encouragement in the course of this project.

I am greatly indebted to the administration of the National Museums of Kenya (NMK), particularly the Director-General, Dr. George Abungu, for the support I have received throughout my studies.

I would like to thank Prof. Frank Brown of the University of Utah (USA) and Dr. Meave Leakey of the National Museums of Kenya for their very kind support and encouragement throughout my studies. A word of thanks is due to my colleagues in the Division of Palaeontology, NMK, for their encouragement.

Very special words of thanks go to my wife Grace and daughter Mercy for their love and encouragement, as well as endurance throughout the many years I have been away from them. My parents Anne and Anthony, together with my siblings, all deserve special thanks for their love and encouragement throughout my studies.

This study has been made possible by financial assistance from the Leakey Foundation. I am most grateful to the Trustees of the Leakey Foundation for awarding me the Baldwin Fellowship for this study and earlier studies. I gratefully acknowledge the financial support extended to me through the Wenner-Gren Foundation Fellowship at the University of Cape Town.

This thesis is dedicated to:

Grace and Mercy – I thank you so much for your great love and endurance

Anne and Anthony – I thank you so much for your wonderful parenting

Table of Contents

CHAPTER THREE

The agency of micromammalian faunal accumulations

CHAPTER FOUR

Taphonomic processes affecting small mammal remains

CHAPTER FIVE

The relationship between taphonomic and ecological analyses in the interpretation of micromammalian faunal assemblages

CHAPTER SIX

Material and methods

CHAPTER SEVEN

Results

CHAPTER EIGHT

Discussion

CHAPTER NINE

Conclusion

List of figures

List of tables

CHAPTER ONE

Introduction

1.1 Background

At many fossil sites including important African Pleistocene localities there are substantial accumulations of microfaunal remains. Because of this, the impetus to study microfauna and more particularly small mammal remains has increased over the passage of time. This has been born out of the realization that small mammal remains have the potential to offer information about palaeoenvironments, site formation processes and a wide range of taphonomic processes to which the remains would have been subjected (Avery 1982, 1987, 2001; Andrews 1990a; Fernandez-Jalvo and Andrews 1992; Fernandez-Jalvo 1995). Additionally, there has been an increasing interest in understanding the environmental contexts in which our early ancestors evolved (e.g. Avery, 1987, 1995, 2001; Black and Krishtalka 1986; Vrba 1989; Wesselman 1995). For these reasons, this research project investigates the taphonomic and ecological aspects of micromammalian faunal remains from the Saldanha Bay Yacht Club site (SBYC), with the intention of making some contribution towards the understanding of the effect of taphonomic processes on micromammalian fauna, as well as enhancing the understanding of the South African west coast palaeoenvironments.

1.1.1 The site

The SBYC site is located on the southwest sheltered extremity of Saldanha Bay (33° 01' S; 17° 56' E), approximately 150 km northwest of Cape Town (see Figure 1.1.1). The site, situated about 7 m above sea level, was chosen for investigation primarily because of the abundant micromammalian remains eroding down a relatively gentle slope. For the purpose of sampling and analysis, the site has been arbitrarily divided into three sampling units namely, Down Slope, Upper Slope, and the Hanging Remnant. The first two units are on the slope on which overwhelmingly large accumulations of microfauna are eroding, whereas the Hanging Remnant is a small

remnant outcrop with micromammalian fauna that are loosely cemented and appear to be largely *in situ*. A radiocarbon date derived from micromammalian remains taken from a section in the Upper Slope has placed the fauna at about 15,540 ± 70 years B.P. (GrA 18075, S. Woodborne, pers. comm., 2001).

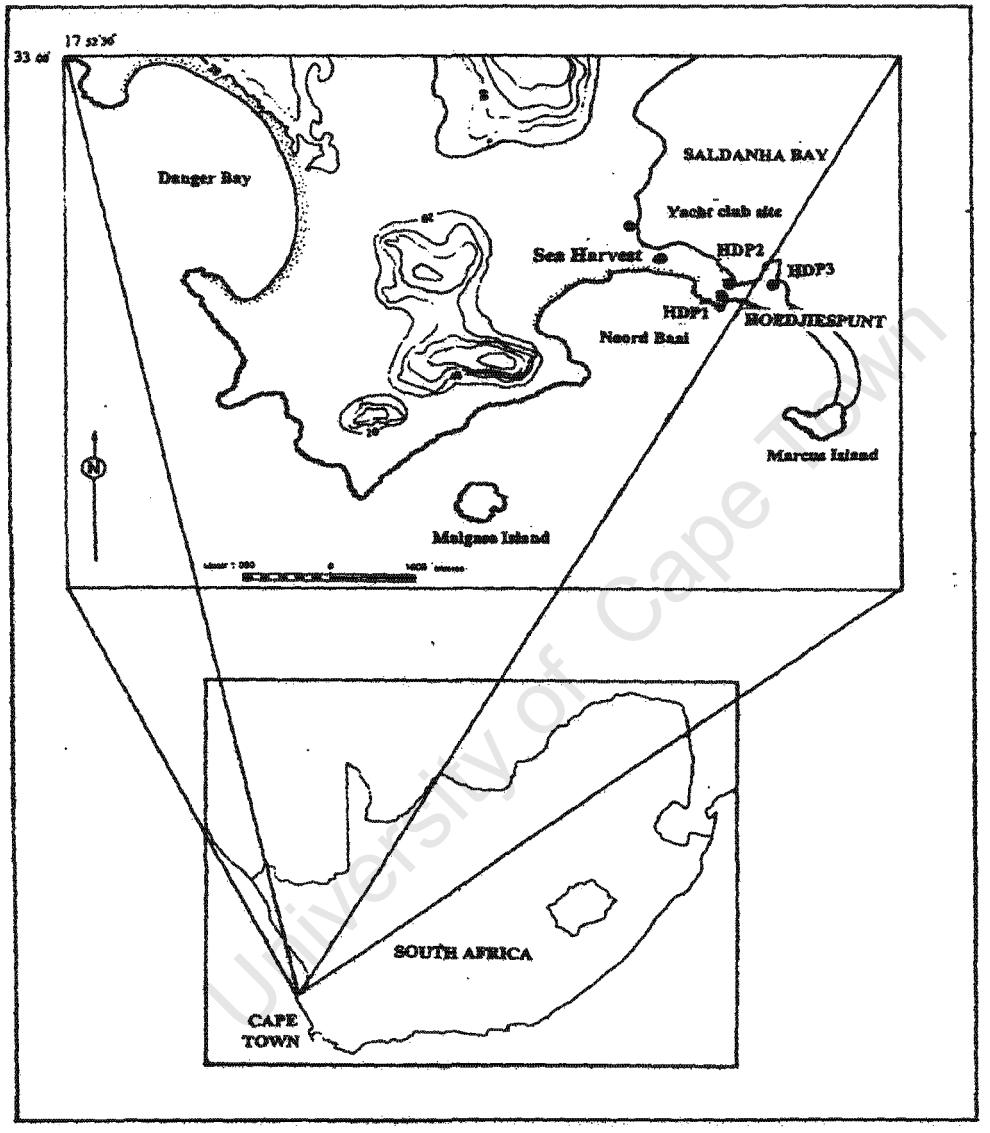

Figure 1.1.1: A regional map showing the location of the SBYC site (information supplied by Cedric Poggenpoel)

1.1.2 Past and present environments

Although a number of scientists have been aware of the microfaunal accumulation at SBYC, no prior palaeontological investigations have been conducted at the site (J. E. Parkington, pers. comm., 2002). For this reason, it has not been possible to find any literature about the site. The geological setting and also the past and modern environments of the site will therefore be given in relation to the general setting of the Saldanha Bay area, as well as the nearby Langebaan area.

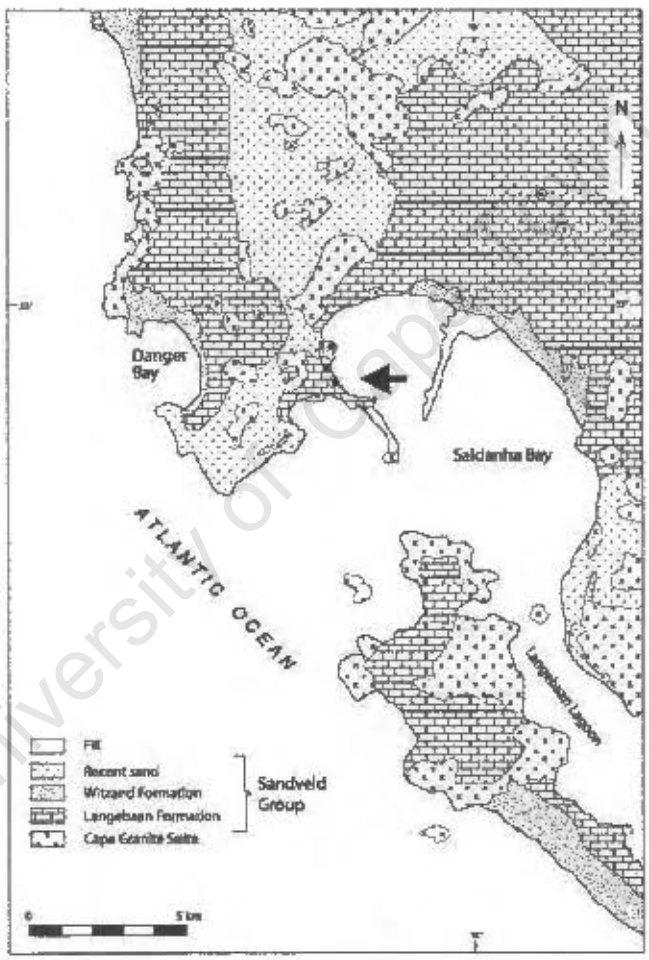

Figure 1.1.2: A map showing the geological setting of the Saldanha region (arrow shows the location of the SBYC site: information supplied by Dave Roberts)

SBYC lies in the Langebaan Formation (Figure 1.1.2), which comprises calcified biocalc-siliciclastic arenites of aeolian origin, with interbedded calcretes representing

palaeosols (Knox 1977; Roberts, In press). According to Du Plessis and De La Cruz (1977), the biogenetic deposits also contain a substantial amount of quartz, and show cross-bedding in some areas but not others. The deposits are believed to have accumulated over a considerable time during the middle or the late Pleistocene (Hendey and Deacon 1977; Knox 1977: 657; Parkington 1999). Most of the Langebaan Formation was deposited during the marine transgressive episodes or in the early phases of regression (e.g. Rogers 1986; Pether *et al.* 2000). According to Flemming (1977), sediment distribution in the area is controlled by waves, and this is mainly determined by the energy level and the refraction patterns of the waves. Echoing Flemming (1977) but not referring to the Saldanha Bay area, Lyman (1994) has noted that coastal blown sand may be deposited in the surrounding areas, as long as the areas lack surface vegetation. Similarly, deposits of blown sand and organic remains such as shell may also accumulate in coastal areas characterized by broad shallow coastal zones or bays (Lyman 1994). It is believed that the calcareous deposits in the Saldanha Bay area developed into a caliche profile and calcrete ridges which over the passage of time formed the hard and strongly indurated surfaces of calcrete that characterizes the whole area (Knox 1977: 657; Low and Pond 2001).

Although climatic conditions in the Saldanha region during much of the Upper Pleistocene were generally cooler than those of today, the later Pleistocene fauna in the Saldanha region were essentially the same as the modern (Hendey and Deacon 1977). According to Parkington (1999), faunal remains occurring in most of the aeolian deposits (calcretes) along the South African west coast are later insertions into the earlier sedimentary deposits. As owls, and more particularly barn owls, prefer to roost under rocky ledges (Steyn 1982), the "continuous pavements of indurated caliche" (Knox 1977: 661) would have provided roosting sites for not only owls, but also other animals (e.g. Parkington 1999).

Currently, the Saldanha Bay area lies within the range of the Thicket Biome of South Africa (Lubke 1996). The Thicket Biome, although not formally recognized as a biome (Lubke 1996), comprises a mosaic of smaller vegetational zones that include the Dune Thicket, which characterizes the Saldanha Bay area (see Figure 1.1.3).

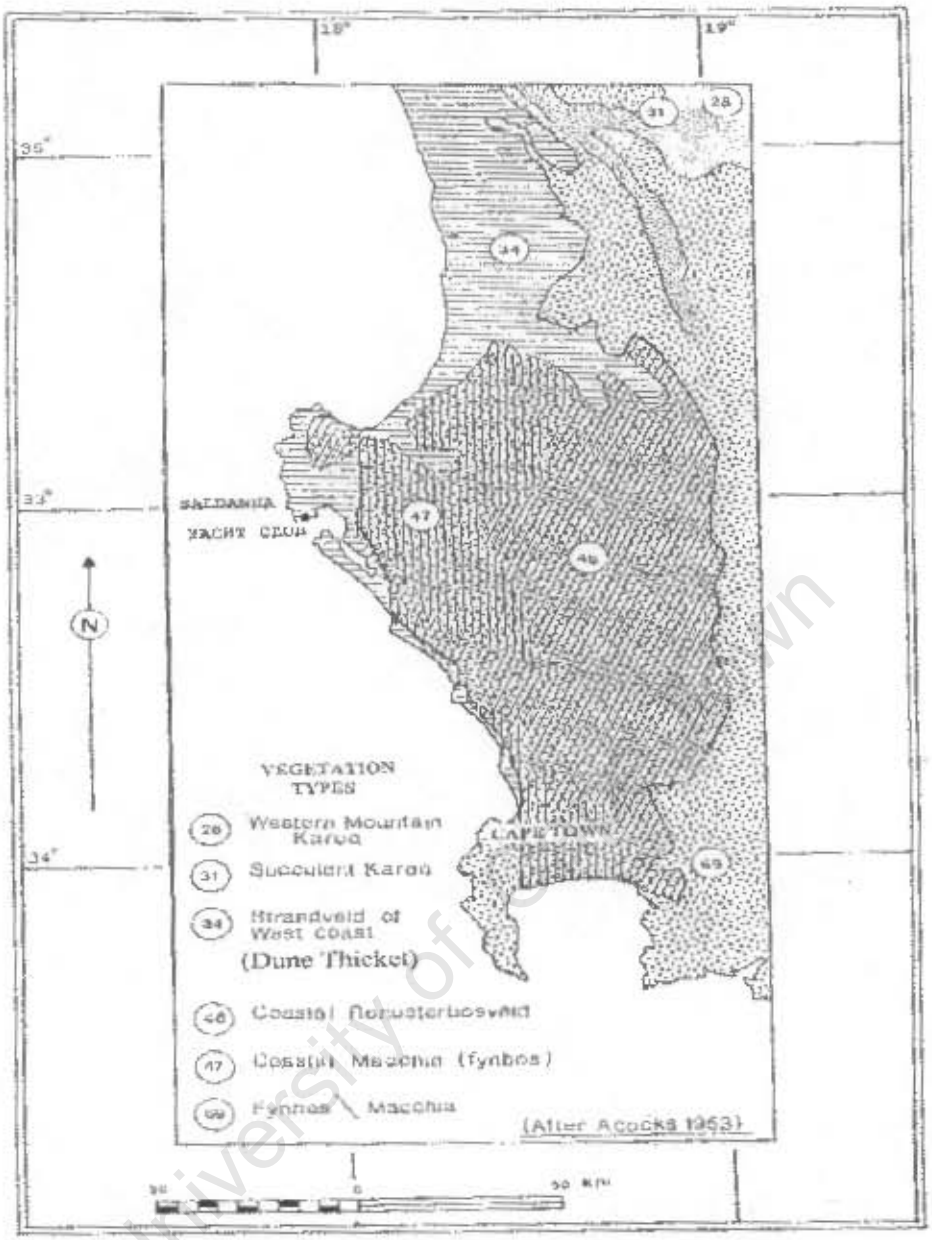

Figure 1.1.3: A map showing the current biomes along the South African west coast (information supplied by Cedric Poggenpoel)

Dune Thicket, comprising dense thicket (e.g. shrubs) stretches from the Western Cape into the KwaZulu-Natal. The region is fairly mesic and is characterized by dunes of altitudes up to 30 m (Lubke 1996). Although the biome lacks the vegetation height and the numerous strata below the canopy that are normally associated with the Forest Biome, it has vegetation ranging from closed shrubs (such as *Rhus glauca* and *Tetragonia spicata*) to dwarf forests, with evergreen, sclerophyllous or succulent

trees, shrubs and vines, many of which have stem spines. These vegetation types tend to replace forest in most areas (Boucher and Jarman 1977; Lubke 1996). According to Low and Pond (2001), the flora in the Saldanha Bay region is mainly restricted to the calcrete and calcareous sands, and is home for some 297 endemic floral species. These species range from limestone shrubs to floral species occupying the stable (e.g. *Pterocelastrus tricuspidatus*) and the unstable (e.g. *Eriocephalus racemosus*) dunes in the Saldanha area (Low and Pond 2001). Inherent in the Thicket Biome area including the dune thicket, are a few endemics, which are predominantly succulents with a Karoo origin (Lubke 1996). Because of the presence of such vegetation types that are characteristic of other major biomes, the Thicket Biome has often been referred to as a "transitional thicket" (Lubke 1996: 14). In some places, the distribution of the dune thicket is confined to a relatively narrow area along the beach (Lubke 1996). Over the passage of time, however, the distribution of the dune thicket in the neighborhood of the SBYC has been disturbed by human activities. Low and Pond (2001) have indicated that modern human activities such as mining and dust-production by factories such as the Saldanha Steel facility may be destabilizing the plant communities around the Saldanha area. This may happen when dust influences the photosynthetic processes of some plant species. Boucher and Jarman (1977) have also indicated that over a long period of time man has greatly influenced the vegetation in the Saldanha area.

The soils in the Saldanha area and the Thicket Biome as a whole are predominantly deep regic dune sands, together with pockets of granites, calcretes, shales and sandstones (Lubke 1996; Low and Pond 2001). Because of the absence of prominent drainage systems in the Saldanha area, the aeolianites that have developed over time contain relatively high levels of bioclastic carbonates, as major rivers would have helped in diluting the bioclastics (Knox 1977; Roberts and Brink, In press). The granite soils are relatively fertile and support a fairly wide range of vegetation types, including some endemic species. Some of the plant species found in the granite soils include *Tetragonia spicata* and *Zygophyllum morgsana*. Biomass production on the granite soils is, however, impeded by the relatively low rainfall (Boucher and Jarman 1977; Low and Pond 2001). The relatively shallow limestone soils support a number

of plant species, including *Zygophyllum flexuosum, Z. morgsana* and *Senecio floribunda*. The plant communities on the limestone soils are distinguishable from other communities by the high dominance of common species such as *Z. morgsana, Z. flexuosum, S. floribunda* and *Ehrharta calycina*, as well as low occurrence of species such as *Rhus glauca* and *Salvia lanceolata* (Boucher and Jarman 1977).

As detailed in Table 1.1.2, the Langebaanweg area experiences winter rainfall, and receives an average annual rainfall up to about 278 mm. Maximum mean annual temperature in the Langebaanweg area is about 23°C (Weather Bureau 1986; www.weathersa.co.za/climat/Climstats/Langebaan_Stats.html).

Table 1.1.2: Temperature and rainfall data for the Langebaanweg area.

	Temperature		Precipitation
Month	Average daily maximum (°C)	Average daily minimum (°C)	Average monthly (mm)
January	28	15	8
February	28	15	4
March	27	14	11
April	25	12	24
May	21	10	40
June	19	8	41
July	18	7	47
August	19	7	45
September	20	9	24
October	23	10	12
November	25	12	12
December	26	14	10
Year	**23**	**11**	**278**

1.2 Chapter summaries

Small mammals living today in various microhabitats and climatic zones have been well studied which has enabled associations between faunal types and ecology to be inferred (e.g. Kingdon 1974; Southern 1979; Smithers 1983; Avery *et al.* 1990; Skinner and Smithers 1990). It has, however, been demonstrated (e.g. Krebs 1996)

that intraspecific and interspecific relations in small mammal communities are far from simple. With a view to shedding some light on the structures and dynamics in small mammal populations, Chapter Two discusses the interactions within and between modern small mammal populations and their environment, and the influence that these interactions may have on the composition of micromammalian faunal assemblages. It is plausible that the same interrelationships existed among the small mammal species represented in the SBYC faunal samples, and these relationships would have influenced the composition of the faunal occurrence. In addition, Chapter Two further looks into the role that predation and other environmental phenomena play in determining the composition of micromammalian faunal assemblages (e.g. Mellet 1974).

Most analyses of small mammal remains in South Africa (e.g. Avery 1982, 1986, 1987, 1990) and elsewhere (e.g. Marean *et al.* 1994) have concluded that barn owls are the major accumulators of micromammalian remains. Taphonomic analyses of micromammalian remains from Elands Bay Cave, South Africa, have, however, favoured the suggestion that several predators might have contributed towards the accumulation of at least some of the faunal assemblages (Matthews 1999). Elsewhere, Andrews (1990a) and Fernandez-Jalvo and Andrews (1992) have suggested that several predators were involved in the accumulation of the Westbury (in England) and the Gran Dolina (in Spain) small mammal remains, respectively. Although no prior palaeontological investigations have been conducted at SBYC, it has been suggested (J. E. Parkington, pers. comm., 2001) that owls, which are major predators and accumulators of small mammal remains (e.g. Avery 1982, 1992; Andrews 1990a, 1990b; Matthews 1999), would have played a significant role in the accumulation of the SBYC microfauna. In view of the debate regarding the accumulation of small mammal remains, and without making reference to any particular micromammalian faunal site, Chapter Three offers some insight into the different processes through which micromammalian remains may accumulate.

Taphonomic processes such as digestion, trampling, weathering, abrasion, diagenesis, as well as damage through the recovery procedures all cause modifications to bones.

These processes may alter the structure, size and texture of skeletal elements (Behrensmeyer 1975; Andrews and Cook 1985; Bonnichsen 1989a; Marshall 1989; Oliver 1989; Andrews 1990a; Fernandez-Jalvo and Andrews 1992; Fernandez-Jalvo 1995; Reitz and Wing 1999). Once identified, diagnostic signatures left by the different taphonomic processes, which may include etching during digestion, breakage caused by the predators and pedogenic corrosion after burial, have the potential to yield information about the taphonomic history of the fauna. The diagnostic features may, for instance, provide information about the potential predators that would have accumulated the faunal assemblages, and also the environments in which the fauna accumulated or were derived (e.g. Andrews 1990a; Fernandez-Jalvo and Andrews 1992; Denys *et al.* 1997b; Matthews 1999). While borrowing largely from Andrews (1990a), Chapter Four discusses the effect of taphonomic processes on small mammal remains.

Because of the taphonomic and ecological factors that influence micromammalian fauna (e.g. Andrews 1990a), interpreting patterns in micromammalian faunal assemblages may not only be fraught with difficulties but may also result in erroneous interpretations about the communities from which the fauna were derived (e.g. Avery 1990). This is essentially because, depending on the taphonomic and ecological factors that would have influenced the fauna, the composition of fossil assemblages may sometimes differ from the living communities from which they came (Marshall 1989; Andrews 1990a). Andrews (1990a) and Wesselman (1995) have noted that a faunal assemblage may sometimes include representatives from a mosaic of palaeocommunities, all representing different palaeo-habitats. Taking into consideration the wide range of taphonomic and ecological factors that influence micromammalian faunal assemblages (e.g. Andrews 1990a), Chapter Five demonstrates the importance of integrating both taphonomic and ecological factors in the attempts to understand patterns evident in micromammalian faunal assemblages and also in the use of micromammalian remains to reconstruct palaeoenvironments (e.g. Avery 2001).

Investigation of the taphonomic and ecological factors that have influenced the SBYC micromammalian fauna followed procedures outlined in Chapter Six. The patterns that characterize the SBYC microfauna are clearly reported in Chapter Seven, and these include a species list that shows the representation of at least 18 micromammalian species in the SBYC faunal samples.

In South Africa and other parts of the world, micromammalian remains have been used in the reconstruction of palaeoenvironments (Avery 1981, 1982; Black and Krishtalka 1986; Andrews 1990a; Fernandez-Jalvo 1995; Wesselman 1995). According to Wesselman (1995: 356), the use of micromammals as "palaeoenvironmental indicators rests on the principle of actualism, which implies that the fossil taxa had ecological requirements similar to those of the contemporary species they most resemble". The theoretical basis for the use of micromammals as palaeoenvironmental indicators is also predicated on the assumption that climate change brings about change in vegetation, which in turn may affect the dynamics and community structures of small mammals, as small mammals are relatively habitat specific and sensitive to environmental fluctuations (e.g. Avery 1990; Marean *et al.* 1994). Using the SBYC micromammalian fauna as an example, faunas that prefer moist environments with dense vegetation (e.g. *Otomys irroratus*) are, for instance, distinct from faunas that prefer sandy substrates with dry grassland (e.g. *Steatomys krebsii*) and when these distinctions are made, it is possible to correlate and discern ecological zones (e.g. Avery 1992). In view of this, although Chapter Eight is largely dedicated to discussing the patterns (results) observed in the SBYC faunal samples, the micromammalian species represented at SBYC are further used to infer palaeoenvironments in the SBYC area.

The main findings that have resulted from this project are summarized in Chapter Nine, and suggestions on issues that need to be investigated or considered while studying micromammalian fauna are made in the same chapter.

CHAPTER TWO

Biological and ecological factors affecting the composition of micromammalian faunal assemblages

2.1 Introduction

Investigations of modern ecosystems have shown that complex ecological, evolutionary, geological and geochemical processes influence the interactions within and between species in biological communities (Huston 1994). Although it is beyond the scope of a thesis to discuss the processes individually, it is important, nevertheless, to point out that biological parameters such as mutualism, commensalism, predation and competition are at play in all living communities and that these may impact either positively or negatively onto the ecosystems or parts of the ecosystems. The removal or introduction of a particular species in a community or even a change of behaviour in a keystone species such as a predator, for instance, may call for certain readjustments in the community, depending on the role the species played in the dynamics of that community (Nel and Rautenbach 1975; Krebs 1978, 1996; Andrews 1990a; Huston 1994; Reitz and Wing 1999). Disruptions of community dynamics and structures may be followed by new patterns of community organization, gradually leading to stability (Nel and Rautenbach 1975; Krebs 1978).

An accurate interpretation of the communities from which micromammalian faunal remains may have been derived will require an understanding of the dynamics and structures in small mammal communities. This understanding will provide a logical basis on which to interpret the composition of small mammal faunal assemblages, as intraspecific and interspecific characteristics and relationships such as predation and competition, together with environmental factors such as the nature of the substrate, may influence the distribution and dynamics of small mammal populations (e.g. Nel and Rautenbach 1975; Krebs 1978; Krohne 1997; Stapp 1997). It is realistic to surmise that the distribution and the dynamics inherent in small mammal communities will influence factors such as prey availability and vulnerability to predators, and

subsequently the micromammalian remains that appear in predator-generated faunal assemblages.

2.2 The small mammal community

As Krohne (1997) has reported, the quest to document spatial dynamics of micromammalian communities requires an understanding of the landscape. This is largely because it is factors associated with the landscape such as the nature of the substrate and moisture conditions that influence, for instance, plant communities. Plant communities may in turn influence spatial distribution, species composition and also species equitability in small mammal populations (Nel and Rautenbach 1975; Krohne 1997). In addition, Huston (1994) has pointed out that the composition of any biological community will be influenced by many environmental parameters, including productivity. It has been suggested (Inouye *et al.* 1997) that variations in the microtopography may influence the available resources for small mammal populations, as demonstrated by the mounds of soil created by the pocket gopher (*Geomys bursarius)* as it burrows. On the mounds, a mosaic of vegetation types develop, leading to numerous discrete microhabitats (Inouye *et al.* 1997). Investigations by Stapp (1997) have revealed how the microtopographic variations created by the pocket gophers influence the dynamics of the northern grasshopper mouse (*Onychomys leocogaster*).

While acknowledging that each individual as well as species in a community responds uniquely to external factors such as the availability of resources, Stapp (1997) investigated habitat use by the northern grasshopper mouse (*Onychomys leocogaster*) inhabiting short-grass prairie in north-central Colorado, in the United States. Investigations revealed that the grasshopper mouse preferred to live in areas where soil had been disturbed by another rodent, the pocket gopher (*Geomys bursarius)*, which according to Inouye *et al.* (1997) builds extensive underground burrow systems, depositing soil on the surface and forming discrete mounds. These mounds and burrows provided homes for a wide range of arthropod species. The grasshopper

mouse, being insectivorous, showed more preference for the burrows and mounds microhabitats (disturbed soils) than to the shrub and other microhabitats in the vicinity (Stapp 1997).

It is important to point out that the dynamics of any particular rodent species are complex, and intraspecific dynamics and population structures may be influenced by factors related to both the macro- and microhabitats. The climate of a large area, for instance, may affect the vegetation of the microhabitats within that area (e.g. Stapp 1997). As an example, Stapp (1997: 1128) has pointed out that, "although the local abundance of the grasshopper mouse is best explained by the availability of suitable foraging microhabitats, the relationships between these microhabitats and the edaphic characteristics are intertwined". According to Stapp (1997), it would be difficult to separate the roles of the microhabitat and macrohabitat for a wide-ranging species such as the grasshopper mouse. Krohne (1997) has also argued that even within micromammalian populations there are fundamental spatial differences in the dynamics and structures of the individual species and that these may vary from one place to another.

It has further been argued (e.g. Krohne 1997) that, although there may be spatial variations in resources between different habitats, boundaries between habitats are not distinct. This is because factors such as behavioural traits within and between micromammalian species may provide opportunities for competition and differential exploitation of resources, with the better adapted and common species having an advantage over the others (Nel and Rautenbach 1975; Krebs 1978; Krohne 1997). Investigations of habitat heterogeneity and habitat use by rodents in the southern Kalahari have, for instance, shown that, although the micromammalian species preferred different and spatially discrete microhabitats, some species showed a widespread occurrence (Nel and Rautenbach 1975). Among the small mammal populations, *Gerbillurus* sp. occurred in high density in the dune crest habitats and was also widespread in other habitats. The high occurrence of *Gerbillurus* sp. in the dune crest microhabitats suggested that it would have faced little competition from other rodent species in that habitat. On the other hand, the very low occurrence of

Gerbillurus sp. in habitats such as the calcrete riverbank suggested that this species would have been foraging possibly in years of low productivity in resident areas, but not living there. The observations made on the micromammalian populations in the southern Kalahari led the researchers to point out that "the number of species in a habitat reflects the availability of niches, but not the relative carrying capacity of the habitat" (Nel and Rautenbach 1975: 15). It is conceivable that predator assemblages derived from habitats with many niches will tend to yield higher species diversity.

The presence or absence of dispersal corridors may further influence the distribution of micromammalian species (Krohne 1997). Because *Gerbillurus* sp. thrives in sandy substrates, the presence of sandy environments in the southern Kalahari would have provided dispersal corridors for this rodent (Nel and Rautenbach 1975). In fact, Hughes *et al.* (1995) have experimentally observed that there are intraspecific differences in the dispersal and foraging patterns among the Namib Desert gerbils (*Gerbillurus tytonis*), which may be significantly influenced by the nature of the substrate particularly in relation to the size of plant seeds that the gerbils preferred to eat. As the size of the substrate sand grains differed from one microhabitat to another, there was competition for the microhabitats in which substrates comprised sand grains larger than the size of seeds. This was largely because the ability for the rodent to discriminate seeds was higher in such substrates, making foraging more efficient. The more dominant members of this species would have inhabited the microhabitats in which foraging was more efficient (Hughes *et al.* 1995).

It is worth emphasizing that the essential feature of the landscape that will determine the distribution of small mammals is the quality of the habitats and niches in terms of their resources. This is largely due to most individuals or species living in just one microhabitat in a heterogeneous landscape that contains habitat patches of significantly different quality (Krohne 1997). Huston (1994) has argued that the most mobile vertebrates tend to minimize the effect of environmental heterogeneity by concentrating their activities in favourable areas that provide their ecological requirements. By so doing, they convert a heterogeneous habitat into a homogeneous one by feeding and living in a restricted area (Huston 1994).

Also important is the relative behavioural plasticity inherent in small mammal populations. As Halle (1995: 88) has argued, the behavioural traits inherent in most small mammal populations are not "a fixed program", but are flexible and subject to change, depending on particular situations. Investigations by Fenn and MacDonald (1995) on the Norway rats (*Rattus norvegicus)* living near a midden in Oxfordshire have, for instance, revealed that this largely nocturnal rat becomes almost entirely diurnal in summer when red foxes (*Vulpes vulpes*), which are also nocturnal, frequent the midden. This is a predator-avoidance behaviour, which is largely determined by the periodic changes in the foraging behaviour of the red foxes, as the rats revert to their nocturnal activity pattern in winter when the red foxes stop visiting the midden. Similarly, Tamura and Yong (1993) have reported that tree squirrels (*Callosciurus* spp.) living in Ulu Gombak, in Malaysia, have developed anti-predator vocalizations and are able to alert one another through staccato barks when a predator has been sighted. In view of this, it may be stated that, although predation may impact negatively on small mammal populations, most small mammals have developed escape mechanisms and this helps in stabilizing the populations (e.g. Fenn and MacDonald 1995).

In spite of predator-avoidance behaviours among micromammalian species, predation continues to be an important phenomenon that significantly directs and influences the dynamics and structures in small mammal communities (e.g. Krebs 1978). Depending on factors such as the reproductive rate of small mammal populations, the effect of predation in small mammal communities may, however, vary. Observations by Krebs (1996) on the collared lemmings (*Dicrostonyx groenlandicus)* and the tundra voles (*Microtus oeconomus)* at Pearce Point in the western Canadian Arctic have revealed that heavy summer predation on the lemmings by predators such as the red fox (*Vulpes vulpes)* and the rough-legged hawk (*Buteo lagopus*) leads to population decline in the rodent communities. The periodic population decline has largely been attributed to heavy predation in summer that does not correspond with the reproductive rate of the rodents. This is because the rodent populations erupt again in winter when the rodents breed (Krebs 1996). It has, however, been argued (e.g. Krebs 1996) that predation alone may not always lead to periodic fluctuations in small

mammal populations. Experiments by Krebs (1996) showed that the removal of predators from vole populations did not lead to a sharp increase in the populations, suggesting that predation by itself may not have an adverse effect on small mammal populations. It is, nevertheless, widely accepted that predation plays a significant role in determining the composition of micromammalian populations and also the kind of predator assemblages that accumulate from such populations (e.g. Mellet 1974).

2.3 Predator and prey habitats

While acknowledging the complexity of the predator-prey relationships (e.g. Andrews 1990a), attempts to understand these relationships should include the investigation of how they are intertwined to their habitats. This is because the kind of habitats that both the predator and the prey species prefer to inhabit may influence species diversity in predator assemblages. Understanding the preferred habitats for each one of them, as well as their hunting areas is therefore imperative, as these phenomena have been shown to govern to a large extent the distribution of both the prey and the predator species (Krebs 1978; Fernandez-Jalvo 1995).

Predators may prefer to live in certain habitats simply because their prey species occupy those areas. Skinner and Smithers (1990) have shown that servals (*Felis serval*) in southern Africa prefer to live in proximity to water and in areas with good vegetation cover. This may be because one of the servals' main prey species, the vlei rat (*Otomys* spp.), is also known to prefer grassy and swampy areas (e.g. Avery 1982, 1987). Conversely, Andrews (1990a) has pointed out that a prey species from a particular microhabitat may be underrepresented in predator faunal accumulations if the habitat does not fall within the hunting range of the predator. Such a phenomenon has been observed in buzzard pellets where the vole, *Clethrionomys glareolus,* is underrepresented essentially because it prefers microhabitats with dense vegetation, whereas the buzzard favours more open environments (Andrews 1990a).

In spite of the poor understanding of the living/foraging ranges of most predators and its effect on species diversity in predator assemblages, it has been acknowledged (e.g. Mellet 1974; Andrews 1990a) that, depending on the size of their hunting territory, predators may increase species diversity in faunal assemblages by including small mammals from areas that are distant from those where the pellets or scats are deposited. In southern Africa, plasticity in habitat selection has been reported among the small-spotted genet (*Genetta genetta*). This small carnivorous mammal occurs in parts of both the southern Savanna Biome and in the South West Arid Biome, where it utilizes a mosaic of environments (Skinner and Smithers 1990). It is plausible that the plasticity exhibited by the small-spotted genet will influence the composition of faunal assemblages accumulated by this carnivore. As noted earlier in the current chapter, plasticity in the selection of habitats has also been observed among small mammal communities. The pygmy mouse (*Mus minutoides*), for instance, is known to occur in a variety of microhabitats, including the Cape fynbos (e.g. Stuart and Stuart 2001). It may therefore be surmised that plasticity in the ecological requirements of both the predator and prey would bear a significant effect on the nature of faunal assemblages that will result from the once living community (e.g. Shotwell 1955), and that this may be determined by the distribution of both the prey and predator species, rather than by the size of the territory (e.g. Andrews 1990a).

2.4 Predator behaviour

Although a considerable amount of time has been expended in trying to understand the behaviour of the predator and how this influences the accumulation of small mammal remains (e.g. Andrews and Evans 1983), the details of predator behavioural traits are far from being understood (Krebs 1978). This deficit may be associated with a lack of understanding of all the structures and dynamics of any particular community (Chaplin 1971; Krebs 1978). In fact, Delcourt and Delcourt (1991) have argued that no modern ecosystem has completely been investigated and therefore the heterogeneous nature of ecosystems is not fully understood. Actualistic investigations of not only predator but also the prey species, have, nevertheless, yielded interesting

information concerning possible behavioural traits that would also have existed in the past communities (e.g. Andrews 1990a). More importantly, it is worth mentioning that predator-prey systems have co-evolved over the passage of time and that the stability existing in these systems has resulted from this continued and gradual co-evolution (Krebs 1978; DiMichele 1994).

In addition to the many physical peri-mortem and post-mortem processes to which small mammals are subjected, predator behaviour may result in faunal assemblages that may not be a true mirror of the original communities from which they were derived (Avery 1982; Andrews 1990a, 1990b; Matthews 1999). Investigations of both faunal accumulations and modern ecosystems have suggested that predators hunt selectively. Hunting behaviour may be influenced by factors such as prey preference, prey availability and vulnerability, prey daily activity pattern (diurnal or nocturnal), seasonal variations, prey size and prey palatability (Krebs 1978; Vrba 1980; Kemp and Calburn 1987; Andrews 1990a). As a result of these factors, among others, predator assemblages will only represent remains of the prey species commonly hunted or available to the predator.

If all taphonomic factors were equal, faunal assemblages accumulated by the more generalized and opportunistic predators such as the tawny owl will tend to yield high species diversity and to exhibit a relatively high micro-spatial heterogeneity (Southern 1954; Andrews 1990a). On the other hand, faunal assemblages accumulated by specialized predators such as the great-grey owl, which prefers voles and particularly *Microtus agrestis*, will tend to yield assemblages with a relatively low species diversity and low micro-spatial heterogeneity. The barn owl, an intermediate predator that preys largely on the more abundant species while at the same time exploiting other available prey species within a certain size range, tends to yield assemblages with a relatively high species richness. Predator assemblages resulting from barn owls also tend to exhibit a relatively high micro-spatial heterogeneity, although equitability may vary with a bias towards the more dominant prey species (Avery 1982, 1990; Andrews 1990a, 1990b). In spite of the prey selectivity exhibited by predators, it is important to point out that whenever preferred

prey species are unavailable, predators, even the very specialized ones revert to other prey species (Southern 1954; Andrews 1990a).

Another factor limiting the range of species diversity in faunal assemblages will be the maximum prey size particular predators can take (Andrews 1990a; Taylor 1994). Although Andrews (1990a: 28) concurs that there is normally a size bias in all predator assemblages, he points out that there is a generally "predictable size equivalence between the predator and the prey". In view of this relationship, Avery (1988, 1993) has reported that the barn owl preys largely on rodents and insectivores whose average body weight is below 150 g. On the other hand, the Cape eagle owl, one of the largest owls, preys on much bigger prey species than does the barn owl and remains of terrestrial mammals as large as the hare have been found in their nest sites (e.g. Kemp and Calburn 1987). The small carnivorous mammals are also known to take prey of a certain size range. Among the viverrids, the white-tailed mongoose takes prey up to the size of the hare (2.6-5.0 kg), while the small-spotted genet takes prey species between 1-2 kg (Andrews and Evans 1983: 297).

The daily activity patterns of both predator and prey will also have an impact on the species represented in predator assemblages. Largely nocturnal predators such as barn owls are likely to miss diurnal prey species. Avery (1987, 1992) has reported that remains of the predominantly diurnal striped field mouse (*Rhabdomys pumilio*) are usually underrepresented in pellets of the barn owl, which is largely nocturnal. Similarly, the diurnal grass mouse (*Arvicanthis niloticus)* is missing from faunal assemblages accumulated by nocturnal eagle owls in the Serengeti (Andrews 1990a). Behavioural traits in one species may, however, vary from one place to another. Steyn (1982) has reported that in England, the barn owl is known to hunt in dull days as well as at dusk. It is therefore realistic to suppose that these behavioural variations will influence species representation in predator assemblages, resulting in predator assemblages in which both nocturnal and diurnal prey species are represented. Table 2.4.1 summarizes some of the factors that may influence prey intake by predators.

Table 2.4.1: Predators, their preferred habitats and prey species (compiled from Appendix 2).

Species	Habitat & activity pattern	Prey preference
Owls		
Barn owl	open country of all environments, largely nocturnal	selects most dominant species, mainly rodents; also takes shrews, birds, lizards, amphibians and insects
Grass owl	lives entirely on the ground; confined mainly in open but moist grassland, bracken and heath; nocturnal, but may also hunt on overcast days	rodents, mainly the vlei rats; small birds, frogs and insects also taken
Marsh owl	stands of rank grass, clumps of weeds, patches of herbs; a crepuscular	rodents e.g. mice and vlei rats; shrews, insects, frogs, lizards and birds are also taken
African Wood owl	lives mainly in forests, including riverine forests, strictly nocturnal	varied prey, but mainly insects, diet also includes birds, small rodents, shrews and frogs.
Spotted eagle owl	a variety of habitats including open woodland and savanna, nocturnal	varied prey, but mainly birds, rodents, shrews, scrub hares, lesser bush babies, fruit bats also taken
Cape eagle owl	favours rocky ledges and wooded gulleys, and near running water, largely nocturnal, but may hunt at dawn or dusk	primarily hares and dassies, rodents, shrews, and small carnivores, e.g. the genet and the civet also taken
Giant eagle owl	drier areas (e.g. savanna acacia woodland), and also in riverine trees; nocturnal, but may also hunt during the day	wide range of prey species including small monkeys, rodents, shrews, birds, hares and insects
Carnivorous mammals		
African wild cat	wide habitat tolerance, but requires some cover, e.g. underbush, stands of tall grass, entirely nocturnal	murids (e.g. *Mastomys* spp., vlei rats, gerbils) dominate; birds also taken
Bat-eared fox	wide habitat range, e.g. open grassland and woodland, and karoo scrub; diurnal and nocturnal	varied diet, including murids, insects, arthropods, wild-fruits and termites
Black-backed jackal	wide habitat tolerance, but more in drier and open terrain; diurnal and nocturnal	varied diet, including grasshoppers, termites, beetles, murids, reptiles, birds and small antelopes
Cape fox	open country (e.g. karoo arid scrub, grassland, fynbos); mainly nocturnal	varied diet, but mainly invertebrates (e.g. arthropods); mice, reptiles, birds and wild-fruits are also taken
Small spotted genet	mainly open and arid areas; also occurs in woodland savanna; strictly nocturnal	small prey, including murids, hares, birds, reptiles, amphibians
Suricate	prefers open, arid (stony or calcareous) and lightly vegetated habitats, diurnal	mainly invertebrates; birds, mice, reptiles and amphibians also taken
Small grey mongoose	wide habitat tolerance (e.g. forest, open scrub, bushy country fynbos), diurnal	mainly invertebrates; small rodents (e.g. murids), birds, amphibians and reptiles are also taken
Yellow mongoose	sandy substrate on open country, e.g. short grassland, semi-desert scrub, largely diurnal	mainly invertebrates, small rodents (rats and mice), reptiles and amphibians also taken

Seasonal changes in diet and degree of prey consumption have also been observed in some predators (e.g. Steyn 1982). Analyses of tawny owl pellets in the northern

temperate zones have suggested that these owls revert to taking moles and rats during their breeding period around May because it becomes difficult to locate mice in the thick vegetation at that time of the year (Southern 1954). Steyn (1982: 241) has also reported that in the Transvaal (South Africa), barn owls' daily consumption was highest in autumn and winter when the birds breed. Of interest to note is that seasonal behavioural changes in some prey species have made them more vulnerable to predation. The relatively high representation of male root rats (*Tachyoryctes splendens)* at the Enkapune Ya Muto rock-shelter in the Kenyan Central Rift, together with the available behavioural data on root rats, led the analysts (Marean *et al.* 1994) to suggest that male rats would have been heavily predated by the owls during the mating season as they would have left their burrows in search of mates. Andrews (1990a) has also noted that in the northern temperate zones moles are heavily predated by birds of prey as they leave their nests to travel on the surface. Although the above phenomena are ephemeral and may not be detected in the fossil record (e.g. Avery 1982), it is plausible that the individuals and therefore species that are heavily predated will appear in relatively higher proportions in the faunal assemblages.

2.5 The physical environment

Environmental factors may influence the diversity of prey species that will be available to the predator and that may end up in the fossil record. It has been reported (e.g. Krebs 1978; Avery 1990; Reitz and Wing 1999) that environments that are unpredictable and have extreme climatic conditions and little vegetation tend to host relatively low numbers of species. Conversely, it has been suggested (e.g. Krebs 1978; Reitz and Wing 1999) that environments that are generally favourable and enjoy a relatively high productivity tend to have quite high species diversity and finer specialisation of faunas. These statements are based on observations that the tropics host relatively higher biotic diversity than do the temperate regions. This has been attributed to the complexity and the stability of the former regions, which has enabled more species to evolve and diversify over time (e.g. Krebs 1978; Avery 1990; Reitz

and Wing 1999). It is thus reasonable to suppose that predator assemblages from regions that are fairly stable will yield relatively high species diversity.

Because micromammalian populations are relatively habitat specific, fluctuations in environmental parameters such as temperature and moisture level may influence the nature of vegetation cover and other ecological requirements of various species (Avery 1987, 1988, 1990, 1992). As an example, investigations of small mammal populations in a semi-arid site in south-central California revealed that the 1989-1991 drought reduced the small mammal populations (White *et al.* 1996). It is realistic to suppose that such changes in small mammal populations will influence the composition of predator assemblages.

It has been suggested (e.g. Kemp and Calburn 1987) that the nocturnal behaviours of micromammalian species may be influenced by physical environmental conditions. Some rodent prey species such as root rats (*Microtus oeconomus*) are known to show reduced levels of activity at full moon (Halle 1995). According to Kemp and Calburn (1987), these seasonal behavioural patterns are associated with the animals' avoidance of predators. It is realistic to surmise that such behavioural changes may influence the prey species that will be available to the predator, with the possibility of a relatively similar influence on species diversity in the predator assemblages.

While acknowledging the complexity in the relations between species diversity, biotic and abiotic factors, as well as underscoring the fact that environmental changes in the past may have triggered changes in mean population densities, Avery (1982, 1990) has argued that long term fluctuations in the mean population densities would have been caused by large scale environmental phenomena. Avery (1982) has further noted that long-term fluctuations are more noticeable in faunal assemblages than short-term fluctuations. Delcourt and Delcourt (1991) have also argued that on a macro-scale, Quaternary ecology would have been disturbed by large scale environmental changes, while at the micro-level, short term disturbances such as fire, would have resulted in the depletion of the vegetation, decimation of nests or burrows, and consequently the disturbance of community dynamics and structures. The latter proposition by Delcourt

and Delcourt (1991) has been echoed by Marean *et al.* (1994) and Matthews (1999), who have argued that fluctuations in micromammalian populations may be caused by factors that have no direct association with large-scale controls on the natural environment. Marean *et al.* (1994) have, for instance, reported that at Enkapune Ya Muto, the pastoral burning of grassland that took place after 5200 years B.P. would have influenced the decline in the relative abundance of the groove-toothed rat *(Otomys irroratus)*, a small mammal species that prefers thick grassland and bush and finds difficulty in living in areas where grass is regularly burned. Krebs (1978) has also noted that changes in climate and/or other environmental variables may bring about small-scale cyclic changes in the internal dynamics of communities, which would affect aspects of the community such as species diversity. Similarly, Osman and Whitlatch (1978) have argued that any form of environmental disturbance, ranging from changes in environmental variables such as temperature to environmental productivity would affect species diversity, especially at the micro-level. This is because such disturbances would influence factors such as predation and species reproductive rates, which are believed to vary in response to changing environment. The effect of the disturbance to the biotas would, however, be determined by the frequency and magnitude of the disturbance, and habitats that are fairly stable would tend to yield relatively high species diversity (Osman and Whitlatch 1978). It may be argued that the environmental changes mentioned above may have some influence on the prey species that will be available to the predator and subsequently the faunal remains that will reach the analyst.

Although environmental factors may have some impact on small mammal populations, it is worth emphasizing that different species react differently to a variety of environmental parameters and may adapt in response to a changing environment (Krebs 1978). Investigations have suggested that species diversity may be relatively high in unstable environments as suggested by the ability of species such as the southern Kalahari *Gerbillurus* sp. to colonize certain optimal areas, and also exploit other areas in the event of unfavourable climatic regimes in the optimal areas (Nel and Rautenbach 1975). In addition, there are environments that are transitional in nature and therefore host relics of ecological characteristics that are, otherwise, found

mainly in adjacent main zones (Chaplin 1971). Such transitional zones, otherwise called ecotones tend to be homes for large numbers of species that have adapted to living together. Although optimum habitats may be modified by micro-climatic changes, adaptation of the faunas to a variety of micro-vegetation zones enables them to survive in the event of climatic changes (Chaplin 1971). Delcourt and Delcourt (1991) have, however, asserted that the extent of stability in transitional zones depends on the magnitude and frequency of the disturbances, and the effect of the disturbances upon the ecotone can be measured by species turnover in the ecotone. It is, therefore, reasonable to conclude that although environmental changes may cause fluctuations in species diversity, which may in turn influence factors such as predation, faunas do adapt to a variety of ecological requirements and this may enable them to become resilient to certain environmental changes (Krebs 1978; Delcourt and Delcourt 1991). Similarly, even though the regulation of the species pool in any particular community may be influenced by both biotic and abiotic factors, individual species react differently to a variety of environmental factors such as climatic fluctuations, since ecological requirements may vary from one species to another (Krebs 1978; Coe 1980; Bonnichsen 1989b).

CHAPTER THREE

The agency of micromammalian faunal accumulations

3.1 Introduction

Origins of micromammalian faunal accumulations may principally be explained through the scatological and fluvial hypotheses. The scatological hypothesis holds that accumulations of micromammalian remains result from the deposition of pellets and scats by avian and mammalian predators respectively. The fluvial hypothesis states that hydraulic transport plays a significant role in the dispersal and ultimate deposition of micromammalian remains (Mellet 1974; Korth 1979; Andrews 1990a). It may, however, be noted that besides these two processes, there is a wide range of other natural means through which micromammalian fauna may accumulate (e.g. Andrews 1990a). This chapter will discuss the predator-induced mechanisms through which micromammalian remains accumulate, as well as other natural processes that may contribute towards the accumulation of micromammalian faunal remains.

3.2 Predators as accumulators of small mammal remains

A substantial amount of literature and research has implicated predation as the main cause of micromammalian faunal accumulations (e.g. Mellet 1974; Behrensmeyer and Dechant Boaz 1980; Avery 1982; Andrews and Evans 1983; Andrews 1990a; Fernandez-Jalvo and Andrews 1992; Matthews 1999). In acknowledging the role of predation in the accumulation of not only micromammalian faunas but also some reptilian and avian species, Mellet (1974: 349) has argued that most or all microvertebrate faunal accumulations would have passed through the digestive tracts of carnivores. Following their consumption by predators, the indigestible remains of small mammals may be deposited in the pellets of avian predators or in the scats of small carnivorous mammals (Andrews and Evans 1983; Andrews 1990a). The behavioural patterns of the predators determine to a large extent the sites on which micromammalian remains will be accumulated. In southern Africa, barn owls, which are presumed to be the main accumulators of small mammal remains (e.g. Avery 1982, 1992; Avery *et al.*

1990), are relatively catholic in their habitat requirements. These owls may roost or nest in many sites, including fissures with crevices, caves and rocky outcrops in relatively open country (Steyn 1982, 1984; Kemp and Calburn 1987). According to Taylor (1994), barn owl pellets may accumulate in the nesting places when the bird is breeding and at roost sites during other times of the year. Andrews (1990a) has reported that regurgitated pellets may also accumulate at the entrances of caves. In Kenya, the Cape or Mackinder's eagle owl (*Bubo capensis mackinderi*) has been reported to nest on tree stumps (Steyn 1982). Both owls may use the same nesting site for long period, resulting in large accumulation of bones of their prey (Steyn 1982, 1984).

Most small carnivorous mammals predominantly prey on small mammal species (e.g. Skinner and Smithers 1990) and studies have shown that small carnivorous mammals may accumulate micromammalian bones in their scats (e.g. Andrews and Evans 1983). Deposition of scats by small carnivorous mammals will greatly be influenced by the behavioural patterns of the predator. The white-tailed mongoose and the genet are, for instance, known to habitually use certain areas as latrines, accumulating large assemblages of scats (Andrews and Evans 1983). Small carnivorous mammals may also accumulate scats at the entrances to their dens (Andrews and Evans 1983), behaviour that has also been recorded among large carnivorous mammals such as hyenas (e.g. Behrensmeyer 1993).

The important role that predator behaviour plays in determining faunal accumulations cannot be over-emphasised. The effect of behavioural traits on the accumulation of micromammalian fauna has further been demonstrated through the tendency of some predators to cache food. Village (1990) has reported that some diurnal raptors such as the European kestrels and falcons choose when to eat and also cache food for later use. Kestrel caches, which may be stacked in crevices, tend to comprise both micromammalian and avian faunal remains (Village 1990). Among the nocturnal birds of prey, the marsh owls are also known to cache their prey, especially if the prey is in abundance (Steyn 1982; Kemp and Calburn 1987). Similar caching of food for later use has been recorded in some small carnivorous mammals. Observations on Ethiopian wolves (*Canis simensis)* have revealed that these canids sometimes cache their prey in

the vicinity of their dens. This they do by digging a hole and then covering the prey with soil or vegetation (Sillero-Zubiri and Gottelli 1995). If caches are not retrieved, skeletal remains of the prey species may accumulate (e.g. Andrews and Evans 1983). Because predator roosting/living sites have significant influence on the accumulation and preservation of micromammalian remains, Table 3.2.1 summarizes different places where predators roost/live.

Table 3.2.1: Predators and their preferred roosting / living places (compiled from Appendix 2).

Species	preferred roosting/living sites
Owls	
Barn owl	roosts in cavities or crevices in trees, buildings, rocky ledges (e.g. caves)
Grass owl	roosts/lives entirely on the ground, mainly in open but moist grassland
Marsh owl	roosts in stands of rank grass, clumps of weeds, patches of herbs
Spotted eagle owl	roosts in rocky ledges, buildings, hollows in large trees, burrows
African wood owl	lives mainly in forests
Cape eagle owl	favours rocky ledges/fissures and wooded gulleys, and near running water
Giant eagle owl	roosts/lives in savanna acacia (woodland) and also in riverine trees
Diurnal birds of prey	
Black-shouldered kite	roosts mainly in reeds; may also roost in trees; communal roosting takes place
The black eagle	prefers rocky or mountainous environments
Steppe buzzard	lives near agricultural activities such as wheat farming
Lesser kestrel	roosts commonly in areas inhabited by humans, e.g. stands of eucalypts
Carnivorous mammals	
Bat-eared fox	sleeps in burrows, underneath vegetation, or just in the open; defecates near resting places
Black-backed jackal	shelters in holes in the ground, rock crevices, under vegetation cover, among piles of boulders
Cape fox	prefers some cover during the day (e.g. holes in the ground or stands of grass
African wild cat	requires some cover, e.g. underbush, rocky hillsides, hollow trees; droppings are usually buried or deposited at latrine sites
Caracal	prefers plains and rocky hills in open country and open wooded savanna
Small spotted cat	prefers some cover, e.g. vegetation and burrows; also lives in hollow termite mounds
Honey badger	may use rock crevices to shelter; an adept digger and may dig holes in which to live
Striped polecat	shelters in burrows under loose and soft sandy/rocky substrate, amongst vegetation, piles of stones
Cape clawless otter	lives predominantly in fresh and marine waters, may also be found foraging on dry environments e.g. wooded and grassland environments); deposits droppings at latrine sites
Small spotted genet	wide habitat tolerance; may occur in open and arid, woodland, riverine & grassland habitats and also in pockets of rocky outcrops on open plains; droppings are deposited at latrine sites
Large-spotted genet	prefers well-watered habitats, relatively dense vegetation cover; droppings deposited at latrine sites
Suricate	digs its own burrow complexes (warrens), and also lives in burrows dug by other small mammals
Small grey mongoose	prefers dry rocky ground where it shelters, e.g. under vegetation cover, in burrows
Yellow mongoose	shelters in communal burrows; scats get deposited in latrines near the entrances to the burrows

It has further been reported that predator species may live communally in areas such as caves (e.g. Southern 1954). The black-shouldered kites (*Elanus caeruleus*), for instance, regularly roost communally throughout the year (Steyn 1982). Because of communal roosting by some predator species, faunal assemblages representing a wide range of prey species may accumulate, leading to a phenomenon referred to as "predation mixture" (Denys *et al.* 1997b: 58). Andrews and Evans (1983) have noted that communal roosting may lead to pellet or scat clusters containing high numbers of micromammalian individuals and species. Interpretations of faunal accumulations resulting from communal roosting may, however, lead to erroneous conclusions especially in situations where avian predator species with different behavioural traits were roosting together (D. M. Avery, pers. comm., 2001).

It is realistic to suppose that owing to the wide range of sites on which pellets or scats may be deposited, the micromammalian faunas that are preserved and become available later to the scholar may only be a small percentage of what was initially deposited. This is because, as it will become evident in Chapter Four, taphonomic processes influence micromammalian faunas differently, and this may depend on factors such as the chemical composition of the area of deposition (e.g. Andrews 1990a).

3.3 The role of scavenging in the accumulation of small mammal remains

Whereas the accumulation of large mammalian bones by large carnivorous mammals and by large rodent species such as the porcupines has been well studied (e.g. Brain 1981; Marshall 1989; Klein and Cruz-Uribe 1991; Behrensmeyer 1993), there is poor understanding of the role that scavenging plays in the accumulation of micromammalian remains. Shipman and Walker (1980) have, however, shown that accumulation of micromammalian fauna is not limited to mammalian and avian predators alone. They have documented harvester ants (*Messor barbarus)* accumulating small mammal remains in a single ant hill in a farm in Athi Plains, near Nairobi, Kenya. Investigations of this rare phenomenon suggested that there would have been high populations of both the harvester ants and the rodents in the Athi Plains, following heavy rains in the area.

An increase in rodent carcasses would have allowed the harvester ants to augment their seed and grain diet by scavenging on the bits of flesh on the small mammal bones. According to Shipman and Walker (1980), the ant hill yielded 1167 bones and teeth belonging to diverse species that included the pygmy mouse (*Mus minutoides)* and the striped field mouse (*Rhabdomys pumilio)*.

3.4 The role of natural deaths

Small mammal remains are also known to accumulate in natural pitfalls after the animals get trapped and die in the pitfalls (Chaplin 1971; Andrews 1990a). Although there is poor documentation, shafts and fissures have been reported as natural death traps for both small and large mammals (e.g. Chaplin 1971). According to Andrews (1990a), factors such as age and visual acuity affect the likelihood that animals will fall into such traps with species such as some shrews, which have poor eyesight being more likely to fall in pitfalls. The fact that some species are more vulnerable to natural pitfalls than others may imply that the assemblages accumulated in this way will tend to yield relatively low species diversity (Andrews 1990a). In view of this, the low frequency of micromammalian fauna from the otherwise thick level TD8 at Gran Dolina, Atapuerca, Spain, led Fernandez-Jalvo and Andrews (1992) to suggest that these accumulations would have been remains of incidental small mammal deaths.

Catastrophic mortality may also cause the accumulation of small mammal remains. This phenomenon, referred by Chaplin (1971: 153) as death *in situ*, may occur in a number of ways such as burrowing rodents being trapped and killed in their burrows by floods (e.g. Andrews 1990a). Such synchronic and passive accumulations may also result from factors such as hibernation or aestivation deaths as well as animals dying as a result of starvation (Andrews and Evans 1983; Andrews 1990a; Lyman 1994). Although such occurrences may be rare in the fossil record (Andrews 1990a), "catastrophocenosis assemblages" (Denys *et al.* 1997b: 63) accumulated during such short periods usually represent single events. The time and the faunas sampled, therefore, may yield distorted information about the palaeoecosystems from which the assemblages were drawn (Vrba 1980; Andrews 1990a; Denys *et al.* 1997b). In fact, Andrews and Evans (1983) have

noted that catastrophic assemblages such as those associated with aestivation may comprise a single species only and, because of that, such assemblages provide minimal information about the communities from which they were derived. Conversely, Western (1980), who has studied large mammals, has argued that, as long as the phenomenon was widespread and instantaneous, catastrophic assemblages tend to represent a true mirror of the living community from which they were drawn. It is also important to note that catastrophic accumulations such as those associated with aestivation or hibernation usually yield assemblages with minimal modifications. Such assemblages often tend to yield faunal assemblages with all skeletal parts relatively well represented (Andrews 1990a).

3.5 Transport as an agent of accumulation of small mammal remains

Agents of transport such as water play a significant role in determining the final resting place of faunal remains (e.g. Hanson 1980; Andrews 1990a; Denys *et al.* 1997b). Although it is difficult to determine the effect of transport on the final resting place of small mammal remains largely because of their small size (Andrews 1990a), it is worth noting that this taphonomic process may significantly determine the kind of faunal assemblages that accumulate in particular areas. As Wolff (1975) has indicated, runoff water disperses bones and teeth of small animals much more easily than those belonging to large animals. While referring to large mammals, Behrensmeyer (1975) has also elucidated how, depending on factors such as their shape and density, different bones from different origins may be differentially transported and deposited in a particular sedimentary deposit. Similarly, Korth (1979), who experimented with the effect of water transport on micromammalian remains, has argued that some skeletal elements, because of their shape and density, may be sorted, resulting in their absence in particular faunal assemblages. It is therefore feasible that differential sorting and deposition of skeletal elements, including those belonging to micromammals, may result in the accumulation of biased faunal assemblages. This, according to Korth (1979), may explain the scarcity of some skeletal elements in some faunal sites. This is because, assuming that faunal remains had been hydraulically transported, the sizes of faunal remains found in any

particular environmental context will always tend to be hydraulically equivalent to the sediments of the deposit (Behrensmeyer 1975; Korth 1979). Following Korth (1979), Table 3.5.1 gives the settling velocities of micromammalian remains belonging to three species, a shrew (*Sorex* sp.), a mouse (*Peromyscus* sp.) and a squirrel (*Sciurus* sp.). Table 3.5.1 shows that skeletal elements are differentially dispersed and this may vary within and between species.

Table 3.5.1: Experimentally determined settling groups of some small mammal remains (After Korth 1979, Table 3).

Genus	I (low)	I/II	II	II/III	III (high)
Sorex					
		atlas	calcaneum	molar (M_2)	mandible
			astragalus		skull
			femur		
Peromyscus					
	rib	metatarsal	maxilla +	molars	tibia-fibula
	scapula	lumbar vert.	calcaneum	maxilla-	
	phalanx	atlas	astragalus	incisors	
		radius	skull	mandible	
		ulna	humerus		
		pelvis	femur		
Sciurus					
		skull	astragalus		tibia
		atlas	calcaneum		mandible
			scapula		
			molar (M^2)		
			femur		

Denys *et al.* (1997b) have shed further light on the nature of faunal assemblages that may accumulate subsequent to transport. They have reported that transport into a channel may form a faunal assemblage with relatively high species diversity, representing a relatively high ecological heterogeneity. This is because through transport, faunas from a wide range of habitats may be deposited together. If such an accumulation takes place over a long period, this results in a phenomenon known as "taphonomic time-averaging" (Behrensmeyer 1993: 402). Such diachronic assemblages may be associated with active large-scale phenomena such as fluvial transport (Lyman 1994). Time-averaged occurrences, however, tend to yield faunal assemblages whose origins are difficult to

determine (Andrews 1990a; Denys *et al.* 1997a). As Andrews (1990a) has pointed out, ecological interpretations from such faunal assemblages can be achieved through taphonomic and microstratigraphic analyses of the faunas. Similarly, an understanding of the depositional and environmental contexts of the site may provide crucial leads that can help in understanding the origins and history of the fauna (e.g. Denys *et al.* 1997a). The importance of understanding the depositional contexts has been demonstrated by Fernandez-Jalvo's (1995) investigations of the micromammalian fauna from La Trinchera de Atapuerca, in Spain. An understanding of the sedimentological context of La Trinchera de Atapuerca helped in the interpretation of the micromammalian fauna, enabling aspects such as the environment at the time of deposition to be discerned (Fernandez-Jalvo 1995). It is therefore important to stress that while investigating the mode of faunal accumulations and the subsequent processes that may have affected the assemblages, understanding the depositional and/or geological contexts is a prerequisite, if a true image of the past is to be realized (Oliver 1989).

CHAPTER FOUR

Taphonomic processes affecting small mammal remains

4.1 Introduction

The faunal samples that reach the analyst are relics of many taphonomic processes. These processes may alter aspects of the fauna such as their shape and chemical composition, leaving faunal remains that essentially differ from their original form. The taphonomic processes start at the time of death and consumption of small mammals and continue after the indigestible skeletal remains have been deposited in the pellets of avian predators or in the scats of small carnivorous mammals. Prior to their burial, micromammalian remains, like their large mammalian counterparts, may be modified by a wide range of taphonomic processes which may act either dependent on or independent of each other. Following burial, further modifications take place, and this may continue until the fauna are recovered by the excavator. Depending on the recovery methods employed, the bones may further be modified during this process (Behrensmeyer 1975; Korth 1979; Behrensmeyer *et al.* 1989; Oliver 1989; Andrews 1990a, 1990b; Fernandez-Jalvo 1995). This chapter will highlight the taphonomic processes that affect small mammal remains prior to and after burial.

4.2 Pre-burial processes

The term pre-burial in this discussion refers to the taphonomic processes and modifications that occur prior to the mineralization of faunal remains (Behrensmeyer *et al.* 1989). These initial taphonomic processes play a crucial role in the life of faunal assemblages and may significantly influence later taphonomic processes (e.g. Denys *et al.* 1997a).

4.2.1 Modifications caused by predators

Investigations of micromammalian fauna encased in modern pellets regurgitated by avian predators (e.g. Dodson and Wexlar 1979; Andrews 1990a; Avery 1992), as well as modern scats deposited by small carnivorous mammals (e.g. Mellet 1974; Andrews and Evans 1983), have yielded crucial information about the modifications inflicted by predators to the bones of their prey. These investigations have suggested that predators modify the bones of their prey differently, and this may depend on factors such as the digestive processes of the predators (Dodson and Wexlar 1979; Andrews 1990a).

Modifications to small mammal bones may start at the time of death (Andrews 1995). It has been reported (Dodson and Wexlar 1979; Andrews 1990a) that a common way of killing prey is either by breaking the neck or piercing the back of the skull. Observations made by Dodson and Wexlar (1979) have revealed that the barn owl holds its prey in its talons, puncturing and damaging the cranium of the prey, after which the prey is swallowed whole. Diurnal raptors including buzzards, falcons and kestrels, whose modifications to the bones of their prey are relatively high, usually kill their prey by their sharp talons, tearing it apart. While feeding, the kestrels hold their prey with their feet, picking flesh off the prey with their beaks, and each small bite causes damage to the bones of the prey (Dodson and Wexlar 1979; Andrews 1990a; Village 1990).

Depending on the predator and its feeding patterns, further modifications may ensue after predators have consumed their prey. This may include digestion, breakage and loss of skeletal elements of the prey. Nocturnal owls, for example, are generally known to swallow their prey whole. Once the prey has been swallowed, the digestive processes separate the nutritious components, leaving the indigestible components that include the bones, feathers and fur. With little dismemberment, the indigestible remains are collected at the bottom of the stomach where they are compacted into pellets and later regurgitated (e.g. Kemp and Calburn 1987; Andrews 1990a). The gastric juice in the stomach causes differential corrosion on the undigested skeletal

remains. The amount of corrosion depends largely on the stomach acidity, as well as the morphology of individual skeletal elements (Andrews1990a; Fernandez-Jalvo and Andrews 1992). Studies have shown that among the owls, the pH of the barn owl's stomach is higher and therefore less acidic than that of many other avian predators. Because of the high pH in the barn owl's stomach most of the regurgitated bones belonging to the owl's prey species are fairly undigested (Dodson and Wexlar 1979; Andrews 1990a).

Depending on the relative size of the prey and predator, differential modifications may occur on prey bones (e.g. Andrews 1990a; Matthews 1999). Investigations of pellets regurgitated by the great horned owl (*Bubo virginianus)* have revealed that bones belonging to larger prey are more broken than those of smaller ones (Korth 1979). Similarly, Dodson and Wexlar (1979) have noted that young owls tend to digest and therefore modify the bones of their prey much more than mature ones. This has been attributed to the need of the young owls to replenish their skeletons with salts in the bones of their prey (Dodson and Wexlar 1979). Overall, as can be seen in Table 4.2.1, barn owls generally cause minimal breakage to the bones of their prey (e.g. Dodson and Wexlar 1979; Andrews 1990a; Matthews 1999).

Modifications of prey bones by small carnivorous mammals may differ from that of avian predators in that the former have teeth that they use to kill and comminute their prey (Andrews and Evans 1983). These predators habitually break and chew their prey and digestion starts in the stomach and continues into the intestines (Andrews 1990a). The prey of small carnivorous mammals are therefore subjected to much more digestion than those of avian predators. The effect of this thorough digestion causes distinctive damage to the bones, such as rounding of exposed edges of bones or the articular ends of limb bones, puncture marks and etching of tooth enamel as a result of acid corrosion (Andrews and Evans 1983; Andrews 1990a, 1990b; Fernandez-Jalvo and Andrews 1992).

Table 4.2.1: Predator breakage categories from least (1) to greatest (5): (After Andrews 1990a, Table 3.16 and Matthews 1998, Table 2.2).

Predator categories

	1	2	3	4	5
Breakage of skulls	BO, SO, LE, GEO, GGO	SE, SEO, EEO, TO	LIT, KES, H	-	MAM
Breakage of mandibles	BO, LE, GEO, GGO	SO, SE, EEO, TO	SEO, KES, H	LIT, MAM	-
Mandibular tooth loss	BO, SO, LE, SE, GGO, EEO	GEO, SEO, TO	LIT, KES, COY, ART, PINE	H, MONG, GEN, BAT, RED	-
Maxillary tooth loss	BO, SO, LE, GEO	GGO, TO	SE, EEO, SEO, BAT, COY	LIT, KES, H, GEN, MONG, RED, ART, PINE	-
Proportions isolated teeth	BO, SO LE, SE GEO, EEO, SEO	GGO, COY, MONG	TO, LIT, BAT	KES, GEN, RED, PINE	H, ART
Post-cranial/ cranial proportions	BO, LE, SE, EEO, GGO, PINE, BAT	TO, GEO, SEO, KES, GEN	H, ART	SO, LIT, MONG, COY, RED	-
Loss of distal elements of Post-crania	BO, SO, LE, GEO, TO	SE, EEO, GGO, COY, ART	LIT, KES	SEO, H, RED	PINE, MONG, GEN, BAT
Breakage of teeth	BO, SO, LE, GGO	SE, GEO, SEO, LIT	EEO, TO	KES, H	MAM
Incisor digestion	BO, SE, SO	LE, GEO, BAT, GGO	EEO, SEO, TO, LIT, PINE, MONG, GEN	KES	H, ART, RED, COY
Breakage of Post-crania	BO, GGO, LE, SE, GEO	SO, EEO	SEO, TO	LIT, KES, H, MONG, GEN, BAT	PINE, ART, RED, COY

Key: BO = Barn owl, LE = Long-eared owl, SO = Snowy owl, SE = Short-eared owl, GEO = Giant eagle owl, SEO = Spotted eagle owl, EEO = European eagle owl, GGO = great grey owl, TO = Tawny owl, LIT = Little owl, COY = Coyote, BAT = Bat-eared fox, PINE = Pine Marten, H = Hen harrier, ART = Artic fox, MONG = Mongoose, GEN = Genet, KES = Kestrel, RED = Red fox, MAM = Mammalian carnivores

In some small carnivorous mammals such as the felids and more particularly the serval (*Felis serval*), bone modification and destruction through digestion is so severe that only the teeth are fairly well represented in scats. Very often, the bones are completely digested and only appear as a powdery admixture bound together with the hair of the rodents that had been consumed (Skinner and Smithers 1990). Among the viverrids, the white-tailed mongoose (*Ichneumia albicauda)* has been reported to cause severe breakage to the bones of its prey, yielding assemblages predominantly represented by the most resistant skeletal elements such as the distal humeri.

Rounding of bones at their edges and bone corrosion are relatively common in micromammalian assemblages accumulated by the white-tailed mongoose (Andrews and Evans 1983). On the other hand, investigations of the small-spotted genet (*Genetta genetta*) have revealed that not all small carnivorous mammals completely destroy the bones of their prey. The small-spotted genet preys on micromammalian species such as gerbils (*Tatera* spp.) and multimammate mice (*Mastomys* spp.). It chops its prey into pieces that can easily be swallowed without much mastication so that small mammal remains found in their scats can be identified (Skinner and Smithers 1990). The effect of comminution among small carnivorous mammals may depend upon the size of the prey relative to that of the predator. Andrews and Evans (1983) have, for instance, reported that the smaller mustelids do not consume prey that are larger than they are but prefer to consume prey with bones that they can easily comminute.

Trampling by predators may cause further modifications to small mammal remains. Although Andrews (1990a) has acknowledged that there is little understanding of the effect of natural trampling on micromammalian remains largely because of their small size, he has reported that owls such as the European eagle owls are known to trample on the pellets in their nest sites, causing a substantial amount of destruction to the small mammal remains encased therein. Fernandez-Jalvo (1995) has also noted that trampling may leave striations and puncture marks on the small mammal remains. As will become more evident when trampling by non-predators is discussed later in this chapter, the effect of trampling on microvertebrate fauna may be influenced by a range of factors, including the hardness of the substrate on which the fauna is resting (e.g. Mellet 1974). It is also conceivable that the effect of trampling on micromammalian remains may also be influenced by factors such as the size of the predator. Because of their weight, large predators are likely to cause more destruction to micromammalian bones than small sized predators.

Modifications to micromammalian bones during and after consumption may therefore be identified through diagnostic features such as breakage and digestion patterns, the presence of superficial tooth marks and rounding or polishing of ends of bones

(Andrews and Evans 1983; Andrews 1990a; Fernandez-Jalvo and Andrews 1992; Fernandez-Jalvo 1995; Matthews 1999).

4.2.2 Modifications resulting from non-predator actions

Following the accumulation of small mammal remains by predators or other agents of accumulation, a wide range of environmental processes shape the faunal assemblages, resulting in ones that may differ from the primary accumulations (Korth 1979; Bonnichsen 1989a; Andrews 1990a; Lyman 1994). The survivability of the bones may be determined by factors such as the chemical and physical properties of the bones, as well as the nature of the environment on which they have been discarded (Chaplin 1971). While acknowledging that different skeletal elements have distinct durabilities in the face of physical environmental processes (e.g. Gifford-Gonzalez 1989b), this section will occasionally borrow from observations made on macromammalian fauna. This will be done with the view to shedding more light on the taphonomic processes other than those associated with the primary predator that may shape the multifaceted micromammalian faunal assemblages. These processes, which may include trampling, weathering and transport may come into play before the faunal accumulations are deposited and buried in their final resting place (e.g. Behrensmeyer 1975).

Depending on the area of deposition, the most immediate modification to mammalian faunas, including those belonging to micromammals, is decomposition. Although decomposition is often associated with the soft tissue, prolonged scavenging by insects tends to accelerate the processes that cause modification to bones. This happens when insect actions result in the disarticulation of skeletal elements, leaving them more vulnerable to a range of sub-aerial processes such as weathering and trampling (e.g. Behrensmeyer 1975, 1978; Korth 1979; Andrews 1990a; Fernandez-Jalvo 1995). The rate of decomposition of bone is dependent upon the chemical and biological properties of the area where the carcase lies (Behrensmeyer 1975; Andrews 1990a). Korth (1979) has experimentally observed that as a result of insect action, small mammal remains in hot climates may disarticulate (if not already disarticulated

by the predator) and start to decompose within a period of eight days. Behrensmeyer (1975), whose focus has been large mammals, has also stated that in humid environments, decay causes the dissolution of the organic material in the bone tissue, while in dry environments, dehydration of the organic material may take place on fresh bones, resulting in cracking and splitting of the bones. Further acknowledging the importance of understanding the effect of decomposition on fossil assemblages, Korth (1979) has noted that the effect of decomposition on faunal assemblages may influence subsequent taphonomic processes that affect faunal assemblages.

Andrews (1990a) has reported further that scavenging by non-predator species may inflict damage on micromammalian bones. Experimentation in which small mammal carcases were deliberately protected from scavenging by diurnal raptors and small carnivorous mammals, revealed that scavenging by shrews caused extensive damage and gnawing to both cranial and post-cranial bones (Andrews 1990a).

Another cause of modification to small mammal bones may be trampling by non-predator species. The effect of trampling on micromammalian faunal remains resulting from species other than the predators is, however, as unclear as the effect of trampling by the predators themselves (e.g. Andrews 1990a). This is largely because the small size and fragility of micromammalian remains make them vulnerable to destruction by a wide range of taphonomic processes (e.g. Western 1980; Andrews 1990a). Hill (1980) has, however, argued that the size of an animal does not always count, as remains of large animals such as the elephant may also be highly modified. The effect of trampling may, nevertheless, vary from one skeletal element to the other and this may be determined by factors such as the intrinsic properties of each skeletal element (e.g. Andrews 1990a, 1995).

Andrews (1990a) has demonstrated that large mammals may cause differential damage to small mammal remains encased in pellets, depending on whether the pellets are wet or dry. Experimentally, Andrews (1990a) has shown that dry pellets trampled by large animals are more resistant to destruction than wet ones, with the former affording more protection to the small mammal remains inside them. The

extent of destruction to the pellets and consequently to the small mammal remains inside them, may also be influenced by the kind of substrate on which the pellets are resting. Those resting on soft substrates tend to be impelled into the substrate with little breakage (Andrews 1990a). Andrews' (1990a) experiments demonstrated that cranial and post-cranial elements may differentially be destroyed by trampling, resulting in almost total absence of the skulls.

The effect of trampling on macromammalian bones (e.g. Andrews and Cook 1985) compare relatively well with Andrews' (1990a) experimental observations on small mammal bones. Andrews and Cook's (1985) studies revealed that on sandy or rocky substrates, the pressure exerted on bones by the feet of ungulates causes damage to macromammalian bones. Trampling on large bones may result in spiral fractures, pitting, scouring, rounding and polishing of the bones (e.g. Behrensmeyer *et al.* 1989; Oliver 1989). The effect of trampling on large bones may be identified through variations in the numbers of scratches and the way they are distributed on the bones as well as the prevalence of superimposed scratches that vary in their orientations (Behrensmeyer *et al.* 1989). Depending on its intensity, the effect of trampling on large bones may depend upon the weathering stage of the bones. Behrensmeyer *et al.* (1989) have reported that relatively unweathered bones tend to show less modification as a result of trampling. While referring to large mammal bones, Hill (1980) has noted that unburied bones that are shielded, for instance, by vegetation are more likely to survive sub-aerial taphonomic processes, including trampling. It is reasonable to suppose that micromammalian remains protected by vegetation may also become buried and therefore protected from sub-aerial taphonomic processes, including trampling (e.g. Andrews 1995).

4.2.3 Mechanical modification

Another taphonomic process that may modify micromammalian remains prior to their burial is weathering. Because of the shortage of literature on the subject, Andrews (1990a) attempted to understand the effect of weathering on small mammal bones by experimenting on barn owl pellets. Barn owl pellets exposed to varying environmental

conditions were left for a period ranging from ten months to two years. It was found that the pellets that had been exposed to weathering on a dry ledge for two years had experienced some weathering, although they were largely intact (Andrews 1990a). On the other hand, the pellets that were exposed to weathering in a damp environment had completely disintegrated after ten months. After further experimentation in which the bones derived from intact pellets were exposed to weathering for 18 months, it was observed that these bones had experienced minimal weathering, including chipping of the molar enamel. Generally, a similar trend of slight splitting and chipping that was evident in the cranial parts was also observed in post-cranial elements such as the femur and the tibia (Andrews 1990a). It is therefore important to point out that the effect of weathering on micromammalian bones may depend on the time of exposure of the bones to the environmental factors that cause weathering and bones that had previously been subjected to some weathering may be more vulnerable than fresh ones (Andrews 1995; Fernandez-Jalvo 1995). Table 4.2.3 summarizes the effect of weathering on micromammalian remains that had been artificially exposed in wet temperate climate.

Table 4.2.3: Weathering stages in small mammal bones artificially exposed in wet temperate climate (After Andrews 1990a, Table 1.3).

Stage	Small mammal bones artificially exposed	Range in yrs.
0	no modification	0-2
1	slight splitting of bone parallel to fibre structure; chipping of teeth and splitting of dentine	1-5
2	more extensive splitting but little flaking; chipping and splitting of teeth leading to loss of parts of crown	3-5+
3	deep splitting and some loss of deep segments or 'flakes' between splits; extensive splitting of teeth	4-5+

Depending on the environmental properties of the area of primary deposition, sub-aerial weathering may introduce changes in the chemical composition of faunal remains (e.g. Andrews 1995; Fernandez-Jalvo 1995). Andrews (1995) has reported that in temperate environments weathering of small mammal bones may cause splitting and decalcification of the bones. Fernandez-Jalvo (1995) has also observed calcite crystal infillings in micromammalian faunal remains from La Trinchera de Atapuerca. The presence of calcite crystals in the bones suggested that they were either deposited during a wet period or were hydraulically transported (Fernandez-Jalvo 1995). Cutler *et al.* (1999) have further shown that large animal bones found in the same occurrence may show variations in the degree of pre-burial weathering. This may be attributed to differences in the intrinsic properties of bones as more compact skeletal elements such as the podials are more resistant not only to sub-aerial weathering but also to other taphonomic processes (e.g. Behrensmeyer *et al.* 1989). It is important to point out that after deposition, small mammal bones cannot withstand long periods of exposure to sub-aerial processes without being completely destroyed and will therefore only be preserved if they have been covered by sediments (Korth 1979).

As micromammalian remains may be dispersed through a wide range of agents, further modifications to the bones may occur. When considering taphonomic processes such as hydraulic transport, which may significantly influence among other factors, the final resting place of bones, it is reasonable to treat faunal remains as sedimentary particles that may be altered by a wide range of geological phenomena that affect other sedimentary particles (Behrensmeyer 1975; Korth 1979; Oliver 1989). Although it is difficult to trace the effect of transport on small mammal remains due to their small size, Andrews (1990a, 1990b) has noted that transport of microfaunal remains by agents such as water may cause damage to the bones.

The dispersal potential of faunal remains, and its effect on skeletal elements may depend upon a multiplicity of factors, including the physical properties of the environment in which the animal died. A skeleton lying in dense vegetation, for instance, is less likely to be dispersed than a skeleton lying on a flood plain. This is

because the vegetation may protect the bones from the extreme hydraulic forces, thereby helping to reduce the effect of dispersal (Behrensmeyer 1975, 1993). Similarly, small mammalian bones transported in a low energy environment such as overbank waters are likely to be less dispersed and modified than those transported in fast moving and high energy channels. High-energy channels tend to disperse bones more, causing relatively high destruction especially to the less durable skeletal elements (Graham 1986). Observations in the Draycott cave system in the U.K. have revealed that small mammal bones deposited in caves show both minimal dispersion and modifications (Andrews 1995).

In an attempt to provide more insight into the hydraulic behaviour of micromammalian remains, and ultimately the modifications caused to microfaunal remains by water transport, Korth (1979) artificially simulated stream action on small mammal bones for 80 hours. He found that there was preferential modification of the bones, with the earliest modification of the skeleton being the disarticulation of the skull bones as well as the loss of teeth from the jaws. As a result of weathering, rounding of the cranial bones that had detached from the crania became prominent and signs of abrasion were evident on the coronoid processes of the jaws. Although breakage did not occur on the major limb bones until advanced stages of the experiment, signs of erosion were evident. The relatively compact bones of the feet, however, showed no clear signs of modification. The experimentation by Korth (1979) further revealed that it was difficult to follow the influence of water transport when bones were being transported at the bottom of the artificially simulated stream. This was mainly because the bones became essentially invisible against the irregular bottom of the stream (Korth 1979: 262). Referring to large bones, Behrensmeyer (1975) has pointed out that bones transported as bed load tend to be more abraded and broken than those transported as suspended load. In general, lack of abrasion on bones may imply that they had not been transported far from their primary site of deposition and that the faunal occurrence may have remained undisturbed (Andrews 1990a).

The level of bone modification resulting from transport may depend on the extent to which preceding taphonomic processes such as weathering, have modified the bone

structurally, with bones that are structurally weak being more prone to breakage. Weathered bones, for instance, having lost much of their organic material, become relatively weak and therefore are easily abraded and destroyed during transport (Behrensmeyer 1975). In view of this, and with regard to small mammal remains, Denys *et al.* (1997a) have pointed out that the examination of modifications caused by taphonomic processes not related to predation must take into consideration how much predation may have influenced the structure of the faunal remains, as the extent of later taphonomic modifications will be influenced by the effect predation has had on the bones. Korth (1979) and Avery (1990) have also stressed the importance of identifying the original source of faunal remains as predation leaves a fairly disarticulated skeleton, more vulnerable particularly to hydraulic transport. It is significant that bones derived from predators such as the barn owls, which cause little modification to the bones of their prey, tend to be structurally strong, and therefore less subject to modification by other taphonomic processes (Andrews 1990a). In addition, Korth's (1979) experiments on the effect of hydraulic transport on micromammalian faunas have revealed that bones belonging to different micromammalian species may differentially be destroyed in hydraulic transport. Observations by Korth (1979) on bones belonging to a vole (*Microtus* sp.) and a mouse (*Peromyscus* sp.), which had been artificially subjected to hydraulic transport, revealed that destruction was more rapid on the bones belonging to the former than those of the latter species. It is therefore reasonable to conclude that during the pre-burial stages, a range of taphonomic factors determine which bones, and ultimately which species, will be available for burial and subsequent fossilisation.

4.3 Post-burial processes

Following Behrensmeyer *et al.* (1989), post-burial processes in this discussion refer to taphonomic processes and modifications that occur during and after fossilization.

4.3.1 Modifications caused by sediments

Although faunal remains are protected from the extreme effect of sub-aerial taphonomic processes following their burial, further modifications resulting from

diagenetic processes may occur, altering the chemical and physical conditions of the fauna (e.g. Andrews 1990a). The sedimentological or depositional contexts on which bones are deposited, buried and mineralised (fossilised) play a significant role in the subsequent history of the bones. This is because different pedogenic environments, depending on their chemical and physical properties modify bones differently (Klein and Cruz-Uribe 1984; Oliver 1989; Andrews 1990a, 1995; Fernandez-Jalvo and Andrews 1992; Fernandez-Jalvo 1995). It has been observed (e.g. Chaplin 1971; Behrensmeyer 1975) that one of the immediate modifications to bone surfaces after burial results from organic decay. The effect of organic decay upon bones may depend on a range of factors, including the chemical properties of the area of burial. Andrews (1990a) has reported that small mammal bones buried under wet pedogenic conditions for a long time become soft and break relatively easily, yielding a very fragmented faunal assemblage. This phenomenon may occur in various environments, including closed environments such as caves. Behrensmeyer (1975) has also noted that when bone is softened by underground water it becomes very weak and therefore breaks very easily. Andrews (1990a) has further reported that bones buried in wet environments tend to accumulate high levels of manganese staining, changing the cortical appearance of the bones. Such changes to the cortical appearance of bones have been observed on the micromammalian fauna from Mumbwa, a Middle Stone Age site in Zambia (Andrews and Jenkins 2000).

Upon burial, the original organic material in bones is replaced by minerals such as calcium carbonate, which not only change the structure of the bones but also help in their preservation or destruction. Modification may result from a range of phenomena, including situations in which bones are caused to "explode by the outward growth of carbonate nodules", a phenomenon that has been observed at East Rudolf (now Turkana), in Kenya (Behrensmeyer 1975: 482). Another phenomenon, post-depositional leaching, has been observed in South African sites. Together with slow sedimentation, post-depositional leaching causes extreme fragmentation of bones (Klein and Cruz-Uribe 1984).

Depending on the sediment type, buried bones may also break as a result of profile compaction (Behrensmeyer 1975; Klein and Cruz-Uribe 1984). Because of the relatively minimal contraction of sand, bones buried in sandy sediments tend to show fairly little breakage. On the other hand, bones buried in clay sediments, whose contraction and expansion is relatively high, tend to be distorted and are often crushed (Chaplin 1971; Behrensmeyer 1975).

Depending on the acidity or alkalinity level of the soils or sediments, a more advanced alteration of bones may result from chemical corrosion. Fernandez-Jalvo and Andrews (1992) have noted that in highly acidic soils, etching by the sediments affects the tooth enamel and, in extreme cases, may also infiltrate bones. High alkalinity causes etching that alters the bone and the dentine more than the enamel. Unlike the localised etching caused by digestion, which tends to be more evident on the tips of incisors, sediments cause etching that affects all surfaces of the bones equally (Fernandez-Jalvo and Andrews 1992; Fernandez-Jalvo 1995).

4.3.2 Biotic-induced modifications

Further modifications to buried bones may result from biological processes such as root action (Fernandez-Jalvo and Andrews 1992; Fernandez-Jalvo 1995). Plants have been reported to leave root marks on bones and, through their organic acids, they may also cause corrosion. The effect of root action may appear as channels that conform to the shape of the roots (Andrews 1990a; Fernandez-Jalvo and Andrews 1992; Fernandez Jalvo 1995). Bone modifications resulting from root action have been observed among the micromammalian fauna from Gran Dolina, where organic acids from roots caused the erosion of bone surfaces and changed the cortical appearance of the bones (Fernandez-Jalvo and Andrews 1992).

Burrowing animals may also contribute towards the destruction of bones, as they churn sediments or soils, disrupting the bones and therefore leaving them weak and vulnerable to other diagenetic processes (Behrensmeyer 1975; Behrensmeyer *et al.* 1989). Fungal action and the activities of micro-organisms such as bacteria may

modify buried bones. These modifications may be localised in any part of the bones (Fernandez-Jalvo 1995). Andrews' (1995) observations on bones deliberately buried in the Overton Down Experimental Earthworks in the U.K. revealed that fungal attack, together with the action of other micro-organisms may differentially modify bones, leaving features such as small-scale grooves on bones.

Pre- and post-burial processes may either act independent of the other or may work together to cause modifications to both unburied and buried bones. In view of this, understanding the microstratigraphy and sedimentological contexts in which fossils are found is very important. Knowledge of these geological conditions will help in the interpretation of both pre- and post-depositional taphonomic processes to which the bones may have been subjected (Klein and Cruz-Uribe 1984; Oliver 1989; Andrews 1990a; Denys *et al.* 1997a). As Oliver (1989) has pointed out, however, one of the main obstacles encountered by taphonomists is the discernment of taphonomic modifications associated with geological and/or depositional processes. This may become more complicated when further modifications to the bones are introduced during recovery processes (Oliver 1989).

4.4 Modifications caused through the recovery methods

Depending on the techniques employed in the recovery of faunal remains, further modifications may ensue from this important stage in the history of faunal remains. Oliver (1989) has argued that retrieval procedures such as excavation may continue to destroy the very record that archaeologists and palaeontologists are trying to understand. Regardless of how carefully the sampling procedures are conducted, sieving, which is the main recovery method for small mammal remains, may cause not only destruction but also loss of some skeletal elements (Andrews 1990a). Payne (1975) has also indicated that, although most fossil sites host a wide range of small mammal remains, many excavators do not suspect their presence. It is, therefore, reasonable to suppose that in such sites, unsuspected breakage will take place, thereby skewing any micromammalian investigations conducted. In view of this, it cannot be

over-emphasised that post-burial processes such as excavation and the associated collection procedures determine to a large extent the kind of faunal samples that will be available to the analyst (Grayson 1984; Reitz and Wing 1999).

4.5 Differential destruction and preservation

Having highlighted the taphonomic processes that influence micromammalian remains, it remains to consider the effect of differential destruction and preservation on faunal assemblages. It is important to note that differential destruction and preservation of skeletal elements may be determined by factors such as the intensity of the taphonomic processes (e.g. digestion) and the microstructure of the skeletal elements (Lasker 1976; Marshall 1989; Andrews 1990a; Avery 1990; Fernandez-Jalvo 1995). Denys *et al.* (1995) have, for instance, noted that the epiphysis of the distal humerus is better preserved than the proximal. This may be associated with the early fusion and development of the distal humerus in most species (e.g. Reitz and Wing 1999). Analyses of remains from the Middle Stone Age Mumbwa Caves in Zambia have also confirmed that the distal humerus and the proximal femur tend to be well represented in micromammalian faunal assemblages (Andrews and Jenkins 2000). Modifications resulting from diagenetic processes may, however, have more severe effect on skeletal elements belonging to mature individuals than to bones belonging to immature individuals. Andrews' (1995) observations on metapodials experimentally buried at Overton revealed that bone degradation was more intense on bones belonging to the mature individual than it was on those of the immature one. Andrews (1995) attributed this phenomenon to the possibility that the mature and more mineralised bones would have been more prone to acid attack than the immature ones.

Studies on predation by Andrews (1990a) have also shown that skeletal elements belonging to different micromammalian prey species are modified differently. Among the insectivores (particularly the shrews) and the rodents, the mandibles of the former rarely break at the inferior border, as they lack the thin alveolar bone that is associated

with rodent incisors (Andrews 1990a). In view of the effect of differential destruction and preservation in faunal assemblages, it may be concluded that species whose elements are more durable, and therefore more often preserved, will stand a better chance of being encountered and/or recovered and that a faunal sample may represent only a small measure of the total species that were actually present (Foote 1992).

CHAPTER FIVE

The relationship between taphonomic and ecological analyses in the interpretation of micromammalian faunal assemblages

5.1 Introduction

As taphonomic and palaeoecological issues are fundamental to any interpretation of micromammalian faunal samples, it is necessary to consider the relationship between them. It is also essential to examine the effect of this relationship on the patterns observed in faunal assemblages, if these patterns are to be used in the reconstruction of ancient environments. This is largely because, as summarized in Figure 5.1.1, the patterns apparent in micromammalian faunal assemblages result from a wide range of taphonomic factors, including breakage and loss of skeletal elements during the recovery/sampling procedures, as well as earlier modifications introduced on bones by both the predator and diagenetic processes. Moreover, ecological factors such as the behaviour of predators to select certain prey species would also have had influence on the patterns evident in micromammalian faunal assemblages (e.g. Krebs 1978; Klein and Cruz-Uribe 1984; Andrews 1990a). In reconstructing ancient environments, attempts should therefore be made to identify and unravel the taphonomic and ecological factors that would have influenced the patterns evident in faunal assemblages. The arrows in Figure 5.1.1 delineate the process that the faunal analyst should follow in the attempt to reconstruct past environments.

It is important to point out that the influence that the collector/analyst may have on patterns evident in faunal assemblages may be fully or partially controllable. Control may be exercised, for instance, through the decisions made during the recovery/sampling and analysis processes. On the other hand, the analyst would have no control over the effect of taphonomic processes that have no direct association with recovery and other associated procedures. This may include modifications (e.g.

breakage) that have resulted from environmental processes such as transport and those caused by the predator. Similarly, patterns in faunal assemblages (e.g. species diversity) that would have resulted from ecological factors such as predator behaviour cannot be controlled.

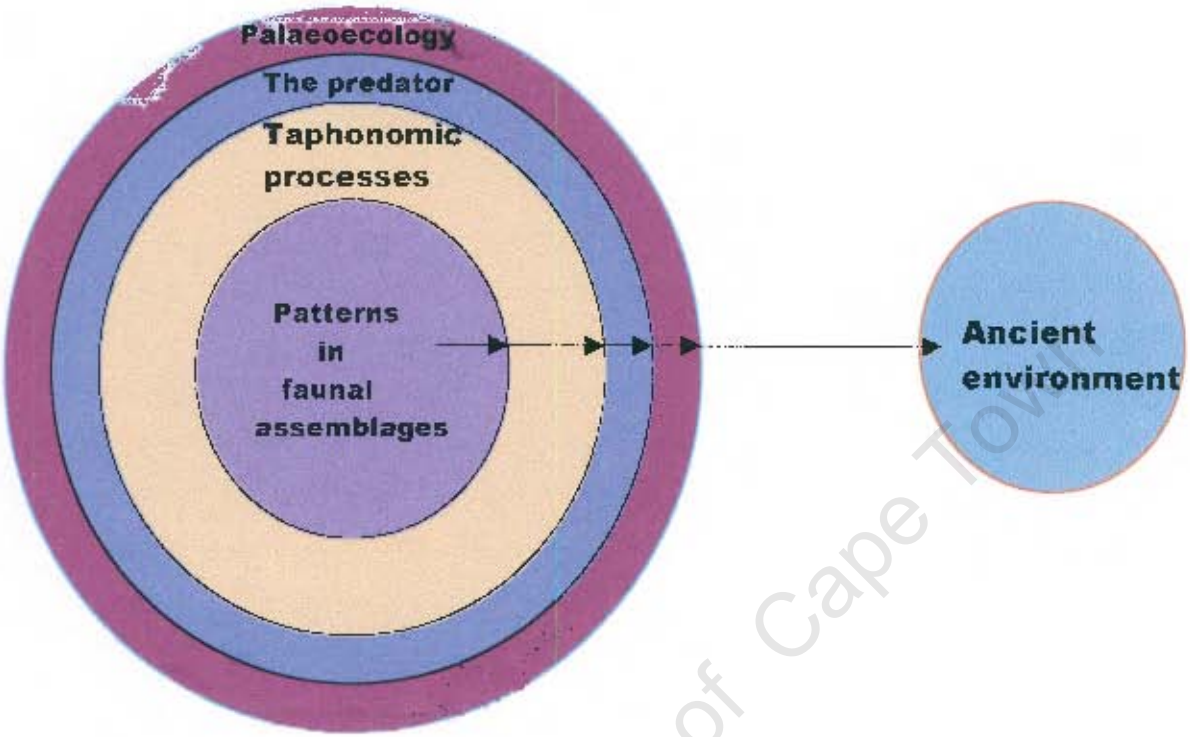

Figure 5.1.1: Factors that influence patterns in micromammalian faunal assemblages

In view of the many obstacles that an analyst is likely to face in the attempt to understand ancient environments (e.g. Figure 5.1.1), Oliver (1989) has stressed the need for taphonomic issues to be sorted out prior to any ecological interpretations of faunal assemblages. In his attempts to demonstrate the importance of micromammalian and macromammalian faunal assemblages in palaeoecological interpretations, Shotwell (1955) also emphasizes the importance of understanding the effect of taphonomic processes on faunal assemblages. According to Shotwell (1955), skeletal elements that are relatively complete suggest that the fauna was deposited in proximity to the habitat of the once living animal and, because of this, the bones had been subjected to minimal taphonomic processes. On the other hand, very fragmented faunas suggest that intense taphonomic processes such as stream action influenced the

fauna and this may have resulted in the deposition of such faunas in sites some distance from the habitat in which the once living individual died or lived (Shotwell 1955).

While appreciating the importance of taphonomic analyses in the reconstruction of palaeoenvironments, Avery (2002) has argued that taking account of mechanical taphonomy (e.g. breakage and acid-etching) alone will not lead to accurate palaeoecological information; taphonomy must be combined with ecological analyses to increase the likelihood of achieving realistic palaeoecological interpretations. Similarly, Andrews (1995) has underscored the importance of understanding the interrelationships between taphonomy and palaeoecology, as past variables, including climate and vegetation will have contributed to past taphonomic processes and hence to the palaeoecology. It may, however, be noted that because of the changing nature of environmental parameters, the effect of taphonomic and ecological processes on the faunal record has changed through time (e.g. Krebs 1978; Gifford-Gonzalez 1989a).

5.2 The changing nature of taphonomic and ecological processes

The actualistic approach employed to understand palaeoecosystems has shed light on the different ecological processes that may have influenced biological communities over the passage of time (e.g. Behrensmeyer 1975, 1993; Andrews 1990a; Avery 1992; Wesselman 1995). Actualistic studies have also provided clues to the taphonomic processes that may have influenced factors such as deposition and breakage of faunal remains (e.g. Gifford-Gonzalez 1989b; Andrews 1990a).

In spite of the regular use of modern taphonomic and ecological analogues in inferring ancient biological communities and their associated physical environmental parameters, the assumption of uniformitarianism has been questioned (e.g. Van Couvering 1980; Gifford-Gonzalez 1989a). The idea that communities and their constituent species as well as environmental parameters have remained constant and linearly ordered over time and that the same biological and physical processes being

observed presently correlate with processes in the past is seen as untenable (Van Couvering 1980; Gifford-Gonzalez 1989a). Following Krebs (1978: 159), "environments in nature are continuously varying; they are never consistently favourable, never consistently unfavourable, but fluctuate between the two extremes". In view of this, although the dependency of faunas on the environment has not changed (e.g. Krebs 1978, 1996; Chapman and Reiss 1992), it is imperative to acknowledge that the environment and its associated parameters have changed over time, and community structures and dynamics, including the biological species, have responded to such changes through processes such as adaptation. The effect of environmental changes should therefore be considered when using modern ecological and taphonomic analogues or patterns to interpret palaeoecosystems (e.g. Krebs 1978, 1985; Van Couvering 1980; Vrba 1980; Andrews 1990a: 29; Delcourt and Delcourt 1991; Reitz and Wing 1999). Similarly, the role played by the human species, which according to Reitz and Wing (1999) has been a factor in promoting environmental modifications, and the impact that this has had on ecosystems, should also be investigated (Chaplin 1971: 145; Delcourt and Delcourt 1991: 15; Reitz and Wing 1999: 306). Steyn (1984) has reported that the specialised habitat required by the grass owl (*Tyto capensis*) in southern Africa has suffered loss or decline and this has been attributed to the effect of human activities. In view of the changing nature of taphonomic and ecological factors, it is realistic to suppose that these changes pose a challenge to the interpretation of patterns evident in faunal assemblages, and generally the reliability of data derived from micromammalian faunal assemblages (e.g. Avery 1990).

5.3 The reliability of data derived from micromammalian faunal remains

Although faunal remains, including small mammal remains, have generally been acknowledged as reservoirs of information relating to the past, the reliability of the information derived from them has been questioned by a number of scholars (e.g. Mellet 1974; Gifford-Gonzalez 1989a; Marshall 1989; Avery 1990). While

acknowledging the potential of faunal remains to yield information about palaeoecosystems, Klein and Cruz-Uribe (1984) have argued that the many taphonomic processes that influence faunal remains can result in loss of some information. Fernandez-Jalvo and Andrews (1992) have also observed that secondary modifications may be superimposed on primary modifications, resulting in modifications to the bones that are unrelated with the cause of death. Additionally, Marshall (1989) has reported mimicry in faunal assemblages, which may result when different taphonomic processes produce similar patterns of modifications. As demonstrated in Figure 5.1.1, it is conceivable that secondary modifications may result from a wide range of taphonomic processes, including the recovery methods employed by the collector/analyst.

As highlighted in Chapter Two and further summarized in Figure 5.1.1, faunal remains will bear a distinctive signature of the behaviour of a particular predator as predators hunt their prey selectively. Before micromammalian faunas are interpreted for palaeoenvironmental reconstruction, it should be acknowledged that the selective behaviour of predators would have influenced the composition of the subsequent predator faunal assemblages (e.g. Mellet 1974; Andrews 1990a). Although one cannot reliably identify and/or quantify the biases introduced by the predator and the wide range of taphonomic processes that influence faunal remains (D. M. Avery, pers. comm., 2002), all these biases significantly influence the faunal assemblage that will be accumulated, preserved, and finally become available to the analyst. Interpretations of such faunas are likely to result in flawed conclusions, such as an averaged and therefore meaningless index of completeness among skeletal elements, especially if remains of some species are underrepresented in the sample because of factors such as an inadequate sample size (e.g. Avery 1984).

5.3.1 Sample size

Although all faunal samples suffer from some bias (e.g. Klein and Cruz-Uribe 1984), it is imperative to note that prior to excavation or any other faunal recovery method, certain decisions must be made by the collector/analyst. These should include the best

way of recovering faunal samples that will provide a relatively clear and valid picture of the original living communities from which the samples were derived (e.g. Payne 1975; Wolff 1975; Avery 1984; Grayson 1984). In fact, the recovery methods should be tailored in such a way that no new biases are introduced (D. M. Avery, pers. comm., 2001). The size of screen used in the sieving of small mammal remains, for instance, will have tremendous effect on the samples retrieved. It is generally accepted that fine sieves tend to recover relatively high numbers of skeletal elements (e.g. Reitz and Wing 1999).

Due to the many factors that influence micromammalian faunal remains, faunal samples will only reflect the number of species in a sediment sample which may or may not be the same as the total richness of the hypothesised community (e.g. Foote 1992). Similarly, a sample will only reflect the faunal remains that reached a certain depositional area and were actually preserved and later retrieved by the analyst (Klein and Cruz-Uribe 1984). Because of essentially these factors, Payne (1975) and Avery (1984) have demonstrated the importance of collecting as large a sample as possible. This is because large faunal samples have a greater potential for yielding high number of identified specimens (NISPs) and minimum number of individuals (MNIs), therefore increasing the possibility of greater species diversity in the sample (Payne 1975; Avery 1984; Grayson 1984; Klein and Cruz-Uribe 1984). Conversely, small samples have less chance of accurately reflecting the proportional representation of each species, and are less likely to include all possible species represented in the faunal assemblage (e.g. Reitz and Wings 1999).

Without completely precluding possible biases in subsequent interpretations, Shotwell (1955) has offered some insights into faunal sampling procedures that will help in ensuring that the number of specimens recovered will be reasonably adequate for palaeoecological investigations. Shotwell (1955) has stressed the need to collect or retain all faunal specimens in a given volume of sediments, including the fragments. The need for not only large samples but also samples with fairly complete skeletal elements may also be emphasized. This is because depending on factors such as the intensity of the taphonomic processes, it is conceivable that relatively complete

skeletal elements will have a greater potential for yielding much more information on the taphonomic history of the fauna than fragmented ones (e.g. Marshall 1989). In view of this, the importance of large samples in all these analyses cannot be over-emphasised, as aspects such as the determination of relative taxonomic richness and equitability, as well as skeletal frequency and equitability may fairly be achieved through relatively large samples. Large samples too, have greater potential to not only include new species but also rare ones (Grayson 1984; Koch 1987; Reitz and Wing 1999). The crucial role that the collector/analyst plays in determining patterns in faunal assemblages therefore continues to be underscored. It is, however, important to point out that the need for a large sample will vary from one faunal occurrence to another and that this will depend on the heterogeneity of the parent population from which the fauna were derived (D. M. Avery, pers. comm., 2002). Interpretations of a faunal sample from a more homogeneous population such as catastrophic assemblage, for instance, may not strictly require a large sample size, as such faunas often represent one or a few species (e.g. Andrews 1990a).

5.4 Micromammalian remains as palaeoenvironmental indicators

In spite of the many taphonomic and ecological factors that influence micromammalian remains, it has become widely accepted that with appropriate caution, small mammal remains are useful in the interpretation and reconstruction of palaeoenvironments (e.g. Kowalski 1971; Avery 1982, 1987, 1993; Thackeray 1987; Andrews 1990a; Reitz and Wing 1999). The recognition of small mammals as palaeoenvironmental indicators is based on the ecological premise that small mammals are relatively habitat-specific and sensitive to climatic and environmental changes that may affect them either positively or negatively, depending on their ecological requirements (e.g. Avery 1982, 1990; Black and Krishtalka 1986).

Small mammals are largely dependent upon vegetation for food, shelter and protection from predators. Because of this, extrinsic factors such as climate tend to affect the structure and dynamics of small mammal communities through their positive or negative impact on vegetation. Rainfall, for example, is known to

influence the vegetation as well as the general biomass of an area (e.g. Nel and Rautenbach 1975; Coe 1980; Avery 1990, 1992, 1993). Because of their great dependence upon vegetation, therefore, small mammals provide indirect evidence for climatic interpretations. The interpretations may be made after discerning fluctuations in vegetation in response to changing environments (Avery 1987, 1993). As an example, the dominance of moist dense vegetation at Boomplaas in the southern Cape some 6200 years ago led to the inference that rainfall may have been an all-year-round phenomenon (Avery 1993). This inference has also been supported by the dominance of Krebs's fat mouse (*Steatomys krebsii)* in the southwestern Fynbos at Byneskranskop since this species is associated with relatively wet summers (Avery 1993). Similarly, micromammalian remains from Klasies River Mouth on the south coast of South Africa have provided a relatively clear sequence of vegetational changes during the Late Pleistocene. The fauna suggest that the environment would have been a mixture of vegetation types comparable with those in modern environment. Because Saunders's vlei-rat (*Otomys saundersiae*) occurs in open vegetation including restioids and small-leaved shrubs, the presence of this species at Klasies River Mouth suggested that the vegetational mosaic during the Late Pleistocene would have included open vegetation associated with Dune Fynbos (Avery 1987). Following Kowalski (1971), the rodent spectrum in faunal assemblages has the potential to offer insights into vegetation fluctuations, including very slight ones. The prominence in faunal assemblages of micromammalian species that are presently known to be generally adapted to extreme but relatively predictable environments may also help in the reconstruction of the palaeoenvironment. Avery (1993: 224) has indicated that because of its breeding characteristics the prominence of the fat mouse (*Steatomys pratensis*) in South African sites may imply that the area received "strongly seasonal but predictable rainfall regime".

Depending on temperature extremes, it has been observed (e.g. Krebs 1978) that the life cycle of mammalian species including micromammals may be impeded, resulting in disruption of important aspects of the community such as reproduction. The Late Quaternary fluctuations in species diversity and equitability in micromammalian fauna in southern Africa have been associated with changes in temperature

(Thackeray 1987). Atmospheric moisture, another key variable in the environment (e.g. Krebs 1978, 1985), is also known to affect small mammal populations. Avery (1982) has, for instance, noted that the broad-niched forest shrew (*Myosorex varius)* is very sensitive to changes in the atmospheric moisture levels and, being an inhabitant of relatively moist environments, would be affected by changes in available moisture. According to DiMichele (1994), however, minor environmental perturbations may not dramatically disrupt biological communities, as some species are able to adapt.

Micromammalian remains accumulated by both avian and mammalian carnivores will tend to offer reliable palaeoecological interpretations (Korth 1979). This is largely because through predation, both avian and mammalian predators sample different micromammalian species and, therefore with all other factors being equal, an assemblage resulting from these predators is more likely to provide a relatively close approximation of the communities from which the micromammalian species were derived (Korth 1979). In view of this, even though micromammalian data will only offer evidence for the subset of the environments within which the predator hunted (e.g. Andrews 1990a), an understanding of not only the habitats from which prey species may have been derived but also those in which the predators lived, will help in deriving relatively accurate interpretations of palaeoenvironments (e.g. Fernandez-Jalvo 1995). By and large, because of the many taphonomic and ecological processes that influence micromammalian fauna, it is worth emphasizing the need to understand patterns evident in micromammalian faunal assemblages, as this will help in reaching more accurate interpretations of ancient ecosystems.

CHAPTER SIX

Material and methods

6.1 Introduction

The material on which this project is based comprises cranial and post-cranial elements of mainly murids (rats and mice) and soricids (shrews), the former being much more abundant than the latter in the SBYC faunal samples. Although Andrews (1990a: 57) has noted that insectivores are much less commonly represented in pellet assemblages, it was felt worth investigating separately the soricids represented in the SBYC faunal samples. Other micromammalian species investigated included the molerats, golden moles, elephant shrews and bats. These micromammalian groups, together with the birds, reptiles and amphibians, are poorly represented in the faunal samples, which explains why they were given little attention.

6.1.1 Specific aims and hypotheses

Because the microfauna at SBYC appears to be eroding down slope (see Figure 6.2.1), one of the main motivations of this study is to determine whether the site represents a single predator faunal accumulation that has been modified subsequently by later processes such as erosion. If this is the case, there should be differences in the representation and condition of bones among the three samples, bearing in mind differences in durability among body parts. These differences will therefore be attributed to the differential effect of taphonomic processes at work during the exposure and down-slope movement of the assemblage. In addition, there should be no significant differences in species composition among the three samples, and because skeletal morphology plays an important role in relative degrees of damage, MNIs based on the same skeletal element should be consistent across taxonomic groups. On the other hand, if several predators were involved in the accumulation of the assemblage, there should be noticeable differences in species composition among the three samples, largely because of the tendency of predators to hunt certain prey species. In addition, although

modifications to skeletal elements subsequent to deposition would have substantially masked the predator-induced modifications, the fauna should also exhibit differences in the levels of breakage and, most importantly etching as a result of predator digestion, because predators differentially modify the bones of their prey.

6.2 Sampling and analysis of the fauna

Two surface samples, termed Upper Slope and Down Slope, were taken from different heights of the slope. A third sample, termed Hanging Remnant, was taken from the believed *in situ* material. In both the Down Slope and the Upper Slope, surface sediments were arbitrarily collected in polythene bags. With the aim of ensuring that minimal damage was caused to the bones, the scooping of sediments into the bags was carefully done with a soft brush and a trowel.

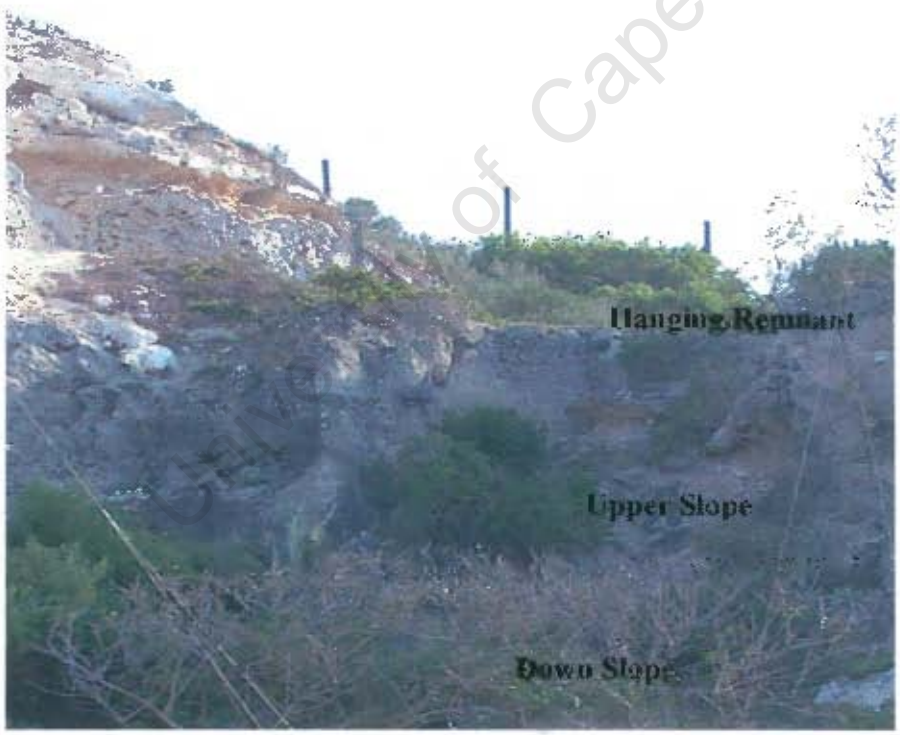

Figure 6.2.1: The SBYC site showing the positions along the slope of the three sampled areas (photo by J. E. Parkington)

Because of the partially cemented nature of the Hanging Remnant (Figure 6.2.2), dental picks were used to supplement the soft brush and trowel. This was done with the intention of extracting sediment samples of relatively the same size as those obtained

from both the Down Slope and Upper Slope, where the loose sediments were easy to sample (see Figure 6.2.3).

Figure 6.2.2: The cemented nature of the Hanging Remnant (outcrop pointed by the arrow: photo by J. E. Parkington)

Figure 6.2.3: The position of the Down Slope relative to the Upper Slope and the loose sediments in both areas (photo by J. E. Parkington)

In the laboratory, two bags of sediment samples from each of the sampled areas were arbitrarily chosen for investigation of the microfauna inside them. These sediment samples were carefully sieved through a 1.5 mm flour sieve, and sorted for microfauna. After sorting, the SBYC microfauna were taken for identification at the Iziko South African Museum in Cape Town, where a comparative collection of modern material was available.

Although every faunal occurrence has its unique characteristics (e.g. Olson 1980), the small mammal remains from SBYC have been analysed following largely the procedures described by Andrews (1990a), supplemented by the work of Matthews (1998), Fernandez-Jalvo and Andrews (1992), and Avery (1982, 1999).

6.3 Number of identified specimens (NISPs)

The number of identified specimens (NISPs) was taken for all skeletal elements represented in the SBYC faunal samples. Because of the fragmented nature of the skulls, a phenomenon that Andrews and Evans (1983) and Andrews (1990a) have also reported, it proved difficult to assign the cranial fragments to any particular taxonomic group, especially in situations where dentition is lacking. Cranial fragments have therefore been counted for each sample, and the few that could certainly be identified assigned to their respective taxonomic groups. The mandibles and the maxillae belonging to murid rodents, insectivores (shrews and golden moles), molerats and bats, were counted and recorded for the three sampled areas. Similarly, loose molars were also counted and recorded. Andrews and Jenkins (2000) have noted that large numbers of incisor fragments may not always indicate their abundance, especially when they are fragmentary. In view of this, because of the large numbers of incisor fragments in the SBYC faunal samples, counts were confined to those incisors that have their tip intact, and were half or more complete. Without separating the rodents and the insectivores, counts were also taken for all post-cranial elements represented in the three samples.

fauna, and more particularly the murids, yielded relatively high numbers of long bones as compared to the jaws, the MNIs derived from the counts of the best represented jaws were further augmented by MNIs derived from the long bones. As Klein and Cruz-Uribe (1984) and Avery (2002) have suggested, the best represented long bone (either from the left or right side) was used to obtain the MNIs in the SBYC faunal samples.

Following Avery (2000), proportional representation of species among the three sampled areas was determined through the Shannon-Wiener index for general diversity, $H= \sum(n_i/N) *LN (n_i/N)* -1$. Here n_i is the number of individuals assigned to each species and N is the total number of individuals in the sample (Avery 2000: 64). Because identification of the micromammalian species represented in the SBYC fauna was based on the jaws, analyses of diversity indices were based on the MNIs derived from the jaws.

6.5 Breakage patterns of the skulls

Investigations of breakage patterns of the skulls were only carried out on the murids and soricids, and not on the rest of the micromammalian fauna in the SBYC samples. As noted earlier, this was largely because the rest of the fauna are poorly represented in the SBYC samples. In addition, because of differences in morphology, it became apparent that the breakage categories developed to suit the large murid and soricid samples (especially the jaws) would not have suited the other fauna without upsetting the categories. It was, however, acknowledged that molerats and golden moles would possibly have exhibited a similar breakage pattern, owing to their similar bone morphology adapted to the burrowing lifestyle (D. M. Avery, pers. comm., 2001).

6.5.1 Breakage of the crania

Andrews (1990a) adapted some categories to define different cranial proportions depending on their degree of completeness. He has, for instance, defined a complete cranium as one that has the maxillae and frontal bones, and approximately half of the cranial vault still intact. Because of the fragmented nature of the crania in the SBYC samples, however, it was difficult to assign them different categories. Most of the cranial portions were therefore counted and assigned to the category of 'cranial fragments'.

Identifiable portions of the cranium such as the zygomatic processes and the auditory bullae were also counted.

Although the available literature (e.g. Andrews 1990a; Matthews 1998) on maxilla breakage does not investigate rodents and insectivores separately, this project attempted to do so. According to Andrews (1990a), the detachment of the maxillae from the cranium is one of the primary stages observable in the breakage of a rodent skull. When this happens, the zygomatic process (see Figure 6.5.1) may remain attached to the maxilla, an aspect that Andrews (1990a) used to investigate maxillae breakage patterns, depending on the retention of the zygomatic process.

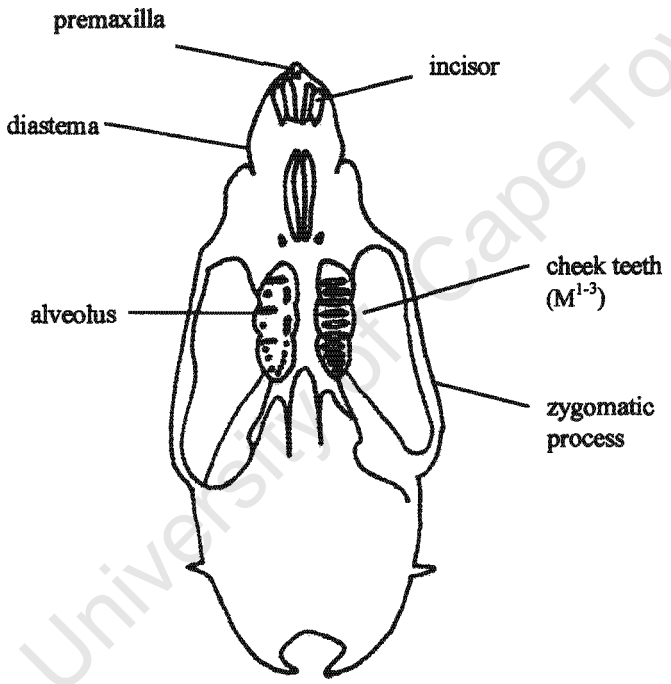

Figure 6.5.1: The ventral view of a rodent cranium showing elements used in the text (labelling after Avery 1982, Figure 7)

Among the SBYC murids, the number of maxillae with zygomatic processes still attached was relatively high, and therefore this phenomenon was used as an important key in the analysis of murid maxillae breakage. The following categories were used:

Category 1 Alveoli (with or without teeth) of M^1-M^3 intact, and a portion of the zygomatic process intact; slight damage on any part of the alveoli was disregarded

Category 2 As Category 1, but zygomatic process missing

Category 3 Alveoli (with or without teeth) of M^1 or M^1-M^2 intact, and a portion of the zygomatic process intact

Category 4 Maxilla fragments; include portions of the premaxilla, and the alveolus of either M^1, M^2 or M^3 or any combination of two of these (with or without teeth)

It was not possible to use the zygomatic process as a key in the investigation of breakage patterns among the soricids. This is largely because, as Meester (1963) has shown, the incomplete zygomatic processes of the soricids (see Figure 6.5.2) posed a difficulty in the analysis of maxillary breakage among the soricids.

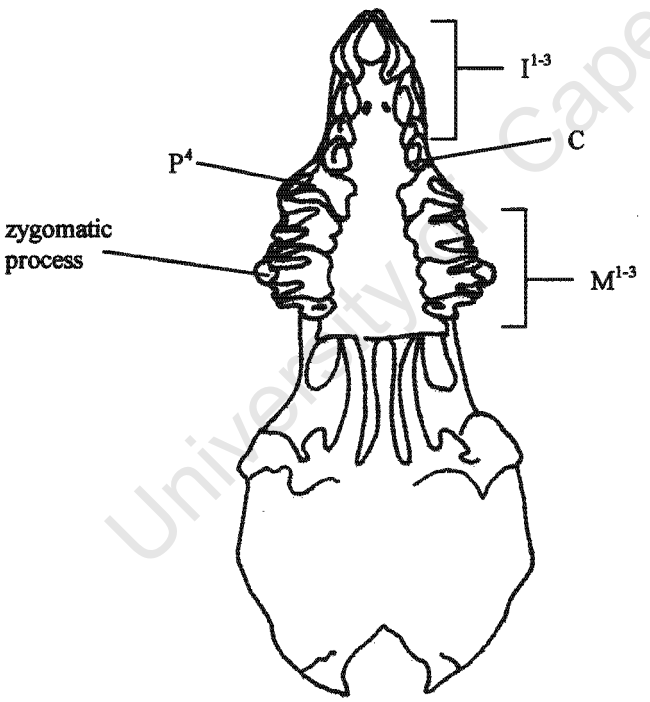

Figure 6.5.2: The ventral view of a soricid cranium showing elements used in the text (labelling after Meester 1963, Figure 12 and text)

Following Andrews' (1990a) and Matthews' (1998) procedures in the analysis of maxilla breakage patterns among small mammals, the breakage of soricid maxillae was investigated mainly by counting the maxillae occurring as part of the cranium as well as

those that were detached from the cranium. The following categories were employed to investigate breakage among soricid maxillae:

Category 1 Left and right maxillae still joined by the palatine bone, with alveoli (with or without teeth) of $I^{1\,2\,3}$: C^{1}: P^{4}: $M^{1\,2\,3}$. These were termed complete, with slight damage on any part of the maxillae disregarded

Category 2 As Category 1, but maxilla detached from the opposite side

Category 3 Alveoli (with or without teeth) of P^{4}-M^{2}

Category 4 Maxilla fragments; include alveoli portions (with or without teeth) of I^{1}-P^{4} or P^{4}-M^{1}, M^{1} or M^{1}-M^{2} or M^{3}

6.5.2 Breakage of the mandibles

Andrews (1990a) indicated that breakage categories resulting from different predators are similar for both rodent and soricid mandibles. While analysing the SBYC mandible samples, however, it became apparent that the breakage categories adopted by Andrews (1990a) and Matthews (1998) required some adjustments to suit the SBYC samples. This was largely because a variety of individual portions of the mandible, and more particularly among the soricids, were fairly well represented in the faunal samples. The breakage categories used by both Andrews (1990a) and Matthews (1998) could therefore not have accommodated all the individual mandible portions in the SBYC samples. A similar phenomenon was also evident among the rodent (murid) mandibles. Due to some differences in the anatomy and morphology of micromammalian mandibles, such as the presence of a diastema in rodent mandibles and not in insectivores (see Figures 6.5.3 and 6.5.4), or the absence in the soricids of the thin alveolar bone associated with rodent incisors (Andrews 1990a: 57), it became necessary to adopt different breakage categories for the murids and the soricids represented in the SBYC faunal samples.

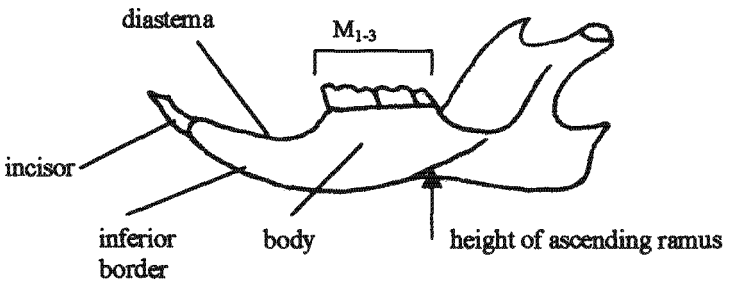

Figure 6.5.3: The lingual view of a rodent mandible showing elements used in the text (labelling after Avery 1982, Figure 7)

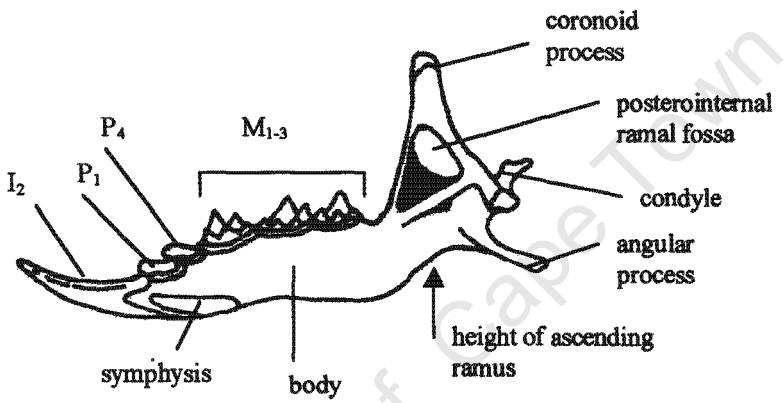

Figure 6.5.4: The lingual view of a soricid mandible showing elements used in the text (labelling after Meester 1963, Figure 14, and Avery 1982, Figure 7)

Following Andrews (1990a: 56) and Matthews (1998: 49), breakage of the murid mandibles was investigated by placing the individual jaws into the following categories, depending on their degree of breakage:

Category 1 Complete mandibles; slight damage on any part of the mandible was disregarded

Category 2 As Category 1, but with ascending ramus missing

Category 3 As Category 2, but with inferior border broken; ascending ramus broken or missing

Category 4 Mandible fragments; include portions of body (with or without teeth) with or without the diastema, and portions of ascending ramus with or without any alveoli

Mandible breakage patterns among the soricids were investigated by grouping them into the following categories:

Category 1 Complete mandibles (with or without teeth); slight damage to the ascending ramus and the anterior part was disregarded

Category 2 As Category 1, but ascending ramus missing; slight damage to the anterior and the posterior part was disregarded

Category 3 Anterior portion with I_2-P_4 missing. M_1 and M_2 may also be missing; ascending ramus intact or slightly damaged

Category 4 Anterior portion with I_2-P_4, and the ascending ramus missing. M_1, M_2, M_3 or any combination of this intact

Category 5 Mandible fragments; include portions anterior to the M_3 (may include the alveoli of I_2 - M_2, with or without teeth), and portions of the ascending ramus without any alveoli.

The above investigations were carried out separately on all jaws from the three sampled areas. No distinction at this stage was made between left and right maxillae and mandibles.

6.5.3 Tooth loss from maxillae and mandibles

According to Avery (1984) and Matthews (1998), determination of the relative number of teeth lost from both the maxilla and the mandible is far from simple. This is because many factors, including the sampling and/or sorting procedures may result in the loss of

teeth. To determine the extent of tooth loss at SBYC, the number of isolated teeth in each faunal sample were counted. This was done without separating the rodent and the insectivore molars, and without the distinction of lower and upper molars.

In this preliminary investigation of the SBYC micromammalian fauna, no comparison was made between the isolated molars and those *in situ*. This was because it was felt that the data obtained from the breakage patterns of the murid and soricid jaws were sufficient to explain the breakage patterns of the jaws.

6.6 Effect of acid-etching

Because of the mineralized nature of tooth enamel, the effect of acid-etching in predator assemblages tends to be relatively higher on teeth than other skeletal elements (e.g. Andrews 1990a). In view of this, this groundwork study investigated the effect of predator digestion only among the incisors. Andrews (1990a) pointed out that among micromammalian species, incisor digestion tends to be restricted to rodents, and different rodent species show less structural differences in the incisors than in the molars. Because of the relatively low numbers of incisors belonging to the non-rodent species in the SBYC faunal samples, only the murid rodent incisors were investigated for acid-etching. The lower incisors were separated from the upper ones as according to Andrews (1990a), there is usually differential incidence of digestion between upper and lower incisors, with upper incisors exhibiting a relatively greater incidence of digestion than the lower ones. The greater incidence of digestion on upper incisors has been ascribed to the higher breakage of the maxillae (Andrews 1990a).

Etching caused by digestion is evident mainly on the tips of the incisors (Figure 6.6.1) and, depending on the predator, may spread along the enamel surface and the dentine of the incisor (Andrews 1990a; Fernandez-Jalvo 1995). For this reason, investigations on acid-etching were only carried out on incisors with intact tips and were half or more complete. Although it is important to note that acid-etching may have been present on other incisor fragments, it is believed that the incisors investigated for acid-etching would provide a clear image on the effect of etching on the SBYC micromammalian fauna.

Figure 6.6.1: A murid incisor showing elements used in the text

Following Matthews (1998: 54), the following categories were used in the investigation of acid-etching among the SBYC murid incisors. A light microscope was used in the investigations and magnifications up to x 40 were employed.

Category 1 No visible etching on the incisor

Category 2 Slight digestion and pitting of the enamel surface (mainly on the incisor tip, but not restricted there); etching has not penetrated the dentine

Category 3 Area of digestion not much greater than Category 2, but etching has slightly penetrated the dentine

Category 4 Much more extensive area of digestion with total removal of the enamel in some areas; underlying dentine exposed and digested

Category 5 Almost total removal of the enamel and extensive digestion of the dentine

6.7 Breakage of post-cranial bones

Investigations of post-cranial breakages started with the long bones, as these are some of the more durable skeletal elements (e.g. Chaplin 1971; Reitz and Wing 1999) that may provide unique information about the taphonomic history of faunal assemblages. Following Andrews' (1990a) procedures, the best represented long bones in the samples, namely humeri, ulnae, femora and tibiae, were chosen for analysis. The fibula, which is

normally attached to the tibia, was not considered in the analysis. This is because, except for a few golden mole tibiae, this very fragile bone was rarely preserved. Due to the relatively poor representation of the radius in the faunal samples, the breakage pattern of this limb bone was not investigated.

Breakage patterns of the soricid and murid humeri and femora of which it was fairly easy to distinguish, were investigated separately. In this exercise, the sides (left or right) of the humeri and femora were also determined. The separate analysis of the murid and soricid long bones was undertaken with the aim of shedding some light on how differential destruction, a phenomenon associated with many taphonomic processes (e.g. Korth 1979; Andrews 1990a), has affected the long bones belonging to the two different taxonomic groups. On the other hand, it proved difficult at this stage to certainly assign elements such as the tibia proximal ends and shafts to taxonomic group. Similarly, it was difficult to certainly assign all proximal ends of the ulnae to taxonomic group. Because of this, the tibiae and the ulnae were at this stage treated as indeterminate micromammalian remains.

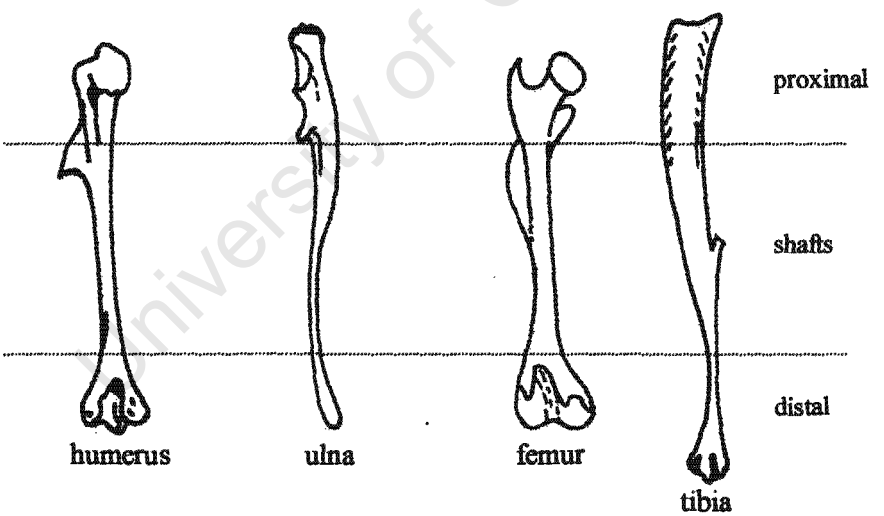

Figure 6.7.1: Categories of long bones represented in the SBYC fauna

In the investigation of breakage among the long bones, the same breakage categories established by Andrews (1990a) and further adopted by Matthews (1998), among others, were used. These are 'complete, proximal, shaft and distal' (see Figure 6.7.1). A long bone was categorised as complete if the shaft contained part or most of the proximal and

distal ends intact. Proximal and distal ends comprised the relevant end with a portion or all the shaft. Long bones lacking both the proximal and articular ends were categorised as shaft. Long bones represented in these different categories were counted for each sampled area in the SBYC. The percentage of each category was calculated against the total of each category.

6.7.1 Analysis of other post-cranial bones

Because scapulae and innominates are relatively abundant in the SBYC faunal samples, it was felt worth investigating their breakage patterns. Although there is little literature on the breakage of the scapula and the innominate, keys were invoked to help analyse the breakage patterns of these two bones.

Following Dodson and Wexlar (1979) and Matthews (1998), but making some adjustments to suit the SBYC samples, the scapulae were grouped into two categories, depending on their degree of breakage. The scapulae with the glenoid fossa (i.e. the proximal end) and less than half of the blade intact (see Figure 6.7.2), were categorized as 'proximal'. On the other hand, those that have the glenoid fossa and half or more of the blade intact were categorised as 'complete'.

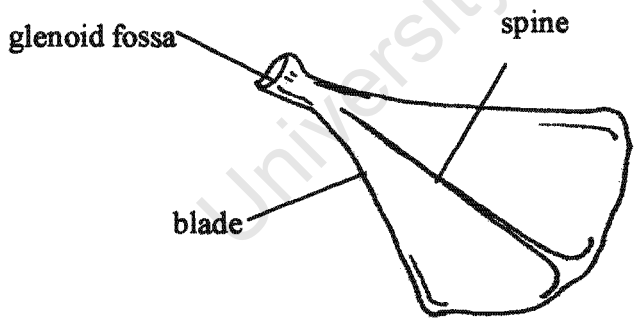

Figure 6.7.2: A rodent scapula showing elements used in the text

The innominates were also grouped into two categories, depending on their degree of breakage. Following Matthews (1998), an innominate was classified as 'complete' if it retained all or most of the acetabulum, ilium, ischium and pubis (see Figure 6.7.3); slight damages were disregarded. Portions of the acetabulum, ilium, ischium or the acetabulum together with part of one or two of the pelvic bones were classified as fragments.

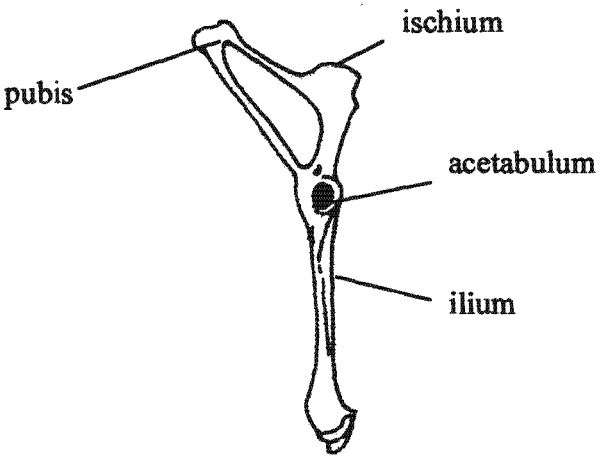

Figure 6.7.3: A rodent innominate showing elements used in the text

Analysis of post-cranial bones other than the long bones, scapulae and innominates, was restricted to taking their counts. In this exercise, patellae, loose epiphyses, metapodials, calcanea, astragali and other associated podials, phalanges, and the vertebrae were counted.

6.8 Epiphyseal fusion in the long bones

The extent of modifications to mammalian remains, including those belonging to small mammals may depend on the age of the individuals at the time of their death. Bones belonging to young individuals are less durable and therefore more likely to be destroyed by taphonomic processes, including the effect of predation (Chaplin 1971; Western 1980; Klein and Cruz-Uribe 1984; Andrews 1990a; Reitz and Wing 1999). In view of this, two of the relatively abundant long bones in the SBYC samples, the humerus and femur, were chosen for investigation of epiphyseal fusion. This aimed at determining whether their abundance may be ascribed to their early fusion and therefore durability and survivability against taphonomic processes (e.g. Klein and Cruz-Uribe 1984). Without determining whether the epiphyseal line was visible or obscure (e.g. Reitz and Wing 1999) as long as the epiphysis was 'fused' to the limb bone, investigations were carried out on each limb bone. Although the distal humeri fuse early in life (e.g. Bates and Harrison 1980: 584-5), investigations of epiphyseal fusion among the humeri were carried out on both the proximal (head of the humerus and its tuberosities) and distal ends. With regard to the

femur, investigations were confined to the femur head and the distal extremity (e.g. Bates and Harrison 1980). Because rates of epiphyseal fusion may differ from one species to another and from one individual to another (Bates and Harrison 1980), investigations of epiphyseal fusion were carried out separately on the murids and the soricids.

In each sampled area, loose epiphyses for both humeri and femora were also counted. Besides lending some support to the relative age classes of the fauna across the three sampled areas, the main aim behind taking the counts for loose epiphyses was to investigate whether their proportions generally corresponded with the proportions of unfused humeri and femora.

6.9 Post-cranial to cranial proportions

In an attempt to investigate the possibility of preferential destruction/preservation between the cranial and post-cranial bones, the relative proportions of post-cranial to cranial elements were determined. Following Andrews (1990a), the relative proportions of post-cranial to cranial elements were established on the premise that if there had been no preferential damage, the numbers of the long bones (i.e. humeri, ulnae, femora and tibiae) should correspond with those of the maxillae and mandibles, and any disparity in this would mean that there has been preferential damage. Proportions <100 have been taken to imply relative loss of skeletal elements, while on the other hand, proportions >100 have been taken to imply surplus skeletal elements. The following indices were investigated:

1) [Humeri + femora]/ [maxillae + mandibles] x 100

In the above exercise, the proportions of post-cranial to cranial elements in each sampled area were determined separately for both murids and soricids, whereas in the two exercises below, all skeletal elements were treated together.

2) [humeri + ulnae + femora + tibiae]/ [maxillae + mandibles + isolated teeth] x 100

Following Andrews (1990a), an index to investigate any possible selection for or against the proximal, as opposed to distal limb bones, was invoked:

3) total numbers of [tibiae + ulnae]/ femora + humeri] x 100

In addition to the investigations of relative proportions between the three samples, chi-squared tests (X^2) were carried out for a number of skeletal elements. Following Weatherburn (1962: 164-184) and Shennan (1988: 65-76), the X^2 tests were carried out with a view to statistically testing the distribution of skeletal elements among the three samples, and whether the distribution of the fauna in the three sampled areas has been dependent on or independent of one another. The following formula was used in the chi-squared (X^2) tests:

$$X^2 = \Sigma \frac{(O-E)^2}{E}$$ where O is the observed number of cases (elements) in each category and E is the expected number of cases (elements) in each category. The chi-squared tests were also augmented by computer-derived gamma analyses. The gamma analyses were carried out with the intention of investigating whether there are statistically discernible directional (ordinal) relationships between the position of the fauna along the slope and the degree of breakage. The gamma statistic is constructed to be sensitive to the proper ordering of categories for two distinct variables, whereas the chi-squared (X^2) is constructed so as to ignore the ordering of categories, and is not able to detect ordinal patterns (T. Dunne, pers. comm., 2002).

6.10 Analysis of other microfauna represented in the SBYC samples

With a view to conclusively understanding the SBYC microfauna, the non-mammalian microfauna were investigated. The analysis of these faunal remains was, however, limited to the identification of the various taxonomic groups. In this exercise, the most commonly preserved skeletal elements were used to determine relative abundance of the different species represented.

6.11 Palaeoenvironmental reconstruction

In reconstructing the microhabitats represented by the SBYC micromammalian species, taphonomic and ecological issues investigated on the SBYC micromammalian fauna will be considered. This will include factors such as the breakage patterns of skeletal elements, modern distribution and microhabitats of the small mammals represented at SBYC, as well as their proportions in the faunal samples (e.g. Avery 2001, 2002). A

general understanding of the habitats of the potential predator/s that may have been involved in the accumulation of the fauna will also aid in the reconstruction of the palaeoenvironment around the SBYC area (e.g. Fernandez-Jalvo 1995).

CHAPTER SEVEN

Results

7.1 Skeletal elements in the SBYC micromammalian faunal samples

Although the faunal samples on which this project is based are portions of the microfaunal occurrence at SBYC, the numbers listed in Table 7.1.1 will give some idea about body-part representation at the site.

Table 7.1.1: Number of identified specimens from SBYC (N).

Skeletal element	Down Slope		Upper Slope		Hanging Remnant	
	N	%	N	%	N	%
Mandibles	280	3.7	860	4.0	135	4.5
Maxillae	198	2.6	398	1.8	66	2.2
Cranial fragments	87	1.1	146	0.7	61	2.0
Zygomatic processes	56	0.7	60	0.3	13	0.43
Auditory bullae	2	0.03	13	0.1	0	0
Isolated molars	1258	16.5	3061	14.2	510	16.9
Isolated incisors	337	4.4	1185	5.5	100	3.3
Scapulae	89	1.2	196	1.0	25	0.83
Humeri	387	5.1	698	3.2	158	5.2
Ulnae	238	3.1	846	3.9	118	4.0
Radii	158	2.1	424	2.0	83	2.7
Innominates	148	1.9	352	1.6	65	2.1
Vertebrae	1329	17.4	3548	16.5	402	13.3
Femora	337	4.4	714	3.3	166	5.5
Patellae	47	0.6	99	0.5	18	1.0
Tibiae	379	5.0	1054	4.9	174	5.8
Astragali	208	2.7	481	2.2	66	2.2
Calcanea	229	3.0	570	2.6	78	2.6
Podials	75	1.0	314	1.5	22	0.72
Metapodials	838	11.0	2680	12.4	448	14.8
Phalanges	961	12.6	3831	17.8	318	10.5
TOTAL	**7641**		**21530**		**3026**	

The percentages in Table 7.1.1 suggest that there are no significant differences in the proportions of number of identified specimens (NISPs) among the three samples. The results further show that in the three samples, there seems to have been preferential destruction of the skull, as indicated by the absence of complete crania, the presence

of low proportions of identifiable cranial fragments and the high proportions of isolated molars. In all the sampled areas, the percentages of isolated molars, vertebrae, phalanges and metapodials are quite high.

Among the long bones, there are relatively low percentages of radii and generally higher percentages of tibiae relative to other long bones. In the three samples, it is interesting to note the minimal differences in the percentages of skeletal elements such as mandibles, radii, ulnae, podials, astragali, calcanea and zygomatic processes.

7.2 Micromammalian species from SBYC and the minimum number of individuals (MNIs)

Table 7.2.1: List of micromammalian species encountered in the SBYC faunal samples (Nomenclature after Meester *et al.* 1986; Skinner and Smithers 1990; Wilson and Reeder 1993).

Order	Family	Genus, species	Common name
Insectivora	Chrysochloridae	*Chrysochloris asiatica*	Cape golden mole
	Soricidae	*Crocidura cyanea*	reddish-grey musk shrew
		Crocidura flavescens	greater musk shrew
		Myosorex varius	forest-shrew
		Suncus varilla	lesser dwarf shrew
Chiroptera	Rhinolophidae	*Rhinolophus clivosus*	Geoffroy's horseshoe-bat
Rodentia			
	Muridae	*Dendromus melanotis*	grey climbing mouse
		Dendromus mesomelas	Brants's climbing mouse
		Steatomys krebsii	Krebs's fat mouse
		Gerbillurus paeba	hairy-footed gerbil
		Tatera afra	Cape gerbil
		Mystromys albicaudatus	white-tailed rat
		Rhabdomys pumilio	striped mouse
		Otomys irroratus	vlei-rat
		Otomys saundersiae	Saunders's vlei-rat
		Otomys unisulcatus	bush Karoo rat
	Bathyergidae	*Bathyergus suillus*	Cape dune molerat
		Cryptomys hottentotus	common molerat
Macroscelidea	Macroscelididae	*Elephantulus edwardii*	Cape rock elephant-shrew

Table 7.2.1 lists the micromammalian species recovered from SBYC. The maxillary and mandibular frequencies of the micromammalian species are recorded in Appendix 3. From the results in Table 7.2.1, it is apparent that small sized rodent species are

well represented in the fauna than any other taxonomic group. Among the insectivores, soricids are fairly well represented in the SBYC faunal samples.

Table 7.2.2 gives the MNI and percentage representation of all micromammalian species from SBYC. Table 7.2.3 presents the Shannon-Wiener indices for general diversity (*H*). The MNIs have been derived from the most represented jaw (upper or lower, left or right). Based on the jaws, Table 7.2.4 further shows the total MNIs for the murids and soricids.

Table 7.2.2: MNI and percentage representation of micromammalian species from SBYC based on maxillae and mandibles.

Taxon	Down Slope		Upper Slope		Hanging Remnant	
	N	%	N	%	N	%
Insectivora						
C. asiatica	2	1.1	12	2.4		
cf. C. cyanea	7	3.7	3	0.6	3	3.4
C. flavescens	4	2.1	5	1.0	1	1.1
M. varius	49	26.0	164	32.7	12	13.5
cf. M. varius	3	1.6	16	3.2	1	1.1
S. varilla	20	10.6	63	12.5	19	21.3
cf. S. varilla			1	0.2		
Chiroptera						
R. clivosus	1	0.53	1	0.2		
Rodentia						
D. melanotis	2	1.1	9	1.8	2	2.25
D. mesomelas			2	0.4		
Dendromus spp.			2	0.4	2	2.25
S. krebsii	8	4.2	22	4.4	3	3.4
G. paeba	7	3.7	9	1.8	3	3.4
T. afra	50	26.5	121	24.1	25	28.1
M. albicaudatus	2	1.1	4	0.8	2	2.25
R. pumilio	4	2.1	4	0.8		
cf. R. pumilio	1	0.53				
O. irroratus	1	0.53	7	1.4	1	1.1
O. saundersiae	10	5.3	24	4.8	12	13.5
O. unisulcatus	5	2.65	6	1.2		
Otomys spp.	9	4.8	17	3.4	3	3.4
B. suillus			1	0.2		
C. hottentotus	4	2.1	8	1.6		
Macroscelidea						
E. edwardii			1	0.2		
TOTAL MNI	**189**		**502**		**89**	

The results in Table 7.2.2 show relatively high MNIs for *Tatera afra, Myosorex varius* and *Suncus varilla* in all the samples. The minimal differences in the percentages of *Tatera afra* among the three samples may also be observed. The results further show that the *Otomys* spp., particularly *Otomys saundersiae*, are fairly well represented at SBYC. The total percentage representation of *Otomys* spp. is highest in the Hanging Remnant and least in the Upper Slope. On the other hand, the relatively low representation of species such as *Dendromus* spp., *Crocidura* spp., *Gerbillurus paeba* and *Rhabdomys pumilio*, as well as the negligible representation of relatively larger species such as *Bathyergus suillus, Cryptomys hottentotus* and *Elephantulus edwardii*, is evident in Table 7.2.2.

Table 7.2.3 shows that there are minor differences in the indices for general diversity (*H*) among the three samples. When the highly represented *Tatera afra* is omitted from the analysis, the diversity indices fluctuate, as indicated by the higher index in the Down Slope and the lower indices in the other samples. On the other hand, when *Myosorex varius* is omitted from the analysis, there is a noticeable decline in the diversity indices in all the samples, and this phenomenon is more prominent in the Hanging Remnant. Among the three samples, the Down Slope yielded the highest diversity indices.

Table 7.2.3: Shannon-Wiener indices for general diversity (*H*).

	Down Slope	Upper Slope	Hanging Remnant
With *T. afra* and *M. varius*	2.16	2.04	1.95
Without *T. afra*	2.24	1.97	1.9
Without *M. varius*	2.07	2.02	1.74

The results in Table 7.2.4 clearly show that in both the Down Slope and the Upper Slope, soricids yielded higher MNIs than did the murids. It is, however, worth mentioning the minimal difference in the MNIs between murids and soricids in the Down Slope. On the other hand, the murids yielded higher MNIs in the Hanging Remnant than did the soricids.

Table 7.2.4: Minimum numbers of murids and soricids (in bold) based on maxillae and mandibles.

Skeletal element	Down Slope		Upper Slope		Hanging Remnant	
	Murids	Soricids	Murids	Soricids	Murids	Soricids
Lmax	73	13	149	43	26	2
Rmax	**80**	16	148	37	35	1
Lman	52	61	**199**	218	32	**33**
Rman	72	**83**	199	**238**	**41**	25

To complement the MNIs derived from the most represented jaw, Table 7.2.5 presents MNIs derived from the most represented distal humeri and proximal femora (left or right). The relatively durable distal end of the humerus and the proximal end of the femur (e.g. Andrews 1990a), of which it is fairly easy to separate the left from the right, were used to obtain the MNIs.

Looking at the MNIs derived from the long bones presented in Table 7.2.5, it is very clear that in all the samples, murids yielded the highest MNIs. The results further show that the Upper Slope yielded the highest MNIs for both murids and soricids, followed by the Down Slope.

Table 7.2.5: Minimum numbers of murids and soricids (in bold) based on humeri and femora.

Skeletal element	Down Slope		Upper Slope		Hanging Remnant	
	Murids	Soricids	Murids	Soricids	Murids	Soricids
Lt. distal humeri	109	**37**	215	**80**	33	**20**
Rt. distal humeri	**133**	31	194	65	49	14
Lt. proximal femora	99	23	**258**	61	**58**	14
Rt. proximal femora	92	30	214	72	42	14

Comparing the MNIs derived from the jaws and those obtained from the long bones (Tables 7.2.4 and 7.2.5, respectively), it may clearly be seen that murid MNIs are greater than those of the soricids when long bones are considered, whereas the soricid MNIs are generally higher than those of the murids when jaws are considered. Overall, among the three sampled areas, the Hanging Remnant yielded the lowest MNIs.

7.3 Breakage patterns of the skulls

As reported in Chapter Six, breakage of the crania was investigated separately for the murids and soricids. Tables 7.3.1 and 7.3.2 record the breakage patterns of the murid and soricid maxillae respectively. N is the number of skeletal elements in each category, and percentage (%) is calculated against the total of each category. These results are further illustrated in Figure 7.3.1 for the murids and Figure 7.3.2 for the soricids.

Table 7.3.1: Breakage patterns of murid maxillae.

Breakage Category	Down Slope N	Down Slope %	Upper Slope N	Upper Slope %	Hanging Remnant N	Hanging Remnant %
1	35	20.5	91	29.2	12	19.0
2	6	3.51	7	2.24	1	1.6
3	82	48.0	151	48.4	26	41.3
4	48	28.1	63	20.2	24	38.1
TOTAL	**171**		**312**		**63**	

Table 7.3.2: Breakage patterns of soricid maxillae.

Breakage Category	Down Slope N	Down Slope %	Upper Slope N	Upper Slope %	Hanging Remnant N	Hanging Remnant %
1	2	7.4	5	5.8	0	0
2	0	0	4	4.7	0	0
3	8	29.6	21	24.4	2	66.7
4	17	63.0	56	65.1	1	33.3
TOTAL	**27**		**86**		**3**	

The amplified results in Figure 7.3.1 show a very interesting trend. Although the percentage of Category 1 murid maxillae is higher in the Upper Slope, the percentages of this category are generally high in all the sampled areas. The results in Figure 7.3.1 further show that percentages of Category 4 murid maxillae are generally high in the three samples, but higher in the Hanging Remnant. Of interest to note are the relatively high percentages of Category 3 maxillae, as well as the minimal disparity in

the percentages of this category between the Down Slope and the Upper Slope. In all the sampled areas, percentages of Category 2 maxillae are the lowest. Overall, the Upper Slope yielded the highest percentage of Category 1 as well as the lowest percentage of Category 4 murid maxillae.

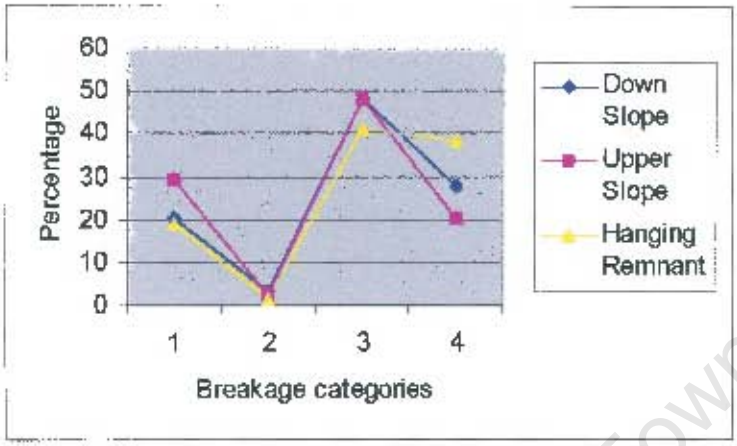

Figure 7.3.1: Relative completeness of the murid maxillae

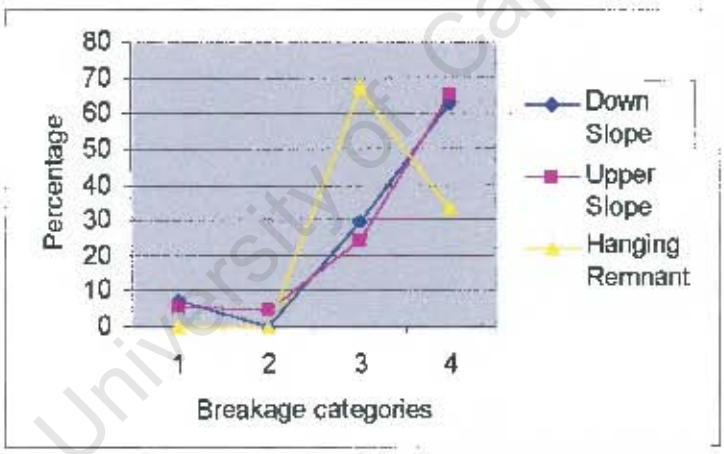

Figure 7.3.2: Relative completeness of the soricid maxillae

Table 7.3.2 indicates that the proportions of soricid maxillae are very low especially in the Hanging Remnant. The clearly exemplified results in Figure 7.3.2 above show that there is high incidence of breakage among the soricid maxillae, as suggested by the relatively low percentages of Categories 1 and 2 maxillae. The high incidence of breakage among the soricid maxillae is further suggested by the high percentages of Category 4 maxillae, especially in the Down Slope and the Upper Slope samples.

Comparing the murids and soricids (Figures 7.3.1 and 7.3.2 respectively), the results show that the former yielded a higher percentage of Category 1 maxillae.

Tables 7.3.3 and 7.3.4 record the breakage patterns of both murid and soricid mandibles respectively. These patterns are further demonstrated in Figures 7.3.3 and 7.3.4.

Table 7.3.3: Breakage patterns of murid mandibles.

Breakage Category	Down Slope N	Down Slope %	Upper Slope N	Upper Slope %	Hanging Remnant N	Hanging Remnant %
1	1	0.76	34	8.56	3	4.0
2	13	9.85	60	15.1	9	12.0
3	12	9.1	45	11.3	11	14.7
4	106	80.3	258	65.0	52	69.3
TOTAL	132		397		75	

Table 7.3.4: Breakage patterns of soricid mandibles.

Breakage Category	Down Slope N	Down Slope %	Upper Slope N	Upper Slope %	Hanging Remnant N	Hanging Remnant %
1	7	4.73	91	19.7	5	8.3
2	7	4.73	102	22.0	6	10.0
3	26	17.6	79	17.1	23	38.3
4	99	67.0	151	32.6	20	33.3
5	9	6.1	40	8.64	6	10.0
TOTAL	148		463		60	

Figure 7.3.3 shows that the Upper Slope yielded a higher percentage of Category 1 murid mandibles than the other samples. This phenomenon has also been observed among the maxillae in Figure 7.3.1. It is also evident in Figure 7.3.3 that the Upper Slope yielded the highest percentage of Category 2 murid mandibles. Although the percentages of Category 4 murid mandibles are generally high in the three samples, Figure 7.3.3 suggests that there has been a higher destruction of mandibles in the Down Slope sample, as indicated by the relatively low percentage of Category 1

mandibles and the very high percentage of Category 4 mandibles. There are minimal differences in the percentages of Category 3 murid mandibles among the three SBYC faunal samples.

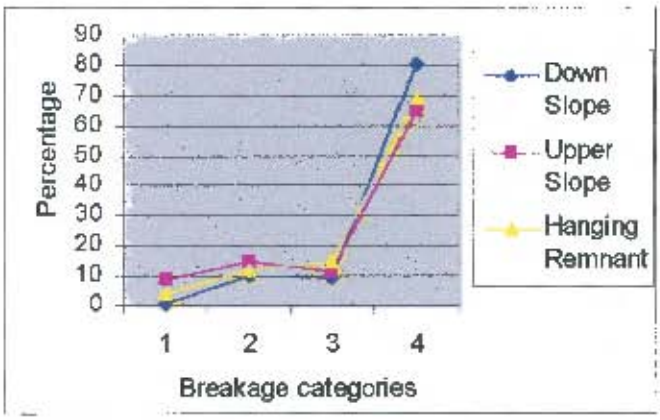

Figure 7.3.3: Relative completeness of the murid mandibles

Figure 7.3.4 shows that there are higher percentages of soricid Categories 1 and 2 mandibles in the Upper Slope than in the other samples. This phenomenon has also been observed among the murid mandibles (Figure 7.3.3). Of interest to note among the soricid mandibles (Figure 7.3.4) are the generally low percentages of Category 5 mandibles in all the samples, and the relatively high percentage of Category 4 mandibles in the Down Slope.

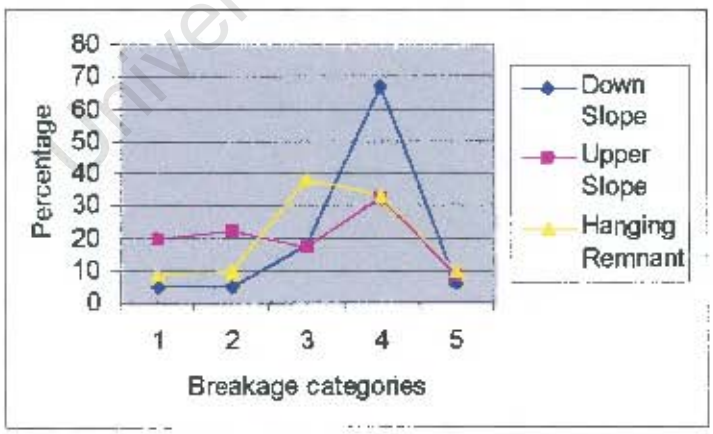

Figure 7.3.4: Relative completeness of the soricid mandibles

7.4 Incisor etching

Table 7.4.1 details etching among the murid lower and upper isolated incisors. Table 7.4.2 reports on etching among *in situ* murid lower and upper incisors. The results for the relatively abundant lower and upper isolated incisors are clearly illustrated in Figures 7.4.1 and 7.4.2 respectively.

Table 7.4.1: Etching of murid isolated incisors.

Etching Category	Down Slope N	Down Slope %	Upper Slope N	Upper Slope %	Hanging Remnant N	Hanging Remnant %
			Lower incisors			
1	93	54.7	165	27.6	7	16.0
2	59	34.7	340	56.9	35	79.5
3	18	10.6	93	15.6	2	4.5
4	0	0	0	0	0	0
5	0	0	0	0	0	0
TOTAL	**170**		**598**		**44**	
			Upper incisors			
1	55	33.0	147	25.0	14	25.0
2	97	58.1	400	68.1	39	70.0
3	15	9.0	40	6.81	3	5.36
4	0	0	0	0	0	0
5	0	0	0	0	0	0
TOTAL	**167**		**587**		**56**	

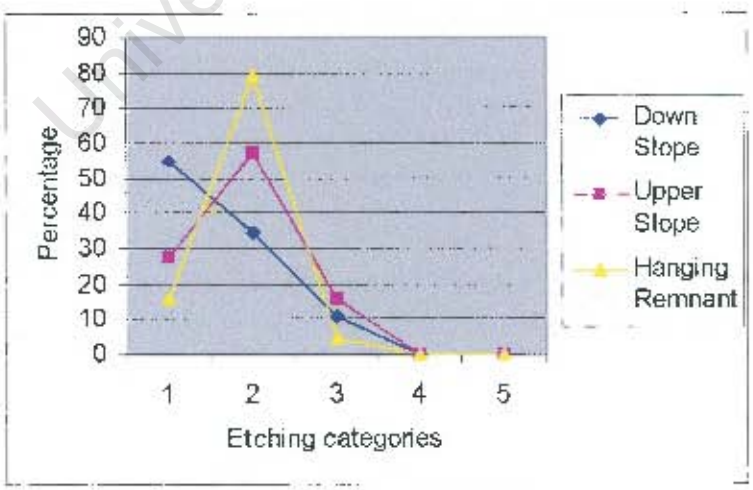

Figure 7.4.1: Etching among isolated lower incisors

The most obvious observation in Figures 7.4.1 and 7.4.2 is the absence in all the samples of Categories 4 and 5 incisors, which following Andrews (1990a) represent high levels of etching. In Figures 7.4.1 and 7.4.2, the results clearly show that the percentages of Category 1 incisors are generally higher among the lower incisors. Among the three sampled areas, the Down Slope yielded the highest percentage of Category 1 lower isolated incisors. Generally, there are high percentages of Category 2 isolated incisors, the highest coming from the Hanging Remnant. The results further show that the percentages of Category 3 incisors are generally low for both lower and upper isolated incisors.

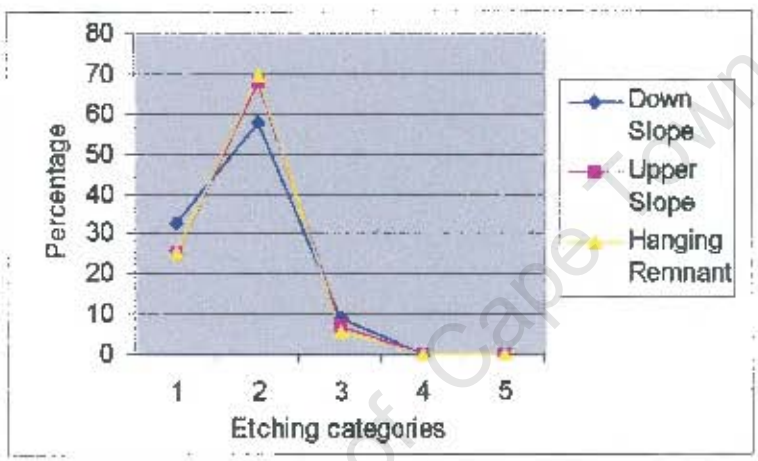

Figure 7.4.2: Etching among isolated upper incisors

Although the counts for *in situ* incisors are quite low, the results in Table 7.4.2 indicate that there are no Categories 4 and 5 *in situ* incisors in the SBYC samples. The results also show that the percentages of Category 1 incisors are relatively lower among the lower incisors. Conversely, the percentages of Category 2 *in situ* incisors are quiet high among the lower incisors.

Table 7.4.2 further suggests that there are higher proportions of lower than upper *in situ* incisors. In all the sampled areas and for all incisors, the percentages of Category 3 incisors are very low. Overall, etching in the SBYC incisors is minimal, as indicated by the percentages of Categories 1 and 2 incisors. Following Andrews (1990a), Appendix 4.2 further elucidates the categories of incisor etching resulting from different predators.

Table 7.4.2: Etching of murid *in situ* incisors.

Etching Category	Down Slope N	Down Slope %	Upper Slope N	Upper Slope %	Hanging Remnant N	Hanging Remnant %
		Lower Incisors				
1	2	18.2	12	16.2	0	0
2	8	72.7	58	78.4	21	87.5
3	1	9.1	4	5.41	3	12.5
4	0	0	0	0	0	0
5	0	0	0	0	0	0
TOTAL	11		74		24	
		Upper Incisors				
1	1	1.0	7	43.8	3	25.0
2	0	0	8	50.0	9	75.0
3	0	0	1	6.25	0	0
4	0	0	0	0	0	0
5	0	0	0	0	0	0
TOTAL	1		16		12	

It is important to point out that among the incisor fragments that were not investigated for etching, there are some incisor fragments in which the dentine has completely been removed, leaving behind the relatively thin enamel. According to D. M. Avery (pers. comm., 2002), this appears to have resulted from mechanical breakage.

7.5 Breakage patterns of the long bones

Table 7.5.1 presents the breakage patterns for murid and soricid humeri. N is the number of skeletal elements in each category, and percentage (%) is calculated against the total of each category. The breakage patterns are amplified in Figures 7.5.1 and 7.5.2.

As shown in Figure 7.5.1, the Upper Slope yielded the highest percentage of complete murid humeri. Of interest to note is the minimal difference in the percentages of complete humeri between the Down Slope and the Hanging Remnant, and also the reduced difference in the percentages between complete and proximal humeri in the Down Slope. The results further show that the Hanging Remnant yielded the highest

percentage of proximal murid humeri. Although there are high percentages of distal humeri in the three samples, the Down Slope sample yielded the highest percentage. The minimal difference in the percentages of distal humeri between the Upper Slope and Hanging Remnant may also be observed.

Table 7.5.1: Breakage patterns of murid and soricid humeri.

	Down Slope		Upper Slope		Hanging Remnant	
	N	%	N	%	N	%
Murid						
Complete	42	14.2	102	19.6	16	14.5
Proximal	40	13.6	89	17.1	24	21.8
Shaft	13	4.41	21	4.0	4	3.64
Distal	200	67.8	308	59.2	66	60.0
TOTAL	**295**		**520**		**110**	
Soricid						
Complete	33	35.9	88	49.4	21	43.8
Proximal	20	21.7	29	16.3	14	29.2
Shaft	4	4.34	4	2.25	0	0
Distal	35	38.0	57	32.0	13	27.1
TOTAL	**92**		**178**		**48**	

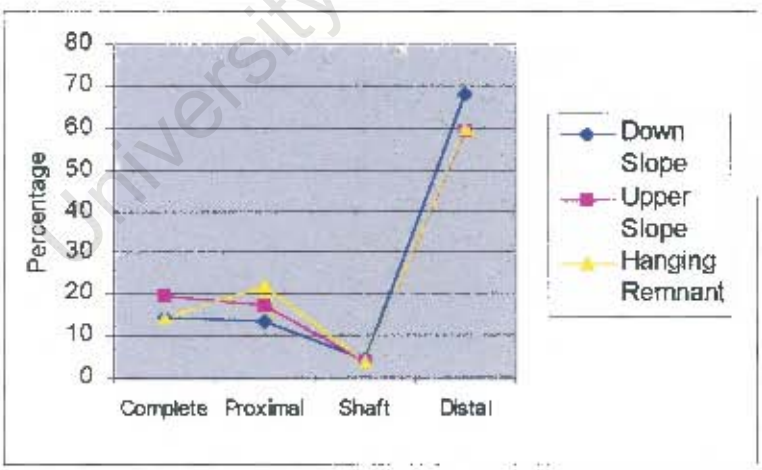

Figure 7.5.1: Relative completeness of the murid humeri

Figure 7.5.2 shows that the percentages of complete soricid humeri are quite high in all the sampled areas, but highest in the Upper Slope. The results further indicate that

the Hanging Remnant yielded the highest percentage of proximal humeri. The Down Slope sample yielded the highest percentage of distal humeri.

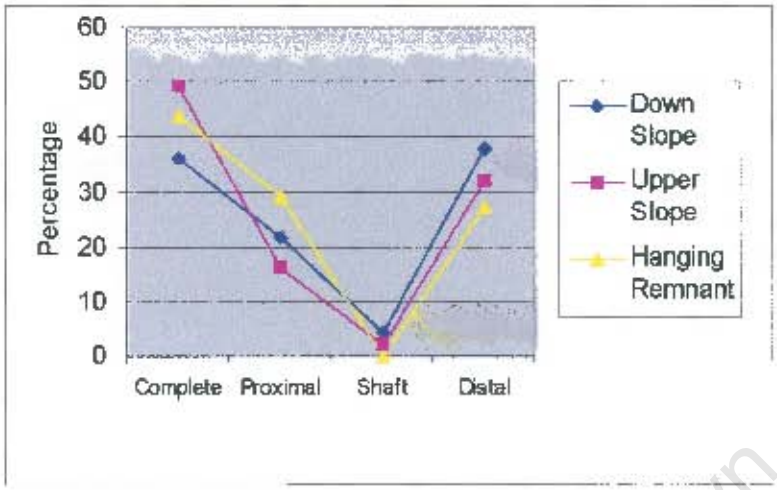

Figure 7.5.2: Relative completeness of the soricid humeri

Comparing Figures 7.5.1 and 7.5.2, it is interesting to note that soricids yielded the highest percentages of complete humeri, as opposed to the relatively low percentages of the same among the murids. In both the murids and soricids, the Hanging Remnant yielded the highest percentage of proximal humeri. The percentages of humeri shafts are quite low. In fact, there are no soricid humeri shafts in the Hanging Remnant. Even though the percentages of distal humeri are high in both the murids and the soricids, the results show that the murids yielded higher percentages of distal humeri than did the soricids. Of particular interest to note are the relatively higher percentages of murid and soricid distal humeri in the Down Slope.

Table 7.5.2 records the breakage patterns for murid and soricid femora. These patterns are further illustrated in Figures 7.5.3 and 7.5.4 respectively.

Figure 7.5.3 shows that the Upper Slope yielded the highest percentage of complete murid femora. There is minimal difference in the percentages of complete femora between the Down Slope and the Hanging Remnant. Of particular notice in Figure 7.5.3 are the relatively high percentages of proximal murid femora, and especially in the Down Slope. The Hanging Remnant yielded the highest percentage of distal murid femora.

Table 7.5.2: Breakage patterns of murid and soricid femora.

	Down Slope		Upper Slope		Hanging Remnant	
	N	%	N	%	N	%
Murid						
Complete	23	8.16	113	19.7	10	7.25
Proximal	228	80.9	359	62.7	90	65.2
Shaft	0	0	10	1.75	5	3.62
Distal	31	11.0	91	15.9	33	23.9
TOTAL	**282**		**573**		**138**	
Soricid						
Complete	14	25.5	67	47.5	12	42.9
Proximal	39	70.9	66	46.8	16	57.1
Shaft	0	0	2	1.41	0	0
Distal	2	3.64	6	4.26	0	0
TOTAL	**55**		**141**		**28**	

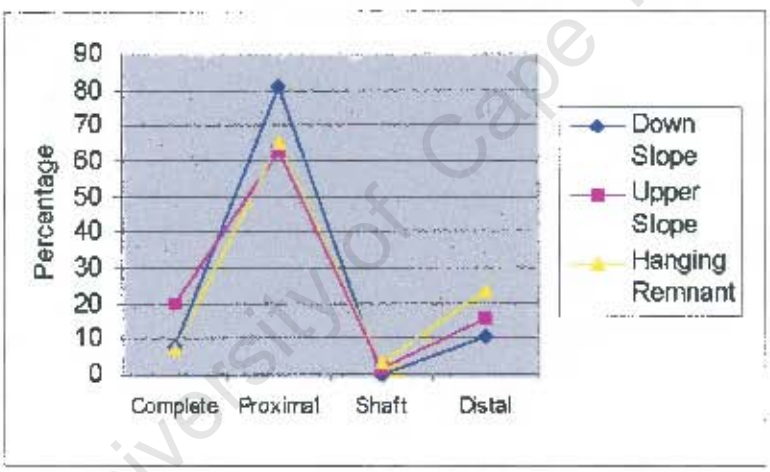

Figure 7.5.3: Relative completeness of the murid femora

Figure 7.5.4 clearly indicates that the percentages of complete soricid femora are quite high. In fact, comparing the murids and the soricids, the latter yielded the highest percentages of complete femora. This phenomenon has also been observed among the humeri (Figures 7.5.1 and 7.5.2). As Figure 7.5.4 further shows, the Down Slope yielded the highest percentage of soricid proximal femora, as it did for murid proximal femora.

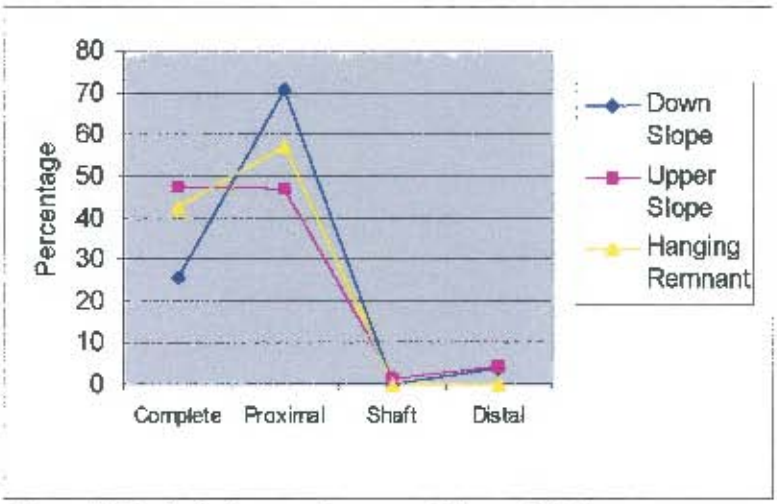

Figure 7.5.4: Relative completeness of the soricid femora

Figures 7.5.3 and 7.5.4 clearly show that the percentages of shafts are very low in all the sampled areas. Although the percentages of distal femora are quite low among the murids and the soricids, the former yielded slightly higher percentages than the latter. Overall, comparing the murids and the soricids, the latter show a greater index of completeness in both the humeri and femora.

Table 7.5.3 reports on the breakage patterns of the tibiae and ulnae. These patterns are clearly shown in Figures 7.5.5 and 7.5.6.

Table 7.5.3: Breakage patterns of the indeterminate micromammalian ulnae and tibiae from SBYC.

Skeletal element	Down Slope		Upper Slope		Hanging Remnant	
	N	%	N	%	N	%
Ulna						
Complete	9	3.78	11	1.3	8	6.8
Proximal	220	92.4	745	88.1	103	87.3
Shaft	9	3.78	87	10.3	7	5.93
Distal	0	0	3	0.35	0	0
TOTAL	**238**		**846**		**118**	
Tibia						
Complete	5	1.32	27	2.56	3	1.72
Proximal	72	19.0	254	24.1	34	19.5
Shaft	133	35.1	322	30.6	49	28.2
Distal	169	44.6	451	42.8	88	50.6
TOTAL	**379**		**1054**		**174**	

The results in Figure 7.5.5 indicate that the proportions of complete ulnae are quite low in all the sampled areas. The results further show that, except for minimal differences in the percentages of proximal ulnae, the percentages are generally high in all the sampled areas. Interestingly, as also observed earlier among the murid and soricid proximal long bones (humeri and femora), the Down Slope yielded the highest percentage of proximal ulnae, which by nature is sturdy (e.g. Andrews 1990a). On the other hand, the very low percentages of ulnae shafts and distal ends are evident in Figure 7.5.5. In fact, there are no distal ulnae in the Down Slope and the Hanging Remnant, and the percentage of distal ulnae in the Upper Slope is negligible.

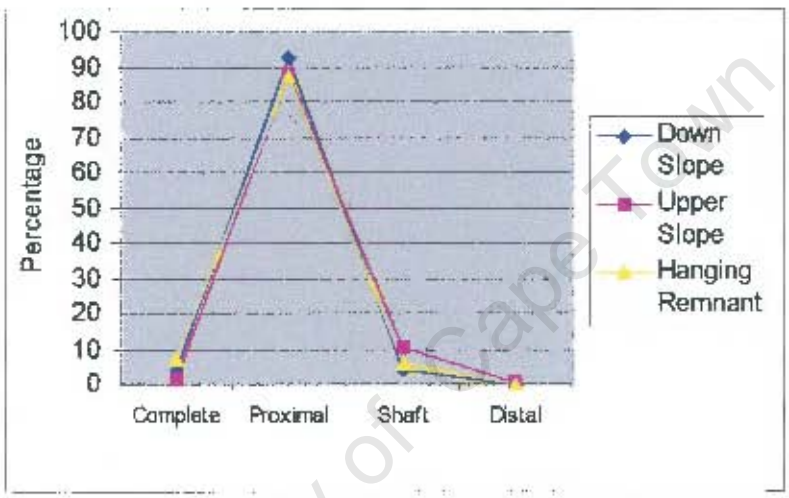

Figure 7.5.5: Relative completeness of the ulnae

Figure 7.5.6 displays a very interesting trend in the breakage of the tibiae. In all the three samples, the percentages of complete tibiae are the lowest. After the complete tibiae, the proximal tibiae are next with the second lowest percentages. The results further indicate that the percentages of distal tibiae and tibia shafts (in that order) are the highest in the three samples. Although the Hanging Remnant yielded the highest percentage of distal tibiae, it is interesting to observe the relatively high percentage of distal tibiae in the Down Slope. Among the three sampled areas, the Down Slope has continued to yield relatively high percentages of the portions of limb bones that are by nature sturdy. Interestingly, the Down Slope yielded the highest percentage of tibia shafts. The high percentages of shafts evident among the tibiae have not been observed in the other long bones.

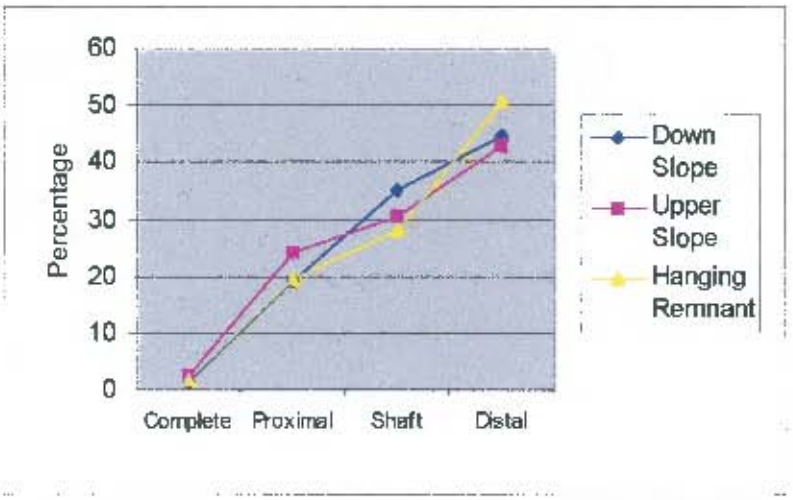

Figure 7.5.6: Relative completeness of the tibiae

7.6 Breakage patterns of other post-cranial bones

As detailed in Table 7.6.1, the percentages of proximal scapulae are quite high in all the SBYC faunal samples. Although the Hanging Remnant yielded the highest percentage of proximal scapulae, generally there are no remarkable differences in the percentages of proximal scapulae among the three samples. On the other hand, even though the percentages of complete scapulae are low in all the samples, the Down Slope yielded a higher percentage. With regard to the innominates, the percentages of innominate fragments are very high in all the sampled areas. In fact, there are no complete innominates in the Hanging Remnant.

Table 7.6.1: Breakage patterns of scapulae and innominates.

	Down Slope		Upper Slope		Hanging Remnant	
	N	%	N	%	N	%
Scapula						
Complete	21	23.6	37	18.9	4	16.0
Proximal	68	76.4	159	81.1	21	84.0
TOTAL	**89**		**196**		**25**	
Innominate						
Complete	4	2.7	15	4.3	0	0
Fragments	144	97.3	337	95.7	65	100.0
TOTAL	**148**		**352**		**65**	

7.7 Epiphyseal fusion in the long bones

Tables 7.7.1 and 7.7.2 detail epiphyseal fusion for humeri and femora belonging to the murids and soricids respectively. In these two tables, it is important to point out that one long bone may be represented twice, depending on whether both the proximal and distal ends are joined. Table 7.7.3 presents the total number of loose epiphyses belonging to the two long bones investigated for epiphyseal fusion.

From Table 7.7.1, all murid distal humeri in the three sampled areas are fused. On the other hand, there are relatively high proportions of murid humeri with proximal ends not fused. It is interesting noting the minimal disparities in the percentages of unfused proximal humeri among the three samples. Although the percentages of fused proximal femora are fairly high, the results show much higher percentages of unfused proximal femora in the three samples. The very high percentages of unfused distal femora may also be noted in Table 7.7.1. Conversely, there are very low percentages of fused distal femora across the three samples.

Table 7.7.1: State of fusion of the murid humeri and femora.

Skeletal element	Down Slope		Upper Slope		Hanging Remnant	
	N	%	N	%	N	%
Humerus						
Proximal fused	3	4.0	11	6.0	2	5.0
Proximal unfused	79	96.0	180	94.0	38	95.0
TOTAL	**82**		**191**		**40**	
Distal fused	160	100.0	360	100.0	62	100.0
Distal unfused	0	0	0	0	0	0
TOTAL	**160**		**360**		**62**	
Femur						
Proximal fused	54	24.0	114	26.0	29	30.0
Proximal unfused	168	76.0	321	74.0	67	70.0
TOTAL	**222**		**435**		**96**	
Distal fused	4	7.0	7	2.0	4	9.0
Distal unfused	50	93.0	290	98.0	39	91.0
TOTAL	**54**		**297**		**43**	

As may be seen in Table 7.7.2, all soricid humeri are fused on the distal end. In all the samples, there are fairly high proportions of proximal humeri that are not fused. Comparing the murids and the soricids, the results indicate that the proportions of fused proximal humeri are much higher among the latter. Table 7.7.2 further shows that except for a negligible percentage in the Hanging Remnant, all soricid proximal femora are fused. This phenomenon has not been observed among the murid proximal femora. Unlike the relatively low percentages of fused distal femora, the percentages of unfused soricid distal femora are quite high in all the three samples especially in the Hanging Remnant. This phenomenon has also been observed among the murid distal femora.

Table 7.7.2: State of fusion of the soricid humeri and femora.

Skeletal element	Down Slope		Upper Slope		Hanging Remnant	
	N	%	N	%	N	%
Humerus						
Proximal fused	17	33.0	45	41.3	10	29.4
Proximal unfused	34	67.0	64	58.7	24	70.6
TOTAL	**51**		**109**		**34**	
Distal fused	64	100.0	179	100.0	34	100.0
Distal unfused	0	0	0	0	0	0
TOTAL	**64**		**179**		**34**	
Femur						
Proximal fused	52	100.0	128	100.0	23	96.0
Proximal unfused	0	0	0	0	1	4.0
TOTAL	**52**		**128**		**24**	
Distal fused	4	25.0	16	22.0	1	8.0
Distal unfused	12	75.0	57	78.0	11	92.0
TOTAL	**16**		**73**		**12**	

The results on loose epiphyses recorded in Table 7.7.3 indicate that there are very high percentages of loose epiphyses from the proximal end of the humerus. There are quite high percentages of loose epiphyses from the distal end of the femur particularly in the Down Slope and the Upper Slope. The proportions of loose epiphyses from the proximal end of the femur are also substantial.

Table 7.7.3: Loose micromammalian long bone epiphyses from SBYC.

Skeletal element	Down Slope N	Down Slope %	Upper Slope N	Upper Slope %	Hanging Remnant N	Hanging Remnant %
Humerus						
Proximal	145	100.0	144	100.0	55	100.0
Distal	0	0	0	0	0	0
TOTAL	**145**		144		**55**	
Femur						
Proximal	80	32.8	153	33.8	26	42.6
Distal	164	67.2	299	66.2	35	57.4
TOTAL	**244**		**452**		**61**	

7.8 Relative proportions of skeletal elements

Table 7.8.1 reports on the relative proportions of both murid and soricid skeletal elements.

Table 7.8.1: Relative proportions of murid and soricid skeletal elements.

	Murids			Soricids		
	Total No. of mandibles & maxillae	Total No. of femora & humeri	% femur + humerus / mandible + maxilla	Total No. of mandibles & maxillae	Total No. of femora & humeri	% femur + humerus / mandible + maxilla
Down Slope	303	577	190.4	175	147	84.0
Upper Slope	709	1093	154.2	549	319	58.0
Hanging Remnant	138	248	180.0	63	76	121.0

The results in Table 7.8.1 show that among the murids, there are excess femora and humeri relative to mandibles and maxillae in the three samples, and this phenomenon is more salient in the Down Slope and the Hanging Remnant. Among the soricids, the relative proportions of femora and humeri to mandibles and maxillae are lower in both the Down Slope and the Upper Slope, with the latter sample showing the least

percentage. On the other hand, the Hanging Remnant shows high proportions of soricid humeri and femora relative to mandibles and maxillae.

Tables 7.8.2 and 7.8.3 show relative proportions of cranial to post-cranial elements. In these tables, all skeletal elements have been treated as micromammalian remains without separating the murids and the soricids.

From Table 7.8.2, it is apparent that the relative proportions of femora and humeri to mandibles and maxillae are quite high in the three sampled areas. This phenomenon is, however, more pronounced in both the Down Slope and the Hanging Remnant. Interestingly, although the Upper Slope yielded the highest numbers of femora and humeri, the relative proportion of these elements to the mandibles and maxillae is lower than in the other samples. In both the Down Slope and the Hanging Remnant, the relative proportions of tibiae and ulnae to femora and humeri are fairly low. Conversely, there are excess tibiae and ulnae relative to femora and humeri in the Upper Slope.

Table 7.8.2: Relative proportions of skeletal elements.

Sampled area	Total No. of mandibles & maxillae	Total No. of femora & humeri	Total No. of tibiae & ulnae	% femur + humerus / mandible + maxilla	% tibia + ulna / femur + humerus
Down Slope	478	724	617	151.5	85.2
Upper Slope	1258	1412	1900	112.2	134.6
Hanging Remnant	201	324	292	161.2	90.1

From Table 7.8.3, it may be observed that the proportions of post-cranial relative to cranial elements are low. It is interesting to note the similar proportions in both the Down Slope and the Upper Slope. As the results further show, the index for relative proportion of post-cranial to cranial elements is greater in the Hanging Remnant than in both the Down Slope and the Upper Slope.

Table 7.8.3: Relative proportions of post-crania to crania.

Sampled area	Total No. of mandibles & maxillae	Total No. of isolated molars	Total No. of femora & humeri	Total No. of tibiae & ulnae	% Total No. of humeri + ulnae + femora + tibiae / Total No. maxillae + mandibles + isolated molars
Down Slope	478	1258	724	617	77.2
Upper Slope	1258	3061	1412	1900	76.7
Hanging Remnant	201	510	324	292	86.6

7.9 Non-micromammalian species at SBYC

Besides the micromammalian species, non-micromammalian species are also represented in the SBYC faunal samples. These include, Reptilia (snakes), Amphibia (frogs), Pisces (fish) and Aves (birds).

Table 7.9.1: Non-micromammalian fauna recovered from the SBYC faunal samples.

Skeletal element	Amphibia N	Aves N	Pisces N	Reptilia N
Humeri	61	35		
Ulnae	54	35		
Femora	1	10		
Tibiae		3		
Vertebrae	42	18	28	192
Phalanges		77		

The results in Table 7.9.1 show that there is a considerable representation of amphibians. Following (Klein and Cruz-Uribe 1984), 61 humeri would account for a MNI of at least 31. Aves as well are reasonably well represented at SBYC, as 35 ulnae would account for a MNI of at least 18.

CHAPTER EIGHT

Discussion

8.1 Introduction

The analysis of the SBYC micromammalian fauna yielded some interesting observations that will form the basis of this chapter. Although there are some differences among the three samples, the depositional contexts (see Figures 6.2.1 and 6.2.3) and patterning of the three samples strongly suggest that the fauna in both the Upper Slope and Down Slope originated from down-slope movement of the fauna in the Hanging Remnant. The Hanging Remnant, because of its partially cemented nature, appears to be *in situ*. In testing the hypothesis on whether or not the SBYC faunal samples belong to one parent population, comparisons will be made between different aspects of the samples. This will include skeletal representation and breakage patterns among the three samples (e.g. Klein and Cruz-Uribe 1984). Besides shedding light on species diversity in the SBYC micromammalian fauna, the species represented in the faunal samples will also be used to test the suggestion that the three SBYC samples represent one faunal occurrence that has been re-distributed across the site by natural taphonomic processes other than the primary agent/s of accumulation (e.g. Andrews 1990a). Based on taphonomic factors such as breakage patterns and ecological factors such as species representation in the SBYC fauna, the predator/s that may have been responsible for the faunal accumulation will be inferred (e.g. Matthews 1999). The species represented in the fauna will further be used to interpret the microhabitats in the SBYC area some 15, 000 years ago.

8.2 Number of identified specimens (NISPs)

In all, 32,197 micromammalian skeletal elements (NISPs) have been investigated from a variety of perspectives. Among the three sampled areas, the Upper Slope yielded generally high proportions of skeletal elements. Even though the sediments sample from the Upper Slope is larger relative to those from the Down Slope and the Hanging Remnant (see Table 8.2.1), the very high NISPs from the Upper Slope sample strongly

suggest a higher faunal density in that part of the site. The higher faunal density in the Upper Slope is confirmed by the 10 NISPs for each gram of coarse material sorted, as compared with approximately 2 and 5 NISPs from the Hanging Remnant and Down Slope respectively.

Table 8.2.1: Mass in grams of unsorted fine sediments (1) from 1.5 mm flour sieve and of coarse sediments sorted for microfauna (2), total NISPs derived from the sediments (3) and approximate NISPs for each gram of sorted coarse sediments (4).

	Down Slope	Upper Slope	Hanging Remnant
1	2307.4	5082.6	2378.3
2	1588.6	2109.2	1737.3
3	7641	21530	3026
4	5	10	2

The higher density of faunal remains in the Upper Slope relative to the other sampled areas is further confirmed by chi-squared (X^2) tests on the distribution of different skeletal elements. The tests show generally higher proportions of observed relative to the expected numbers of skeletal elements in the Upper Slope, as opposed to the generally lower numbers of observed relative to the expected numbers of skeletal elements in both the Down Slope and Hanging Remnant (see e.g. Appendices 5.1.1-4 and 5.2.1).

As Table 7.1.1 clearly shows, the percentages of isolated molars, foot bones and vertebrae are generally high in the three samples. Although there are minor differences among the SBYC samples, the high percentages of phalanges, metapodials and vertebrae in all the samples may be attributed to a range of factors. While there are large numbers of these bones in the body, their frequent preservation in the SBYC samples is a feature of barn owl collections (e.g. Dodson and Wexlar 1979; Korth 1979). In addition, it has been noted (Korth 1979; Behrensmeyer *et al.* 1989) that the durability of foot bones enables them to survive many taphonomic processes, including abrasion during transport. With regard to the high percentages of isolated molars in the SBYC samples, this phenomenon may be ascribed to the loss of teeth from the jaws as a result of post-depositional breakage of the jaws (e.g. Andrews 1990a). Overall, the generally consistent percentages of NISPs across the three sampled areas and, more particularly those of the

four most abundant skeletal elements (isolated molars, vertebrae, phalanges and metapodials) support the suggestion that the three SBYC samples represent one faunal occurrence.

8.3 Damage to the skull

8.3.1 Breakage of the crania

There seems to be high breakage of murid crania at SBYC. This is clearly demonstrated by the absence in all the samples of murid maxillae or maxilla fragments that are still attached to the cranium. Similarly, the paucity in all the samples of cranial fragments that could certainly be associated with a particular taxonomic group further confirms the high degree of cranial breakage in the SBYC fauna. This agrees with observations by Dodson and Wexlar (1979) as well as Andrews (1990a) that complete skulls of small mammals rarely occur in predator assemblages. This is essentially because the most common way of killing prey is by breaking the neck and piercing through the back of the skull (Dodson and Wexlar 1979). Additionally, Korth (1979) has also noted that post-depositional processes such as hydraulic transport easily destroy the skull. In view of this, it may be concluded that damage resulting from post-depositional processes has exacerbated predator-induced modifications, resulting in severe breakage of the crania at SBYC.

Even though the SBYC samples yielded fairly high percentages of complete murid maxillae and generally maxillae with a portion of the zygomatic process still intact, murid maxillae breakage among the samples is generally high. Because Andrews' (1990a) modern predator assemblages show generally high proportions of complete maxillae and maxillae with the zygomatic process intact (see Appendix 4.1), the relatively lower proportions of these maxillae in the SBYC samples suggests that post-depositional processes have also contributed towards the damage of the SBYC maxillae. The higher percentage of murid maxilla fragments in the Hanging Remnant relative to the other sampled areas suggests a greater breakage of murid maxillae in this sample. It is possible that the use of dental picks to extract sediment samples from the Hanging Remnant may have partially contributed towards the higher breakage of not only the maxillae in this

sample, but also other skeletal elements. Comparing the Down Slope and Upper Slope, the relatively higher breakage of murid maxillae in the former sample is suggested by the lower percentage of complete maxillae as well as the higher percentage of maxillae fragments. It is conceivable that down-slope movement of the maxillae would have partially contributed towards the higher breakage evident in the Down Slope sample. The relatively high percentages of murid maxillae with a portion of the zygomatic process still intact in all the SBYC samples, nevertheless, support the suggestion that the zygomatic process is one of the most durable parts of the skull (e.g. Andrews 1990a). It is, however, important to point out that since *Tatera afra* yielded the highest number of maxillae (see Appendix 3), the results obtained from the breakage patterns may have been significantly influenced by this dominant species (e.g. Avery 1999).

Although there are a few complete soricid maxillae (see Table 7.3.2), the much higher breakage of soricid crania in all the samples as compared to those of the murids, probably reflects the more delicate nature of soricid skulls (pers. observ.). At this stage, although there is no clear explanation for the low proportions of soricid maxillae in the Hanging Remnant, it is plausible that both predator-induced breakage and breakage resulting from post-depositional processes (including recovery procedures) would have adversely contributed towards this phenomenon. Because of the fragility of soricid maxillae, the lower proportions of these jaws in the Down Slope relative to the Upper Slope may also be explained by the greater distance of the former from the presumed source in the Hanging Remnant.

8.3.2 Breakage of the mandibles

Because the morphology of mandibles makes them less susceptible to damage, mandibles tend to be commonly preserved in predator assemblages (e.g. Dodson and Wexlar 1979; Andrews 1990a). In the SBYC faunal samples, the low percentages of complete murid mandibles, together with the generally high percentages of mandible fragments, especially in the Down Slope, suggests that post-depositional factors have compounded the effect of predator-induced processes to significantly influence the number of complete murid mandibles. It has been shown (Andrews and Jenkins 2000) that post-

depositional processes may cause extensive breakage to mandibles. It should, however, be noted that mandible breakage patterns may vary from one species to another (e.g. Korth 1979). In all the SBYC samples, mandibles belonging to the most common murid, *Tatera afra,* are not only abundant (see Appendix 3) but are also generally well preserved. This is largely because these mandibles are big and robust (D. M. Avery, pers. comm., 2002). Overall, unlike in the modern predator assemblages (Appendix 4.1), there are relatively low proportions of complete murid mandibles in the SBYC faunal samples and generally high percentages of murid mandibles of which the ascending rami are missing or broken, which further confirms the higher breakage of the SBYC murid mandibles.

The occurrence of generally high proportions of soricid mandibles in all the SBYC samples agrees with Andrews' (1990a: 57) postulation that because of the morphology of insectivore mandibles, these jaws tend to be more common in predator assemblages. Nevertheless, although there are fairly high percentages of complete or nearly complete soricid mandibles, especially in the Upper Slope, the effect of predator and post-depositional breakage on the soricid mandibles is suggested by the relatively high percentages of Category 4 mandibles, especially in the Down Slope, and the fairly high percentages of Category 5 mandibles in all the samples.

By and large, the percentages of different elements of the skull in the three SBYC faunal samples point to a relatively high breakage of the skull. Following Andrews (1990a) and Fernandez-Jalvo (1995), the high breakage of the skull has largely contributed towards the high proportions of isolated molars in all the SBYC faunal samples. It is also likely that the high breakage of the skulls may have resulted in the loss of cranial elements (e.g. Andrews 1990a). In view of the breakage patterns among murid mandibles, the down-slope movement may have contributed towards the much higher proportion of mandible fragments as well as the very low proportion of complete mandibles in the Down Slope. Similarly, among the soricid mandibles, the very low percentage of complete mandibles in the Down Slope and the much higher percentages of mandible portions (Categories 4 and 5) indicate that there has been an increase in breakage as the jaws moved down slope, a proposition that has been confirmed by the gamma analyses.

Although the gamma analyses on both the murid and the soricid maxillae suggest that there are no statistically discernible directional relationships between the position on the slope and the degree of breakage, the corresponding gamma analyses on both murid and soricid mandibles show statistically discernible evidence of directional (ordinal) relationships between the position of the fauna at the site and the degree of breakage (see Appendix 5.3.5). These statistically significant relationships indicate an increase in breakage as the bones erode down slope. As reported in Tables 7.3.3 and 7.3.4, the high proportions of both soricid and murid mandible fragments in the Upper Slope and Down Slope support the statistical evidence of increased breakage as the bones move down slope. Contrasts in the levels of breakage as the fauna moved down slope are further suggested by the chi-squared (X^2) tests. The chi-squared results (e.g. Appendices 5.1.1, 5.2.1 and 5.3.1) show that although the proportions of the observed murid and soricid complete jaws relative to the expected are lower in both the Down Slope and the Hanging Remnant, the differences in the proportions are generally more pronounced in the former sample. Additionally, comparing the Down Slope and the Upper Slope, the chi-squared tests suggest higher breakage of the jaws as the fauna moved down slope, as strongly indicated by the generally lower numbers of the observed relative to the expected Category 1 maxillae and mandibles in the former sample. The overall image reflected by the results on cranial elements is, therefore, that the SBYC faunal samples belong to one parent assemblage and that taphonomic processes, including post-post-depositional processes (e.g. the down-slope movement) have not only contributed towards the current location of the fauna along the slope but have also differentially modified the fauna.

8.4 Etching of the incisors

Examination of incisors for acid-etching strongly shows that in all the SBYC samples etching is minimal. This is indicated by the generally high percentages of Categories 1 and 2 incisors. Although there are some differences in the percentages of etching among the three samples, the generally high percentages of incisors that show either no evidence of etching and/or pitting or very light etching and/or pitting imply that the predator/s responsible for the accumulation of the SBYC fauna belonged to the lower etching categories (see Appendix 4.2). Moreover, because etching and/or pitting on the SBYC

incisors are not restricted to the tips of the incisors, post-depositional corrosion by the alkaline sediments at SBYC cannot be ruled out. This is because, unlike the localized effect of digestion, corrosion resulting from non-digestive processes such as alkaline sediments tends to affect all parts of the element (Andrews 1990a; Fernandez-Jalvo and Andrews 1992). In addition, because the Hanging Remnant yielded higher percentages of incisors (isolated and *in situ*, lower and upper) that show light etching and/or pitting, it is likely that longer presence of the incisors in the partially cemented Hanging Remnant may have contributed towards this phenomenon. Since heavier digestion by predators such as the barn owl and giant eagle owl (Category 1 predators) may sometimes penetrate the dentine, the incisors in the SBYC samples in which etching has slightly infiltrated the dentine (Category 3) may have resulted from either digestion by such predators or from corrosion by sediments (e.g. Andrews 1990a; Fernandez-Jalvo and Andrews 1992). On the whole, the high percentages of Categories 1 and 2 incisors and the low percentages of Category 3 incisors in all the samples indicate minimal etching of the SBYC incisors. This phenomenon further strengthens the contention that the SBYC faunal samples belong to one faunal accumulation that may have been accumulated by the same agent/s and that the apparent differences in the percentages of etching may have resulted from factors such as the differential effect of predator-induced corrosion as well as post-depositional processes.

8.5 Post-cranial elements

8.5.1 Breakage of the long bones

As clearly illustrated in Figures 7.5.1-7.5.4, the analysis of breakage patterns among the humeri and the femora yielded some very interesting results. As further demonstrated in Figures 8.5.1 and 8.5.2, even though there are some differences in the percentages among the three SBYC samples, overall the soricids yielded higher proportions of complete humeri and femora than did the murids. Given that the faunal remains at SBYC appear to have been subjected to generally similar taphonomic processes, the higher proportions of complete humeri and femora among the soricids relative to the murids suggest that there has been preferential preservation of the soricid proximal long bones.

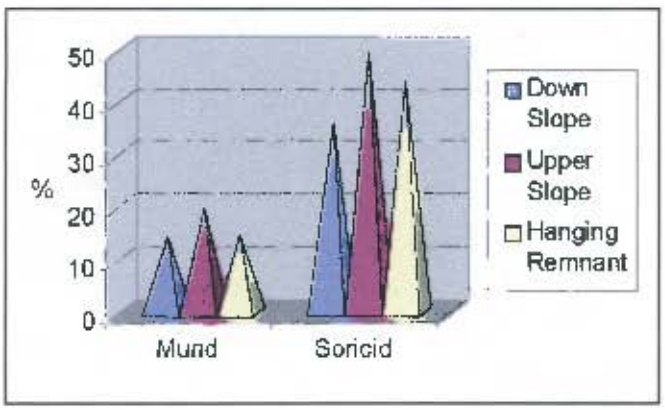

Figure 8.5.1: A comparison between the percentages of complete murid and soricid humeri across the three sampled areas

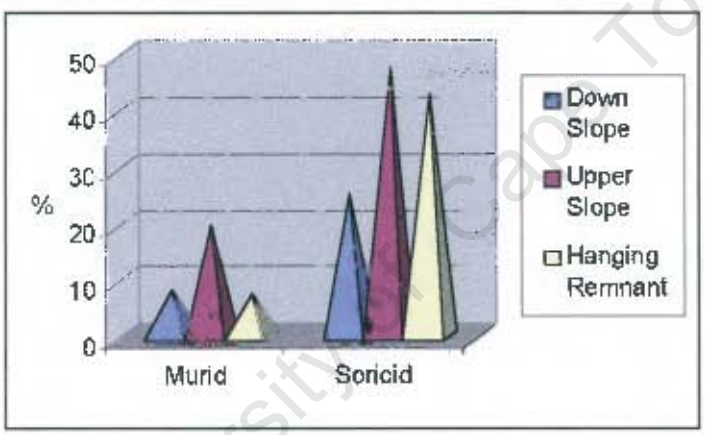

Figure 8.5.2: A comparison between the percentages of complete murid and soricid femora across the three sampled areas

Because the material in the Down Slope lies at the foot of the slope, the generally lower percentages of complete humeri and femora in this sample, especially among the soricids (Figures 8.5.1 and 8.5.2), suggest an increase in breakage as the bones moved down slope. On the other hand, the higher percentages of distal humeri and proximal femora in the Down Slope sample (Figures 8.5.3 and 8.5.4) should have been influenced by the durability of these portions of the long bones (e.g. Andrews 1990a; Andrews and Jenkins 2000).

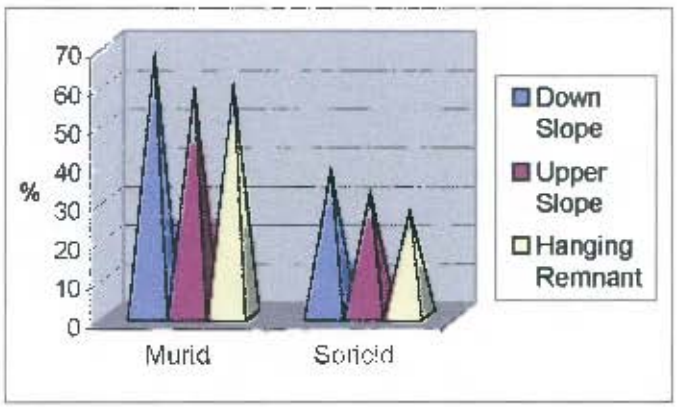

Figure 8.5.3: A comparison between the percentages of murid and soricid distal humeri across the three sampled areas

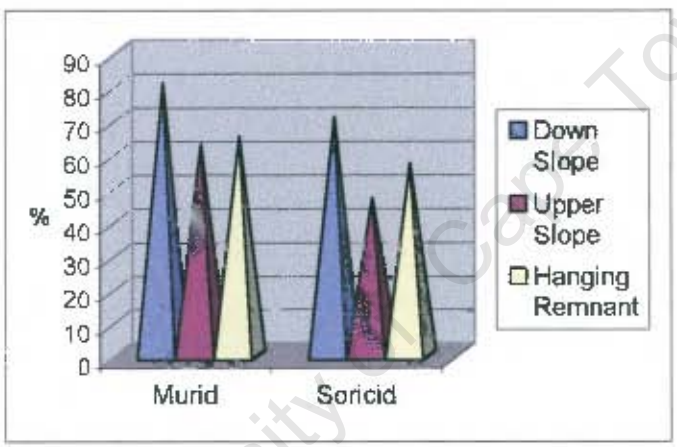

Figure 8.5.4: A comparison between the percentages of murid and soricid proximal femora across the three sampled areas

The generally low percentages of distal femora (see Figures 7.5.3 and 7.5.4) may have resulted from the preferential destruction of that part of the bone. Dodson and Wexlar (1979) have reported that as a result of predator activity, the distal end of the femur tends to sustain damage. It is therefore apparent that, besides the modifications to the long bones that would have resulted from the predator/s or other modes through which the SBYC fauna may have been accumulated, both post-depositional processes (e.g. diagenesis) and post-post-depositional factors (e.g. erosion) have influenced the breakage patterns of the long bones. Additionally, it is evident that survival of not only down-slope movement but also the preceding taphonomic processes such as predator-induced

breakage favoured the more robust and therefore durable skeletal elements (i.e. distal humerus and proximal femur).

The chi-squared tests of the murid and soricid humeri (Appendices 5.4.1 and 5.5.1) indicate that there are no statistically discernible correlations between position on the slope and the types of bone (complete, proximal, shaft or distal) commonly represented there. Conversely, the tests of the murid and soricid femora (Appendices 5.6.1 and 5.7.1) show high statistical evidence of correlation between position on the slope and the types of bone highly represented there. As an example, the higher than expected numbers of complete murid femora in the Upper Slope and the lower than expected numbers in the Down Slope illustrate this relationship (see Appendix 5.6.1). In sum, the chi-squared tests for both murids and soricids show generally lower numbers of observed relative to the expected complete humeri and femora in the Down Slope. In addition, the chi-squared tests show higher numbers of observed relative to the expected distal humeri and proximal femora (sturdy ends of the bones) in the same sample (see e.g. Appendices 5.4.1-2 and 5.5.1-2). Figures 8.5.1 and 8.5.2 clearly demonstrate the low percentages of soricid complete humeri and femora in the Down Slope. These observations agree with the suggestions that there has been an increase in breakage as the fauna moved down slope and also that there has been a selective bias for the more durable elements. The generally lower numbers of observed relative to the expected complete humeri and femora in the Hanging Remnant, on the other hand, may be attributed to a range of factors, including the poor representation of skeletal elements that characterizes this sampled unit (see e.g. Table 8.2.1).

Although the percentages of complete ulnae and tibiae are very low in all the SBYC samples, the generally high percentages of proximal ulnae and distal tibiae indicate preferential preservation of these two ends of the bones. Among the three samples, the higher percentage of proximal ulnae and the fairly high percentage of distal tibiae in the Down Slope provide further support for the hypothesis that there has been a selective bias for the more durable portions of the long bones in the Down Slope. With regard to the generally high proportions of proximal ulnae, this end of the bone fuses early in life and is therefore more durable (Andrews 1990a). On the other hand, the distal end of the ulna

tends to be more prone to damage by predators (through e.g. digestion) than the proximal end (Dodson and Wexlar 1979), which may explain the high percentages of proximal relative to distal ulnae in the three SBYC faunal samples. Andrews and Jenkins (2000) have also reported high proportions of distal tibiae from Mumbwa Caves, which agrees with the situation at SBYC.

Andrews (1990a) has noted that lower proportions of shafts in a faunal assemblage may imply secondary breakage rather than predator-induced damage, which tends to yield relatively high proportions of shafts. This phenomenon tends to be more apparent among avian predators such as hen harriers, kestrels, little owls and also many of the small carnivorous mammals (Andrews 1990a). Following Andrews (1990a), although the fairly high percentages of tibia shafts in the SBYC fauna contrasts with the very low proportions of shafts from the rest of the long bones, it is apparent that both predator and post-depositional destruction have influenced the SBYC fauna. The very low percentages of long bone shafts (except for the tibiae) in the SBYC faunal samples correlate with results from the Dark Brown Breccia, Unit 12, at Westbury (Andrews 1990a) and from Elands Bay Cave (Matthews 1998). Generally, comparing the breakage patterns in the SBYC samples with the results from modern predator assemblages (Appendix 4.3), there seems to have been greater destruction of the long bones in the SBYC samples. The patterns clearly indicate that both predator-induced and post-depositional processes have differentially influenced the breakage patterns among the SBYC faunal samples, as demonstrated by the preferential preservation and/or destruction of elements such as proximal and distal humeri and femora.

8.5.2 Breakage of other post-cranial bones

Although the scapulae show higher index of completeness than the innominates, the high percentages of scapula and innominate fragments indicate high incidence of breakage in these two bones. This could be associated with the effect of both predation and post-depositional processes. Dodson and Wexlar (1979) have reported that, except for those accumulated by barn owls, most predator assemblages tend to yield scapulae and innominates that are badly damaged. Because of the relatively delicate nature of the

scapulae and the innominates (e.g. Dodson and Wexlar 1979), it has also been demonstrated (Korth 1979) that post-depositional processes such as transport easily abrade these bones. It may therefore be concluded that, in all the sampled areas, the effect of both predation and post-depositional processes on these bones has largely been influenced by their fragility.

8.6 Epiphyseal fusion in the long bones

The absence of distal humeri without epiphysis in both the murids and the soricids is ascribed to the early fusion of that part of the bone (e.g. Andrews 1990a). Bates and Harrison (1980), who have investigated epiphyseal fusion in wild mice (*Apodemus sylvaticus)* observed no unfused epiphyses on the distal end of the humerus, implying that this end of the bone fuses early in life. Although the percentages of fused and unfused humeri and femora suggest that both mature and young individuals are represented in the SBYC faunal samples, the relatively higher proportions of unfused murid proximal humeri in all the samples indicate that a considerable percentage of the murids were juveniles at the time of their death (e.g. Chaplin 1971). The high proportions of unfused proximal and distal murid femora in all the samples further supports the suggestion that young individuals are fairly well represented at SBYC.

The percentages of fused and unfused humeri and femora among the soricids also suggest that young individuals are well represented in the SBYC faunal samples. The very high percentages of fused soricid proximal femora, however, indicate that proportions of soricid juveniles are lower than those observed among the murids. Overall, although skeletal remains of young individuals are more vulnerable to taphonomic processes such as digestion, Avery (1992) has shown that at Geelbek B in the West Coast National Park, young *Otomys irroratus* are fairly well represented in barn owl pellets. Following Avery (1990: 410), "the rates of early post-natal development and maternal practices will influence the likelihood of the very young being caught by predators". In spite of the suggestion that both mature and young individuals are represented at SBYC, it is imperative to point out that the age at which epiphyseal fusion occurs is variable and that

this may be influenced by factors such as individual variation, as well as those associated with the environment (e.g. Chaplin 1971; Bates and Harrison 1980).

With regard to the loose epiphyses, the high proportions of these elements from the proximal end of the humerus correlate with the high percentages of unfused proximal humeri. The relatively high proportions of loose epiphyses from the distal end of the femur compare with the fairly high percentages of unfused distal femora especially among the murids. Similarly, the generally high proportions of loose epiphyses from the proximal end of the femur correspond with the relatively high percentages of unfused murid proximal femora. Generally, it may therefore be concluded that the proportions of loose epiphyses are comparable with the unfused ends of the humeri and femora, particularly among the murids.

8.7 Relative proportions of skeletal elements

Because the SBYC samples, especially the Down Slope, show excess murid humeri and femora (proximal long bones) relative to mandibles and maxillae (Table 7.8.1), this supports the suggestion that there has been differential destruction or loss of jaws at SBYC and that this phenomenon is more pronounced in the Down Slope. Among the soricids, the excess of maxillae and mandibles over humeri and femora in the Down Slope and Upper Slope is expected. This is largely because there has been generally a selective bias for soricid jaws, and more particularly the mandibles (see e.g. Tables 7.2.4 and 7.2.5). The higher proportions of soricid humeri and femora relative to maxillae and mandibles in the Hanging Remnant, on the other hand, shows that there has been a selective bias against soricid jaws in the Hanging Remnant, a suggestion supported by the low proportions of soricid jaws in this particular sample relative to the other samples. Overall, comparing the SBYC faunal samples with modern predator assemblages (Appendix 4.4), the proportions of femora and humeri relative to mandibles and maxillae in the SBYC fauna indicate that predator-induced and post-depositional processes have selected against the jaws.

When murids and soricids are combined (Table 7.8.2), the excess of femora and humeri over mandibles and maxillae in all the faunal samples further indicates that jaws are poorly represented at SBYC. Although the excess of femora and humeri over the jaws is more prominent in both the Hanging Remnant and the Down Slope, it may be noted that the generally high proportions of murid long bones relative to the jaws in the three samples may have influenced the indices for relative proportions (e.g. Andrews 1990a). Except for assemblages accumulated by a few predators such as the mongoose (see Appendix 4.4), the proportions of excess humeri and femora relative to mandibles and maxillae are generally higher in the SBYC samples than they are in modern predator assemblages. Again, this may be partially an artifact of the generally high proportions of humeri and femora in the SBYC samples, which as Andrews (1990a) also noted on the Westbury Pink Breccia Unit 11 fauna, may be associated with the sturdy nature of these two long bones.

The proportions of femora and humeri relative to tibiae and ulnae (distal long bones) indicate excess of the former in both the Down Slope and the Hanging Remnant (Table 7.8.2). Conversely, the indices indicate higher proportions of tibiae and ulnae relative to femora and humeri in the Upper Slope. It may therefore be concluded that there is differential representation of long bones in the three samples and that this may be associated with the differential effect of taphonomic processes on the bones across the site. Additionally, the low proportions of post-cranial to cranial elements (Table 7.8.3) reflect the high proportions of isolated molars in all the three sampled areas (e.g. Andrews 1990a). This is because relative proportions of post-cranial to cranial elements are quite high in cases where isolated molars have not been considered (see Table 7.8.2).

8.8 The microfaunal species and the minimum number of individuals (MNIs)

8.8.1 Micromammalian species

Even though there are some differences in the percentages based on MNIs among the three SBYC faunal samples (Table 7.2.2), the dominance of *Tatera afra*, *Myosorex varius*

and *Suncus varilla* in all the samples is evident. Importantly, when murid and soricid MNIs are compared, it is apparent that the jaws yielded generally higher MNIs for soricids than for murids (Table 7.2.4), but the humeri and femora gave higher MNIs for murids (Table 7.2.5). In view of this, it may strongly be argued that for one to arrive at MNIs that are likely to be accurate, both jaws and long bones should be considered, and attempts should be made where possible to identify the taxa represented by these elements at least to family level. This is largely because faunal remains are relics of a wide range of ecological and taphonomic processes, and these processes differentially influence the composition of faunal assemblages (e.g. Korth 1979; Andrews 1990a).

From the perspective of the predator-prey relationship, the high representation of *Tatera afra, Myosorex varius* and *Suncus varilla* in the three samples indicates that the predator/s that accumulated the fauna had a preference for these three micromammalian species or that these species were particularly abundant (e.g. Andrews 1990a). If all taphonomic processes at SBYC affected the remains of the different species equally (e.g. Korth 1979), the relatively low proportions of the other rodent and insectivore species in all samples suggest that either the predators avoided them or they occurred in low proportions around the SBYC area. Similarly, the negligible representation of molerats and Cape rock elephant-shrews shows that these two species were rarely taken by the predator/s that accumulated the SBYC microfauna (e.g. Andrews 1990a; Avery *et al.*1990).

As indicated in Table 8.8.1, the micromammalian species represented in the SBYC fauna have been derived from a wide range of microhabitats. Investigations of barn owl pellets recovered from the West Coast National Park have, however, suggested a co-occurrence of different micromammalian species (Avery *et al.* 1990; Avery 1992). The investigations suggested that species such as *Myosorex varius* and *Otomys irroratus* tended to co-exist. *Suncus varilla* and *Otomys unisulcatus* were both found to occur together, while *Steatomys krebsii* co-occurred with *Suncus varilla.* The investigations further revealed that in some areas, *Tatera afra, Otomys unisulcatus* and *Steatomys krebsii* co-occurred (Avery 1992). Following these observations, it is likely that in the neighborhood of the SBYC faunal site some 15,000 years ago, the co-existence of species

would have influenced the sampling by the predator of the most preferred and possibly abundant species in each microhabitat, resulting in the evidently high representation of *Tatera afra*, *Myosorex varius* and *Suncus varilla*. Overall, the dominance of *Tatera afra*, *Myosorex varius* and *Suncus varilla* in all the samples together with the relatively low representation of other micromammalian species strongly support the suggestion that the three SBYC faunal samples represent one occurrence that would have been accumulated by one predator species.

Table 8.8.1: Micromammalian species from SBYC, their preferred modern habitat, activity pattern and mean individual mass (Mass* to the nearest 5g. See Appendix 1 for further details).

Taxon	Preferred modern habitat	Activity pattern	Mass*
Insectivora			
Chrysochloris asiatica	sandy soil loosened by e.g. cultivation; fairly open grass or semi-arid scrub		50
Crocidura cyanea	wide habitat tolerance; grass or fynbos	diurnal and nocturnal	10
Crocidura flavescens	dense vegetation	diurnal and nocturnal	25
Myosorex varius	moist, dense vegetation	largely nocturnal	15
Suncus varilla	open grassland		5
Chiroptera			
Rhinolophus clivosus	caves, rock crevices, mine adits etc.	largely nocturnal	15
Rodentia			
Dendromus melanotis	tall dense grass in riverine conditions	nocturnal	5
Dendromus mesomelas	rank vegetation of tall grass or bushes	nocturnal	10
Steatomys krebsii	dry sandy grassland and sandy alluvium	nocturnal	25
Gerbillurus paeba	loose sand; sparse grassland	nocturnal	25
Tatera afra	loose sandy or sandy alluvium soils; open grassland	nocturnal	100
Mystromys albicaudatus	savanna grassland	nocturnal	80
Rhabdomys pumilio	dense vegetation	largely diurnal	45
Otomys irroratus	moist dense vegetation	largely diurnal	120
Otomys saundersiae	mountainous areas; grass or fynbos	diurnal	100
Otomys unisulcatus	sparse semi-arid shrub or fynbos	largely crepuscular	125
Bathyergus suillus	soft coastal sandveld		650
Cryptomys hottentotus	sandy soils; sparse vegetation	largely nocturnal	200
Macroscelidea			
Elephantulus edwardii	rocky outcrops; sparse semi-arid scrub	largely nocturnal	50

Although the Shannon-Wiener indices for general diversity (*H*) suggest that the three samples are not absolutely the same, the lower index (*H*) in the Hanging Remnant may be

attributed to the much smaller faunal sample from this part of the site. According to Avery (1982), the number of species can be affected by sample size even when evenness of representation is not. It is, however, interesting that the Down Slope sample yielded slightly higher index (*H*) than did the Upper Slope one, considering that the latter sample is the largest of all. Avery (1999) demonstrated that there is a lower species diversity index in modern faunal samples when a dominant species is included in the analysis, and higher when this species is omitted. The slightly lower diversity index (*H*) in the SBYC Upper Slope sample may therefore be attributed to the much higher *Myosorex varius* MNIs in this sample (see Table 7.2.2). This does not, however, explain the continued lower index (*H*) in the Upper Slope relative to the Down Slope when *Myosorex varius* is omitted from the analysis (Table 7.2.3). The fluctuating indices depending on whether or not *Myosorex varius* and *Tatera afra* are included in the analyses, nevertheless, agree with Avery's (1987) observations on the micromammalian fauna from the Klasies River Mouth. These studies showed fluctuations in species indices (*H*), depending on whether or not the dominant species, *Otomys irroratus,* was included in the analysis. This demonstrates the effect that high representation of particular species may have on faunal interpretations.

8.8.2 Non-micromammalian fauna

Even though the representation of non-micromammalian fauna appears to have been minimal at SBYC, its presence confirms that the predator/s that accumulated the SBYC fauna were not restricted to micromammalian species (e.g. Steyn 1982; Andrews 1990a). Because amphibians and birds (in that order) are the best represented, this may suggest either that the two were more highly favoured than the others or that they were more abundant. Although accidental inclusions of not only micromammalian but also other microfaunal remains may result in their occurrence in predator assemblages (e.g. Fernandez-Jalvo and Andrews 1992), the relatively high MNIs for both amphibians and birds in the SBYC fauna compared to micromammalian species such as the Cape rock elephant-shrews, strongly indicate the involvement of some predator/s. As summarized in Appendix 2, most avian and mammalian predators prey on a wide range of microfaunal species.

8.9 Identifying the predator

Given that post-depositional factors will have obscured some characteristic signatures left by predators (e.g. Andrews 1990a), the attempt to infer the potential predator/s that may have been responsible for the SBYC micromammalian fauna will be based on both ecological and taphonomic patterns evident in the fauna (e.g. Matthews 1999).

Appendix 2 gives modern ecological data for some avian and mammalian predators that could have been responsible for the accumulation of the SBYC micromammalian remains. Although most small carnivorous mammals prey on a wide range of micromammalian species (e.g. Skinner and Smithers 1990), the likelihood that these predators would have been responsible for the accumulation of the SBYC fauna is ruled out by a range of factors. As highlighted in Chapter Four, most small carnivorous mammals cause considerable damage to the bones of their prey. Through consumption and digestion the mustelids, for instance, cause so much damage to the bones of their prey (Andrews 1990a) that they are unlikely accumulators of the micromammalian remains at SBYC. The destruction of micromammalian bones found in scats of mustelids such as polecats is so high that it is difficult to positively identify skeletal elements. Likewise, the felids cause great damage to the bones of their prey, to the extent that it is difficult to obtain any meaningful samples. Micromammalian bones derived from canid scats have also shown large-scale destruction (Andrews and Evans 1983; Andrews 1990a).

The range of prey species taken by small carnivorous mammals also makes them unlikely candidates for the SBYC micromammalian faunal accumulation. Among the felids, although the caracal's diet may include micromammals such as mice, the absence in the SBYC fauna of larger prey species (e.g. small antelopes and dassies) that commonly occur in the diet of the caracal, calls into question the involvement of this carnivore in the accumulation of the SBYC fauna (see Appendix 2). Among the canids, the largely nocturnal black-backed jackal preys on larger prey species such as young antelopes and hares (Stuart and Stuart 2001). The Cape fox and the bat-eared fox, on the other hand, are predominantly insectivorous (Kingdon 1997; Stuart and Stuart 2001). Among the

viverrids, the largely diurnal and insectivorous small-grey mongoose and yellow mongoose (Stuart and Stuart 2001) are not potential accumulators of the SBYC fauna. The suricate is completely diurnal, living in burrow complexes (warrens) and preying predominantly on insects and other invertebrates (Stuart and Stuart 2001).

Studies have also shown that scats of many small carnivorous mammals yield micromammalian incisors that exhibit high levels of etching. Canid scats, for instance, have generally yielded micromammalian incisors that are highly etched (Category 4). One exception is the largely insectivorous bat-eared fox, which causes Category 1 or 2 etching. The viverrids yield intermediate incisor etching that falls between Category 2 and 3 (Andrews 1990a).

Since most of the micromammalian species at SBYC are largely nocturnal (Table 8.8.1), the possibility that diurnal raptors would have accumulated the fauna is minimal. Analyses done on diurnal raptors' pellets (e.g. Dodson and Wexlar 1979) have yielded very few micromammalian bones, largely because through digestion, these birds cause considerable destruction to the bones of their prey (Dodson and Wexlar 1979; Andrews 1990a). In addition, although most diurnal raptors prey on micromammals, the generally mobile existence of these birds makes them less potential accumulators of micromammalian bones (e.g. Steyn 1982).

Among the owls, the small size of the micromammalian species represented in the SBYC samples does not suggest large owls such as the Cape eagle owl (*Bubo capensis capensis*) and the giant eagle owl (*Bubo lacteus)* as potential accumulators of the micromammalian fauna at SBYC. This is largely because these owls feed primarily on larger prey species such as molerats, red hyraxes, vervet monkeys, warthog piglets, dassies, mongoose, scrub hares, red rock hares and springhares (Steyn 1982, 1984; Kemp and Calburn 1987).

On their present distribution, the grass owl (*Tyto capensis*), marsh owl (*Asio capensis*) and wood owl (*Strix woodfordii*) may be ruled out as potential accumulators of the SBYC micromammalian fauna on the premise that the first two species roost and nest in open expanses of moist grassland while the largely insectivorous wood owl occurs mostly in

forests. The marsh owl is also one of the most mobile owls in southern Africa, and therefore its roost sites usually contain few pellets (Steyn 1982; Kemp and Calburn 1987).

Because of the catholic diet associated with the spotted eagle owl (*Bubo africanus*), this owl may have contributed towards the accumulation of the micromammalian fauna at SBYC. This owl takes a wide range of prey species including rats, mice, shrews, birds, amphibians, molerats, and also arthropods. Depending on their abundance, species such as the gerbils may also be taken in large numbers by this owl (Steyn 1982). Although molerats are represented at SBYC, their negligible representation, and the total absence of small mammalian prey species such as scrub hares which occasionally occur in the diet of this owl (Steyn 1982), does not favour the spotted eagle owl as a potential accumulator of the SBYC micromammalian fauna. As also recorded in Table 4.2.1, the spotted eagle owl causes considerable damage to the bones of its prey (e.g. Grindley *et al.* 1973; Dean 1989; Andrews 1990a). Andrews (1990a: 75) has reported further that the spotted eagle owl causes extensive enamel digestion over the entire incisor, a phenomenon that is not evident among the SBYC incisors. In addition, the large accumulations of bones at SBYC tend to rule out the spotted eagle owl. This owl has a tendency to use various nest sites (Steyn 1982), and therefore not to accumulate large clusters of pellets, which further calls into question the candidacy for this owl as a potential accumulator of the SBYC micromammalian fauna.

Overall, considering all the factors highlighted above and the relative completeness of the SBYC micromammalian fauna, particularly the long bones, the possibility that any of these predators would have been responsible for the SBYC fauna is minimal. Because of the factors discussed below, the most probable accumulator of the SBYC micromammalian fauna is the barn owl. The barn owl occurs in a wide range of habitats but its hunting over-emphasizes riverine environments (Steyn 1982; Kemp and Calburn 1987; Avery 2002). The owl preys largely on rodent and insectivore species with mean body mass below 150 g (e.g. Avery 1988, 1990, 1993). As shown in Table 8.8.1, the micromammalian fauna from the three sampled areas at SBYC represent largely micromammalian species weighing below 150 g, with negligible representation of larger

rodent species such as the molerats. Table 8.9.1 further shows that nearly all the micromammalian species represented at SBYC have also been recorded in barn owl pellets from the region.

Table 8.9.1: Micromammalian species encountered in modern barn owl pellets from the West Coast National Park (After Avery *et al.* 1990, Table 2) and in the SBYC faunal samples.

Species	Common name	In owl pellets	In SBYC fauna
Insectivora			
Chrysochloris asiatica	Cape golden mole	#	#
Eremitalpa granti	Grant's golden mole	#	
Crocidura cyanea	reddish-grey musk shrew		#
Crocidura flavescens	greater musk shrew		#
Myosorex varius	forest shrew	#	#
Suncus varilla	lesser dwarf shrew	#	#
Chiroptera			
Rhinolophus clivosus	Geoffroy's horseshoe bat		#
Eptesicus hottentotus	long-tailed serotine bat	#	
Rodentia			
Dendromus melanotis	grey climbing mouse	#	#
Dendromus mesomelas	Brants's climbing mouse	#	#
Steatomys krebsii	Krebs's fat mouse	#	#
Gerbillurus paeba	hairy-footed gerbil	#	#
Tatera afra	Cape gerbil	#	#
Mystromys albicaudatus	white-tailed rat		#
Rhabdomys pumilio	striped mouse	#	#
Otomys irroratus	vlei-rat	#	#
Otomys saundersiae	Saunders's vlei-rat		#
Otomys unisulcatus	bush Karoo rat	#	#
Mus musculus	house mouse	#	
Mus minutoides	pygmy mouse	#	
Bathyergus suillus	Cape dune molerat		#
Cryptomys hottentotus	common molerat	#	#
Georychus capensis	Cape molerat	#	
Macroscelidea			
Elephantulus edwardii	Cape rock elephant-shrew		#

Although the barn owl takes a wide range of micromammalian species, it tends to over-emphasize the most abundant prey species, particularly rodents and shrews (Steyn 1982; Andrews 1990a). The relatively high representation of *Tatera afra*, *Myosorex varius* and *Suncus varilla* (Table 7.2.2) may be interpreted as implying that these three species were

abundant around SBYC when the fauna was accumulated, and the barn owl would have preferred the three micromammalian species to others (e.g. Andrews 1990a). At Steenbokfontein, situated on the western coast of South Africa, Avery (1999) has also recorded a relatively high representation of *Suncus varilla* in some of the layers, indicating that this species formed a significant part of the diet for the predator/s at Steenbokfontein. Investigations of modern barn owl pellets from Steenbokfontein (Avery 1999) have also shown a fairly high representation of *Tatera afra*, indicating that this species occupies a significant part in the diet of the barn owl in certain parts of the Western Cape.

Most of the micromammalian species represented in the three sampled areas at SBYC are largely nocturnal (Table 8.8.1) and, because the barn owl is largely nocturnal (e.g. Kemp and Calburn 1987), this further strengthens the contention that this owl is the most likely accumulator of the SBYC micromammalian fauna. The presence at SBYC of largely diurnal micromammalian species such as *Rhabdomys pumilio* (e.g. Avery 1992) can be explained by the fact that the barn owl is known to hunt during dull days (Steyn 1982). Because the barn owl may roost in one site for a very long time, large quantities of pellets can accumulate (e.g. Steyn 1982). It is therefore conceivable that the barn owls could have been responsible for the large quantities of microfauna at SBYC. Because of the nature of the depositional context, however, it is difficult to determine how long it would have taken for the SBYC fauna to accumulate.

According to Andrews (1990a), Category 1 predators, including the barn owls, cause minimal digestion to the incisors of their prey (see Appendix 4.2). Although not frequent, etching resulting from the barn owl "may be distributed over the whole enamel surface" (Andrews 1990a: 74). Because the SBYC faunal samples yielded high proportions of both un-etched incisors and incisors with very slight etching and pitting, this phenomenon lends further support to the suggestion that the barn owl was responsible for the accumulation of the fauna. Given that heavier etching by Category 1 predators including the barn owl may sometimes penetrate the dentine, the presence of low proportions of incisors in the SBYC faunal samples in which etching has penetrated the dentine are generally consistent with barn owl behaviour. Investigations of incisor

etching among the Mumbwa Caves micromammalian fauna have also suggested that, because of the low incidences of etching, the barn owl would have been the most probable accumulator of the fauna (Andrews and Jenkins 2000). Following Andrews and Jenkins (2000), the differences in levels of etching evident in the SBYC incisors may have resulted from physiological differences in the barn owl, as nesting and roosting owls tend to yield different degrees of etching. In addition, although the effect of post-depositional breakage has substantially influenced the SBYC micromammalian fauna, the relatively high proportions of complete long bones, especially among the soricids, and also the high proportions of foot bones and vertebrae in the three samples correlate with those from barn owl pellets (e.g. Dodson and Wexlar 1979; Korth 1979; Avery 2002). Overall, the above observations provide further support to the hypothesis that the SBYC micromammalian faunal samples belong to one faunal accumulation.

8.10 Palaeoenvironments in the SBYC area

The barn owl has been reported to hunt up to a maximum of 16 km from the roost site (e.g. Kemp and Calburn 1987). Assuming that the behaviour of the barn owl has not changed over time and that this was the responsible predator, it is reasonable to suppose that the micromammalian species represented at SBYC may have been derived from within a range of no more than 16 km.

Although the micromammalian species represented at SBYC may presently occur in a wide range of microhabitats (Appendix 1), the environment around SBYC when the fauna was accumulated appears to have been largely open vegetation and dry sandy soils on flat ground and hillsides. This is indicated by the preference of the barn owl for hunting in open habitats and also the high representation of micromammalian species such as *Tatera afra* and *Suncus varilla*, which currently inhabit sandy ground and open scrub environments. The occurrence of sandy and fairly open scrub microhabitats around SBYC is further suggested by the presence, although in generally low proportions, of *Crocidura cyanea*, *Gerbillurus paeba*, *Steatomys krebsii*, *Otomys saundersiae*, *Mystromys albicaudatus*, *Chrysochloris asiatica*, *Bathyergus suillus* and *Cryptomys hottentotus*. In addition to the scrub microhabitats, there would have been areas with

closed vegetation, as indicated by the presence of *Rhabdomys pumilio*, *Dendromus melanotis* and *Dendromus mesomelas*. More particularly, grassy microhabitats in flat grounds are suggested by *Dendromus melanotis*. Conditions in the grassy environments would have varied, and sparse and possibly semi-arid grassy environments are suggested by *Otomys unisulcatus* and *Elephantulus edwardii* (see Appendix 1).

On the other hand, lusher vegetation and moist microhabitats on slopes as well as on flat ground and riverine environments are indicated by the high representation of *Myosorex varius* and also the occurrence of *Otomys irroratus* in the SBYC samples. Although *Dendromus melanotis* may occur in a range of microhabitats, its presence at SBYC further emphasizes mesic microhabitats on flat grounds. The common association of *Crocidura cyanea* and *Crocidura flavescens* with habitats such as vleis, as well as the close association of *Otomys saundersiae* with sedge fields in heathlands further emphasize mesic microhabitats (see Appendix 1). The presence of these microhabitats at SBYC agrees with the tendency of the inferred predator, the barn owl, to also hunt in riverine environments (e.g. Avery 2002).

The Shannon-Wiener indices for general diversity (*H*), particularly those from the Down Slope and Upper Slope, are comparable with other Holocene or interglacial values from the entire southern Cape region (e.g. Avery 1987). These indices, which suggest moderate climatic conditions, generally correlate with those of the micromammalian fauna from both Byneskranskop 1 and Steenbokfontein (Avery 1982, 1999). In sum, although Talma and Vogel (1992) have noted that late Quaternary temperature along the southernmost part of South Africa would have been 2 degrees lower until about 13,800 years B.P., over all the SBYC micromammalian fauna supports the contention of Hendey and Deacon (1977) that climatic conditions in the SBYC region at the time the fauna accumulated were essentially modern.

CHAPTER NINE

Conclusion

9.1 Findings

This thesis has sought to reach an understanding of the many factors that have influenced the accumulation, transformation and structure of the SBYC micromammalian faunal assemblage. It has been shown that, although there are some differences in aspects such as the percentages of NISPs, MNIs, breakage patterns and etching on incisors, the three SBYC faunal samples exhibit a clear picture of a unitary faunal occurrence. The differences that exist may be explained in terms of the differential effect of largely taphonomic processes. In addition, even though the chi-squared and gamma analyses show some differences that do not perfectly support the suggestion of a single faunal occurrence, these tests generally indicate that there has been an increase in breakage as the fauna eroded down slope. The gamma analyses have generally shown statistically discernible directional relationships between the breakage patterns of the fauna and their position along the slope, a suggestion that is also supported by the high representation of the most durable skeletal elements in the Down Slope. The preferential preservation of the more durable elements as the fauna eroded down slope is more apparent when the Down Slope and Upper Slope samples are compared. At this stage, there seems to be no clear explanation of the differences between the Hanging Remnant and the other two sampled areas. Nevertheless, the fact that the fauna from the Hanging Remnant was derived from partially cemented sediments, as opposed to the loose sediments from which the Down Slope and Upper Slope fauna were derived, may explain the patterns evident in the Hanging Remnant fauna.

Species diversity and equitability among the SBYC faunal samples, together with the levels of acid-etching among the incisors, have strongly suggested that the SBYC micromammalian fauna was accumulated by the barn owl. The high representation of *Tatera afra*, *Myosorex varius* and *Suncus varilla* in the SBYC faunal samples is a feature of the barn owl, which tends to over-emphasize certain prey species depending

on their abundance. Moreover, because the barn owl is largely nocturnal, the high representation of *Tatera afra* and *Myosorex varius* in the SBYC fauna has been ascribed to the nocturnal activity pattern of these micromammalian species, which would have made them more vulnerable to predation by the barn owl. Ecological factors such as predator preference for certain prey species may have led to poor representation of other prey species that may have occurred in the SBYC area. The deduction that the barn owl was responsible for the SBYC micromammalian fauna lends further support to the hypothesis of a unitary faunal assemblage.

Even though taphonomic studies of African micromammalian material are greatly hindered by the lack of modern comparative data (Avery 2002), this thesis has presented a wide range of taphonomic factors that affect micromammalian faunal remains. The study of the SBYC micromammalian fauna has provided more clarification of the fact that, beginning from the time of death up to the time when micromammalian bones are recovered by the analyst/s, taphonomic processes including those resulting from the recovery procedures, differentially affect bones. These processes may lead to phenomena such as loss of skeletal elements and greater destruction of some skeletal elements than others. The latter phenomenon has been demonstrated through the differential preservation of skeletal elements at SBYC, as strongly indicated by the higher proportions of complete soricid humeri and femora relative to murid humeri and femora and also the generally higher soricid MNIs based on the jaws relative to the long bones. It has also been shown that taphonomic processes may yield similar patterns on bones, or new patterns including breakage may be superimposed on earlier ones. In view of this, as has been suggested by the high proportions of the most durable skeletal elements in the SBYC Down Slope sample, emphasis has been made on the importance of understanding the environmental contexts in which faunal assemblages have been deposited. This understanding has the potential to help in discerning the taphonomic processes that may have influenced the composition of faunal assemblages.

Because of the many taphonomic and ecological processes that influence micromammalian faunal assemblages, the importance of relatively large samples has

been expressed through this thesis. From the relatively low proportions of soricid maxillae in the Hanging Remnant, for instance, it has become apparent that small samples are more likely to yield erroneous interpretations of the taphonomic history of the fauna and ultimately the communities from which the fauna were derived. Additionally, the importance of integrating mechanical (e.g. breakage patterns) and ecological data (e.g. species diversity) from micromammalian faunal assemblages has been emphasized. This integration has helped in inferring the barn owl as having being responsible for the accumulation of the SBYC micromammalian fauna, as well as in reconstructing the microhabitats from which the micromammalian species were derived.

The SBYC fauna includes species that have wide vegetational tolerance (e.g. *Suncus varilla)*, species whose distribution is controlled by physical features such as nature of substrate rather than vegetation type (e.g. *Tatera afra* and *Cryptomys hottentotus*), and species adapted to moist and closed vegetation (e.g. *Otomys irroratus* and *Myosorex varius*). In view of this, the general picture of the SBYC area some 15,000 years ago has been suggested to have been a mosaic of microhabitats including well-vegetated and moist microhabitats, fairly dry and moderately open grass and scrub (sandveld), and an admixture of bush and sandy flats. In addition, drier and karroid microhabitats would have existed, as suggested by the presence of *Otomys unisulcatus.* Overall, climatic conditions in the SBYC area 15,000 years ago were moderate, as further suggested by the Shannon-Wiener indices for general diversity (*H*).

9.2 Recommendations

In acknowledgement of the possible use of average body size and morphological changes in faunal remains in the interpretation of palaeoenvironmental changes (e.g. Avery 1982, 1990; Klein and Cruz-Uribe 1984; Thackeray 1987; Marean *et al.* 1994), it is worth pointing out that possible variation in mean body size is an important area that may in future be investigated on the SBYC fauna. This will augment the findings that have resulted from this first study of the SBYC micromammalian fauna.

Because the SBYC soricids yielded generally higher MNIs than did murids when jaws are considered and the opposite when long bones are considered, this demonstrates the great need for all faunal analyses to compliment MNIs based on the jaws with those derived from the long bones, and vice versa. Similarly, because the soricid proximal long bones (humerus and femur) showed higher levels of completeness relative to those of the murids, micromammalian faunal analyses should attempt to examine insectivore and rodent faunal remains separately. Such analyses will have a higher potential for providing accurate interpretations of the taphonomic history of the bones. Additionally, because soricids yielded higher proportions of fused proximal long bones relative to the murids, studies on modern skeletons should investigate whether this may have been caused by early fusion of the soricid bones relative to those of the murids.

In summary, this thesis has indicated further areas of investigation in the study of micromammalian fauna, including the need for future studies to analyse micromammalian bones or species separately. At the same time, this study has shown that, with appropriate caution in the analysis and interpretation of micromammalian fauna, the multivariate faunal record has great potential for yielding information about palaeoenvironments and the many taphonomic processes that have influenced the fauna.

REFERENCES

Andrews, P. 1990a. Owls, Caves and Fossils. Natural History Museum. London.

Andrews, P. 1990b. Small Mammal Taphonomy. In E. H. Lindsay *et al.* (Eds.), *European Neogene Mammal Chronology,* 487-494. Plenum Press, New York.

Andrews, P. 1995. Experiments in Taphonomy. *Journal of Archaeological Science*, **22**, 147-153. Academic Press, London.

Andrews, P. and Evans, E. M. N. 1983. Small mammal bone accumulations produced by mammalian carnivores. *Paleobiology,* **9**(3), 289-307.

Andrews, P. and Cook, J. 1985. Natural modifications to bones in a temperate setting. *Man (N.S.),* **20**, 675-91.

Andrews, P. and Jenkins, E. 2000. The taphonomy of the small mammal faunas. In L. Barham (Ed.), The Middle Stone Age of Zambia, South Central Africa. Western Academic & Specialist Press Ltd., Bristol, England.

Apps, P. 1997. African wild cat, *Felis lybica*. In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 188. Struik Publishers, Cape Town 8001.

Avery, D. M. 1981. Holocene micromammalian faunas from the northern Cape Province, South Africa. *South African Journal of Science*, 77, 265-273.

Avery, D. M. 1982. Micromammals as palaeoenvironmental indicators and an interpretation of the Late Quaternary in the southern Cape Province, South Africa. *Annals of the South African Museum,* **85**(2), 183-374.

Avery, D. M. 1984. Sampling procedures and cautionary tales. In M. Hall, G. Avery, D. M. Avery, M. L. Wilson & A. J. B. Humphreys (Eds.), *Cambridge Monographs in African Archaeology,* **10**, 375-379. BAR International Series 207.

Avery, D. M. 1987. Late Pleistocene Coastal Environment of the Southern Cape Province of South Africa: Micromammals from Klasies River Mouth. *Journal of Archaeological Science*, **14**, 405-421.

Avery, D. M. 1988. The Holocene environment of central South Africa: Micromammalian evidence. *Proceedings of the VIIIth biennial conference held at the University of Bloemfontein, 20-24 March 1987. Palaeoecology of Africa,* **19**, 335-345.

Avery, D. M. 1990. Holocene climatic change in Southern Africa: the contribution of micromammals to its study. *South African Journal of Science,* **86**, 407-412.

Avery, D. M. 1992. Ecological data on micromammals collected by barn owls *Tyto alba* in the West Coast National Park, South Africa. *Israel Journal of Zoology,* **38**, 385-397.

Avery, D. M. 1993. Last Interglacial and Holocene altithermal environments in South Africa and Namibia: micromammalian evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **101**, 221-228.

Avery, D. M. 1995. Southern Savannas and Pleistocene Hominid Adaptations: The Micromammalian Perspective. In E. S. Vrba, G. H. Denton, T. C. Partridge & L. H. Burckle (Eds.), *Paleoclimate and evolution with emphasis on human origins.* Yale University Press: New Haven & London.

Avery, D. M. 1999. Holocene coastal environments in the Western Cape Province, South Africa: micromammalian evidence from Steenbokfontein. *Archaeozoologia,* Vol. **X**, 163-180.

Avery, D. M. 2000. Past and present ecological and environmental information from micromammals. In L. Barham (Ed.), The Middle Stone Age of Zambia, South Central Africa. Western Academic & Specialist Press Ltd., Bristol, England.

Avery, D. M. 2001. The Plio-Pleistocene vegetation and climate of Sterkfontein and Swartkrans, South Africa, based on micromammals. *Journal of Human Evolution*, **41**, 113-132.

Avery, D. M. 2002. The taphonomy of micromammals from Kabwe (Broken Hill) and Twin Rivers cave deposits in central Zambia. *Journal of Archaeological Science*, **29**(5), 537-544.

Avery, D. M., Rautenbach, I. L. and Randall, R. M. 1990. An annotated check list of the land mammal fauna of the West Coast National Park. *Koedoe*, 33/1, 1-18.

Bates, P. J. J. and Harrison, D. L. 1980. The potential value of routine examination of limb bones of rodents in systematic research. *Mammalia*, **44**(4), 581-590.

Behrensmeyer, A. K. 1975. The Taphonomy and Paleoecology of Plio-Pleistocene Vertebrate Assemblages East of Lake Rudolf, Kenya. *Bulletin of the Museum of Comparative Zoology*, **146**(10), 473-578.

Behrensmeyer, A. K. 1978. Taphonomic and ecologic information on bone weathering. *Paleobiology*, **4**(2), 150-162.

Behrensmeyer, A. K. 1993. The Bones of Amboseli. *National Geographic Research and Exploration*, **9**(4), 402-421.

Behrensmeyer, A. K. and Dechant Boaz, D. E. 1980. The recent bones of Amboseli Park, Kenya, in relation to East African paleoecology. In A. K. Behrensmeyer, & A. P. Hill (Eds.), Fossils in the Making: Vertebrate Taphonomy and Paleoecology, pp.72-92. University of Chicago Press.

Behrensmeyer, A. K., Gordon, K. D. and Yanagi, G. T. 1989. Nonhuman Bone Modification in Miocene Fossils from Pakistan. In R. Bonnichsen & M. H. Sorg (Eds.), Bone Modification, pp. 99-120. Peopling of the Americas Publication.

Black, C. and Krishtalka, L. 1986. Rodents, bats and insectivores from the Pleistocene sediments to the East of Lake Turkana, Kenya. *Science,* **37,** 1-15. Natural History Museum of Los Angeles County, Los Angeles, California.

Bonnichsen, R. 1989a. An Introduction to Taphonomy with an Archaeological Focus. In R. Bonnichsen & M. H. Sorg (Eds.), Bone Modification, pp. 1-5. Peopling of the Americas Publication.

Bonnichsen, R. 1989b. Constructing taphonomic models: Theory, Assumptions, and Procedures. In R. Bonnichsen & M. H. Sorg (Eds.), Bone Modification, pp. 515-526. Peopling of the Americas Publication.

Boucher, C. and Jarman, M. L. 1977. The vegetation of the Langebaan area, South Africa. *Transactions of the Royal Society of South Africa,* **42,** 241-272.

Brain, C. K. 1981. The hunter or the hunted: An introduction to African cave taphonomy. University of Chicago Press.

Bronner, G. 1997. Cape golden mole, *Chrysochloris asiatica.* In G. Mills & L. Hes (Eds.), The Complete Book of southern African Mammals, pp. 56. Struik Publishers, Cape Town 8001.

Chaplin, R. E. 1971. The study of animal bones from archaeological sites. New York: Seminar Press.

Chapman, J. L. and Reiss, M. J. 1992. Ecology: Principals and applications. Cambridge University Press.

Coe, M. 1980. The role of modern ecological studies in the reconstruction of paleoenvironments in Sub-Saharan Africa. In A. K. Behrensmeyer, & A. P. Hill (Eds.), Fossils in the Making: Vertebrate Taphonomy and Paleoecology, pp.55-67. University of Chicago Press.

Cutler, A. H., Behrensmeyer, A. K. and Chapman, R. E. 1999. Environmental information in a recent bone assemblage: roles of taphonomic processes and ecological change. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **149,** 359-372.

Davies, R. 1997. Caracal, *Felis caracal.* In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 186-7. Struik Publishers, Cape Town 8001.

Dean, W. R. J. 1989. Spotted Eagle Owl, *Bubo africanus.* In P. J. Ginn, W. G. McIlleron & P. le S. Milstein (Eds.), The Complete Book of Southern African Birds, pp. 341. Struik Winchester, Cape Town 8001.

De Graaf, G. 1997a. Grey climbing mouse, *Dendromus melanotis.* In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 159. Struik Publishers, Cape Town 8001.

De Graaf, G. 1997b. Brants's climbing mouse, *Dendromus mesomelas.* In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 159. Struik Publishers, Cape Town 8001.

De Graaf, G. 1997c. Krebs's fat mouse, *Steatomys krebsii.* In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 161. Struik Publishers, Cape Town 8001.

De Graaf, G. 1997d. White-tailed rat, *Mystromys albicaudatus.* In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 156. Struik Publishers, Cape Town 8001.

De Graaf, G. 1997e. Striped mouse, *Rhabdomys pumilio.* In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 140. Struik Publishers, Cape Town 8001.

Delcourt, H. R. and Delcourt, P. A. 1991. Quaternary Ecology: A paleoecological perspective. Chapman & Hall, New York.

Denys, C., Fernandez-Jalvo, Y. and Dauphin, Y. 1995. Experimental taphonomy: preliminary results of the digestion of micromammal bones in the laboratory. *C.R.Acad. Sci. Paris*, t.**321**, series II a, 803-809.

Denys, C., Andrews, P., Dauphin, Y., Williams, T. and Fernandez-Jalvo, Y. 1997a. Towards a site classification: comparison of stratigraphic, taphonomic and diagenetic patterns and processes. *Bull. Soc. geol. Fr.* **6**, 751-757.

Denys, C., Fernandez-Jalvo, Y. and Laudet, F. 1997b. Biochronology and Taphonomy: Problems and Solutions. *Mem. Trav. E.P.H.E., Inst. Montpellier*, **21**, 55-65.

DiMichele, W. A. 1994. Ecological patterns in time and space. *Paleobiology*, **20**(2), 89-92.

Dippenaar, N. J. 1997a. Reddish-grey musk shrew, *Crocidura cyanea.* In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 50. Struik Publishers, Cape Town 8001.

Dippenaar, N. J. 1997b. Greater red musk shrew, *Crocidura flavescens.* In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 50. Struik Publishers, Cape Town 8001.

Dippenaar, N. J. 1997c. Forest shrew, *Myosorex varius*. In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 47. Struik Publishers, Cape Town 8001.

Dippenaar, N. J. 1997d. Lesser dwarf shrew, *Suncus varilla.* In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 48. Struik Publishers, Cape Town 8001.

Dodson, P. and Wexlar, D. 1979. Taphonomic investigations of owl pellets. *Paleobiology,* **5**(3), 275-284.

Du Plessis, A. and De La Cruz, M. A. 1977. Geophysical investigations in Saldanha Bay. *Transactions of the Royal Society of South Africa,* **42**: 285-302.

Fenn, M. G. P. and MacDonald, D. W. 1995. Use of middens by red foxes: Risk reverses rhythms of rats. *Journal of Mammalogy,* **76**(1), 130-136.

Fernandez-Jalvo, Y. and Andrews, P. 1992. Small Mammal Taphonomy of Gran Dolina, Atapuerca (Burgos), Spain. *Journal of Archaeological Science,* **19**, 407-428.

Fernandez-Jalvo, Y. 1995. Small mammal taphonomy at La Trinchera de Atapuerca (Burgos, Spain). A remarkable example of taphonomic criteria used for stratigraphic correlations and palaeoenvironmental interpretations. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **114**, 167-195.

Flemming, B. W. 1977. Distribution of recent sediments in Saldanha Bay and Langebaan Lagoon. *Transactions of the Royal Society of South Africa,* **42**, 317-340.

Fodgen, M. 1973. Fishing Owls, Eagle owls and the Snowy owls, *Ketupa, Scotopelia, Bubo, Nyctea.* In J. A. Burton (Ed.), Owls of the World; their evolution, structure and ecology. Clarke, Irwin & Company Ltd, Toronto and Vancouver.

Foote, M. 1992. Rarefaction analysis of morphological and taxonomic diversity. *Paleobiology,* **18**(1), 1-16.

Gargett, V. 1989. Black Eagle, *Aquila verreauxii.* In P. J. Ginn, W. G. McIlleron & P. le S. Milstein (Eds.), The Complete Book of Southern African Birds, pp. 132. Struik Winchester, Cape Town 8001.

Gifford-Gonzalez, D. 1989a. Modern analogues: Developing an Interpretive Framework. In R. Bonnichsen & M. H. Sorg (Eds.), Bone Modification, pp. 43-52. Peopling of the Americas Publication.

Gifford-Gonzalez, D. 1989b. Ethnographic Analogues for Interpreting Modified Bones: Some Cases from East Africa. In R. Bonnichsen & M. H. Sorg (Eds.), Bone Modification, pp. 179-246. Peopling of the Americas Publication.

Graham, R. W. 1986. Response of mammalian communities to environmental changes during the Late Quaternary. In J. Diamond & T. J. Case (Eds.), Community Ecology. Harper & Row, Publishers, New York.

Grayson, D. K. 1984. Quantitative Zooarchaeology: Topics in the analysis of archaeological faunas. Academic Press, Inc., Orlando, Florida 32887.

Grindley, J., Siegfried, W. R. and Vernon, C. J. 1973. Diet of the barn owl in the Cape Province. *Ostrich* **44**, 266-67.

Halle, S. 1995. Effect of extrinsic factors on activity of root voles. *Microtus oeconomus. Journal of Mammalogy,* **76**(1), 88-99.

Hanson, C. B. 1980. Fluvial Taphonomic Processes: Models and Experiments. In A. K. Behrensmeyer & A. P. Hill (Eds.), Fossils in the Making: Vertebrate Taphonomy and Paleoecology, pp.156-181. University of Chicago Press.

Hartley, R. R. 1989a. Yellowbilled Kite, *Milvus migrans parasitus*. In P. J. Ginn, W. G. McIlleron & P. le S. Milstein (Eds.), The Complete Book of Southern African Birds, pp. 128. Struik Winchester, Cape Town 8001.

Hartley, R. R. 1989b. Rock kestrel, *Falco tinnunculus*. In P. J. Ginn, W. G. McIlleron & P. le S. Milstein (Eds.), The Complete Book of Southern African Birds, pp. 172. Struik Winchester, Cape Town 8001.

Hendey, Q. B. and Deacon, H. J. 1977. Studies in palaeontology and archaeology in the Saldanha region. *Transactions of the Royal Society of South Africa,* **42** (3&4), 371-381.

Hill, A. P. 1980. Early postmortem damage to the remains of some contemporary East African mammals. In A. K. Behrensmeyer & A. P. Hill (Eds.), Fossils in the Making. Vertebrate Taphonomy and Paleoecology, pp.131-152. University of Chicago Press, Chicago 60637.

Hughes, J. J., Ward, D. and Perrin, M. R. 1995. Effects of substrate on foraging decisions by a Namib Desert gerbil. *Journal of Mammalogy,* **76**(2), 638-645.

Huston, M. A. 1994. Biological Diversity: the coexistence of species on changing landscapes. Cambridge University Press.

Inouye, R. S., Huntly, N. and Wasley, G. A. 1997. Effects of pocket gophers (*Geomys bursarius*) on microtopographic variation. *Journal of Mammalogy,* **78**(4), 1144-1148.

Jarvis, J. 1997a. Cape dune molerat, *Bathyergus suillus*. In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 121. Struik Publishers, Cape Town 8001.

Jarvis, J. 1997b. Common molerat, *Cryptomys hottentotus.* In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 122. Struik Publishers, Cape Town 8001.

Jensen, R. A. C. 1989. Greater kestrel, *Falcon rupicoloides.* In P. J. Ginn, W. G. McIlleron & P. le S. Milstein (Eds.), The Complete Book of Southern African Birds, pp. 172-3. Struik Winchester, Cape Town 8001.

Kemp, A. and Calburn, S. 1987. The Owls of Southern Africa. Struik Winchester, Cape Town 8000.

Kerley, G. 1997a. Vlei rat, *Otomys irroratus*. In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 136. Struik Publishers, Cape Town 8001.

Kerley, G. 1997b. Karoo bush rat, *Otomys unisulcatus*. In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 137. Struik Publishers, Cape Town 8001.

Kingdon, J. 1974. East African Mammals. *An Atlas of Evolution in Africa.* Vol. **2**, Part B. Academic Press, London.

Kingdon, J. 1997. A Kingdon Field Guide to African Mammals. Academic Press Ltd., 24-28 Oval Road, London NW1 7DX.

Klein, R. G. and Cruz-Uribe, K. 1984. The Analysis of Animal Bones from Archaeological Sites. University of Chicago Press.

Klein, R. G. and Cruz-Uribe, K. 1991. The Bovids from Elandsfontein, South Africa, and their implications for the age, palaeoenvironment, and origins of the site. *The African Archaeological Review*, **9**, 21-79.

Knox, G. J. 1977. Caliche profile formation, Saldanha Bay (South Africa). *Sedimentology*, **24**, 657-674.

Koch, C. L. 1987. Prediction of sample size effects on the measured temporal and geographic distribution patterns of species. *Paleobiology*, **13**(1), 100-107.

Korth, W. W. 1979. Taphonomy and microvertebrate fossil assemblages. *Annals of Carnegie Museum.* **48**, 235-285.

Kowalski, K. 1971. The biostratigraphy and paleoecology of Late Cenozoic mammals of Europe. In K. K. Turekian (Ed.), The Late Cenozoic Glacial Ages, pp.465-477. Yale University Press, New Haven and London.

Krebs, C. J. 1978. Ecology: The Experimental Analysis of Distribution and Abundance. Second Edition. Harper International Edition.

Krebs, C. J. 1985. Ecology: The experimental analysis of distribution and abundance. Third Edition. Harper & Row, Publishers, Inc., 10 East 53 Street, New York, NY 10022.

Krebs, C. J. 1996. Population cycles revisited. *Journal of Mammalogy*, 77(1), 8-24.

Krohne, D. T. 1997. Dynamics of metapopulations of small mammals. *Journal of Mammalogy*, **78**(4), 1014-1026.

Lasker, H. 1976. Effects of differential preservation on the measurement of taxonomic diversity. *Paleobiology*, **2**, 84-93.

Liversidge, R. 1989. Factors Influencing Migration of "Wintering" Raptors in Southern Africa. In B. U. Meyburg & R. D. Chancellor (Eds.), Raptors in Modern World. WWGBP: Berlin, London & Paris.

Low, B. and Pond, U. 2001. Proposed Expansion of Portnet Iron Ore Handling Facility in Saldanha: Specialist Vegetation Study. A report by the coastal and environmental consultants (COASTEC), P.O Box 370, Rondebosch 7701.

Lubke, R. 1996. The Dune Thicket. In A. B. Low and A. G. Rebelo (Eds.), Vegetation of South Africa, Lesotho and Swaziland, pp 14-15. Department of Environmental Affairs and Tourism, Pretoria.

Lyman, R. L. 1994. Vertebrate Taphonomy. Cambridge University Press.

MacDonald, D. W. 1997. Suricate, *Suricata suricatta*. In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 208-9. Struik Publishers, Cape Town 8001.

Maddock, A. 1997a. Small-spotted genet, *Genetta genetta*. In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 206. Struik Publishers, Cape Town 8001.

Maddock, A. 1997b. Large-spotted genet, *Genetta tigrina*. In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 207. Struik Publishers, Cape Town 8001.

Marean, C. W., Mudida, N. and Reed, K. E. 1994. Holocene Paleoenvironmental change in the Kenyan Central Rift as indicated by micromammals from Enkapune Ya Muto Rockshelter. *Quaternary Research*, **41**, 376-389.

Marshall, L. G. 1989. Bone Modification and "The Laws of Burial". In R. Bonnichsen & M. H. Sorg (Eds.), Bone Modification, pp.7-24. Peopling of the Americas Publication.

Martin, R. 1989. Black harrier, *Circus maurus*. In P. J. Ginn, W. G. McIlleron & P. le S. Milstein (Eds.), The Complete Book of Southern African Birds, pp. 163. Struik Winchester, Cape Town 8001.

Matthews, T. 1998. A taphonomic investigation of the agency of microfaunal accumulation at Elands Bay Cave. Thesis presented for a MA degree at the University of Cape Town, South Africa.

Matthews, T. 1999. Taphonomy and the micromammals from Elands Bay Cave. *South African Archaeological Bulletin*, **54**, 133-140.

McKenzie, A. 1997. Black-backed jackal, *Canis mesomelas*. In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 198-199. Struik Publishers, Cape Town 8001.

Meester, J. 1963. A systematic revision of the shrew Genus *Crocidura* in Southern Africa. *Memoir* **13.** Transvaal Museum, Pretoria.

Meester, J. A. J., Rautenbach, I. L., Dippenaar, N. J. and Baker, C. M. 1986. Classification of Southern African Mammals. Transvaal Museum Monograph 5.

Mellet, J. S. 1974. Scatological Origin of Microvertebrate Fossil Accumulations. *Science*, **185**, 349-350.

Mendelsohn, J. M. 1989. Population Biology and Breeding Success of the Blackshouldered Kites *Elanus caeruleus*. In B. U. Meyburg & R. D. Chancellor (Eds.), Raptors in Modern World: WWGBP: Berlin, London & Paris.

Mills, G. 1997a. Cape fox, *Vulpes chama*. In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 196. Struik Publishers, Cape Town 8001.

Mills, G. 1997b. Honey badger, *Mellivora capensis*. In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp.202. Struik Publishers, Cape Town 8001.

Nel, J. A. J. and Rautenbach, I. L. 1975. Habitat use and community structure of rodents in the southern Kalahari. *Mammalia*, **39**(1), 9-29.

Nel, J. A. J. 1997. Bat-eared fox, *Otocyon megalotis*. In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 191. Struik Publishers, Cape Town 8001.

Oliver, J. S. 1989. Analogues and Site Context: Bone Damages from Shield Trap Cave (24CB91), Carbon County, Montana, U.S.A. In R. Bonnichsen & M. H. Sorg (Eds.), Bone Modification, pp. 73-98. Peopling of the Americas Publication.

Olson, E. C. 1980. Taphonomy: Its history and role in community evolution. In A. K. Behrensmeyer & A. P. Hill (Eds.), Fossils in the Making: Vertebrate Taphonomy and Paleoecology, pp.5-19. University of Chicago Press.

Osman, R. W. and Whitlatch, R. B. 1978. Patterns of species diversity: fact or artifact?. *Paleobiology*, **4**, 41-54.

Parkington, J. 1999. Western Cape Landscapes. *Proceedings of the British Academy,* **99,** 25-35.

Payne, S. 1975. Partial recovery and sample bias. In A. T. Clason (Ed.), Archaeozoological Studies: Papers of the Archaeozoological Conference 1974, held at the Biologisch-Archaeologisch Instituut of the State University of Groningen, pp.7-17. North-Holland Publishing Company - Amsterdam.

Perrin, M. 1997a. Pygmy hairy-footed gerbil, *Gerbillurus paeba.* In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 152. Struik Publishers, Cape Town 8001.

Perrin, M. 1997b. Cape gerbil, *Tatera afra.* In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 155. Struik Publishers, Cape Town 8001.

Perrin, M. 1997c. Cape rock elephant shrew, *Elephantulus edwardii.* In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 66. Struik Publishers, Cape Town 8001.

Pether, J., Roberts, D. L. and Ward, J. D. 2000. Deposits of the West Coast. In T. C. Partridge & R. R. Maud (Eds.), The Cenozoic of southern Africa, pp. 406. Oxford University Press.

Prestt, I. and Wagstaffe, R. 1973. Barn and Bay owls, *Tyto, Phodilus.* In J. A. Burton (Ed.), Owls of the World; their evolution, structure and ecology. Clarke, Irwin & Company Ltd, Toronto and Vancouver.

Rautenbach, N. 1997. Geoffroy's horseshoe bat, *Rhinolophus clivosus.* In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 97. Struik Publishers, Cape Town 8001.

Reitz, E. J. and Wing, E. S. 1999. Zooarchaeology. Cambridge University Press.

Roberts, D. L. (In press). Lithostratigraphy of the Langebaan Formation (Sandveld Group). South African Committee for Stratigraphy Lithostratigraphic Series.

Roberts, D. L. and Brink, J. (In press). Coastal Miocene aeolianites and palaeo-sea levels in southwestern Africa. *South African Journal of Geology.*

Rogers, J. 1986. Cenozoic geology of the southern Cape coastal plain, particularly the area between the Kafferkuils and Gouritz estuaries. *Palaeoecology of Africa*, **17**, 3-11.

Rowe-Rowe, D. 1997. Striped polecat, *Ictonyx striatus*. In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 204. Struik Publishers, Cape Town 8001.

Shennan, S. 1988. Quantifying Archaeology. Edinburgh University Press, 22 George Square , Edinburgh.

Shipman, P. and Walker, A. 1980. Bone-collecting by harvesting ants. *Paleobiology,* **6**(4), 496-502.

Shotwell, J. A. 1955. An approach to the paleoecology of mammals. *Ecology,* **36**(2), 327-337.

Sillero-Zubiri, C. and Gottelli, D. 1995. Diet and feeding behavior of Ethiopian wolves (*Canis simensis*). *Journal of Mammalogy*, **76**(2), 531-541.

Skinner, J. D. and Smithers, R. H. N. 1990. The mammals of the Southern Africa region. University of Pretoria, Republic of South Africa.

Sliwa, A. 1997. Black-footed cat, *Felis nigripes*. In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 189. Struik Publishers, Cape Town 8001.

Smithers, R. H. 1983. The mammals of the Southern African Subregion. University of Pretoria, Republic of South Africa.

Somers, M. J. 1997. Cape clawless otter, *Aonyx capensis*. In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 200-1. Struik Publishers, Cape Town 8001.

Southern, H. N. 1954. Tawny owls and their prey. *Ibis*, **96**, 384-409.

Southern, H. N. 1979. The stability and instability of small mammal populations. In: M. Stoddard (Ed.), Ecology of small mammals, pp. 103-132. Chapman & Hall, London.

Stapp, P. 1997. Habitat selection by an insectivorous rodent: Patterns and mechanisms across multiple scales. *Journal of Mammology*, **78**(4), 1128-1143.

Steyn, P. 1982. Birds of prey of Southern Africa: Their identification and life histories. David Philip, Publisher (Pty) Ltd., 217 Werdmuller Centre, Claremont, Cape, 7700 South Africa.

Steyn, P. 1984. A delight of Owls: African Owls observed. David Philip, Publisher (Pty) Ltd. Claremont Cape, 7700 South Africa.

Stuart, C. T. 1997a. Yellow mongoose, *Cynictis penicillata*. In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 211. Struik Publishers, Cape Town 8001.

Stuart, C. T. 1997b. Small grey mongoose, *Galerella pulverulenta*. In G. Mills & L. Hes (Eds.), The Complete Book of Southern African Mammals, pp. 214. Struik Publishers, Cape Town 8001.

Stuart, C. and Stuart, T. 2001. Field Guide to Mammals of Southern Africa. Struik Publishers (Pty) Ltd., Cornelis Struik House, 80 McKenzie Street, Cape Town 8001.

Talma, A. S. and Vogel, J. C. 1992. Late Quaternary Paleotemperatures Derived from a Speleothem from Cango Cave, Cape Province, South Africa. *Quaternary Research* **37**, 203-213.

Tamura, N. and Yong, H. 1993. Vocalizations in response to predators in three species of Malaysian *Callosciurus* (Sciuiridae). *Journal of Mammalogy*, **74**(3), 703-714.

Tarboton, W. R. 1989a. Martial eagle, *Polemaetus bellicosus*. In P. J. Ginn, W. G. McIlleron & P. le S. Milstein (Eds.), The Complete Book of Southern African Birds, pp. 140-1. Struik Winchester, Cape Town 8001.

Tarboton, W. R. 1989b. Jackal buzzard, *Buteo rufofuscus*. In P. J. Ginn, W. G. McIlleron & P. le S. Milstein (Eds.), The Complete Book of Southern African Birds, pp.150. Struik Winchester, Cape Town 8001.

Taylor, I. 1994. Barn Owls: Predator-prey relationships and conservation. Cambridge University Press, New York.

Thackeray, J. F. 1987. Late Quaternary environmental changes inferred from small mammalian fauna, Southern Africa. *Climatic Change*, **10**, 285-305.

Van Couvering, J. A. H. 1980. Community evolution in East Africa during the Late Cenozoic. In A. K. Behrensmeyer & A. P. Hill. (Eds.), Fossils in the Making: Vertebrate Taphonomy and Paleoecology, 272-298. University of Chicago Press.

Village, A. 1990. The Kestrel. Published by T & A D Poyser Ltd., 24-28 Oval Road, London NW1.

Vrba, E. S. 1980. The significance of Bovid remains as indicators of environment and predation patterns. In A. K. Behrensmeyer & A. P. Hill (Eds.), Fossils in the Making: Vertebrate Taphonomy and Paleoecology, 247-271. University of Chicago Press.

Vrba, E. S. 1989. The Environmental Context of the Evolution of Early Hominids and Their Culture. In R. Bonnichsen & M. H. Sorg (Eds.), Bone Modification, pp. 27-42. Peopling of the Americas Publication.

Weatherburn, C. E. 1962. A First Course In Mathematical Statistics. Cambridge University Press, Bentley House, 200 Euston Road, London, N.W. 1.

Weather Bureau 1986. Climate of South Africa. WB 40. Government Printer, Pretoria.

Wesselman, H. B. 1995. Of Mice and Almost-Men: Regional Paleoecology and Human Evolution in the Turkana Basin. In E. S. Vrba, G. H. Denton, T. C. Partridge & L. H. Burckle (Eds.), *Paleoclimate and evolution with emphasis on human origins.* Yale University Press: New Haven & London.

Western, D. 1980. Linking the ecology of past and present mammal communities. In A. K. Behrensmeyer & A. P. Hill (Eds.), Fossils in the Making: Vertebrate Taphonomy and Paleoecology, pp.41-54. University of Chicago Press.

White, P. J., White, C. A. V. and Ralls, K. 1996. Functional and numerical responses of kit foxes to a short-term decline in mammalian prey. *Journal of Mammalogy,* 77(2), 370-376.

Wilson, D. E. and Reeder, D. M. (Eds.). 1993. Mammal species of the World. Second Edition. Smithsonian Institution Press, Washington and London.

Wolff, R. G. 1975. Sampling and sample size in ecological analyses of fossil mammals. *Paleobiology*, **1**(2), 195-204.

APPENDIX 1

Short notes on the southern African modern habitats, behaviour and diets of the small mammal species represented in the SBYC faunal samples

Insectivora

Cape golden mole (*Chrysochloris asiatica*)

Cape golden moles are endemic to the southwestern Cape Province, extending up to the Namaqualand coastal plain. The total length of an adult is about 110 mm, and a mean body weight of about 50 g. Females are usually smaller than males. Cape golden moles may occur (solitarily) in a variety of preferably flat habitats, including sandy fynbos, succulent karroid veld types, and grasslands. These moles also live in cultivated lands and may thrive in the neighborhood of man. The Cape golden moles are fossorial, and are more active after rains. In the southern Cape, these moles occur in areas with annual rainfall up to 600 mm. Although they are generalist feeders, their diet comprises predominantly insects, earthworms and millipedes (Information compiled from: Avery 1982; Avery *et al.* 1990; Skinner and Smithers 1990; Bronner 1997; Kingdon 1997; Stuart and Stuart 2001).

Reddish-grey musk shrew (*Crocidura cyanea*)

This shrew is widely distributed in southern Africa, including the Western Cape Province. It has a total length of up to about 130 mm, and a mean body weight of about 9 g. It is tolerant to a wide variety of environments, and may occur in montane forests and grasslands or fynbos, vleis, dense shrubs, savanna grasslands and rocky outcrops. It may also occur in relatively dry areas. In the southern part of the Western Cape Province, its areas of residence (preferably rocky slopes) receive annual rainfall up to 500 mm. Although this species of the shrews has been trapped during the day, it is predominantly nocturnal, solitary and a terrestrial forager, preying largely on insects. It is also known to prey on small vertebrates (Information compiled from: Avery 1982; Smithers 1983; Skinner and Smithers 1990; Dippenaar 1997a; Stuart and Stuart 2001).

Greater musk shrew (*Crocidura flavescens*)

This is a large and predominantly nocturnal shrew, which is endemic to southern Africa, including the southwestern part of the Cape. Its total length is about 160 mm, and an average body mass of about 26.7 g for males and 22.2 g for females. It occurs in a mosaic of vegetation types, including habitats with dense vegetation cover in fynbos, temperate and subtropical grassland, coastal forest (or along vleis), woodland and savanna. In the southern Cape, it prefers rocky grounds and generally habitats that receive rainfall of more than 400 mm. It is also known to exploit drier environments. It is predominantly solitary, preying largely on insects and small vertebrates (Information compiled from: Avery 1982; Skinner and Smithers 1990; Dippenaar 1997b; Kingdon 1997).

Forest shrew (*Myosorex varius*)

Myosorex varius is endemic to southern Africa, occurring widely in the region, including the Western Cape Province. It has a total body length of about 120 mm, and an average body mass of about 15 g. This shrew is largely nocturnal. It is active beginning from dusk, and by dawn, activity starts to decline. It is an aggressive species and, although it prefers moist habitats (e.g. riverine) with dense vegetation, it may occur in a wide range of vegetation types, including grassland. In the Western Cape Province, it occurs under drier conditions on coastal mountains, preferring areas with dense continuous vegetation cover of low succulent bushes. This shrew makes nests with grass, and may habitually burrow even when in captivity. Although this shrew is an opportunistic feeder, it preys predominantly on invertebrates including beetles, grasshoppers, termites, earthworms and spiders. The forest shrew also preys on small vertebrates such as lizards and frogs. Remains of forest shrews often appear in barn owl pellets. Small carnivorous mammals such as the water mongoose and the polecat are also known to prey on forest shrews (Information compiled

from: Avery 1982; Smithers 1983; Avery *et al.* 1990; Skinner and Smithers 1990; Dippenaar 1997c; Stuart and Stuart 2001).

Lesser dwarf shrew (*Suncus varilla)*

The lesser dwarf shrew is widely distributed in the southwestern, southern and eastern parts of southern Africa, including the Western Cape Province. Its average body length is about 89 *mm*, and an average body mass of about 6.5 g. Because of its catholic ecological requirements, it occurs in a wide range of environments and vegetation types, including open grassland. In the central Free State, for instance, it has been found to nest in termite mounds that are in disuse. It is predominantly insectivorous. *Suncus varilla* lives for about 24 to 30 months. Its activity pattern is not known (Information compiled from: Skinner and Smithers 1990; Dippenaar 1997d; Stuart and Stuart 2001).

Chiroptera

Geoffroy's horseshoe bat (*Rhinolophus clivosus)*

This is the commonest of the horseshoe bats in southern Africa. It occurs in parts of the sub-region including South Africa, Zimbabwe and Mozambique. In South Africa, it occurs in a number of areas, including the Transvaal and the Western Cape Province. The total length of an adult *Rhinolophus clivosus* is about 97 *mm*, with an average body mass of about 17 g. In the Western Cape Province, this species most commonly live in colonies. It usually roosts during the day, preferring a range of roosting sites that offer shelter such as caves, hollow trees and abandoned mines. Generally, *Rhinolophus* spp. may inhabit all kinds of vegetation types, but those species living in temperate regions prefer warm roosts especially when they are active. *Rhinolophus clivosus* is predominantly a savanna woodland bat. Like most horseshoe bats living in temperate regions, *Rhinolophus clivosus* is known to hibernate during the winter. It is predominantly insectivorous, and like most *Rhinolophus* spp, its diet may include mosquitoes, moths, spiders and beetles (Information compiled from: Skinner and Smithers 1990; Kingdon 1997; Rautenbach 1997; Stuart and Stuart 2001).

Rodentia

Grey climbing mouse (*Dendromus melanotis)*

The grey climbing mouse is a very successful species and has a wide distribution in southern Africa. In South Africa, it occurs in a number of areas including KwaZulu-Natal, northern Free State, and Eastern and Western Cape. Adults of this species have a total body length of about 150 mm, and an average body mass of about 8 g. This is a nocturnal and terrestrial mouse and prefers living in tall grassland and rank vegetation on valley floors. In Botswana, this mouse occurs in dry grassland along the edges of marshy areas and/or rivers. It is a successful climber, being able to climb even grass stalks, and also build nests between grass stems. This mouse is also known to burrow especially when taking cover from veld fires. Although it is largely insectivorous, it is also known to consume seeds, grass, and a wide range of invertebrates. Some of the predators that prey on this mouse include the barn owls and a range of snakes (Information compiled from: Avery 1982; Smithers 1983; Skinner and Smithers 1990; De Graaf 1997a; Kingdon 1997; Stuart and Stuart 2001).

Brants's climbing mouse (*Dendromus mesomelas*)

In southern Africa, this mouse occurs in a number of areas, including the northern part of Botswana, northeastern parts of Namibia, northern part of South Africa, and in the Western Cape Province. Its total body length is about 170 mm, and the average adult body mass is about 14 g. It is a nocturnal mouse, although also active during the day. This mouse is a successful climber especially in low vegetation. It uses its long tail in its skillful climbing maneuvers. It prefers living in rank vegetation and more preferably in tall grass and shrubby habitats, where it uses the grass to build its nests. It is mainly insectivorous, although its diet may also include grass and seeds. Some of the predators that prey on this mouse include snakes, the

barn owls and the grass owls (Information compiled from: Smithers 1983; Skinner and Smithers 1990; De Graaf 1997b; Kingdon 1997; Stuart and Stuart 2001).

Krebs's fat mouse (*Steatomys krebsii*)

Although there is poor understanding of the distribution of the Krebs's fat mouse in southern Africa, its occurrence is known in South Africa, Angola and Zambia. In South Africa, its distributional range includes much of the country except KwaZulu-Natal. This species weighs about 24 g and has an average body length of about 130 mm. This nocturnal and terrestrial mouse prefers dry environments, especially ones with sandy substrate (e.g. dry sandy grassland and sandy alluvium). Its diet is not clearly known, but like that of other *Steatomys* spp., may include insects, seeds, bulbs, roots and grass (Information compiled from: Smithers 1983; Skinner and Smithers 1990; De Graaf 1997c; Kingdon 1997; Stuart and Stuart 2001).

Hairy-footed gerbil (*Gerbillurus paeba*)

The hairy-footed gerbil is a solitary, very aggressive and active gerbil, which occurs widely in arid areas. In southern Africa, its distributional range includes Namibia, Botswana and Zimbabwe. In South Africa alone, it is widely distributed in the western half of the country. Its average body mass is about 25 g. This gerbil is nocturnal and terrestrial. It usually spends its diurnal hours in burrows. Although the distribution of the hairy-footed gerbil may extend to the relatively moist southern coastal zone, this gerbil prefers dry sandy or sandy alluvial substrate, with sparse grass, scrub or some form of cover. The hairy-footed gerbil is, however, scarce around calcareous river banks. It occurs in high densities on vegetated dunes that may be conducive for burrowing. In the southern part of the Western Cape Province, this gerbil prefers habitats that are flat, and also the sandy slopes. Its diet comprises seeds, vegetable matter as well as insects (Information compiled from: Avery 1982; Avery *et al.* 1990; Skinner and Smithers 1990; Kingdon 1997; Perrin 1997a; Stuart and Stuart 2001).

Cape gerbil (*Tatera afra*)

The Cape gerbil is endemic to the Western Cape Province and more particularly the Cape Macchia zone, which stretches "southward from Niewoundtville in the northwest of the Western Cape to the Cape Peninsula, and eastward along the coast to Herold's Bay" (Perrin 1997b: 155). This gerbil has an average body length of about 300 mm, and a mean body mass of about 100 g. Males are slightly heavier than females. Cape gerbils are extensive burrowers and are predominantly confined to areas with loose, sandy soils, or sandy alluvium, especially in cultivated areas. Cape gerbils are nocturnal and terrestrial, preferring areas of open grassland with well-drained sandy soils. The diet of this gerbil includes grass, bulbs, roots, seeds, and other vegetable matter. The Cape gerbils are also partly insectivorous (Information compiled from: Skinner and Smithers 1990; Kingdon 1997; Perrin 1997b; Stuart and Stuart 2001).

White-tailed rat (*Mystromys albicaudatus*)

This rat is endemic to South Africa, Lesotho and Swaziland. Throughout its distributional range, it occurs in low densities. In South Africa, the distribution of this rat includes the low-lying areas in the southern parts of the Eastern and Western Cape, as well as the Free State and the northern provinces. Adult white-tailed rats have an average length of about 220 mm, and an average body mass of about 78 g. Mature males may, however, measure up to 111 g. This rat is nocturnal and terrestrial. It is mainly confined to the highveld and montane grassland, but may also occur in the savanna grassland. The white-tailed rat prefers living in burrows and in crevices on the ground, where it builds a nest with shredded materials. Its diet includes insects, seeds and green vegetable matter. It is frequently preyed upon by the barn owl (Information compiled from: Smithers 1983; Skinner and Smithers 1990; De Graaf 1997d; Kingdon 1997; Stuart and Stuart 2001).

Striped mouse (*Rhabdomys pumilio*)

This mouse is widely distributed in southern Africa, occurring in a number of regions in the sub-region including Namibia, Mozambique and Botswana. In South Africa, it occurs over much of the country. Its

average body mass is about 35 g. It is largely diurnal and a grassland mouse (closed vegetation) occurring in a wide variety of habitats as long as there is some grass cover. It is also known to dig burrows. Although the striped mouse is opportunistic in its diet requirements, it is generally granivorous. It also takes green plant material, including stems, leaves and berries, as well as some small invertebrates. The striped mouse is preyed upon by a wide range of predators, including snakes, diurnal birds of prey, owls, as well as small carnivorous mammals such as the caracal and the mongoose (Information compiled from: Smithers 1983; Avery 1987; Skinner and Smithers 1990; De Graaf 1997e; Kingdon 1997; Stuart and Stuart 2001).

Vlei rat (*Otomys irroratus*)

This moderate to large-sized stocky rat is widely distributed in southern Africa. In South Africa, its occurrence is absent only in the more arid western and north-western regions; it is widely distributed throughout the Western Cape Province. Its total average body length is about 240 mm, with a body mass of about 120 g for males, and 114 g for females. This rat prefers mainly vleis or marshy environments, but may also occur in grassland. The vlei rat is terrestrial, although to some extent may also be referred as semi-aquatic. It is predominantly diurnal, but may also show some activity at night. It is completely omnivorous, and its diet includes succulent stems of grasses (e.g. green grass, reeds), seeds, and sedges. Predators for vlei rats include small carnivorous mammals, snakes, diurnal birds of prey, and also nocturnal birds of prey and more particularly the barn owl and the spotted eagle owl (Information compiled from: Smithers 1983; Avery *et al.* 1990; Skinner and Smithers 1990; Kerley 1997a; Kingdon 1997; Stuart and Stuart 2001).

Saunders's vlei rat (*Otomys saundersiae)*

The distribution of the Saunders's vlei rat is mainly in two disjointed areas in South Africa. These are the southwestern part of the Western Cape Province and the eastern parts of the Eastern Cape Province up to the Free State. This rat has an average body length of about 250 mm and 220 mm for males and females, respectively. Average body mass for this rat is about 111 g for males and 95 g for females. Although very little is known about the habitat, the diet and the behaviour of this rat, it may occur in the mountains and in close association with sedge fields in heathlands. It is generally herbivorous and diurnal (Information compiled from: Smithers 1983; Skinner and Smithers 1990; Stuart and Stuart 2001).

Bush Karoo rat (*Otomys unisulcatus*)

The bush Karoo rat is endemic to South Africa and is confined largely to the drier bushy habitats of the Western and Northern Cape provinces, and more particularly in the Karoo and the west coast. Adults have an average body length of about 240 mm, and an average body mass of 125 g. This rat is associated with the fynbos and grassy habitats, preferring drier environments and avoiding moist and damp environments. It builds its nest by accumulating heaps of twigs. It takes refuge under the heaps in the event of possible attack by a predator, and also when taking cover from the harsh desert environment. This rat is largely crepuscular and terrestrial. Being exclusively herbivorous, the diet of the bush Karoo rat comprises a wide variety of plants, including the green foliage of succulent plants (Information compiled from: Avery 1982; Skinner and Smithers 1990; Kerley 1997b; Stuart and Stuart 2001).

Cape dune molerat (*Bathyergus suillus)*

The Cape dune molerat is largely a fossorial rat confined to the coastal areas of the southwestern part of the Western Cape Province, South Africa. It is particularly widespread in the West Coast National Park. This molerat is the largest of all the bathyergids, with a body mass ranging between 550 and 750 g. It occurs only in areas with sandy substrate such as the coastal sandveld, or riverine alluvial sands. When burrowing, its presence is announced by numerous mounds of soil, which accumulate as it pushes soil on to the surface. It is also during mound formation when most predators catch this molerat, as the exercise betrays its presence. It is very territorial, and its vegetarian diet includes leaves, stems, tubers and bulbs. A range of predators including snakes, jackals, caracal and man prey on the Cape dune molerat. This molerat is beyond the size limit of the barn owls (Information compiled from: Avery *et al.* 1990; Skinner and Smithers 1990; Jarvis 1997a; Kingdon 1997; Stuart and Stuart 2001).

Common molerat (*Cryptomys hottentotus*)

The common molerat is widely distributed in the southern Africa sub-region, occurring in places such as eastern Botswana and much of South Africa. Generally, body mass ranges between 100 and 300 g. *Cryptomys hottentotus* live in small colonies of about 14 individuals, and are able to inhabit a mosaic of sparsely vegetated substrates ranging from sandy soils to heavy and compacted soils. This molerat, however, prefers granitic sands where it burrows, throwing up mounds of soil. *Cryptomys hottentotus* is more active during the night. Because of its vegetarian diet, the distribution of the common molerat is greatly influenced by the availability of food items such as corms, tubers and bulbs (Information compiled from: Avery 1982; Smithers 1983; Avery *et al.* 1990; Skinner and Smithers 1990; Jarvis 1997b; Kingdon 1997; Stuart and Stuart 2001).

Macroscelidea

Cape rock elephant-shrew (*Elephantulus edwardii*)

This elephant shrew is endemic to South Africa, and occurs in disjointed areas in the southwestern and central parts of the Western Cape, Little Namaqualand as well as the region around Port Elizabeth in the Eastern Cape. Adults' total body length is about 250 mm, with an average body mass of about 50 g. This species prefers habitats with pockets of layered rocks in either dwarf shrubs, karroid (semi-arid scrub) vegetation, or relatively open environments. It is terrestrial and mainly solitary, although pairs have been recorded. It is crepuscular, diurnal and nocturnal. Although this shrew is predominantly insectivorous, it also preys on a wide range of other invertebrates with a notable preference for ants and termites. In captivity, this shrew readily eats vegetable matter, including seeds (Information compiled from: Skinner and Smithers 1990; Perrin 1997c; Stuart and Stuart 2001).

APPENDIX 2

Short notes on the behavior, diet and preferred habitats of possible predators of small mammals around the SBYC area (based on their present distribution)

The Owls

Barn owl (*Tyto alba*)

The barn owl is a cosmopolitan owl, occurring in most parts of the world. Although this owl is very widespread and can thrive in varied conditions, it prefers open habitats especially for hunting. It is most common in open savanna adjacent to grassland or low scrub. It may also occur in deserts, but not in forests. As barn owls require some form of cavity for their nesting and roosting needs, this greatly influences their habitat choice. The presence of some cavities or crevices in trees, buildings or rocky outcrops are sufficient for barn owls to roost or nest in. The barn owl is largely nocturnal (although may hunt at dusk), and is generally opportunistic in its hunting behaviour. In southern Africa, its catholic diet comprises largely nocturnal rodents and shrews, and to a lesser extent, birds, reptiles, amphibians and arthropods. Other mammals that may also be taken by barn owls include some diurnal rats and mice, golden moles, bats, young hares and hedgehogs, although the last two are taken in rare cases. In southern Africa, it has been estimated that the barn owl requires about 42 g of food per night, and this figure may rise during winter and also during the nesting period for the females. The barn owl preys on the most abundant prey species. It usually regurgitates one pellet a day and, through this, skeletal remains of its prey accumulate at the roost site or below the roost site. The foraging range of barn owls may vary from one place to another, and their roost sites which are usually used for a long time, may be located up to about 16 km from their hunting area (Information compiled from: Prestt and Wagstaffe 1973; Steyn 1982; Kemp and Calburn 1987; Andrews 1990a; Skinner and Smithers 1990; Taylor 1994).

Grass owl (*Tyto capensis*)

The grass owl superficially looks like the barn owl, although it is biologically different. It roosts and nests entirely on the ground in vast and open grasslands and more preferably in long grass. It also prefers living in the vicinity of some water. It is largely nocturnal (although occasionally hunts during the day), and roosts in hollows or tunnels in the long grass. This owl is resident, but when its residence is decimated, it often shifts to another area within the local range. In South Africa, its distribution stretches from the southwestern part of the Western Cape Province through the eastern part of the country, and northwards towards Zimbabwe. This owl preys mainly on rodents and shrews. As a result of its habitat specialization, the grass owl often takes more vlei rats (*Otomys* spp.) whose habitat preference tend to be similar to that of the owl. Similarly, the climbing mice (*Dendromus* spp.), which may also occur abundantly in moist grassland, occupy an important part in the diet of the grass owl. Like its phenotypically related cousin, the barn owl, the grass owl also takes a wide variety of birds and insects. Frogs appear very rarely in the diet of this owl. Generally, although the grass owl does not take a wide range of prey species like the barn owl largely because of its more specialized habitat requirements, it may take similar prey species as the barn owl. This owl uses particular roost sites for a long time, and in these sites, pellets may accumulate (Information compiled from: Prestt and Wagstaffe 1973; Steyn 1982, 1984; Kemp and Calburn 1987).

Marsh owl (*Asio capensis*)

In southern Africa, the marsh owl is thought to be one of the most nomadic owls, and this often happens when its habitat has been disturbed, for instance, by fire. It prefers habitats similar to those of the grass owl, and these include stands of rank grass, clusters of weeds and patches of herbs, all of which tend to be relatively transient in the southern African region. It can, however, cope with fluctuations in the quality of its favoured habitats by making local migrations. In southern Africa, this owl is widespread and its occurrence ranges from southwestern South Africa to Zimbabwe and westwards into both the northern parts of Botswana and Namibia. This owl is mostly crepuscular, as this is the time when most small vertebrates and also arthropods are most active. It may, however, extend its hunting up to daylight. Its diet

comprises mostly small rodents (including multimammate mice and vlei rats), shrews, and birds. Other small vertebrate species, such as the striped polecat and young scrub hares may also be taken. It also takes termites, small beetles, and generally a wide variety of arthropods. It occasionally takes frogs and lizards. When hunting, a marsh owl may often rest on the ground to regurgitate a pellet. The roosts of marsh owls tend to be temporary, and are mainly hollows in the grass. The roosts usually contain very few pellets (Information compiled from: Steyn 1982, 1984; Kemp and Calburn 1987).

African wood owl (*Strix woodfordii*)

The African wood owl occurs commonly in forests, but it is not entirely confined there. It may occur in a mosaic of forest habitats, including coastal bushes, dense woodland, pine plantations and wooded riverine belts. In South Africa, its distributional range extends from the southwest through the Eastern Cape and northwards towards Zimbabwe. This owl is strictly nocturnal. It prefers to roost in dense foliage, where it may roost in one site for a long time. Although this owl is largely insectivorous, it also preys on small rodents, shrews, frogs and birds. Because of its predominantly insectivorous diet, the roost sites of this owl rarely yield pellets and if they do, the pellets usually contain very few and highly fragmented bones (Information compiled from: Steyn 1982, 1984; Kemp and Calburn 1987).

Spotted eagle owl (*Bubo africanus*)

Among the three southern African eagle owls, the spotted eagle owl is the smallest of all. This owl is widespread and common, and occurs in a wide range of places, including lightly wooded savanna areas, and also in desert; it does not occur either in evergreen forest or open flat grassland. It is most common on rocky ledges, and also on steep slopes, hollows in large trees, burrows, old nests belonging to other species, and generally on rocky substrates in areas of broken terrain. In southern African, it has also adapted to living in urban areas, where it roosts on buildings. This owl is largely nocturnal, roosting in pairs during the day, and starting to hunt at dusk. Hunting sometimes may also take place during the day. The spotted eagle owl is opportunistic in its diet requirements, and may prey on a wide variety of species, including relatively large-sized prey. Rodents, including gerbils and vlei rats, shrews, birds (including some large birds such as the speckled and feral pigeons) and arthropods form the main diet in most places. This owl may also take small mammals such as scrub hares, lesser bush babies, and fruit-bats. Other prey species taken by this owl include reptiles such as geckos and snakes. The diet of this owl is greatly influenced by the available prey species, and this enables the owl to inhabit one area for a long time, in spite of changes in prey species (Information compiled from: Fodgen 1973; Steyn 1982, 1984; Kemp and Calburn 1987).

Cape eagle owl (*Bubo capensis capensis*)

The Cape eagle owl is one of the largest and powerful owls confined to South Africa. It occurs mainly in rocky and fragmented mountainous terrain, and also more often in montane grassland, as well as thick woodland in riverine environments. In the southwestern part of the Western Cape Province, this owl occurs in the fynbos mountains stretching down to the sea. The Cape eagle owl is resident and during the day, it prefers to roost in isolated spots on the ground behind some cover, and also in fissures or ledges. It hunts between dusk and dawn. As it prefers hunting the locally abundant and large prey of particular types, its distribution may to some extent be influenced by the distribution of such prey species. It preys on a wide diversity of prey species, including the red rock hares, rock dassies, scrub hares, springhares, small antelopes, hedgehogs, genets, golden moles, tree squirrels, vlei rats, mice and shrews (including the elephant shrew). It also takes birds such as barn owls and the Cape robins, and reptiles such as lizards, and a wide variety of arthropods. As this owl may commonly occur in rocky environments, prey species inhabiting such environments are highly preyed upon. Such prey species may include the scrub hares and hyraxes. The presence of this owl may be recognized by the white droppings of the owl, which may be deposited on rocks within its roosting, nesting or hunting ranges. In the droppings are large accumulations of bones belonging to the larger prey species. Some of these bones such as the hind limbs of the hares may still be articulated with the feet. The presence of such faunal accumulations, together with some pellets, help to distinguish nests belonging to the Cape eagle owls from those belonging to other smaller owls such as the spotted eagle owl (Information compiled from: Fodgen 1973; Steyn 1982, 1984; Kemp and Calburn 1987).

Giant eagle owl (*Bubo lacteus*)

The giant eagle owl is the largest of all owls in Africa. It is sedentary, and prefers to inhabit mainly drier savanna woodland and more preferably acacia. It may also occur abundantly in large trees in riverine belts. It is, however, not found in forests. This owl is nocturnal, and may roost in pairs, or close to one another. It is opportunistic in its feeding behaviour and its prey may range from larger species such as the hedgehogs (most favoured), vervet monkeys, springhares, hares, hyraxes, cane rats, warthog piglets, large birds (e.g. secretary birds), to shrews, small birds, ground squirrels, fruitbats, insects, frogs, snakes, gerbils, rats and mice. It may also prey on other owls such as the barn owl, grass owl, marsh owl and the spotted eagle owl (Information compiled from: Fodgen 1973; Steyn 1982, 1984).

Diurnal birds of prey

Black-shouldered kite (*Elanus caeruleus*)

In southern Africa, this bird is one of the most widespread and common among the birds of prey. Although it is very mobile, it roosts mainly in reeds, and may also roost in trees. Communal roosting takes place throughout the year. When hunting, it may solitarily perch on trees or other high vantage points from where it locates its prey. Its prey comprises mainly rodents, including the vlei rats, striped mouse, and the multimammate mouse. Other prey species may include reptiles (e.g. lizards), birds and insects (Steyn 1982; Mendelsohn 1989).

Yellow-billed kite (*Milvus migrans parasitus*)

The yellow-billed kite is an intra-African migrant. This bird occurs in most habitats in southern Africa, including the coastal regions. It is, however, most common in during the summer. In South Africa, it occurs in a mosaic of areas, including the Western Cape Province. Its diet includes a wide range of insects, fish, frogs, small birds, small mammals and reptiles, and may also scavenge on carrions (Steyn 1982; Hartley 1989a).

The Black eagle (*Aquila verreauxii)*

The black eagle is widespread in South Africa, occurring in areas of high rainfall as well as semi-arid areas. It prefers mainly rocky or mountainous environments. Its habitat preference, just like the black eagle population in the Zimbabwe's Matobo Hills, is greatly influenced by the distribution of its principal prey, the dassies. Besides the dassies, its diet may also include young baboons, vervet monkeys, mongoose, suricates, small antelopes, cane rats, ground and tree squirrels, birds (e.g. chicks of Cape vultures), young springboks and bushbucks (Steyn 1982; Gargett 1989).

Booted eagle (*Hieraaetus pennatus*)

This eagle is widespread in South Africa. In the Western Cape Province, it occurs both in the dry parts of the fynbos and the semi-arid Karoo. In other parts of southern Africa, it may occur in a variety of habitats, including the desert and the woodland environments. In southern Africa, this eagle preys on a wide variety of birds, lizards, rats, mice and insects (Steyn 1982).

Martial eagle (*Polemaetus bellicosus*)

This is the largest eagle in Africa. The martial eagle occurs throughout southern Africa, and is most common in bushveld. Its diet varies from one place to another, and may include large birds (e.g. black-headed heron), small or young antelopes (e.g. red duikers, steenbok, oribi, impala and springbok), young baboons, vervet monkeys, ground and tree squirrels, greater cane rat, snakes, lizards, black-backed jackals, and a wide array of small carnivorous mammals (Steyn 1982; Tarboton 1989a).

Steppe buzzard (*Buteo buteo*)

The steppe buzzard is a seasonal migrant into southern Africa from the Palearctic, arriving in October and leaving by early April. It occurs in open country, and more particularly in places where there are agricultural activities such as wheat farming. It may also occur in light wooded habitats. This buzzard is widespread in southern Africa, including the Western Cape Province. Its prey comprises mainly small rodents, birds, small snakes, lizards, and a wide variety of insects (Steyn 1982).

Jackal buzzard (*Buteo rufofuscus)*

This species of the buzzards occurs in hilly or mountainous environments, including high mountain ranges. It may also prefer to hunt in montane grassland or flat country. It is restricted to South Africa and the southern part of Namibia. The jackal buzzard is widespread in South Africa, including the Western Cape. Its diet includes rodents such as mice, rats, and the greater cane rat. Other mammalian species taken by this bird include young mongoose and dassies. The jackal buzzard also preys on reptiles, other birds, and occasionally termites (Steyn 1982; Tarboton 1989b).

Red-breasted sparrowhawk (*Accipiter rufiventris*)

In South Africa, this bird occurs in a number of places, including eastern Free State, the northern provinces and the Western Cape. It prefers living in stands of exotic trees, including pines and eucalypts, where it may be found nesting. It preys almost entirely on birds of varying sizes; mice, bats and insects particularly termites, may occasionally appear in its diet (Steyn 1982).

Rock kestrel (*Falco tinnunculus*)

Although this species of the kestrels prefers mainly mountainous environments or adjacent areas, it may also occur in open country away from mountains. Its diet comprises small rodents, small birds, lizards, bats, and a variety of arthropods, including spiders and locusts (Steyn 1982; Hartley 1989b).

Lesser kestrel (*Falco naumanni*)

In southern Africa, this species of the kestrels occurs in open country, preferring the 'sweet' grassland of the highveld. Although it is very mobile, it shuns well-wooded habitats, but may be found living/roosting in areas inhabited by humans (e.g. urban areas), especially if there are stands of eucalypts or other trees in which it can roost. It is widely distributed in the south-west of South Africa from where its distribution extends towards the northern parts of southern Africa. In southern Africa, this bird preys mostly on insects, although it may sometimes also catch some rodents (Steyn 1982: Liversidge 1989).

Greater kestrel (*Falcon rupicoloides*)

The greater kestrel is widespread in southern Africa, and occurs principally in open country with short vegetation cover. It does not, however, occur in wooded habitats. Its wide distribution in southern Africa also extends into the semi-desert and desert environments. This bird preys largely on arthropods, with a particular preference for grasshoppers and termites. The greater kestrels also prey on rats (e.g. vlei rats), lizards and also the small snakes (Steyn 1982; Jensen 1989).

African marsh harrier (*Circus ranivorus*)

The distribution of the African marsh harrier is largely confined to south and east of southern Africa. Although this bird occurs mainly in marshlands and other moist areas, it may also venture into the surrounding dry country to hunt. The African marsh harrier preys largely on rats, mice and birds. Other prey species include reptiles, frogs and insects (Steyn 1982).

Black harrier (*Circus maurus*)

Unlike most harriers that are more dependent on marshlands, the black harrier occurs mainly in dry country such as the Karoo scrub and other dry areas with short grassveld. This harrier may, however, hunt on the borders of wet areas. In South Africa, the distributional range of this bird includes the Western Cape Province. In the south-west Cape, the black harrier occurs in mountainous areas. It is an opportunistic hunter, and its prey species include birds, small rodents (particularly rats and mice), amphibians and insects (Steyn 1982; Martin 1989).

Small carnivorous mammals

Canidae

Bat-eared fox (*Otocyon megalotis*)

The bat-eared fox is a common carnivore, which is widely distributed in southern Africa. It occurs in a wide range of areas in this sub-region including Mozambique, Botswana, Zimbabwe and South Africa. In South Africa, it occurs widely, including in the Cape Peninsula. Its body mass may range between 3 to 5.3 kg. In autumn, winter and spring, it is active beginning from late morning to the early hours of the evening, becoming more nocturnal in summer. It occurs in dry and open country, and especially in areas (e.g. valleys) with acacia savannas and short grasslands, where it may be found living/sheltering in burrows, under vegetation cover, or just in the open. The bat-eared fox, however, avoids densely wooded and forested areas. Bat-eared foxes are sociable animals and hunt in groups or pairs, relying on their acute sense of hearing to locate their prey. Their diet comprises largely insects, and also rodents, reptiles, wild fruits, and a wide range of invertebrates. They defecate near their resting/sheltering places, and therefore their droppings accumulate at these sites (Information compiled from: Andrews and Evans 1983; Skinner and Smithers 1990; Kingdon 1997; Nel 1997; Stuart and Stuart 2001).

Cape fox (*Vulpes chama*)

The Cape fox (despite its name) is not confined to the former Cape Province, as it also occurs in other parts of the southern African sub-region including Namibia and Botswana. In South Africa, it also occurs in areas such as KwaZulu-Natal, the Western Cape and the northern provinces. Its total body length is in the range of 860 to 970 mm, with body mass ranging between 2.5 to 4.0 kg. Although difficult to observe, the Cape fox is largely nocturnal. It prefers to lie in holes in the ground or in the cover of stands of grass during the day. Preferring mainly open country, including arid scrub (e.g. of the Karoo), acacia grasslands and the fynbos areas of the Western Cape, this asocial fox hunts solitarily. Although it predominantly preys on invertebrates and mice, its diet may also include reptiles, birds, wild fruits and a wide range of small mammals (Information compiled from: Skinner and Smithers 1990; Kingdon 1997; Mills 1997a; Stuart and Stuart 2001).

Black-backed jackal (*Canis mesomelas*)

In southern Africa, the black-backed jackal occurs in different parts of the region including Zimbabwe, Namibia, South Africa and Botswana. In South Africa, this jackal occurs over much of the country, including the Western Cape Province. This medium-sized carnivore has a body mass ranging between 6.5 to 13.5 kg. Although it prefers drier areas with acacia savannas, it has a wide habitat tolerance. In the southern part of its distributional range, it may occur in moist areas. This jackal is both diurnal and nocturnal, and occurs solitarily or in pairs, or in family groups. When resting, it may be found in burrows dug by other mammalian species, in rock crevices, under vegetation cover, and also among piles of boulders. This very adaptable animal is omnivorous, and preys on a wide range of items, including wild fruits and berries, small vertebrates such as hares, birds, rodents, reptiles, as well as a wide variety of invertebrates (Information compiled from: Skinner and Smithers 1990; Kingdon 1997; McKenzie 1997; Stuart and Stuart 2001).

Felidae

African wild cat (*Felis lybica)*

Felis lybica, also known in some literature as *Felis silvestris lybica* (e.g. Kingdon 1997; Stuart and Stuart 2001), is widely distributed in southern Africa. It occurs in different parts of the sub-region, including Namibia, Botswana, South Africa and Mozambique. In South Africa, this cat occurs in a number of areas, including KwaZulu-Natal, Free State, and the Western Cape Province where it is widely distributed. This cat has a body mass ranging between 2.5 to 6 kg. It is a largely nocturnal and solitary cat. It has a wide habitat tolerance, and may occur in habitats such as woodlands, savannas and grasslands; but does not occur in true deserts. Throughout its distributional range, it requires some form of cover and this may be in the form of rocky hillsides, hollow trees, crevices, and stands of tall grass. Droppings are usually buried, but may also be deposited at latrine sites. It hunts silently, and its ever-changing catholic diet comprises mainly murids, hare-sized mammals, birds, and to a lesser degree, frogs, reptiles and insects (Information compiled from: Skinner and Smithers 1990; Apps 1997; Kingdon 1997; Stuart and Stuart 2001).

Caracal (*Felis caracal)*

In southern Africa, the caracal is very successful and widely distributed, occurring in many areas including South Africa, Namibia, Botswana and Zimbabwe. In South Africa, it occurs over much of the country, including the Western Cape Province. It is a robustly built carnivore, with an average adult weight of about 17 kg and 11.5 kg for males and females, respectively. *Felis caracal* is largely nocturnal, and very secretive in its solitary habits. It can withstand arid environments, although it generally prefers plains and rocky hills in open country and open wooded savanna, with a higher preference for open vleis and open grassland. Its diet depends on the available prey species, and may include dassies, small antelopes, hares, birds, small carnivores, shrews, and rodents such as the *Otomys* spp. and *Tatera afra* (Information compiled from: Avery *et al.* 1990; Skinner and Smithers 1990; Davies 1997; Kingdon 1997).

Small spotted cat/ black-footed cat (*Felis nigripes)*

This cat, also known in some literature as the black-footed cat (e.g. Sliwa 1997; Kingdon 1997) is endemic to the arid western parts of southern Africa, including, Botswana, Namibia and South Africa. In South Africa, it occurs marginally in the Transvaal, but has a wide occurrence further south, including the west coast. Its body mass may range between 1 to 2 kg. It occurs mainly in arid regions and more particularly open habitats with some vegetation cover such as grass. It is nocturnal, solitary and very secretive in its habits, and may be found lying in termite mounds and also in burrows dug by other species. *Felis nigripes* is an opportunistic hunter, and its diet comprises largely rodents (particularly gerbils); other prey species include birds, spiders, reptiles and insects (Information compiled from: Skinner and Smithers 1990; Kingdon 1997; Sliwa 1997; Stuart and Stuart 2001).

Mustelidae

Cape clawless otter (*Aonyx capensis)*

This otter is widely distributed in southern Africa, occurring in areas such as Zimbabwe, Mozambique and Botswana. It is absent in most of the dry and interior parts of the sub-region. In South Africa, the wide distributional range of this otter includes the Western Cape Province. Its body mass may be up to 16 kg. It occurs predominantly in fresh and marine waters (e.g. rivers, lakes and swamps), although it may also be found on dry land (e.g. wooded and grassland environments) looking for food. It is both diurnal and nocturnal. As these otters move widely, accumulations of droppings associated with them may be rare and if they are found, they largely contain crab shells. Latrine sites associated with this otter, however, have been reported. Its diet comprises mainly crabs and frogs, and to a lesser extent, fish, insects, birds, reptiles, small mammals and mollusks (Information compiled from: Skinner and Smithers 1990; Somers 1997; Stuart and Stuart 2001).

Honey badger (*Mellivora capensis*)

In southern Africa, the honey badger is widely distributed, and occurs in parts of the region including South Africa, Botswana, Mozambique and Zimbabwe. In South Africa, the honey badger also occurs over much of the country, including the Western Cape Province. Its body mass ranges between 7 to 16 kg. It is catholic in its habitat requirements. It may occur in montane forests, in waterless desert steppe (but not extreme deserts), and is most common in open woodland. *Mellivora capensis* often uses crevices in rocks to shelter itself. It is also an adept digger, and may dig holes in which to live. The honey badger is predominantly nocturnal, but may also hunt during the day. In widely overlapping ranges, this carnivore hunts solitarily, although pairs have also been observed hunting together. It is an opportunistic omnivore, and its diet includes murids, reptiles, insects, beetles, spiders, birds and wild fruits (Information compiled from: Skinner and Smithers 1990; Kingdon 1997; Mills 1997b; Stuart and Stuart 2001).

Striped polecat (*Ictonyx striatus*)

The striped polecat occurs throughout the southern African sub-region, including the Western Cape Province. Its body mass ranges between 0.5 to 1.4 kg. It has a wide habitat tolerance, and occurs in all major habitat types including areas with scrub cover, savanna woodland and cool upland grasslands. It is not common in areas with dense vegetation, and it is absent in deserts. The striped polecat may burrow under loose and soft sandy substrate, or take shelter in burrows belonging to other species that are not in use. It may also take shelter amongst matted vegetation, piles of stones, and under tree roots or fallen logs. This carnivore is strictly nocturnal. Polecats are largely solitary, although they may occur in pairs or in family groups. Polecats' diet comprises mainly invertebrates and mice, although reptiles, amphibians, birds, and a wide variety of small animals are also taken (Information compiled from: Skinner and Smithers 1990; Kingdon 1997; Rowe-Rowe 1997; Stuart and Stuart 2001).

Viverridae

Small-spotted genet (*Genetta genetta*)

The small-spotted genet is widely distributed in southern Africa, occurring in parts of the region such as Namibia, Swaziland, Botswana, South Africa and Lesotho. In South Africa, its wide distribution includes areas such as KwaZulu-Natal and the Western Cape Province. Its body mass is in the range of 1.5 to 2.6 kg. This genet has a wide habitat tolerance and may occur in open and arid, woodland, riverine and grassland habitats, and also in pockets of rocky outcrops on open plains. Although rarely seen, this genet is strictly nocturnal and occurs mostly solitarily or in pairs. Its diet includes largely insects and rodents; reptiles, shrews, birds, amphibians, bats, and a wide range of invertebrates, may also be part of its diet. It deposits droppings at latrine sites, which are usually in open and conspicuous places (Information compiled from: Skinner and Smithers 1990; Maddock 1997a; Stuart and Stuart 2001).

Large-spotted genet (*Genetta tigrina*)

In southern Africa, this genet occurs in discrete areas in different parts of the region, including South Africa, Namibia, Botswana and Zimbabwe. In South Africa, it occurs in KwaZulu-Natal, as well as in the Western Cape Province. Its body mass ranges between 1.5 to 3.2 kg. This nocturnal and solitary genet prefers habitats that are well-watered, receive high rainfall, and have relatively dense vegetation cover. It is generally well adapted to the arboreal habitat. The diet of the large-spotted genet comprises mainly rodents (particularly murids), insectivores and insects. This genet also preys on birds, reptiles, amphibians, wild fruits and a wide range of invertebrates. It deposits droppings at latrine sites, which are usually in open and conspicuous places (Information compiled from: Skinner and Smithers 1990; Maddock 1997b; Stuart and Stuart 2001).

Yellow mongoose (*Cynictis penicillata*)

This mongoose is widely distributed in southern African, and frequently sighted in most parts of the region. It occurs in most parts of southern Africa, including South Africa, Namibia, Botswana and Zimbabwe. In

South Africa, its widespread distribution includes KwaZulu-Natal and the Western and Northern Cape provinces. Its body mass is in the range of 450 to 950 g. It prefers sandy substrates and open country with short grass, or semi-desert scrub. It does not, however, occur in desert or in areas with dense vegetation. It has, however, penetrated the fairly dense but low scrub fynbos of the Western Cape. This mongoose may dig burrows, and may also communally occupy burrows belonging to other species. Droppings are deposited in latrines near the entrances to the burrows. Although the yellow mongoose may live in groups, foraging is a solitary affair. It is predominantly diurnal, although it is also known to hunt at night. It is known to forage in large areas far from its den and depending on the season, its diet mainly comprises insects and a wide range of invertebrates, small rodents (including murids), amphibians and reptiles (Information compiled from: Skinner and Smithers 1990; Kingdon 1997; Stuart 1997a; Stuart and Stuart 2001).

Small grey mongoose (*Galerella pulverulenta*)

This mongoose is often referred to as the Cape-grey mongoose, and this is because the type specimen of this species was found at the Cape of Good Hope. It is widely distributed in South Africa, apart from the more northerly parts. Its body mass may range between 500 to 1000 g. This mongoose has a wide habitat tolerance, ranging from forest to open scrub. It prefers overgrown bushy country, and also occurs abundantly in dry rocky ground and hillside coastal plains, where it may be found sheltering under vegetation cover, in burrows, and other holes. In the southwestern part of the Western Cape, this mongoose also occurs in fynbos areas with relatively little annual rainfall. It is diurnal, terrestrial, and largely solitary, although pairs have been sighted. Its diet comprises largely invertebrates (insects, crabs and earthworms) and small rodents (rats, including the vlei rats, and mice). Other prey species include reptiles, amphibians and birds (Information compiled from: Skinner and Smithers 1990; Kingdon 1997; Stuart 1997b; Stuart and Stuart 2001).

Suricate (*Suricata suricatta*)

The distributional range of the suricate is mainly within the semi-arid regions of southern Africa, including the Namib and the pro-Namib deserts. In South Africa, it marginally occurs in the northwestern parts of KwaZulu-Natal, but is widespread in the Western and Northern Cape provinces. Its body mass ranges between 620 to 960 g. The suricate prefers areas with stony or calcareous substrate, and inhabits open, arid, and lightly vegetated country where it digs its own burrow complexes (warrens). It may also be found living in burrows made by other small mammals such as the ground squirrels. It avoids dense vegetation and deserts, although its distributional range includes the Namib Desert. Suricates are diurnal and hunt in groups, traveling up to about 6 km from their dens to forage. They, however, return to the same dens to sleep after their diurnal foraging. The diet of the suricates predominantly comprises insects, and a wide range of invertebrates (e.g. spiders and scorpions). Other prey species include birds, amphibians, mice and reptiles particularly geckos (Information compiled from: Skinner and Smithers 1990; Kingdon 1997; MacDonald 1997; Stuart and Stuart 2001).

APPENDIX 3

SBYC maxillary and mandibular frequency according to species (Key: Lmax = Left maxilla, Rmax = Right maxilla, Lman = Left mandible, Rman = Right mandible).

Taxon	Down Slope				Upper Slope				Hanging Remnant			
	Lmax	Rmax	Lman	Rman	Lmax	Rmax	Lman	Rman	Lmax	Rmax	Lman	Rman
Insectivora												
C. asiatica			2				12	7				
cf. C. cyanea			1	7		3		2			1	3
C. flavescens	2	2	1	4	1	3	3	5	1	1	1	1
M. varius	7	10	41	49	27	24	135	164	1		12	9
cf. M. varius			1	3			16	4				1
S. varilla	4	4	17	20	15	7	63	62			19	11
cf. S. varilla							1	1				
Chiroptera												
R. clivosus				1				1				
Rodentia												
D. melanotis	2	1	1	1	9	4	9	7	2	2	1	1
D. mesomelas						2	2					
Dendromus spp.							2				2	2
S. krebsii	2	8	2	3	12	8	17	22	2	2	2	3
G. paeba	7	5			5	7	9	9	2	1	3	2
T. afra	40	50	34	50	84	85	112	121	9	15	10	25
M. albicaudatus	2	2	1	1	4	4	4	3	2		1	1
R. pumilio	4	1			1	2	1	4				
cf. R. pumilio			1									
O. irroratus			1	1	4	7	4	1			1	
O. saundersiae	7	10	4	6	20	24	20	14	8	12	9	7
O. unisulcatus	5	2	5	1	6	2	4	1				
Otomys spp.	4	1	3	9	4	3	15	17	1	3	3	
B. suillus							1					
C. hottentotus			4	4			8	8				
Macroscelidea												
E. edwardii					1		1	1				

APPENDIX 4

This appendix records results from work by Andrews (1990a) on a wide range of modern predator faunal assemblages

Appendix 4.1: Rodent cranial breakage in predator assemblages (*Maxillae still present in skulls: After Andrews 1990a, Tables 3.5 and 3.7).

Predator species	% complete *Maxillae	% maxillae with zygomatic	% complete mandibles	% mandibles with ramus missing	% mandibles with inferior border broken
Barn owl	75	90	78	6	3
Snowy owl	80	80	58	5	21
Long-eared owl	74	94	81	2	2
Short-eared owl	24	24	24	38	10
Verreaux eagle owl	85	94	84	6	3
Spotted eagle owl	17	48	7	62	27
European eagle owl	27	64	38	18	14
Great grey owl	83	83	89	0	7
Tawny owl	64	69	19	18	14
Little owl	0	0	0	33	50
Kestrel	5	19	4	71	44
Hen harrier	9	30	2	55	69
Mongoose	0	10	0	95	100
Genet	0	24	0	94	75
Bat-eared fox	0	10	0	95	86
Coyote	0	12	0	100	75
Red fox	0	0	0	75	100
Artic fox	0	0	0	100	100
Pine marten	0	0	0	100	100

Appendix 4.2: Predator categories based on the digestion of micromammalian incisors (After Andrews 1990a, Table 3.14 and Matthews 1998, Table 2.3).

Predator Category	Percentage of incisor digestion
Category 1	
barn owl, short-eared owl, snowy owl	absent or light digestion; incisor % etched = 8 - 13%
bat-eared fox - intermediate	light digestion; incisor % etched = 19%
Category 2	
long-eared owl, giant eagle owl, great grey owl	moderate digestion (tips only); incisor % etched = 20 - 30%
mustelids	intermediate between Categories 2 and 3; incisor % etched = 24%
viverrids	intermediate between Categories 2 and 3; incisor % etched = 34 - 40%
Category 3	
tawny owl, little owl, European and spotted eagle owls	moderate/heavy digestion; incisor % etched = 50 - 70%
Category 4	
kestrels and peregrines	heavy/extreme digestion; incisor % etched = 60 - 80%
canids - coyote, red fox, artic fox	intermediate, may fall either in Categories 4 or 5; extreme digestion with incisor % etched = 70 - 100%
Category 5	
buzzards, kites, hen harriers	extreme digestion; incisor % etched = 100%; dentine corroded

Appendix 4.3: Breakage patterns of the major long bones in modern predator assemblages (%) (Key: C = Complete, P = Proximal, S = Shaft, D = Distal: After Andrews 1990a, Table 3.3 and Matthews 1998, Appendix 4, Table 6).

Predator species	Humerus				Ulna				Femur				Tibia			
	C	P	S	D	C	P	S	D	C	P	S	D	C	P	S	D
Barn owl	99	0	0	1	97	3	0	0	97	1	2	0	98	1	1	0
Snowy owl	75	4	8	12	76	24	0	0	88	4	0	8	88	8	4	0
Long-eared owl	96	0	1	3	95	4	1	0	96	3	1	0	93	6	1	0
Short-eared owl	88	3	2	7	92	8	0	0	93	7	0	0	87	4	5	4
Verreaux eagle owl	96	0	2	2	98	2	0	0	97	2	1	0	99	1	0	0
Spotted eagle owl	44	7	11	38	85	12	3	0	66	32	2	0	71	0	29	0
European eagle owl	82	7	0	11	97	3	0	0	83	12	3	2	86	9	0	5
Great grey owl	89	4	4	4	96	4	0	0	90	8	2	0	93	7	0	0
Tawny owl	53	7	12	28	69	31	0	0	52	22	6	20	85	7	4	4
Little owl	33	33	16	16	100	0	0	0	12	64	12	12	33	8	50	8
Hen harrier	22	7	39	32	60	40	0	0	20	40	20	20	22	22	33	22
Kestrel	44	4	27	25	32	52	8	8	20	48	24	7	31	29	25	14
White-tailed mongoose	30	29	9	32	8	92	0	0	12	52	13	23	37	25	38	-
Small spotted genet	33	13	10	44	54	46	0	0	12	51	20	17	57	27	16	-
Bat-eared fox	26	7	15	52	57	43	0	0	3	87	3	7	10	80	10	-
Coyote	7	38	17	38	25	75	0	0	0	42	28	30	0	90	10	-
Red fox	0	8	9	83	0	67	33	0	0	53	21	26	0	67	33	-
Pine marten	0	30	19	51	25	75	0	0	0	50	50	0	0	82	18	-

Appendix 4.4: Relative proportions of post-cranial to cranial elements (After Andrews 1990a, Table 3.2).

Predator species	No. of pellet samples	proportions of post-cranial to cranial elements femur + humerus / mandible + maxilla	proportion of distal limb elements tibia + radius / femur + humerus
Barn owl	4	93	105
Snowy owl	1	133	98
Long-eared owl	2	102	92
Short-eared owl	2	111	82
Verreaux eagle owl	2	80	100
Spotted eagle owl	1	74	52
European eagle owl	2	111	75
Great grey owl	1	92	89
Tawny owl	3	82	92
Little owl	1	164	70
Kestrel	3	74	72
Hen harrier	1	33	58
Mongoose	1	138	30
Genet	1	76	44
Bat-eared fox	1	92	25
Coyote	1	133	79
Red fox	1	233	50
Artic fox	1	36	75
Pine marten	1	114	25

APPENDIX 5

This appendix records chi-squared (X^2) results and other data relevant in the interpretation of the SBYC micromammalian fauna

Appendix 5.1.1: Chi-squared analysis comparing the distribution of murid maxillae between the three SBYC faunal samples.

	Down Slope		Upper Slope		Hanging Remnant		
Category	Observed	Expected	Observed	Expected	Observed	Expected	TOTALS
1	35	43	91	79	12	16	138
2	6	4	7	8	1	2	14
3	82	81	151	148	26	30	259
4	48	42	63	77	24	16	135
TOTAL	171		312		63		546
	X^2 = 13.851		df = 6	p = 0.031354			

Appendix 5.1.2: Chi-squared analysis comparing the distribution of murid maxillae between the Down Slope and Upper Slope.

	Down Slope		Upper Slope		
Category	Observed	Expected	Observed	Expected	TOTALS
1	35	45	91	81	126
2	6	5	7	8	13
3	82	82	151	151	233
4	48	39	63	72	111
TOTAL	171		312		483
		X^2 = 6.85	df = 3	p = 0.1	

Appendix 5.1.3: Chi-squared analysis comparing the distribution of murid maxillae between the Down Slope and Hanging Remnant.

	Down Slope		Hanging Remnant		
Category	Observed	Expected	Observed	Expected	TOTALS
1	35	34	12	13	47
2	6	5	1	2	7
3	82	79	26	29	108
4	48	53	24	19	72
TOTAL	171		63		234
		X^2 = 2.56	df = 3	p = 0.5	

Appendix 5.1.4: Chi-squared analysis comparing the distribution of murid maxillae between the Hanging Remnant and Upper Slope.

	Hanging Remnant		Upper Slope		
Category	Observed	Expected	Observed	Expected	TOTALS
1	12	17	91	86	103
2	1	1	7	7	8
3	26	30	151	147	177
4	24	15	63	72	87
TOTAL	63		312		375
		$X^2 = 9.87$	df = 3	p = 0.02	

Appendix 5.2.1: Chi-squared analysis comparing the distribution of murid mandibles between the three SBYC faunal samples.

	Down Slope		Upper Slope		Hanging Remnant		
Category	Observed	Expected	Observed	Expected	Observed	Expected	TOTALS
1	1	8	34	25	3	5	38
2	13	18	60	54	9	10	82
3	12	15	45	45	11	8	68
4	106	91	258	273	52	52	416
TOTAL	132		397		75		604
		$X^2 = 17.19$	df = 6	p = 0.008603			

Appendix 5.2.2: Chi-squared analysis comparing the distribution of murid mandibles between the Down Slope and Upper Slope.

	Down Slope		Upper Slope		
Category	Observed	Expected	Observed	Expected	TOTALS
1	1	9	34	26	35
2	13	18	60	55	73
3	12	14	45	43	57
4	106	91	258	273	364
TOTAL	132		397		529
		$X^2 = 14.95$	df = 3	p = 0.002	

Appendix 5.2.3: Chi-squared analysis comparing the distribution of murid mandibles between the Down Slope and Hanging Remnant.

	Down Slope		Hanging Remnant		
Category	Observed	Expected	Observed	Expected	TOTALS
1	1	3	3	1	4
2	13	14	9	8	22
3	12	15	11	8	23
4	106	101	52	57	158
TOTAL	132		75		207
		$X^2 = 4.90$	df = 3	p = 0.2	

Appendix 5.2.4: Chi-squared analysis comparing the distribution of murid mandibles between the Upper Slope and Hanging Remnant.

	Upper Slope		Hanging Remnant		
Category	Observed	Expected	Observed	Expected	TOTALS
1	34	31	3	6	37
2	60	58	9	11	69
3	45	47	11	9	56
4	258	261	52	49	310
TOTAL	397		75		472
		$X^2 = 2.87$	df = 3	p = 0.41	

Appendix 5.3.1: Chi-squared analysis comparing the distribution of soricid mandibles between the three SBYC faunal samples.

	Down Slope		Upper Slope		Hanging Remnant		
Category	Observed	Expected	Observed	Expected	Observed	Expected	TOTALS
1	7	23	91	71	5	9	103
2	7	25	102	79	6	10	115
3	26	28	79	88	23	11	128
4	99	60	151	186	20	24	270
5	9	12	40	38	6	5	55
TOTAL	148		463		60		671
	$X^2 = 87.4445$		df = 8	p = 0.00000			

Appendix 5.3.2: Chi-squared analysis comparing the distribution of soricid mandibles between the Down Slope and Upper Slope.

	Down Slope		Upper Slope		
Category	Observed	Expected	Observed	Expected	TOTALS
1	7	24	91	74	98
2	7	26	102	83	109
3	26	25	79	80	105
4	99	61	151	189	250
5	9	12	40	37	49
TOTAL	148		463		611

$X^2 = 67.53$ df = 4 p = 0.0000

Appendix 5.3.3: Chi-squared analysis comparing the distribution of soricid mandibles between the Upper Slope and Hanging Remnant.

	Upper Slope		Hanging Remnant		
Category	Observed	Expected	Observed	Expected	TOTALS
1	91	85	5	11	96
2	102	96	6	12	108
3	79	90	23	12	102
4	151	151	20	20	171
5	40	41	6	5	46
TOTAL	463		60		523

$X^2 = 19.87$ df = 4 p = 0.00053

Appendix 5.3.4: Chi-squared analysis comparing the distribution of soricid mandibles between the Down Slope and Hanging Remnant.

	Down Slope		Hanging Remnant		
Category	Observed	Expected	Observed	Expected	TOTALS
1	7	9	5	3	12
2	7	9	6	4	13
3	26	35	23	14	49
4	99	85	20	34	119
5	9	11	6	4	15
TOTAL	148		60		208

$X^2 = 20.0$ df = 4 p = 0.001

Appendix 5.3.5: Results for gamma analyses on murid and soricid jaws.

	Gamma value	Level of significance (p)
Murid mandibles	-0.188	0.007
Murid maxillae	-0.022	0.738
Soricid mandibles	-0.269	0.000
Soricid maxillae	-0.040	0.833

Appendix 5.4.1: Chi-squared analysis comparing the distribution of murid humeri between the three SBYC faunal samples.

	Down Slope		Upper Slope		Hanging Remnant		
Category	**Observed**	Expected	**Observed**	Expected	**Observed**	Expected	**TOTALS**
Complete	**42**	51	**102**	90	**16**	19	**160**
Proximal	**40**	49	**89**	86	**24**	18	**153**
Shaft	**13**	12	**21**	21	**4**	5	**38**
Distal	**200**	183	**308**	323	**66**	68	**574**
TOTAL	**295**		**520**		**110**		**925**
	X^2 = 9.67550		df = 6	p = 0.139012			

Appendix 5.4.2: Chi-squared analysis comparing the distribution of murid humeri between the Down Slope and Upper Slope.

	Down Slope		Upper Slope		
Category	**Observed**	Expected	**Observed**	Expected	**TOTALS**
Complete	**42**	52	**102**	92	**144**
Proximal	**40**	47	**89**	82	**129**
Shaft	**13**	12	**21**	22	**34**
Distal	**200**	184	**308**	324	**508**
TOTAL	**295**		**520**		**815**
		X^2 = 6.88	df = 3	p = 0.76	

Appendix 5.4.3: Chi-squared analysis comparing the distribution of murid humeri between the Down Slope and Hanging Remnant.

	Down Slope		Hanging Remnant		
Category	Observed	Expected	Observed	Expected	TOTALS
Complete	42	42	16	16	58
Proximal	40	47	24	17	64
Shaft	13	12	4	5	17
Distal	200	194	66	72	266
TOTAL	295		110		405
		$X^2 = 4.32$	df =3	p = 0.229	

Appendix 5.4.4: Chi-squared analysis comparing the distribution of murid humeri between the Upper Slope and Hanging Remnant.

	Upper Slope		Hanging Remnant		
Category	Observed	Expected	Observed	Expected	TOTALS
Complete	102	97	16	21	118
Proximal	89	93	24	20	113
Shaft	21	21	4	4	25
Distal	308	309	66	65	374
TOTAL	520		110		630
		$X^2 = 2.41$	df = 3	p = 0.5	

Appendix 5.5.1: Chi-squared analysis comparing the distribution of soricid humeri between the three SBYC faunal samples.

	Down Slope		Upper Slope		Hanging Remnant		
Category	Observed	Expected	Observed	Expected	Observed	Expected	TOTALS
Complete	33	41	88	79	21	21	142
Proximal	20	18	29	35	14	10	63
Shaft	4	2	4	4	0	1	8
Distal	35	30	57	59	13	16	105
TOTAL	92		178		48		318
	$X^2 = 9.67207$		df = 6	p = 0.13917			

Appendix 5.5.2: Chi-squared analysis comparing the distribution of soricid humeri between the Down Slope and Upper Slope.

	Down Slope		Upper Slope		
Category	**Observed**	Expected	**Observed**	Expected	**TOTALS**
Complete	**33**	41	**88**	80	**121**
Proximal	**20**	17	**29**	32	**49**
Shaft	**4**	3	**4**	5	**8**
Distal	**35**	31	**57**	61	**92**
TOTAL	**92**		**178**		**270**
		$X^2 = 5.032$	**df = 3**	**p = 0.2**	

Appendix 5.5.3: Chi-squared analysis comparing the distribution of soricid humeri between the Down Slope and Hanging Remnant.

	Down Slope		Hanging Remnant		
Category	**Observed**	Expected	**Observed**	Expected	**TOTALS**
Complete	**33**	35	**21**	19	**54**
Proximal	**20**	22	**14**	12	**34**
Shaft	**4**	3	**0**	1	**4**
Distal	**35**	32	**13**	16	**48**
TOTAL	**92**		**48**		**140**
		$X^2 = 4.42$	**df = 3**	**p = 0.22**	

Appendix 5.5.4: Chi-squared analysis comparing the distribution of soricid humeri between the Upper Slope and Hanging Remnant.

	Upper Slope		Hanging Remnant		
Category	**Observed**	Expected	**Observed**	Expected	**TOTALS**
Complete	**88**	86	**21**	23	**109**
Proximal	**29**	34	**14**	9	**43**
Shaft	**4**	3	**0**	1	**4**
Distal	**57**	55	**13**	15	**70**
TOTAL	**178**		**48**		**226**
		$X^2 = 4.92$	**df = 3**	**p = 0.2**	

Appendix 5.6.1: Chi-squared analysis comparing the distribution of murid femora between the three SBYC faunal samples.

	Down Slope		Upper Slope		Hanging Remnant		
Category	Observed	Expected	Observed	Expected	Observed	Expected	TOTALS
Complete	23	41	113	84	10	20	146
Proximal	228	192	359	391	90	94	677
Shaft	0	4	10	9	5	2	15
Distal	31	44	91	89	33	22	155
TOTAL	282		573		138		993
	X^2 = 51.1576		df = 6	p = 0.00000			

Appendix 5.6.2: Chi-squared analysis comparing the distribution of murid femora between the Down Slope and Upper Slope.

	Down Slope		Upper Slope		
Category	Observed	Expected	Observed	Expected	TOTALS
Complete	23	45	113	91	136
Proximal	228	194	359	393	587
Shaft	0	3	10	7	10
Distal	31	40	91	82	122
TOTAL	282		573		855
		X^2 =33.1	df =3	p = 0.00000	

Appendix 5.6.3: Chi-squared analysis comparing the distribution of murid femora between the Upper Slope and Hanging Remnant.

	Upper Slope		Hanging Remnant		
Category	Observed	Expected	Observed	Expected	TOTALS
Complete	113	99	10	24	123
Proximal	359	362	90	87	449
Shaft	10	12	5	3	15
Distal	91	100	33	24	124
TOTAL	573		138		711
		X^2= 16.1	df = 3	p = 0.0011	

Appendix 5.6.4: Chi-squared analysis comparing the distribution of murid femora between the Down Slope and Hanging Remnant.

	Down Slope		Hanging Remnant		
Category	Observed	Expected	Observed	Expected	TOTALS
Complete	23	22	10	11	33
Proximal	228	214	90	104	318
Shaft	0	3	5	2	5
Distal	31	43	33	21	64
TOTAL	282		138		420
		X^2 = 23.46	df = 3	p = 0.00003	

Appendix 5.7.1: Chi-squared analysis comparing the distribution of soricid femora between the three SBYC faunal samples.

	Down Slope		Upper Slope		Hanging Remnant		
Category	Observed	Expected	Observed	Expected	Observed	Expected	TOTALS
Complete	14	23	67	58	12	12	93
Proximal	39	30	66	75	16	16	121
TOTAL	53		133		28		214
	X^2 = 8.859518		df = 2	p = 0.01192			

Appendix 5.7.2: Chi-squared analysis comparing the distribution of soricid femora between the Down Slope and Upper Slope.

	Down Slope		Upper Slope		
Category	Observed	Expected	Observed	Expected	TOTALS
Complete	14	23	67	58	81
Proximal	39	29	66	76	105
Shaft	0	1	2	1	2
Distal	2	2	6	6	8
TOTAL	55		141		196
		X^2 = 9.77	df = 3	p = 0.021	

Appendix 5.7.3: Chi-squared analysis comparing the distribution of soricid femora between the Down Slope and Hanging Remnant.

	Down Slope		Hanging Remnant		
Category	**Observed**	Expected	Observed	Expected	**TOTALS**
Complete	**14**	17	**12**	9	**26**
Proximal	**39**	36	**16**	19	**55**
Shaft	**0**	0	**0**	0	**0**
Distal	**2**	1	**0**	1	**2**
TOTAL	**55**		**28**		**83**
		$X^2 = 3.34$	df = 2	p = 0.2	

Appendix 5.7.4: Chi-squared analysis comparing the distribution of soricid femora between the Upper Slope and Hanging Remnant.

	Upper Slope		Hanging Remnant		
Category	**Observed**	Expected	Observed	Expected	**TOTALS**
Complete	**67**	66	**12**	13	**79**
Proximal	**66**	68	**16**	14	**82**
Shaft	**2**	2	**0**	0	**2**
Distal	**6**	5	**0**	1	**6**
TOTAL	**141**		**28**		**169**
		$X^2 = 2.21$	df = 3	p = 0.53	

Appendix 5.8.1: Chi-squared analysis comparing the distribution of indeterminate micromammalian ulnae between the three SBYC faunal samples.

	Down Slope		Upper Slope		Hanging Remnant		
Category	**Observed**	Expected	Observed	Expected	Observed	Expected	**TOTALS**
Complete	**9**	6	**11**	19	**8**	3	**28**
Proximal	**220**	223	**745**	737	**103**	108	**1068**
TOTAL	**229**		**756**		**111**		**1096**
	$X^2 = 15.0639$		df = 2	p = 0.000536			

Appendix 5.8.2: Chi-squared analysis comparing the distribution of indeterminate micromammalian tibiae between the three SBYC faunal samples.

	Down Slope		Upper Slope		Hanging Remnant		
Category	**Observed**	Expected	**Observed**	Expected	**Observed**	Expected	**TOTALS**
Complete	**5**	8	**27**	23	**3**	4	**35**
Proximal	**72**	85	**254**	236	**34**	39	**360**
Shaft	**133**	119	**322**	331	**49**	55	**504**
Distal	**169**	167	**451**	464	**88**	77	**708**
TOTAL	**379**		**1054**		**174**		**1607**
	$X^2 = 10.6700$		**df = 6**	**p = 0.099140**			