Cave Usage and the Implications of Multiple Taphonomic Agents on a Faunal Assemblage

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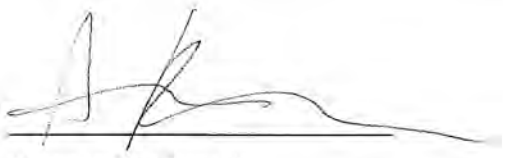
DECLARATION

I declare that this dissertation is my own unaided work. It is being submitted for the Degree of Master at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.



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9th Day of July 2012

ABSTRACT

The means in which fossil accumulations in the caves of southern Africa have formed is of great importance. One method of accumulation is via the collecting behaviours of a variety of mammalian species. The core of said behaviour is in the use of caves by these species. This project was designed to give insight to the way that animals in the Cradle of Humankind, South Africa are using caves today. The objective of this research is to give a new understanding to the amount that caves are used by various taxa in South African cave systems, with particular regard to taphonomic agents and potential taphonomic agents. This study was accomplished over a 20-month period by setting up motion sensor cameras outside of cave entrances at the Malapa Nature Reserve. Results have shown that animals use caves at high frequencies, crucial to recognize when examining fossil accumulations.

I dedicate this to my family.
Wherever in the world I may be I love them dearly.

ACKNOWLEDGEMENTS

The Phillip and Melanie Nash Memorial Trust, Doctor Brian Kuhn (for all that he has done as my supervisor and for donating the camera trap photos for use in this project), Professor Lee Berger, Professor Terence “Spike” McCarthy, University of the Witwatersrand, School of Geosciences, the Institute for Human Evolution, and special thanks to the Nash family for access to the reserve.

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CHAPTER 1: INTRODUCTION

1.1 Background

Caves have been used for millions of years by numerous species, for a variety of reasons, and in nearly every part of the world (Dart, 1954; Sutcliffe, 1970; Kruuk, 1972a; Kruuk, 1972b; Winkler & Adams, 1972; Cumming, 1975; Vrba, 1975; Kruuk, 1976; Maguire, 1976; Vrba, 1976; Klein, 1978; Mills & Mills, 1978; Owens & Owens, 1979; Maguire *et al.*, 1980; Skinner *et al.*, 1980; Brain, 1981; Mills, 1982a; Mills, 1982b; Straus, 1982; Skinner *et al.*, 1986; East *at al.*, 1989; Skinner & van Aarde, 1991; Berger, 1993; Doncaster & Woodroffe, 1993; Berger, 1994; Berger *et al.*, 1995; Stiner *et al.*, 1996; Jagnow, 1998; Skinner *et al.*, 1998; Latham, 1999; de Ruiter & Berger, 2000; Pickering *et al.*, 2000; Avery *et al.*, 2001; Begg, 2001; Berger *et al.*, 2002; Hilton-Barber & Berger, 2002; Lacruz, 2002; Lacruz *et al.*, 2002; Pickering, 2002; d'Errico & Backwell, 2003; Berger *et al.*, 2003; Barrett *et al.*, 2004; Pickering *et al.*, 2004a; Pickering *et al.*, 2004b; Kuhn, 2005; Lacruz & Maude, 2005; Rohland *et al.*, 2005; Skinner & Chimimba, 2005; Strong & Goodbar, 2005; Boydston *et al.*, 2006; Skinner, 2006; Fleminger, 2006; Kerbis Peterhans & Singer, 2006; Wiesel, 2006; Pickering *et al.*, 2007; Pokines & Kerbis Peterhans, 2007; Pruetz, 2007; Backwell & d'Errico, 2008; de Ruiter *et al.*, 2008; Kuhn *et al.*, 2008; Steininger *et al.*, 2008; Backwell *et al.*, 2009; Berger *et al.*, 2009; de Ruiter *et al.*, 2009; Diedrich, 2009; Herries *et al.*, 2009; Kibii, 2009; Kuhn *et al.*, 2009; O'Regan & Menter, 2009; O'Regan & Reynolds, 2009; Avery *et al.*, 2010; Kuhn *et al.*, 2010; Wiesel, 2010; Kuhn, 2011; Kuhn *et al.*, 2011a; Pickering *et al.*, 2011; Val *et al.*, 2011; Villaluenga *et al.*, 2011). Caves also play a significant role in the natural behaviour of many species. When animals use caves, especially for the birthing and rearing of young, higher amounts of food remains (i.e. bones) are left behind. This is due to the young being kept inside of caves, as they are unable to protect themselves (East *et al.*, 1989). In addition to bringing food back for the young, mother hyaenas have been observed feeding in the natal den as opposed to the communal den (East *et al.*, 1989). Adult hyaenas will often bring food back to the dens for the young to feed upon or for the mother to feed upon to gain appropriate nutrients to milk feed her young (Sutcliffe, 1970; Kruuk, 1976; Mills & Mills, 1978; Owens & Owens, 1979; Skinner *et al.*, 1980; Brain, 1981; Mills, 1982b; East *et al.*, 1989; Skinner & van Aarde, 1991; Skinner *et al.*, 1998; Skinner & Chimimba, 2005). The size and rate of accumulation of said faunal assemblages depends upon the species doing the primary collecting, location of den, and time of collection

(Sutcliffe, 1970; Mills & Mills, 1978; Skinner *et al.*, 1980; Skinner *et al.*, 1986; Skinner & van Aarde, 1991; Brain, 1981; Kibii, 2009; Kuhn, 2011).

As not all fossil assemblages are due to collecting behaviour of certain species, there are various other scenarios that allow faunal remains to be collected in a cave environment. These scenarios are vast and can range from animals falling into a death trap, to material being washed in by fluvial action, wind action, or animal movement. Some, or all, of these actions combined can be the cause of any cave accumulation. Due to the nature of dolomite caves the entrance is opened by erosion followed by a collapse and closing of the entrance (Martini & Kavalieris, 1976; Brain, 1981; Martini & Keyser, 1989; Latham, 1999; Pickering *et al.*, 2007; McCarthy, pers. comm., 2011). This process is repeated over time giving many opportunities for different kinds of accumulations to form. This means that accumulations can be derived from more than one source and often times this can be seen in the stratigraphy of the cave (Maguire *et al.*, 1980; Brain, 1981; Berger, 1993; Berger & Tobias, 1994; Avery *et al.*, 2001; Lacruz *et al.*, 2002; d'Errico & Backwell, 2003; Crawford *et al.*, 2004; Pickering *et al.*, 2007; de Ruiter *et al.*, 2008; de Ruiter *et al.*, 2009). What can be seen is that there are different breccias within cave accumulations that relate to different periods of accumulation (Maguire *et al.*, 1980; Brain, 1981; Berger, 1993; Berger & Tobias, 1994; Avery *et al.*, 2001; Lacruz *et al.*, 2002; d'Errico & Backwell, 2003; Crawford *et al.*, 2004; Pickering *et al.*, 2007; de Ruiter *et al.*, 2008; de Ruiter *et al.*, 2009), giving more than one animal or generation of animals the opportunity to use said caves.

When using a fossil accumulation to derive knowledge about the past, how the accumulation was formed is one of the most relevant things to explore. Determining the accumulator and/or modifier and also how an accumulation was made and/or modified (death trap, carnivores, porcupines, water action, wind action, animal movement, or trampling) can yield critical insight into the past landscape of the area. The huge time periods given for fossil accumulations exhibit how long some of the caves in the Cradle of Humankind have been accessible to animals, and the collecting and/or modifying of faunal remains. Some examples of how long some cave sites have been accumulating (with periods being open and closed to exposure): 567,000 years for Gladysvale Internal Deposits (Lacruz *et al.*, 2002; Pickering *et al.*, 2007), 130,000 years for Gladysvale External Deposits (Lacruz *et al.*, 2002; Pickering *et al.*, 2007), 24,800 years for Plovers Lake (de Ruiter *et al.*, 2008), 100,000 years for Kromdraai (Herries *et al.*, 2009), 400,000 years for Makapansgat Limeworks Member 3 (Crawford *et al.*, 2004), 800,000 years for

Swartkrans (Avery, 2001; d'Errico & Backwell, 2003), 1.8 million years for Sterkfontein Members 1 through 5 (Avery, 2001; Pickering *et al.*, 2006), and 100,000 years for Cooper's Cave D accumulations (de Ruiter *et al.*, 2009), all of these sites, except Makapansgat, are located in the Cradle of Humankind.

The caves in the Cradle of Humankind have been studied for many years, and accumulators and/or modifiers of faunal remains have been speculated for many of these sites based on remains, carnivore/ungulate ratios, preferred prey, and coprolites (Maguire *et al.*, 1980; Brain, 1981; de Ruiter & Berger, 2000; Lacruz *et al.*, 2002; Pickering *et al.*, 2004b; de Ruiter *et al.*, 2008; Backwell *et al.*, 2009; Berger *et al.*, 2009).

Gladysvale cave, located on the Malapa Nature Reserve, was a lime-mining site for a short period in the early 20th century and was excavated intermittently until 1988 when long-term and extensive excavations began (Berger & Tobias, 1994). Deposits at Gladysvale like the Gladysvale External Deposits and the Gladysvale Internal Deposits, are thought to range from ~570 to 700 kya and ~7 to 570 kya respectively, and include fossils that have been attributed to the accumulations of porcupines and carnivores (Lacruz *et al.*, 2002; Pickering *et al.*, 2007). The Gladysvale Internal Deposits are located inside the cave close to the entrance, and the Gladysvale External Deposits are the deroofed section outside of the entrance to the cave (Lacruz *et al.*, 2002; Pickering *et al.*, 2007).

Cooper's Cave D has a wide range of species identified in the fossil assemblage, and was originally believed to be aged between 1.6 and 1.9 mya based on biostratigraphy, and the correlation of faunal remains with sites of known ages (Berger *et al.*, 2003; Steininger *et al.*, 2008; de Ruiter *et al.*, 2009; Val *et al.*, 2011). Further studies indicate that this accumulation was formed between 1.4 and 1.5 mya (de Ruiter *et al.*, 2009), a time period of 100,000 years. The examination of remains has led researchers to believe that based on carnivore/ungulate ratios and high quantities of smaller carnivores that this cave accumulation was mostly likely made by hyaenas, although not exclusively (de Ruiter *et al.*, 2009).

Plovers Lake is a Middle Stone Age site, aged between 63.9-88.7 kya (de Ruiter *et al.*, 2008). Faunal material from the site has both cut marked specimens and specimens that appear to have been modified by carnivores (Brophy *et al.*, 2006). Despite evidence of human activity, this site is believed to have been mainly a brown hyaena (*Parahyaena brunnea*) accumulation (de Ruiter *et al.*, 2008). These conclusions have

been made due to the presence of coprolites, carnivore damaged bones, and the high frequency of carnivore remains found within the assemblage (de Ruiter *et al.*, 2008).

Kromdraai is reported to be 1.7-1.8 mya (Herries *et al.*, 2009), which like Cooper's Cave D gives a range of 100,000 years to accumulate. Kromdraai is considered to be a hyaenid and felid accumulation based on the live weight of bovid remains found and the carnivore/ungulate ratio (Brain, 1981).

Makapansgat Limeworks Member 3, often referred to as the Grey Breccia, is reported to be 2.8-3.2 mya (Crawford *et al.*, 2004), 400,000 years, and mainly believed to be a hyaena accumulation; this is based on observations that the damaged specimens collected from Makapansgat resembled the damage found on bones from modern hyaena dens (Maguire *et al*., 1980).

Swartkrans accumulations have been reported at 1-1.8 mya (Avery, 2001; d'Errico & Backwell, 2003) and were hypothesized by Brain (1981) to have been accumulated by both hyaenids and felids. This is based on the remains of at least 14 hyaenas and the high proportion of hyracoid skulls (which are usually thought to be indicative of leopards (*Panthera pardus*)) (Brain, 1981). Based on carnivore/ungulate ratios, carnivore damage, tooth marks, and hyracoid skulls it is believed that Member 1 was likely made by felids and hyaenids (Brain, 1981). Based on similar criterion Swartkrans Member 2 was likely also accumulated by leopards, human hunters, and possibly brown hyaenas (Vrba, 1975; Vrba, 1976; Brain, 1981).

The cave system at Sterkfontein is divided into six members, each representing a different time period. The overall age of the cave accumulations (Members 1-5) is between 1 and 2.8 mya (Avery, 2001; Pickering *et al.*, 2006), Member 6 being much younger at ~100,000 kya. With one of the largest collections of hominid remains (Pickering *et al.*, 2004a) Sterkfontein Cave has given researchers much in terms of faunal and palaeoecological histories (Avery, 2001). It has been hypothesized, based on tooth marks, by Brain (1981) and Vrba (1976) that Member 4 was made by a large felid. Further work by Pickering *et al*. (2004a) also suggests that carnivores were involved in the accumulation. However for Pickering *et al.* (2004a) this evidence is not strong enough to point to a specific carnivore as the principal accumulator.

Lastly mentioned is the Malapa site, which appears to have been formed in a very short period of time and is the only site mentioned here that is considered a death trap. Malapa is believed to be made by the dissolution of dolomite, which led to an underground cavern that was at some period an open hole exposed at the surface where animals could fall into the cave and perish (Dirks *et al.*, 2010). This site has been dated using Uranium-Lead and palaeomagnetic techniques to reach an age of 1.977 mya (Kuhn *et al.*, 2011a; Pickering *et al.*, 2011). The fossils recovered from this site show no evidence of carnivore damage (Dirks *et al.*, 2010), which indicates that fauna was not scavenged upon post deposition.

1.2 Cave use

Although cave accumulations are often attributed to just a handful of animals, there are many animals that use caves for an array of reasons. Whether it is called a cave, a den, a lair, a burrow or a warren, these structures are very important to the species' that use them. Some of the most well preserved fossils and evidence of past life have come from caves sites, this is due to the fact that they can provide a place for fossilization to occur without being constantly exposed to the elements. Caves are however not places that are as easily observable as the open air; caves are protected and thus what animals do while they are inside these underground shelters is not as well known. For example honey badgers use small burrows to eat their prey, often taking larger prey (that will take longer to consume) below ground to protect it from being scavenged (Begg, 2001). This behaviour also prevents researchers from observing how the honey badgers affect the remains of larger prey (Begg, 2001). There is a great deal of archaeological and palaeontological research showing evidence that animals, including hominids, have used caves for millions of years in the Cradle of Humankind and South Africa (Dart, 1954; Maguire *et al.*, 1980; Brain, 1981; Berger, 1993; Berger & Tobias, 1994; Berger *et al.*, 1995; Avery, 2001; Berger *et al.*, 2002; Hilton-Barber & Berger, 2002; Berger *et al.*, 2003; Pickering *et al.*, 2007; Steininger *et al.*, 2008; Berger *et al.*, 2009; Herries *et al.*, 2009; O'Regan & Menter, 2009; O'Regan & Reynolds, 2009; Avery *et al.*, 2010). Cave sites in South Africa such as Cooper's Cave (Berger *et al.*, 1995; Berger *et al.*, 2003; Steininger *et al.*, 2008; de Ruiter *et al.*, 2009; Herries *et al.*, 2009; O'Regan & Reynolds, 2009), Drimolen (Herries *et al.*, 2009; O'Regan & Menter, 2009), Sterkfontein (Brain, 1981; Avery, 2001; Berger *et al.*, 2002; Herries *et al.*, 2009; O'Regan & Reynolds, 2009), Kromdraai (Brain, 1981; Herries *et al.*, 2009), Gladysvale (Berger, 1993; Berger & Tobias, 1994; Pickering *et al.*, 2007; Berger *et al.*, 2009; Herries *et al.*, 2009), Swartkrans (Brain, 1981; Avery, 2001; Herries *et al.*, 2009), and Makapansgat (Dart, 1954; Maguire *et al.,* 1980; Herries *et al.*, 2009) just to name a few caves that have been discovered and have yielded evidence of past use.

1.2.1 Wildlife in caves

Organisms acclimate to their environments, often using caves and whatever else is available to the greatest advantage for their survival. As caves are often part of said environments many organisms have learned to take advantage of caves for many purposes (Sutcliffe, 1970; Kruuk, 1972a; Winkler & Adams, 1972; Cumming, 1975; Brain, 1981; Straus,

1982; Skinner *et al.*, 1986; Skinner & van Aarde, 1991; Doncaster & Woodroffe, 1993; Jagnow, 1998; Latham, 1999; de Ruiter & Berger, 2000; Begg, 2001; Barrett *et al.*, 2004; Kuhn, 2005; Lacruz & Maude, 2005; Rohland *et al.*, 2005; Skinner & Chimimba, 2005; Boydston *et al.*, 2006; Wiesel, 2006; Pokines & Kerbis Peterhans, 2007; Pruetz, 2007; Backwell *et al.*, 2009; Berger *et al.*, 2009; Diedrich, 2009; Herries *et al.*, 2009). Various reasons for cave usage include: hibernaculums (Winkler & Adams, 1972; Stiner *et al.*, 1996; Jagnow, 1998; Villaluenga *et al.*, 2011), latrines (Kuhn, 2005; Bryant & Dean, 2006; Backwell *et al.*, 2009; Berger *et al.*, 2009), places to cache food (de Ruiter & Berger, 2000; Wiesel, 2006; Pokines & Kerbis Peterhans, 2006), places to feed (Brain, 1981; East *et al.*, 1989), thermoregulation (Haim *et al.*, 1992; Jagnow, 1998; Barrett *et al.*, 2004; Pruetz, 2007; Villaluenga *et al.*, 2011), and as maternity dens (Sutcliffe, 1970; Kruuk, 1972a; Kruuk, 1976; Mills & Mills, 1978; Owens & Owens, 1979; Skinner *et al.*, 1980; Brain, 1981; Mills, 1982b; East *et al.*, 1989; Skinner & van Aarde, 1991; Holekamp *et al.*, 1996; Skinner *et al.*, 1998; Sunquist & Sunquist, 2002; Begg, 2005a; Skinner & Chimimba, 2005; Boydston *et al.*, 2006; Kuhn, observations, 2006).

When caves are explored evidence of many fauna other than hominids occurring has frequently been found, whether in recent years or millions of years ago. Of the numerous animals that utilize caves, a few are listed here: bats (Winkler & Adams, 1972; Jagnow, 1998; Latham, 1999; Barrett *et al.*, 2004), hyaenas (Sutcliffe, 1970; Skinner & van Aarde, 1991; Rohland *et al.*, 2005; Boydston *et al.*, 2006; Wiesel, 2006; Pokines & Kerbis Peterhans, 2007; Backwell *et al.*, 2009; Berger *et al.*, 2009), chimpanzees (*Pan troglodytes verus*) (Pruetz, 2007), hominids (Pickering *et al.*, 2007; Herries *et al.*, 2009), Chacma baboons (*Papio hamadryas ursinus)* (Barrett *et al.*, 2004), leopards (*Panthera pardus*) (de Ruiter & Berger, 2000), warthogs (*Phacochoerus africanus*) (Kruuk, 1972b; Cumming, 1975; Skinner *et al.*, 1986), porcupines (*Hystrix africaeaustralis*) (Brain, 1981), badgers (Doncaster & Woodroffe, 1993; Begg, 2001), large-spotted genets (*Genetta tigrina*) (Skinner & Chimimba, 2005), and black-backed jackals (*Canis mesomelas*) (Brain, 1981; Wiesel, 2006; Pokines & Kerbis Peterhans, 2007). These animals use caves for a variety of reasons listed previously, and at times animals will use caves for more than one of these reasons.

Bats have been known to use caves as a winter hibernaculum in the Torgac Cave of New Mexico, USA (Jagnow, 1998). Aside from just a winter hibernaculum, bats will use caves year round, and can often be

prey to animals looking for an easy target (Winkler & Adams, 1972). It is believed that now extinct cave bears (*Ursus* sp.) also used caves as winter hibernaculums (Stiner *et al.*, 1996; Villaluenga *et al.*, 2011). Caves provide shelter for animals from the cold during the winter months when they hibernate; many caves in France still have evidence of use by cave bears (*Ursus spelaeus)* from the Neolithic.

It has been reported that brown hyaenas have used caves as latrines at Gladysvale Cave (Backwell *et al.*, 2009; Berger *et al.*, 2009). Striped hyaenas (*Hyaena hyaena*) have also been reported to make latrines inside of caves different than the sections that are used for feeding, said latrine areas are distinctly devoid of faunal remains (Kuhn, 2005). There is evidence of human usage of caves as latrines throughout the modern world (Bryant & Dean, 2006). Coprolites preserved in these cave latrines can be used to run analyses that can help to determine many things about the past such as the date of the deposit, what the animals diet consisted of, and pollen concentrations (Bryant & Dean, 2006; Berger *et al.*, 2009), hair has also been identified in coprolites (Backwell *et al.*, 2009).

Caves are also used by animals to cache food, examples of caching and feeding in caves can be observed throughout Africa; in the Cradle of Humankind at the Malapa Nature Reserve a leopard was reported to have used caves to cache food (de Ruiter & Berger, 2000). This behaviour has also been observed in spotted hyaenas in Kenya (Pokines & Kerbis Peterhans, 2007), and the brown hyaena on the coast of Namibia (Wiesel, 2006). Aside from caching food, animals will feed inside the caves and use them as a shelter from external elements, such as heat, cold, rain, shelter from predators (Winkler & Adams, 1972; Cumming, 1975; Skinner *et al.*, 1980; Brain, 1981; Skinner & van Aarde, 1991; Haim *et al.*, 1992; Stiner *et al.*, 1996; Jagnow, 1998; Skinner *et al.*, 1998; de Ruiter & Berger, 2000; Barrett *et al.*, 2004; Begg *et al.*, 2005a; Skinner & Chimimba, 2005; Boydston *et al.*, 2006; Wiesel, 2006; Kuhn, 2006; Pokines & Kerbis Peterhans, 2007; Pruetz, 2007; Villaluenga *et al.*, 2011), and of special interest to taphonomic studies is the use of caves as maternity dens (Sutcliffe, 1970; Kruuk, 1972a; Kruuk, 1976; Mills & Mills, 1978; Owens & Owens, 1979; Skinner *et al.*, 1980; Brain, 1981; Mills, 1982b; East *et al.*, 1989; Skinner & van Aarde, 1991; Holekamp *et al.*, 1996; Skinner *et al.*, 1998; Sunquist & Sunquist, 2002; Begg *et al.*, 2005a; Skinner & Chimimba, 2005; Boydston *et al.*, 2006; Kuhn pers. comm., 2011).

Research done on a Chacma baboon population in the southern Cape, South Africa, has shown these primates using caves to thermoregulate

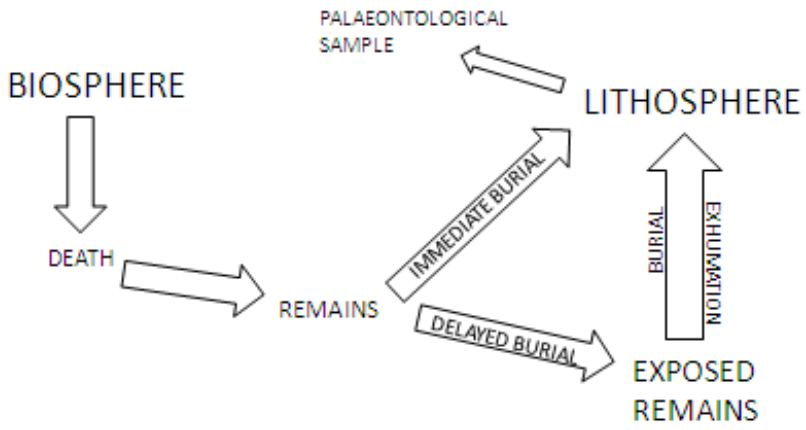
when the external temperatures became too warm (Barrett *et al.*, 2004). Likewise in Fongoli, Senegal, savanna chimpanzees (*Pan troglodytes verus*) use caves to thermoregulate for similar reasons (Pruetz, 2007). Temperatures in caves remain almost constant year round and are a good place to go to find refuge from the elements, this is also what makes caves a stable environment for animals such as bats and bears to hibernate in the winter (Jagnow, 1998; Villaluenga *et al.*, 2011). Newborn porcupines are sensitive to heat loss and are kept huddled in burrows to prevent this from happening (Haim *et al.*, 1992).

Boydston *et al.* (2006) discusses the intricate use of natal dens vs. communal dens in the spotted hyaenas of the Masai Mara National Reserve, Kenya. Aside from hyaenas (Sutcliffe, 1970; Kruuk, 1976; Mills & Mills, 1978; Owens & Owens, 1979; Skinner *et al.*, 1980; Brain, 1981; Mills, 1982b; East *et al.*, 1989; Skinner & van Aarde, 1991; Holekamp *et al.*, 1996; Skinner *et al.*, 1998; Skinner & Chimimba, 2005; Boydston *et al.*, 2006) honey badger (Begg *et al.*, 2005a), black-backed jackal (Kuhn, observations 2006), leopard, (Skinner & Chimimba, 2005), porcupine (Haim *et al.*, 1992), caracal (Sunquist & Sunquist, 2002), and large-spotted genet also utilize caves as a place to birth and rear their young (Skinner & Chimimba, 2005).

1.3 Taphonomy

Taphonomy is "the study of the transition, in all details, of organics from the biosphere into the lithosphere or geological record"- Lyman (1994a, p.1). The word taphonomy stems from the Greek words for burial (*taphos*) and laws (*nomos*). It is with this in mind that any process occurring on a bone after death is the act of a taphonomic agent, therefore any carnivore is by nature a potential if not justified taphonomic agent. When fossil accumulations are examined the whole picture is almost never what is seen, what is seen is just a small amount of what is left from the bigger picture.

Figure 1.1: Pathway from biosphere to lithosphere



Adapted from Behrensmeyer & Kidwell, 1985, p. 108

"Only a small part of what once existed was buried in the ground; only a part of what was buried has escaped the destroying hand of time; of this part all has not yet come to light again; and we all know only too well how little of what has come to light has been of service for our science" (Montelius, 1888, p.5 and quoted by Lyman, 1994a, p. 1). This quote and interpretations by Behrensmeyer & Kidwell (1985) (see Figure 1.1) show us that through the many processes leading to what will eventually be part of a palaeontological sample many things are lost and only a very small fraction remains for examination by researchers. When fossils are found it is possible that researchers are only seeing a sample that remains from a

specific climate and area that favours preservation (Behrensmeyer & Kidwell, 1985).

The study of taphonomy is extremely beneficial because it is the basis of what palaeontologists and archaeologists use to evaluate the past in regards to fossil remains (Behrensmeyer & Kidwell, 1985; Lyman, 1994a; Behrensmeyer *et al.*, 2000). As stated above, all that remains is the remnants of what once was, therefore, the better the processes of taphonomy is understood the better those remains can aid in the evaluation of the assemblages that are found. Taphonomy begins with the deposition of bones; which is the placement of bones, and can occur via many channels including water, wind, and faunal deposition (Lyman, 1994a). In all three of these cases the deposition refers to where and/or how the bones are deposited after death, many times not involving burial (Lyman, 1994a). Deposition is often followed by burial, which in some cases can be the same as deposition; some examples are when an animal dies in a tunnel collapse it is deposited and simultaneously buried, when an animal is purposefully buried, when there is a natural disaster such as Pompeii when the city was quickly covered with ash from the eruption of Mt. Vesuvius (Jashemski & Meyer, 2002), or when an animal is mired in mud which can be seen at the lake found at Snowmass Village, Colorado (Johnson *et al.*, 2011). All of these types of burials can be identified with the finds of complete or nearly complete skeletons (Lyman, 1994a). Once a bone has been buried, if the circumstances are in favor of fossilization, the bone can then turn from bone to fossil (Lyman, 1994a). The third stage is diagenesis defined by Lyman (1994a) as the "chemical and physical changes that occur in animal remains as they alter from their original state and become fossilized" (p. 506). Once bone remains become fossilised all of the organic material is gone and has been replaced by inorganic minerals, this process often keeps the shape of the bone intact, in theory turning the bone into a mineralized cast of itself (Lyman, 1994a).

1.3.1 Abiotic taphonomic factors; Climate, Fluvial action, Eolian action, and Burial

Climate is also related to survivorship of fossils; science can often use evidence of bone weathering on fossils as a way to examine surface exposure of bone before fossilisation (Behrensmeyer, 1978; Lyman & Fox, 1989). Weathering is described as "the process by which the original microscopic organic and inorganic components of a bone are separated from each other and destroyed by physical and chemical agents operating on the bone *in situ*, either on the surface or within the soil zone."

(Behrensmeyer, 1978, p. 153). A wide range of bone weathering can imply that an accumulation was made over time, and not instantaneously (Behrensmeyer, 1978). Instantaneous burial can be seen at natural disaster sites, and bones found here will most likely have similar stages of weathering (Behrensmeyer, 1978), although it has also been seen that different species' bones will weather differently (Lyman, 1994a).

Like a stone polisher polishes stone, fluvial action on bone will polish, or abrade, the entire surface of the bone (Lyman, 1994a). It is also believed that the action of water will move bones and other debris from one place to another, often to the back of caves (Behrensmeyer, 1978; Behrensmeyer, 1982; Lyman, 1984; Lyman & Fox 1989; Cruz-Uribe, 1991; Chase *et al.*, 1994; Eriksson *et al.*, 1995; Farrand, 2001; Goldberg & Sherwood, 2006), however it is believed by McCarthy (pers. comm., 2011) that this movement is caused by animals moving within caves.

Eolian action is the action of wind on bone remains. It may not always be the specific action of wind on the bone, but the action of sand on the bone (Gifford, 1981; Lyman, 1994a). It is thought that wind can also move bones, especially when bones have a small enough size and density (Lyman, 1994a).

Hominids and modern humans are different than many animals due to cultural burial of their dead (Lyman, 1994a); most animals do not bury their deceased. When caching, some animals will bury their prey (Kruuk, 1972b), an example of this can be seen with the Sexton beetle (*Microphorus* sp.), which will bury rodents (Milne & Milne, 1976). However many animals that become buried are animals that already live underground, and at death are (as mentioned previously) deposited and buried simultaneously (Lyman, 1994a). This later type of burial, accidental, is most often abiotic and can be caused in caves by such things as structural collapse, and outside of caves by burial by volcanic lava or ash, and sinkholes.

1.3.2 Animal (or biotic) action

Animal action is very important in the study of taphonomy as it can translate to a better understanding of the landscape when the taphonomic agents are known. Animal movement of bones can alter them in many ways including bone orientation, dip, breakage, and marking (Lyman, 1994a; Blumenschine *et al.*, 1996; McCarthy, pers. comm., 2010). When an animal walks over bones it can change the original placement of said

bone and also affect the directionality and dip of said bone (Lyman, 1994a; McCarthy, pers. comm., 2010). It is thought that breakage of bones is more common once weathering has occurred (Lyman, 1994a, p. 380). When bones are trampled they can produce scratch marks that are more apparent than marks cause by wind or water action on bones (Lyman, 1994a). The hope of the researcher is to identify at what stage the bones were broken and what effect different stages of bone weathering, or lack thereof, have on the breakage pattern of the bone.

Other kinds of taphonomic processes that occur due to animal action include gnawing (together with tooth pit marks), crushing, partial digestion, cut marks, and movement of bones. Hyaena jaws and teeth are designed to crush bones which enable them to gain access to nutrients unavailable to other carnivores, and this action will frequently leave broken and shattered bones (Sutcliffe, 1970; Blumenschine, 1988; Lyman, 1994a; Kuhn, 2005; Kuhn *et al.,* 2009; Kuhn *et al.,* 2010; Kuhn, 2011). These are not the only animals that can cause bone breakage however, many animals including hominids, via tool use, also cause breakage patterns in bone (Sutcliffe, 1970; Blumenschine, 1988). Hyaenids and canids will regurgitate bones that they cannot digest and animals such as the wolf (*Canis lupus*) will regurgitate to feed their young (Sutcliffe, 1970; Horwitz, 1990), this can leave acid etching marks or evidence of partial digestion on bones (Sutcliffe, 1970; Horowitz, 1990; Kuhn, 2011). The process of digestion also involves the remains of food remains found in faecal matter (Horwitz, 1990). Feeding can also cause marks to be made on the bones such as tooth scores and tooth pits (Blumenschine, 1988; Kuhn, 2005; Kuhn *et al.*, 2009; Kuhn, 2011), and when an animal is eaten by hominids cut marks from tool usage are often found (Blumenschine, 1988; Pickering *et al.*, 2000; Abe *et al.*, 2002). When animals feed they will occasionally take the prey from the kill site to another site, either for caching, or to eat the food in a safer place such as a den, a tree, or some sort of ground cover (Sutcliffe, 1970; Kruuk, 1976; de Ruiter & Berger, 2000; Mills & Harvey, 2001; Wiesel, 2006; 2010; Pokines & Kerbis Peterhans, 2007). Movement of smaller bones can also happen when one animal eats the remains of another animal, thus moving its remains, as animals are not likely to return to where it ate its meal to relieve itself (Winkler & Adams, 1972).

When all of these processes (abiotic and biotic), which contribute to the sediment of a cave, are understood, the environment that existed during sedimentation can also be understood.

1.3.3 Cave taphonomy

Cave taphonomy is unique in that it happens in enclosed spaces and what is inside the cave is not exposed to surface elements. Meaning that in caves there are fewer external forces acting on remains once they have been deposited. This is because caves act as a form of protection from outside elements, which a bone left exposed would not have. For example: if a bone were to be deposited in the middle of a bushveld it would likely be trampled, exposed to the elements, and exposed to any animal that may have interest in it. In addition the process of taphonomy in a cave is significant because it is the minerals that occur in dolomitic caves and groundwater therein, that lead to the fossilization of bones at much higher rates than elsewhere in the ecosystem (Stiner *et al.*, 1996).

Many researchers believe that sediments in caves are brought in by fluvial or eolian action (Lyman, 1994a), it is less recognized that sediments would be carried in by surface movement; i.e. as animals walk and move about they also move the sediments (McCarthy, pers. comm., 2010). It is the belief of McCarthy (pers. comm., 2010) that accumulations occurring in the rear of caves are in large part due to animals walking inside of a cave and moving sediments that already exist inside of the cave, or near to the caves entrance.

All the animals observed in this project are known to use caves and are essential to examine when looking at faunal accumulations within caves.

1.4 Leopard (*Panthera pardus*)

The leopard is among the larger felids with a live weight varying between 20 kg to 90 kg (Stuart & Stuart, 2000). This cat is widely distributed throughout Africa and Asia (Brain, 1981; Mills & Harvey, 2001; Skinner & Chimimba, 2005), giving it the most extensive home range of the large felids (Mills & Harvey, 2001). Leopards have been present in Africa for the past 4.0 mya (Turner, 1990), and in the Cradle of Humankind for at least 1.977 million years (Kuhn *et al.*, 2011), making the leopard a major player in the African carnivore guild. The leopard is a nocturnal and solitary predator (Skinner & Chimimba, 2005) living in single animal territories and rarely making contact with others of its kind (Mills & Harvey, 2001). The territory of an adult female leopard varies in size from 10 km^2 to 200 km^2, and forms a mosaic that is overlaid by the larger territories of the male leopard (Mills & Harvey, 2001). Male leopards are often found to be encompassing more than one female territory, but when food is scarce female and male leopards may share the same size territory (Mills & Harvey, 2001).

The leopard has a very wide range of food sources (Mills & Harvey, 2001; Hayward *et al.*, 2006); according to Hayward *et al.* (2006) this felids diet includes over 100 prey species most often between 10 and 40 kg. Leopard prey includes many animals in this study; brown hyaena, black-backed jackal, honey badger (although these are mostly avoided due to the possibility of injury when preying on them), porcupine, warthog, kudu, sable, baboon, and vervet monkey (Hayward *et al.*, 2006). Leopards tend to be quite adept to changing their dietary behaviour in order to fit its environment (de Ruiter & Berger, 2000; Mills & Harvey, 2001), which is of great benefit to these animals during times of duress when other carnivores may feel stress based on lack of dietary needs. “Their ability to survive on virtually any form of carnivorous diet is probably what allows leopards to survive in areas long after other large bodied carnivores have been forced to move, usually in the face of human encroachment.” (de Ruiter & Berger, 2000, p. 683). Evidence of this can be seen in their largely varied diet depending on what is available to them in their surroundings with reported diets ranging from mainly fish to hyraxes or duikers (Mills & Harvey, 2001).

1.4.1 Leopards as cave users

In the Tswana language the leopard is called ‘*the spotted one of the caves’* (Cole, pers. comm., 2010) which shows this species’ well-known

affinity with caves by native peoples of Africa. For many years paleoanthropological research relating to leopards was focused on the belief that leopards used trees that hung over cave entrances to cache their prey (Brain, 1981). Today there is increasing evidence that in addition to using trees leopards are utilizing cave systems to cache food (de Ruiter & Berger, 2000), thus most likely being directly responsible for selected faunal accumulations found within cave environments.

Leopard remains have been found in cave accumulations within the Cradle of Humankind ranging in age from thousands to millions of years (Brain, 1981; Cruz-Uribe, 1991; de Ruiter & Berger, 2000; Pickering *et al.*, 2004; de Ruiter *et al.*, 2008; 2009; O'Regan & Reynolds, 2009; Werdelin & Peigné, 2010). Turner (1990) puts the leopard in Africa at ~4.0 mya and evidence from Kuhn *et al.* (2011) shows the leopard in the Cradle of Humankind at Malapa 1.977 mya. Leopard has occurred at other Cradle sites such as Swartkrans (Brain, 1981), Sterkfontein (Brain, 1981; Pickering *et al.*, 2004), Swartklip 1 and Equus (Cruz-Uribe, 1991), Kromdraai (Brain, 1981; O'Regan & Menter, 2009) and Plovers Lake (de Ruiter *et al.*, 2008).

Research conducted in 2000 by de Ruiter and Berger at the Malapa Nature Reserve was significant in recognizing leopards' use of caves. The leopard was found to use a cave on the reserve to store complete carcasses that it killed and subsequently dragged to the recesses of the cave. This study showed nearly complete skeletons, ranging from class II sized bovids (see Table 1.1) to porcupines, in the recesses of the dolomite cave (de Ruiter & Berger, 2000), again illustrating the leopards varying diet preferences.

Table 1.1 Bovid size class weights

Bovid size class	**Weight range in Kg**
Class I	4.5-19
Class II	18-84
Class III	170-299
Class IIII	367-945

Adapted from Brain, 1981

Rearing young in caves is an important time for bone accumulations to be formed since it is when food must be brought into the den in higher quantities to feed the cubs (Skinner & Chimimba, 2005). Leopard cubs are born in caves (or sheltered areas) and will suckle until around 3 months of age, but do not usually go with their mother on the hunt until approximately

nine months of age (Skinner & Chimimba, 2005). This means that for at least six months the mother is the main source of food for the young.

1.4.2 Leopard as taphonomic agent

This weight restriction, mentioned above, in preferred prey of the leopard is due to the solitary hunting of the leopard and is thought to be a measure taken to protect itself against injury from potential prey (Hayward *et al.*, 2006). The fact that leopards have such a broad range in diet also means that they have overlap with many other animals in terms of prey and are often the victims of kleptoparasitism (Caro & Stoner, 2003). This has been observed by Owens & Owens (1978) when a lone female brown hyaena chased a leopard away from its kill, an adult springbok (*Antidorcas marsupialis*), and up a tree, and then took said kill.

When looking at leopard assemblages among sub-Saharan predators the leopard has the widest range in diet amongst the felids (Hayward *et al.*, 2006). In the Western Cape Province, South Africa, observed leopard kills versus scat analysis show very different results; in East Africa most leopard kills observed by Kruuk & Turner (1967) were also of class size I or II bovids (see Table 1.2). However scat analysis done in South Africa shows that leopards prefer hyraxes to bovids (Stuart & Stuart, 1993). This indicates that, with regards to the leopard, it is not always suitable to rely on observed kills as a measure of actual kills as they vary regionally.

Skinner & Chimimba (2005) also discuss the variation in hunting times amongst leopards in different areas with a range of every 1.5 days to every 13 days. This much variation within this species makes it difficult to ascribe a specific feeding trait to said species, which is turn makes it equally as difficult to speculate the preferred prey and behaviour of leopards in the past.

Leopard teeth are designed for de-fleshing rather than for bone crushing and de-marrowing (Pickering *et al.,* 2004b) indicating that they get nutrition more from eating the flesh of their prey more than from the nutrients that are in the bones. This is very different than the bone collecting hyaenas whose teeth and jaws are more designed to gnaw on and crush bone to get nutrients from bone and marrow (Sutcliffe, 1970; Haynes, 1983; Cruz-Uribe, 1991; Binder & Van Valkenburgh, 2000; Wiesel, 2006; Tanner *et al.*, 2008).

Pickering *et al.* (2004b, p.601) state that leopards "were not major contributors of the large animal remains" from Swartkrans Member 3 due to lack of tooth pit evidence, the article also states that "leopard tooth marks on limb bone midshafts occur in low frequencies in all these modern samples" (p.601). Tooth pits may be useful in showing carnivore involvement, however tooth pit evidence can only be used to distinguish between large and small carnivores and not to determine which exact carnivore made the tooth pit on the bone (Dominguez-Rodrigo & Piqueras, 2003; Pickering *et al.*, 2004b). Tooth pit sizes will vary depending on factors such as the age of the prey, the age of the bone (if it is weathered, if it is greasy or de-fatted, etc.), the part of the bone that is being acted on (diaphysis, epiphysis), which bone it is, the bone density, the age of the carnivore acting on the bone, the sex of the carnivore, how hungry the carnivore was, in what setting it acted on the bone (was it the sole predator, or was it sharing with others, or was the animal scavenging) and how deep the tooth actually goes into the bone (which can be affected by many of the above reasons). So although tooth-pits, and other tooth marks, can indicate carnivore involvement it is very difficult to use these alone to determine the specific modifier.

1.5 Brown hyaena (*Parahyaena brunnea*)

The current study deals specifically with brown hyaenas since they are the only hyaena occurring on the Malapa Nature Reserve today, however all three extant bone-collecting hyaenas will be discussed as they are all cave users, taphonomic agents, and bone collectors. In addition all three bone-collecting hyaenas occur in the fossil record of the Cradle of Humankind (Maguire *et al.*, 1980; Brain, 1981; Pickering, 2002; Berger *et al.*, 2003; Crawford *et al.*, 2004; O'Regan & Reynolds, 2005; de Ruiter *et al.*, 2008; 2009; Dirks *et al.*, 2010; Werdelin & Peigné, 2010; Kuhn *et al.*, 2011a; Kuhn, unpublished).

There are four extant species of Hyaenidae; brown hyaena (*Parahyaena brunnea*), striped hyaena (*Hyaena hyaena*), spotted hyaena (*Crocuta crocuta*), and aardwolf (*Proteles cristatus*) (Leaky *et al.,* 1999; Skinner, 2006). Brown hyaenas, the least widely distributed of the four Hyaenidae, are found only in southern Africa (Turner, 1990; Mills & Harvey, 2001; Skinner & Chimimba, 2005; Wiesel, 2006; O'Regan & Reynolds, 2009; van der Merwe *et al.*, 2009). The home ranges of the other three extant Hyaenidae are as follows; striped hyaena home range includes southern Asia, the Middle East, India, and both northern and eastern Africa (Turner, 1990; Mills & Harvey, 2001), the spotted hyaena occurs mainly in sub-Saharan Africa (Turner, 1990; Skinner & Chimimba, 2005), and lastly aardwolf distribution is southern and eastern Africa (Turner, 1990; Skinner & Chimimba, 2005). Of the four different hyaenid species three are recognized bone collectors and modifiers, while the aardwolf is mainly an insectivore (Skinner, 2006). Brown hyaenas are thought to mostly be nocturnal and extremely shy (Mills & Mills, 1978; Mills, 1982a; Skinner & Chimimba, 2005) making them difficult to observe in much of their range. Brown hyaenas and striped hyaenas are better known for being scavengers as opposed to hunters like the spotted hyaenas (Kruuk, 1976; Skinner & Chimimba, 2005; Wiesel, 2006; Kuhn, 2005). It is also true that brown hyaenas and striped hyaenas, as with many animals, can become hunters when the necessity arises, however both of these hyaenas have very low success rates reported when hunting (Kruuk, 1976; Owens & Owens, 1978; Lacruz & Maude, 2005).

The brown hyaena has been living in Africa for over two million years (Turner, 1990), this is supported by the brown hyaena occurring in fossil accumulations from the Plio-Pleistocene cave sites of Makapansgat (Maguire *et al.*, 1980; Crawford *et al.*, 2004), Cooper's Cave (Berger *et al.*, 2003; de Ruiter *et al.*, 2009), Plovers Lake (de Ruiter *et al.*, 2008;

Werdelin & Peigné, 2010), Malapa (Dirks *et al.,* 2010, Kuhn *et al.*, 2011a), Swartkrans Member 2 and 3 (Werdelin & Peigné, 2010), Sterkfontein Member 4 (Werdelin & Peigné, 2010) and Member 5 (Pickering, 2002; Werdelin & Peigné, 2010).

1.5.1 Hyaenas as cave users

Hyaenas and their association with caves has been studied for many years (Sutcliffe, 1970; Owens & Owens, 1979; Maguire *et al.*, 1980; Brain, 1981; East *et al.*, 1989; Skinner, 1991; Villa & Bartram, 1996; Latham, 1999; Pickering, 2002; Berger *et al*., 2003; Rohland *et al.*, 2005; Kuhn, 2005; Wiesel, 2006; Boydston *et al.*, 2006; Pokines & Kerbis Peterhans, 2007; de Ruiter *et al.*, 2008; Kuhn *et al.*, 2008; Kuhn *et al.,* 2009; Berger *et al.*, 2009; Dirks *et al.*, 2010; Kuhn *et al.*, 2010; Kuhn, 2011; Kuhn *et al.*, 2011a) and are crucial to examine when looking at fossil accumulations found at cave sites. All three hyaenas, brown, striped, and spotted, are typically born and reared in dens (either caves or modified burrows) (Sutcliffe, 1970; Kruuk, 1976; Owens & Owens, 1979; East *et al.*, 1989; Knight *et al.*, 1992; Boydston *et al.*, 2006; Kuhn, 2011) spending the first eight to 12 months of life in a den (Pokines & Kerbis Peterhans, 2007). Hyaenas also use caves as latrines (Kuhn, 2005; Backwell *et al.,* 2009; Berger, 2009), as well as feeding places (Pokines & Kerbis Peterhans, 2007), shelters (Boydston *et al.*, 2006), and resting places (Wiesel, 2006). In addition, all three extant bone collecting hyaena species dens have shown evidence of varying rates of accumulation (Kuhn *et al.*, 2009).

Spotted hyaenas, striped hyaenas, and brown hyaenas will all use different kinds of dens including; cave dens, burrow dens, and artificial dens (Pokines & Kerbis Peterhans, 2007; Kuhn, pers. comm.). Cave dens support bone accumulations as the shelters protect the bones from destruction, often hyaena burrow dens are used for cubs and are not accessible to adults making accumulations there not as prevalent (Pokines & Kerbis Peterhans, 2007). The opposite can be seen as well, when studying accumulations in Jordan; Kuhn (2005) found that a burrow den had the second largest accumulation of the five dens studied. Therefore not only does the length of time these caves persist give more time for accumulations to form, but also gives more species a chance to occupy any given cave.

Communal denning and its importance has been observed in brown hyaenas by Owens & Owens (1979) and Wiesel (2006), where they report on the benefits of this communal behaviour. Examples of benefits

discussed by Owens & Owens (1979) and Wiesel (2006) were food provision, protection, and developing social ties as most social interactions between brown hyaenas appear to occur at den sites. These social ties are valuable to the young as the social behaviour of the brown hyaena allows for the care of the young by all clan members (Owens & Owens, 1979; Mills, 1982b). It has been observed that the communal dens do not include newborn brown hyaenas, and that they are initially kept in isolated natal dens before being moved to the communal dens (Owens & Owens, 1979). This type of den structure has been observed in spotted hyaena clans as well (East *et al.*, 1989; Holekamp *et al.*, 1997a; Boydston *et al.*, 2006), where spotted hyaena newborns spend the first one to five weeks of life in natal dens before being moved to the communal den (Kruuk, 1972a). It is at the communal den where young will stay until they start to leave the den at eight to 12 months in spotted hyaenas (Boydston *et al.*, 2006) and 14-20 months in brown hyaenas (Owens & Owens, 1979).

Understanding the den use patterns and the behaviour of hyaenas when there are young present is beneficial when examining the fossil record. All three bone-accumulating hyaenas are known to bring food back to the den for their young or to nourish the mother, often increasing the rate of accumulation (Sutcliffe, 1970; Kruuk, 1976; Mills & Mills, 1978; Owens & Owens, 1979; Skinner *et al.*, 1980; Brain, 1981; Mills, 1982b; East *et al.*, 1989; Skinner & van Aarde, 1991; Skinner *et al.*, 1998; Skinner & Chimimba, 2005). The increased rate of accumulation in maternity dens is due to the fact that not only are adult hyaenas feeding within the cave, but young hyaenas are feeding there as well. Juvenile spotted hyaenas leave different marks on bone than adult spotted hyaenas because they still have their deciduous teeth (Sutcliffe, 1970). The teeth of young animals will always leave different marks on bones, as all mammal young begin with deciduous dentition. Research done by Mills & Mills (1978) shows that brown hyaena cubs are fed similar diets to the adults, but with increased instances of insects and small mammals. All members of brown hyaena clans participate in feeding the young, as both males and females without cubs have been observed bringing food to the den (Owens & Owens, 1979; Mills, 1982b). Female spotted hyaenas have been observed bringing food back to the birth den, which they ate themselves, as the cubs were still milk fed at the time (East *et al.*, 1989). The pattern is that more food is brought back to the den when there are young present, regardless of whether the food is for the adult mother, or for the young (Sutcliffe, 1970; Kruuk, 1976; Mills & Mills, 1978; Owens & Owens, 1979; Skinner *et al.*, 1980; Brain, 1981; Mills, 1982b; East *et al.*, 1989; Skinner & van Aarde, 1991; Skinner *et al.*, 1998; Skinner & Chimimba, 2005).

This is not the only difference between brown hyaenas and spotted hyaenas. Brown hyaenas are known to suckle cubs other than their own (Owens & Owens, 1979), while spotted hyaenas have only rarely been reported exhibiting this behavior in times of duress or when something has happened to the genetic mother (Kruuk, 1972a; Knight *et al.*, 1992). This can also be attributed to the condition that spotted hyaena cubs are highly dependent on milk (Kruuk, 1972a; Holekamp *et al.*, 1997b) and thus sharing milk with cubs that are not genetically related can be a burden on the mother. Although brown hyaena cubs are raised on a milk diet, the nutritional value of the milk is poor in comparison to the spotted hyaena, thus the cubs are supplemented with food brought back to the dens by adults (Brain, 1981; Skinner & van Aarde, 1991; Skinner *et al.*, 1998; Skinner & Chimimba, 2005). It is due to this behaviour that the rate of bone accumulation in brown hyaena dens is often higher than that of in spotted hyaenas dens.

Carnivores tend to use caves with multiple entrances to be able to escape if necessary (Owens & Owens, 1979; East *et al.*, 1989; Skinner *et al.*, 1996; Kuhn, pers. comm., 2010). Skinner *et al.* (1986) mention that spotted hyaena dens often have more than one entrance, where East *et al.* (1989) refer to the natal dens of spotted hyaenas also having more than one entrance. Multiple entrances have also been observed by Owens & Owens (1979) with regards to a brown hyaena den in the central Kalahari Desert. It has also been noted by Kuhn (pers. comm., 2010) that carnivores tend to prefer two or more entrances at caves.

1.5.2 Hyaena as taphonomic agents

It was once thought that hyaenas could not have been responsible for fossil bone accumulations (Dart, 1954). However, today hyaenas are well known accumulators of bone as well as taphonomic agents (Sutcliffe, 1970; Mills & Mills, 1978; Owens & Owens, 1978; Owens & Owens, 1979; Skinner *et al.*, 1980; Maguire *et al.*, 1980; Brain, 1981; Skinner *et al.*, 1986; Skinner & van Aarde, 1991; Skinner *et al.*, 1998; Burgener & Gusset, 2003; Kuhn, 2005; Skinner & Chimimba, 2005; Skinner, 2006; Wiesel, 2006; Pokines & Kerbis Peterhans, 2007; Kuhn *et al.*, 2009; Kuhn *et al.*, 2010; Kuhn, 2011). Hyaenas are known to leave behind signatures like crushed bones (Sutcliffe, 1970), tooth marks (Haynes, 1983; Selvaggio, 1994; Selvaggio & Wilder, 2001; Faith *et al.*, 2007; Pokines & Kerbis Peterhans, 2007; Villa *et al.*, 2009), high frequencies of gnaw marks (Sutcliffe, 1970; Haynes, 1983; Villa & Bartram, 1996; Pokines &

Kerbis Peterhans, 2007), bone fragmentation (Villa & Bartram, 1996), and partially digested bone (Sutcliffe, 1970; Cruz-Uribe, 1991; Villa & Bartram, 1996; Pokines & Kerbis Peterhans, 2007). Brown hyaenas are typically opportunistic scavengers (Mills & Mills, 1978; Mills, 1982a; Mills, 1982b; Mills & Harvey, 2001; Lacruz & Maude, 2005) and thus collect many different taxa from the landscape often taking parts back to their den to feed. When meat is unavailable the hyaena will scavenge from carcasses left by other carnivores often preferring bones that have the most nutritional value such as the pelvis, vertebrae and ribs (Kruuk, 1972a; Bearder, 1977; Marean *et al.*, 1992, Faith *et al.*, 2007). Due to this often non-selective scavenging it has been suggested that brown hyaena accumulations are a good representation of the local fauna (Lacruz & Maude, 2005). Currently researchers are finding it is more difficult to analyze carnivore tooth marks, and specifically hyaenas gnaw marks, than previously hypothesized (Faith *et al.*, 2007; Kuhn *et al.*, 2009; Kuhn, 2011). The variation in tooth mark frequencies within the family Hyaenidae show that one hyaena species influence on a given faunal assemblage may be different than that of another species (extant or extinct) on bone, and that there may even be variation within a species (Kuhn *et al.*, 2009; Kuhn, 2011).

It is important to examine the differences and similarities between the hyaenid species, because it is the differences between the species that make the identification of the taphonomic agent in an assemblage more accurate. The more efficient hunting by the spotted hyaena may lie with the fact that this species of hyaena live in more structured social groups and thus hunt in said groups (Kruuk, 1972a), making hunting easier as there is less risk of injury. When speaking of the brown hyaena “Group sociality is elastic in that members may spend considerable periods foraging solitarily while meeting frequently to greet and otherwise reinforce social ties, or they may scavenge communally.” (Owens & Owens, 1978, p. 114). So although the brown hyaena does hunt it does so solitarily, and successful attempts observed by Owens & Owens (1978) were only 13.7% of total observed attempts.

As dry and arid weather can cause hyaenas, and many other animals, to be more pressed for food it is important that they are able find ways to acquire nutrients from whatever source is available. In Binder & Van Valkenburgh’s (2000) study, as well as Sutcliffe’s (1970), bone gnawing and crushing by the spotted hyaena is discussed, but the practice of gnawing and modifying bone is common amongst all three extant hyaenas that modify bones (Mills & Harvey, 2001; Kuhn *et al.*, 2009; Kuhn, 2011).

In a study of captive spotted hyaenas, ribs and vertebrae were often consumed first, as these bones are greasy and therefore hold the most nutrients (Marean *et al.*, 1992). Hyaena jaws and dentition have evolved in such a way that when necessary they can use their bite force to procure nutrients from the bones of their prey as well as flesh (Sutcliffe, 1970; Haynes, 1983; Binder & Van Valkenburgh, 2000; Tanner *et al.*, 2008). When bones have been stripped of flesh, cracking open the bone to obtain nutrients from the marrow and bone itself become essential to the survival of the non-hunting bone accumulating hyaenas.

It is not always the case that the hyaena is left with only bones, they often scavenge from kills with flesh still remaining (Owens & Owens, 1978). Food caching is a practice done by many animals including the leopard (de Ruiter & Berger, 2000) and while coastal brown hyaenas have a tendency to cache food, it is not known if they return to their caches afterwards (Wiesel, 2006). Elsewhere brown hyaena caching practices have been observed to be more primitive than their close relatives (Kruuk, 1976), yet despite this clumsy storing of food black-backed jackals in Namibia have not been observed stealing food from hyaena caches (Wiesel, 2006). The reason for the black-backed jackal ignoring hyaena caches is unclear, however it is possible that they do not steal from hyaena caches because there is such an abundance of the Cape fur seal (*Arctocephalus pusillus pusillus*) from which they can prey on (Wiesel, 2006).

1.6 Honey badger or ratel (*Mellivora capensis*)

Honey badgers are part of the family Mustelidae, and they can range in size from 6-12 kg, falling into the category of a medium sized predator (Begg, 2001). The honey badger distribution is quite large, encompassing much of Africa and extending into the Middle East and India (Begg *et al.*, 2005a; Skinner & Chimimba, 2005). This mustelid can be found inhabiting almost any environment from forests and mountains, to deserts, savannas, and woodlands and are often active during the twilight hours of dusk and dawn (Caro & Stoner, 2003). The honey badger is characterized by its body colouring, black with a grey and white stripe down its back (Begg, 2001).

There has not been an abundant amount of research done on honey badgers to date, what work there is includes Kruuk & Mills (1983) and more recently by C. and K. Begg (Begg, 2001; Begg, *et al.,* 2003a; Begg, *et al.,* 2003b; Begg, *et al.,* 2005a; Begg, *et al.,* 2005b) and all take place in southern Africa. Honey badgers are foragers and dig for their food using their strong claws, they are mainly carnivorous except for tsama melons, which is believed are eaten for their high water content (Begg, 2001). A consistent intake of food throughout the year requires this animals diet to vary depending on the season (Skinner & Chimimba, 2005).

The honey badgers strength can be seen in its destruction of honeybee hives, and they have been sought after by beekeepers for destroying their livelihood (Begg, 2001; Skinner & Chimimba, 2005). Their knife like claws can easily penetrate a beehive, so people have had to develop different ways of storing hives, and it is these knife-like claws and strength that make the honey badger a formidable threat to other animals and is not a common prey item (Begg, 2001). These claws may also produce their own taphonomic signatures on the bones of honey badger prey.

The honey badger is unlike the European badger (*Meles meles*) (Kruuk & Mills, 1983) in its den use patterns, as the European badger will return to the same den and the honey badger, much like the American badger (*Taxidea taxus*), changes dens often if not every day (Sargeant & Warner, 1972; Kruuk & Mills, 1983; Begg *et al.*, 2005a). Honey badgers also occupy a much greater area than the American badger, in some cases 35 times larger than the average American badgers home range (Begg *et al.*, 2005a). In fact, aside from the wolverine (*Gulo gulo*), the home range of the honey badger is one of the largest of the mustelid family (Begg *et al.*, 2005a).

1.6.1 Honey badgers as cave users

The honey badger is mentioned in the fossil record at the early cave sites of Swartklip 1 (Cruz-Uribe, 1991; Werdelin & Peigné, 2010) and Plovers Lake (de Ruiter *et al.*, 2008; Werdelin & Peigné, 2010). Like hyaenas, honey badgers use caves as natal or breeding dens and the young do not surface from the den until three months of age when they are weaned from the mother and begin foraging (Begg *et al.*, 2005b). The young remain with the mother for the first 12-16 months of life (Begg *et al.*, 2005b; Skinner & Chimimba, 2005). Unlike the hyaena, the honey badger will continue to regularly change dens when there are young, but often only every three days instead of everyday (Begg *et al.*, 2005a).

These mustelids will use dug out dens or holes that they have dug themselves or reuse holes that have been dug by another species and will then adapt them to suit their needs (Begg, 2001; Skinner & Chimimba, 2005). Honey badgers have been noted to dig a new den each day and rarely reuse the same den (Kruuk & Mills, 1983, Minta *et al.*, 1992), unless, as mentioned above, there are cubs in the den (Begg *et al.*, 2005a), which has implications for the way they may or may not share dens with other taxa.

1.6.2 Honey badger as taphonomic agent

European badgers in Scotland are known to scavenge on sheep carcasses (Hewson & Kolb, 1976; Hewson, 1984), but the evidence for the honey badger as a taphonomic agent is limited at best. Although it has not been observed in published studies that the honey badger modifies bones, they are known carnivores (Kruuk & Mills, 1983; Caro & Stoner, 2003; Begg *et al.*, 2005a; Begg *et al.*, 2005b; Skinner & Chimimba, 2005) and as such are in contact with the bones of their prey. The analysis of the honey badger diet done on faecal remains, includes rodents, reptiles, small antelope, and water mongoose, (Kruuk & Mills, 1983) indicating that there are bone remains in their faeces, which shows that they are essentially working on the bones themselves. According to Begg (2001) the larger prey of the honey badger is often eaten underground, so it is hard to know what is left of the prey. Food can be a limiting resource for honey badgers, which may in turn push them to scavenge and possibly modify bones to get to the nutrients (Begg *et al.*, 2005b), much like scavenging hyaenas.

1.7 Warthog (*Phacochoerus africanus*)

Warthogs have lived in South Africa from at least 1.8 million years ago to the present as evidenced by deposits such as Swartkrans, Kromdraai and Gladysvale (Hilton-Barber & Berger, 2002). This suid is distributed in sub-Saharan Africa and its habitat consists of open woodlands and bushlands as well as dry African savannah grasslands (Cumming, 1975; Skinner & Chimimba, 2005). The warthog is primarily omnivorous and can be found active during the day, often retreating to caves after sun down (Cumming, 1975).

1.7.1 Warthogs as cave users

In a pilot study that took place in 2008 and 2009 (L. Berger & B. Kuhn) on the Malapa Nature Reserve warthogs were documented in and around numerous caves. Kruuk (1972b) observed a warthog exiting a hole and Skinner *et al.* (1986) observed warthogs using a culvert (a passageway that allows water to pass beneath things such as roads and railways). The use of caves by warthogs has been documented for many years (Kruuk, 1972b; Cumming, 1975; Skinner *et al.*, 1986). Cumming (1975) has done work involving warthogs and caves, what he often refers to as holes, and observed that holes are rather important to warthogs as they provide many different things such as sleeping, birthing, thermoregulation, and protection from predators. Warthog remains have been found at many caves in South Africa including Equus Cave (Cruz-Uribe, 1991), Plovers Lake (de Ruiter *et al.*, 2008) and the Boomplaas Stone Age cave site (Klein, 1978), with extinct suid remains also found throughout many South African caves (Herries *et al.,* 2009). Although there is evidence of warthog in caves since at least the Pleistocene (Cruz-Uribe, 1991) it is not clear if they were cave users or if they were brought into the caves by predators. It has been thought that hunting by spotted hyaenas (Holekamp *et al.*, 1997b) and leopards (Hayward *et al.*, 2006) could very well explain the occurrence of warthogs in palaeontological cave sites. However there is evidence of warthog occupation of inactive hyaena dens in the Masai Mara National Reserve in Kenya (Boydston *et al.*, 2006; Pokines & Kerbis Peterhans, 2007), along with other modern cave usage (Kruuk, 1972b; Cumming, 1975; Skinner *et al.*, 1986).

1.7.2 Warthogs as taphonomic agents

Suids have long been underestimated as bone modifiers, and little research has been done to test this theory. Dominguez-Solera &

Dominguez-Rodrigo did work in 2009 and Galdikas in 1978 with both of these papers focusing on suids as taphonomic agents. Dominguez-Solera & Dominguez-Rodrigo (2009) explain that bone modification by suids (domestic pig (*Sus scrofa*), wild boar (*Sus scrofa*), and hybrids of the two) can appear similar to the damage caused by canids and hyaenids. In a study done in 1978 by Galdikas it was observed that the Bornean bearded pig (*Sus barabtus*) scavenged remains of orangutans in the Tanjung Puting Reserve of Central Indonesian Borneo. Although warthogs were not included in these studies, it is important to consider that as members of the family Suidae they could also act as modifiers of bones. Dominguez-Solera & Dominguez-Rodrigo (2009, p. 359) noted, "modern wild boars and pigs also seem to be able to modify bone shafts to a higher degree than reported for hyaenas". Cumming (1975) discusses that tame warthogs have on occasion eaten animals and animal remains, discussing the scavenging of a carcass, bone fragments in warthog faecal samples, and chewing on bones by young warthogs.

In Uganda at the Queen Elizabeth National Park tame warthogs have been observed acting on bones 11 times in what is believed to be the practice of osteophagia (Field, 1970). Osteophagia being when an animal will gnaw on bone to get nutrients that are otherwise not available to them, i.e. phosphorus and calcium, which are known to be deficient in southern African soil (Du Toit & Bisschop, 1929). Since these warthogs were tame and not captive it is reasonable to infer that other wild or non-tame warthogs would act on bones in the same way. Even if only to collect minerals from the bones, the act of "eating" the bones will still produce a taphonomic effect on the bone and thus the warthog becomes a taphonomic agent.

The Plio-Pleistocene Suidae family was more diverse and larger than modern Suidae (Harris & White, 1979). The larger size of these suid ancestors would have given them greater jaw strength and possibly the power to modify the bones of even larger animals than modern suids (Harris & White, 1979).

1.8 Porcupine (*Hystrix africaeaustralis*)

This Old World porcupine, also known as the Cape porcupine or South African Porcupine, inhabits much of the sub-Saharan regions in Africa (Brain, 1981; Skinner & Chimimba, 2005) and is a nocturnal forager (Grubb *et al.*, 2008). The quills of this porcupine can get as long as 30 cm (Hawks, 1987) often deterring predators. Cape porcupines are the largest rodents in southern Africa and spend the first nine weeks of their lives in their burrows (Haim *et al.*, 1992).

The porcupine is one of the many animals that occurs at cave sites in the Cradle of Humankind from past to present (Maguire *et al.*, 1980; Cruz-Uribe *et al.*, 1991; Pickering, 2002; Backwell & d'Errico, 2008; J. Kibii, pers. comm., 2011). Porcupines in South Africa are known for their high-volume collecting of bones as well as modification of said bone (Maguire *et al.*, 1980; Skinner *et al.*, 1980; Brain, 1981; Cruz-Uribe 1991; Lotan, 2000; Kerbis Peterhans & Singer, 2006; Pokines & Kerbis Peterhans, 2007; de Ruiter *et al.*, 2008; Diedrich, 2009), and as such play an important role in the taphonomy within the Cradle of Humankind.

1.8.1 Porcupines as cave users

Porcupines are known to use caves worldwide (Skinner *et al.*, 1980; Diedrich, 2009) and there is substantial evidence of them having used caves for many years (Maguire *et al.*, 1980; Brain, 1981; Skinner *et al.*, 1986; Cruz-Uribe, 1991; Haim *et al.*, 1992; Kerbis Peterhans & Singer, 2006; Pokines, 2007; Diedrich, 2009). Porcupines can also be found in the Plio-Pleistocene to the Holocene records of cave sites throughout southern Africa; Equus Cave (Cruz-Uribe *et al.*, 1991), Drimolen (Backwell & d'Errico, 2008), Fish Hoek Lair (Kerbis-Peterhans & Singer, 2006), Sterkfontein Member 5 (Pickering, 2002), Makapansgat (Maguire *et al.*, 1980), and Malapa (Kibii, pers. comm., 2011) which dates back 1.977 Mya (Pickering *et al.*, 2011; Kuhn *et al.*, 2011a).

In Germany late Pleistocene porcupines are found to have used old hyaena dens, evidence of porcupine gnawed bones can be found on bones that are assumed to have been collected by the hyaenas (Diedrich, 2009). Skinner *et al.*, (1980) reported on porcupines using vacated striped hyaena dens in Israel. The porcupine is thought to be a significant collector and modifier, along with the leopard, of the assemblage at Fish Hoek Lair, Western Cape Province, South Africa (Kerbis Peterhans & Singer, 2006). This shows not only that porcupines and hyaenas use the

same den sites, but also that they act on the same accumulations. Porcupines are known for bone collecting strategies, however are not always the first accumulator at a site, often taking over the den of another accumulator and acting on bones left behind while also continuing to collect bones (Skinner *et al.*, 1980; Diedrich, 2009).

1.8.2 Porcupine as taphonomic agent

Porcupines are well known taphonomic agents in southern Africa (Brain, 1981), leaving behind very distinct taphonomic signatures, such as high amounts of gnawed bones, at times higher than 60% of any given assemblage (Maguire *et al.*, 1980; Brain, 1981; Cruz-Uribe, 1991; Leaky *et al.*, 1999; Lotan, 2000; Kerbis Peterhans & Singer, 2006; de Ruiter *et al.*, 2008). The reason for this high amount of gnawing is thought to be that these rodents gnaw bones to hone their incisors, otherwise they would continue to grow, and also likely in part due to osteophagia (Brain, 1981; Degraaf, 1981; Gow, 1992). Unlike other animals that practice osteophagia when they have mineral deficiencies porcupines collect and gnaw on bones even when they are not deficient (Duthie & Skinner, 1986). There is no evidence of porcupines in Israel gnawing on bones (Skinner *et al.*, 1980), and in Kenya most pieces found in porcupine dens are plastics (Kibii, 2009), because of this it is suggested that the gnawing and collecting of bones by porcupines in southern Africa may serve a dual purpose, honing the incisors as well as being brought about by phosphorus deficiencies in the soil (Skinner *et al.*, 1980).

Lyman (1984) suggests that unlike many other taphonomic agents porcupines are not choosey about the size or weight of the bones that they gnaw, although typically do not collect micro fauna (Kerbis Peterhans & Singer, 2006) most likely because micro fauna would not help with honing the incisors. Brain (1981, p. 115) suggests that “although porcupines collect large quantities of small bone pieces, they prefer to gnaw on the larger ones”. As the porcupine collects bones from many different predators it is possible that they are only collecting the bones that are dry regardless of size or weight, and that is why we are seeing such a broad spectrum of bone variation in porcupine collections (Brain, 1981).

Drier and de-fatted bones are preferred to greasy and fatted bone because porcupines are using said bones to hone their teeth and possibly acquire phosphorus (Brain, 1981). It has been shown that grease left on the bones can cause botulism so they tend to be avoided by the porcupine (Skinner *et al.*, 1980). Accumulations made by porcupines are collected from a

diverse array of predators and can possibly help give a clearer picture of the prey animals available and predators of the past (Brain, 1981; Kerbis Peterhans & Singer, 2006). The more bones in an accumulation the less gnawing by the porcupines will occur, this is due to the higher the availability of bones the less need to gnaw on all bones present (Maguire, 1976; Brain, 1981).

1.9 Large-spotted Genet (*Genetta tigrina*)

Genetta encompasses a group of semi-arboreal insectivore-carnivores (Wemmer, 1977). The common genet or small-spotted genet (*Genetta genetta*) has been reported to have a home range of less than 1 km^2 in Ethiopia (Ikeda *et al.*, 1983). Identifying genet species has been a problem for many years (Gaubert *et al.*, 2001; Gaubert, 2002; Gaubert *et al.*, 2002). The genet seen in this study has been identified as a large-spotted genet given the black at the tip of its tail, with the small-spotted genet having a white tip (Stuart & Stuart, 2001) (see Plate 1). The Cape genet or South African large-spotted genet occurs mainly in southern Africa and is a nocturnal solitary animal (Hawks, 1987; Gaubert *et al.*, 2002; Skinner & Chimimba, 2005). The large-spotted genet has also been recorded in Cradle cave sites such as Plovers Lake and Swartkrans Member 3 (Werdelin & Peigné, 2010).

1.9.1 Genets as cave users

This nocturnal Viverridae will rest in holes or caves during daytime hours (Skinner & Chimimba, 2005). The females tend to litter in places that are protected including ground holes (Skinner & Chimimba, 2005).

1.9.2 Genets as taphonomic agents

The genet is not a proven taphonomic agent, but a potential one. The genet is a carnivore that preys on small mammals and birds (Hawks, 1987) and has not been recorded scavenging (Skinner & Chimimba, 2005). The common genet has a variation of prey frequencies in the Mediterranean ranging from small mammals to arthropods (Virgós *et al.*, 1999), showing its non-specific feeding habits. The common genets main prey includes arthropods, amphibians, reptiles, birds, rabbits, and other small mammals (Rosalino & Santos-Reis, 2002).

1.10 Black-backed jackal (*Canis mesomelas*)

The black-backed jackal is found in eastern and southern Africa (Ferguson *et al.*, 1988; Skinner & Chimimba, 2005) and as with other canids the black-backed jackal is especially aggressive around food sources, even toward other jackals (Ferguson, 1978). The black-backed jackal is an opportunistic hunter/scavenger with variable prey throughout the year depending on external factors (Kaunda & Skinner, 2003; Skinner & Chimimba, 2005). If there are other predators in the area the jackal is most often a scavenger, however if there are less predators to scavenge from it will hunt (Kaunda & Skinner, 2003). It has been recorded that these canids can be quite prolific hunters, although usually not hunting animals larger than a hare (Hilton-Barber & Berger, 2002). In groups jackals are considered more of a threat than a lone hyaena, despite the hyaenas greater strength (van der Merwe *et al.*, 2009), however they often scavenge for their food (Kaunda & Skinner, 2003) and are not often found in such groups (Skinner & Chimimba, 2005). These canids compete with other animals that also scavenge, such as hyaenas, for food sources (Hilton-Barber, 2002; Hunter *et al.*, 2007; van der Merwe *et al.*, 2009), and on the Namibian coast jackal have been reported following brown hyaena to scavenge from their kills (Wiesel, 2006). In the southern Kalahari black-backed jackals will also often follow honey badgers to catch the food that is escaping from the burrows being dug by the badger (Begg, 2001). In this example of honey badger and black-backed jackal the jackal is not scavenging per-say, but it is doing the least it can to attain a food resource (Begg, 2001). The jackal uses human settlements for food as well (Kaunda & Skinner, 2003). Home range size depends on available prey, for example home ranges in the Kalahari Gemsbok National Park were smaller than home ranges in the Transvaal due to greater availability of prey species (Ferguson *et al.*, 1983).

The black-backed jackal has been reported at Plovers Lake and comparable remains have been found at Kromdraai A, Swartkrans Member 2 and Member 3, as well as Sterkfontein Member 4 and Member 5 (Werdelin & Peigné, 2010).

1.10.1 Black-backed jackals as cave users

As with other animals black-backed jackals are born and reared in dens, the cubs usually staying within the natal den for two to three months before leaving (Wiesel, 2006). Once they have left the den they stay in close proximity for up to six months of age (Ferguson *et al.*, 1983).

Spotted hyaena dens in the Masai Mara National Reserve, Kenya, have evidence of jackal occupation (Pokines & Kerbis Peterhans, 2007). In addition to this evidence from the Masai Mara, jackals with pups have been observed inside brown hyaena dens on the Namibian coast (Kuhn, pers. comm.). Taking both of these observations into consideration shows not only that jackals use dens, but that they also use the same dens as hyaenas. This is one example of two different carnivores using the same den within the same time period.

1.10.2 Black-backed jackals as taphonomic agent

The black-backed jackal tooth-pit dimensions and patterning has been explored for use in taphonomic studies, which is indicative of its significance as a taphonomic agent in the fossil record (Dominguez-Rodrigo & Piqueras, 2003; Delaney-Rivera *et al.*, 2009). While it is known that this canid is a taphonomic agent, many prey items of the black-backed jackal are rather small (Bothma *et al.*, 1984) and the remaining bones may not survive to be present in the fossil record since, due to their small nature, they are more prone to destruction over time. Jackals are also known to scavenge from other carnivores such as the honey badger (Begg, 2001) and brown hyaena (Wiesel, 2006), which suggests that any bone that was scavenged from one of these animals has the potential to show marks from both that animal and the black-backed jackal.

The black-backed jackal is thought to reproduce at time when food supply is higher (Skinner & Chimimba, 2005) in order to keep their pups fed. The young pups are weaned at eight to nine weeks, and start foraging by the age of 14 weeks, meaning that they are dependent on their parents as well as other 'helpers' to make sure that they are fed (Skinner & Chimimba, 2005). Both parents are involved in the raising of young and will bring food back to the den for the young pups to eat, indicating that a maternity den for a black-backed jackal would have an accumulation different than that of a non-maternity black-backed jackal den.

1.11 Interspecific interactions/competition

Competition for similar food resources is what pushes interspecific competition (Mills & Harvey, 2001; Donadio & Buskirk, 2006), and means that more than one agent may be accessing bones due to the overlapping food niche. There are many animals living in the Cradle of Humankind, and specifically on the Malapa Nature Reserve, and as such there is bound to be overlap in niche and prey. It is these subtle balances that affect the populations of not just prey animals, but predators as well. This competition can be detrimental to the animals that become prey or victims of kleptoparasitism, but it can also benefit animals that are scavengers (Kruuk, 1972b; Mills, 1978; Owens & Owens, 1978; Skinner & van Aarde, 1991; Palomares & Caro, 1999; Begg, 2001; Caro & Stoner, 2003; Hunter *et al.*, 2007; Kuhn, 2011).

When one species gains fitness benefits from working with another species it will continue to do so and eventually develop some sort of relationship with said species. This has been observed in many situations; in the ocean with larger fish and cleaner fish (*Echeneis naucrates*) (Sazima *et al.*, 1999) as well as with anemones and clown fish (subfamily Amphiprioninae) (Dunn, 1981), and can also be seen with honey badger and black-backed jackal (Begg, 2001). Although black-backed jackals will use honey badgers as "hunting assistants" they have also been found to be the prey of the honey badger (Begg, 2001; Begg *et al.*, 2003a) and visa versa (Begg, 2001). Black-backed jackals however most often gain when hunting with a honey badger, catching 69% of prey that escaped while the honey badger was digging (Begg, 2001). This has also been seen with the honey badger and the pale chanting goshawk (*Melierax canorus*), but again the honey badger does not appear to gain from this relationship (Begg, 2001). The black-backed jackal can also be seen benefiting on the Namibian coast where both the black-backed jackal and the brown hyaena lose and gain from each others kills of Cape fur seal pups, but the jackal is thought to be the one to benefit most of the time (Wiesel, 2006).

Donadio & Buskirk (2006) discuss that predation is more common between a larger and a smaller predator because if they are of similar size than there is more chance of injury with no extra benefit to the predating animal, which could be why so many sub-adults are the victims of interspecific killings (Palomares & Caro, 1999). That an animal would not often choose to enter into a fight with another animal that could cause it harm is sound, but the situation changes when animals hunt/predate in packs. A solitary animal is not as much of a threat as a group (Palomares

& Caro, 1999), thus it must put more caution into hunting to prevent injury. This can be seen when animals hunt and also when they leave prey upon the arrival of a stronger or more dangerous competitor (Owens & Owens, 1978; Caro & Stoner, 2003; Hunter *et al.*, 2007). Despite leopards' prowess as a hunter they have been known to retreat to the safety of nearby trees in the presence of the brown hyaena (Owens & Owens, 1978), this occurs both when the leopard is feeding and also when there is no feeding involved. Behaviour like this has also been seen with spotted hyaenas and warthogs, when four spotted hyaenas moved out of the area for a warthog displaying, and only returning when the warthog had entered its warren (Deane, 1962). Although spotted hyaena (especially in a group of four) is more a formidable opponent than warthog, and leopard more so than a lone brown hyaena, these examples show what would appear to be the animal not willing to risk injury because the other animal could cause harm to them.

Carnivore killing and high incidences of dietary overlap mean animals that are less specialized, like leopard and hyaena, are in less danger of extinction while animals with a more specialized diet like African wild dog are currently endangered (Hayward & Kerley, 2008).

Brown hyaena and black-backed jackal are considered competitive species when resources are low (Owens & Owens, 1978; van der Merwe *et al.*, 2009), and will feed on the same carcasses (Owens & Owens, 1978). It is also noted that the interactions between brown hyaena and black-backed jackal are dependent on other predators in the region, if there are larger predators than black-backed jackal and brown hyaena these two are classified as mid-sized predators, while without larger predators present these two carnivores will become classified as the apex predators (van der Merwe *et al.*, 2009). These differences are more obvious in the hunting and scavenging patterns of the black-backed jackal and brown hyaena, as the jackals diet changes dramatically when it and the brown hyaena are not apex predators because brown hyaena will scavenge from the apex predators and black-backed jackals are forced to hunt (van der Merwe *et al.*, 2009).

The competition between animals changes depending on the landscape that they live on and what other animals are present or absent (van der Merwe *et al.*, 2009). It has also been reported that all six of the extant larger southern African carnivores have been known to kill or be killed by one another (Palomares & Caro, 1999). It is crucial to know that many carnivores, both hunting and scavenging, have high amount of overlap in

dietary preferences and this implies that bones can experience taphonomic action from more than just one agent.

1.12 Aims & Objectives

The aim of this study has been to gain a better understanding of modern cave usage by a variety of mammals on the Malapa Nature Reserve in the Cradle of Humankind, South Africa, and the implications of multiple taphonomic agents use of said caves over a short period of time. It is important to acknowledge that while this data can be useful in the interpretations of past accumulations, only modern equivalents of animals that once existed on the landscape in the past can be observed.

This study was conducted with hopes that this data could be used to help interpret new, and reinterpret past, fossil faunal accumulations. By examining how animals use caves in modern times we can surmise that the same species in the past were using caves in a similar, if not the same, fashion. Cave usage patterns of large carnivores and other animals found using caves at the Malapa Nature Reserve have been documented over a period of 20 months. Of special interest are animals that are considered to be taphonomic agents and any new potential taphonomic agents that may have been discovered in the process of evaluating cave usage at the Malapa Nature Reserve. The Cradle of Humankind has a large number of fossil cave sites, Sterkfontein, Malapa, Swartkrans, Kromdraai, Cooper's, and Gladysvale just to name a few, and thus becomes a strategic place to run this study. Two of these sites, Malapa and Gladysvale, are located on the Malapa Nature Reserve, which is also home to Uitkomst Cave, a site with both Stone Age and Iron Age deposits.

From the beginning of this research a number of questions were asked, such as: Do animals utilize caves? Is there a preferred time of year for cave use? Which animals are using caves today at the Malapa Nature Reserve? Do the selected study animals prefer one cave type to another? Are there any specific factors that appear in any or all of the caves that could be said are a proxy for the cave being used by specific animals? What animals use the same cave more than once and which only appear sporadically? Are the animals of the Malapa Nature Reserve using the same caves within short time periods? How many individuals are using the caves within short time periods? It is by condensing these questions into two hypotheses to examine that this project began.

* For these questions a "short time period" refers to 20 months.

1.13 Hypotheses

A) More than one species uses the same caves within a relatively short period of time.

It is thought that the animals on the Malapa Nature Reserve are using the same caves in relatively short time periods. If the caves are being used within the same time period it is fair to suggest that there will be times when they are in the same cave at the same time. If this is the case there must be some sort of co-operation or mutualism between the animals if they are occupying the same small space. It is known that these animals all use caves and sometimes the same caves, but there are as yet no publications discussing whether they are occupying the caves at the same time. It is believed that the bones porcupines are gnawing on have been brought into the caves by larger carnivores (Diedrich, 2009); therefore they are deriving a fitness benefit from the larger carnivores.

B) Animals prefer certain cave types.

Some animals will use many different kinds of caves types, but it is most likely that there is a specific cave type that animals prefer to another. When preferred caves are available it is thought that these caves will be used more frequently than other non-preferred caves.

1.14 Methods & Materials

1.14.1 Limitations

As with any research there are always limitations. The largest limitation faced by this project is time. The more time spent observing caves the more would be seen in terms of cave usage by taphonomic agents. Also time was also a factor as it is not possible to observe the behaviour of these extant animals on the ancient landscape, nor is it possible to observe now extinct animals.

The motion sensor cameras had some operational malfunctions, beginning from three minutes after activation the cameras would take a sequence of three photographs when triggered and then reset (lapsing about five seconds), which meant that some photo opportunities were missed. There were several photos that were over exposed and thus difficult to get data from. Over exposed photos will still be included in this research when enough information can be taken. When the camera was initially tripped it was possible that an animal could be out of sight before the first photograph was taken. This gap in photographs also meant that animals were not always captured entering and exiting, sometimes it was just one or the other.

1.14.2 Transportation

The first thing that had to be done to begin this research was to get to the site. The Cradle of Humankind is located 45 km from Johannesburg. With the University of the Witwatersrand in Johannesburg being where this study is based getting out to the Malapa Nature Reserve was something that could be done with relative ease. The cameras were checked every 20 to 30 days.

1.14.3 Animals chosen

The animals that have been focused on in this research are animals that are typically found using caves and are either confirmed or potential taphonomic agents. These animals include leopards, brown hyaenas, black-backed jackals, honey badgers, warthogs, porcupines, and large–spotted genets. What has been looked at prior to data analysis is general information regarding these animals as well as their history of cave usage and their taphonomic potential.

1.14.4 Locating Caves

1.14.4.1 Tracking spoor

The first step was tracking spoor to find the best places to put camera traps. This was done anywhere that the soil would hold a track, however due to the geology and vegetation at the Malapa Nature Reserve there were not many places like this. To track spoor the vehicle would stop anytime there was thought to be spoor on the path. There were usually at least two people present on the trips out to the Malapa Nature Reserve because of the danger involved if one of the persons were injured.

1.14.4.2 Word of mouth

The geology the Malapa Reserve is not very conducive for tracking spoor so it was also necessary to rely more heavily on word of mouth from the people that work or live on the property. It has been invaluable to have eyewitness accounts from farm workers, caretakers, and other researchers with a history of working on the Malapa Nature Reserve to help in spotting animals that were being targeted for, and providing locations of known caves. The people working on the Malapa Nature Reserve are the ones who know it best, so this was the most useful method for locating caves for this study. At times both of these methods combined helped to determine the best locations to place camera traps.

1.14.5 Collecting Data

1.14.5.1 Cameras

This study was largely based on the use of motion sensor camera traps set out at the Malapa Nature Reserve in the Cradle of Humankind, South Africa. As such the initial part of this project was placing eight camera traps throughout the reserve, and specifically at cave entrances, with the intention of capturing the movement patterns of the various mammals. Initially two of the eight cameras were placed at cave entrances, and the remaining six were placed on game trails throughout the Malapa reserve. Four additional cameras were obtained in March 2011 and placed at cave entrances that April. Cameras stayed up for a minimum of 20 days, and were left up for a longer period of time if there were promising results.

The cameras used to capture animal movement on the Malapa Nature Reserve were made by Bushnell®, Lynx Optics®, and Moultre® (All three of

these cameras run on batteries, with the batteries in the Bushnell® having the option to attach a solar panel. Both the Moultre® and the Bushnell® use D cell batteries, while the Lynx Optics® uses eight AA batteries). When a motion sensor camera took a photograph the time, date, and ambient temperature (except for the Bushnell®) were recorded on the photograph. The Moultre® camera was up at the reserve for nine months previous to the commencement of this research and was used throughout this research as well. Not all cameras were placed at cave entrances as this project was run simultaneously with another project based at the Malapa Nature Reserve also using motion sensor cameras.

Through the advice of Professor Lee Berger, two caves that had been identified previously were the first two to be monitored. When additional caves were identified they were added to the study by placing cameras outside of the entrance. All of the caves monitored were mapped using traditional compass and clinometer mapping methods. The mapping occurred at the end of the field portion of the study to limit any disturbance to the animals that may have been using said caves. The mapping portion of this study provided cave structure, entrance type, slope (when not flat) and any sedimentary debris (i.e., current faunal accumulations). This has many implications for further examination of the paleontological record with regards to taphonomy. Not only is it expected to identify animals that may be collecting faunal material, but also to obtain a record of all taphonomic or potential taphonomic agents accessing caves and any faunal remains that may be inside of said caves.

The field portion of this project was run over a period of 20 months (not including the pilot study that was run previously) by placing and relocating motion sensor cameras (when results were not obtained) throughout the Malapa Nature Reserve at cave entrances. The camera results have shown what animals were using the caves over the time period of this study.

1.14.5.2 Camera complications

Cameras were attached to trees or fences with an elastic band that ran through the backing of the camera case and was tightened to minimize movement of the camera. Cameras were then locked onto a tree or fence with a padlock and length of chain to ensure their safety.

The cameras did not always work without problems, thus it was important to have batteries and/or an extra camera on hand when cameras were

checked. As mentioned above there were twelve cameras used for this research, but rarely were all twelve cameras up at one time. There is tall grass throughout the Malapa Nature Reserve so many times photos were taken of grass moving, these pictures were not used for this research, but have been retained. The only times that this may have caused a problem was if the photo taken of the grass moving triggered the camera to take a burst of three photos and a passing animal was missed, as the cameras have a 5 second delay between sets of photographs. Grasses occurred most often on the game trails and not at cave entrances so did not affect the outcome of this project, however is worth noting for any possible future research in a similar biome.

There were sporadic occasions of batteries in the cameras dying, either from the solar panel being blocked or disconnected (most likely by baboons) or the battery set running out of power. These were all simple fixes that did not alter the research and only required replacing the batteries.

There was one instance of a baboon that ripped the casing of the camera apart and it had to be taken down and the casing replaced. Baboons also punched out the sensors on the cameras on numerous occasions, which required the camera to be removed for repairs. The camera set above the Porcupine Cave often took blurry photographs; this motion likely caused by wind or possibly by baboons moving the tree that the camera was mounted to.

Lastly locations of cameras were given to the caretaker at the Malapa Nature Reserve incase of a brushfire or any unforeseen issue that would cause a need for the cameras to be removed so that they would not be lost or damaged.

1.14.5.3 Mapping

Caves were mapped using the traditional method of mapping meter by meter with a compass, clinometer, measuring tape, and graph paper. The guidelines used were width, depth, entrance type (vertical or horizontal), and slope/gradient of the caves from the entrance to the bottom where necessary (i.e. unless they have been previously mapped, are in use, or are flat). These maps showed the type of cave being used by the animals, to look for specific patterns in caves chosen by certain animals, if any.

This system of mapping forces the researcher to observe the cave with

their own eyes which in turn gives the researcher a better understanding of the cave being mapped.

The method of mapping employed involves the use of a compass (for directionality) and a clinometer (for degree of slope) to map out the cave. A long measuring tape is placed in the middle of the cave, usually the longest width, and then stabilized at both ends, this is done so that there is as little movement as possible while mapping. From this point you begin at one side and map out from the centerline with a second measuring tape every meter on both sides while drawing the shape of the rocks as well. At every meter a clinometer reading is taken so that the slope of the cave is documented. The middle line is read with the compass so that north and south can be seen when the drawing is finalized.

1.14.6 Assessment of data

The data was assessed on two levels as individual caves and a whole picture. This data will help in the perceptions of animal cave usage regarding fossil accumulations and more specifically the taphonomy of said accumulations. The data was assessed using Excel tables.

1.14.6.1 Excel

The results from the motion sensor cameras were placed in an excel spreadsheet and Pivot Tables were used. Data included: time of photograph, date of photograph, ambient temperature, species entering cave, species exiting cave, and number of said species. The dates of camera placement and removal are listed in the discussion.

The extrapolated information from the raw data was:

-Frequency of appearances for each animal (total)
-Frequency of appearances of animals at each cave (total number of animals seen)
-Time of day most common for cave use
-Season most common for cave use
-Time cameras were up at each cave

1.15 Brief overview of this study

This study captures animals entering and exiting caves at the Malapa Nature Reserve Gauteng Province, South Africa, with motion sensor cameras and has taken into consideration the taphonomic capabilities, and potential taphonomic capabilities, of said animals. By understanding the way that modern animals are using caves in the Cradle of Humankind insight can be gained into how caves were being utilized in the past, when the fossil accumulations were forming. The idea being that if there is significant cave use by various species over a short period of time than assigning collecting and/or modifying agents becomes much more complicated than has been thought. The implications are vast given that this study is the first of its nature taking place in the Cradle of Humankind, examining many different animals as cave users and taphonomic agents simultaneously. With this study past fossil accumulations must be re-evaluated to include all possible cave users as accumulators and/or modifiers, given many species use caves.

Here modern cave usage has been considered and the implications of multiple taphonomic agents on a faunal assemblage. The main focus of this research was regarding mammals (birds were recorded at caves, but were not used in this study as only mammals were considered) that are currently using caves at the Malapa Nature Reserve located in the Cradle of Humankind World Heritage Site, South Africa. Of particular interest in this study are leopards, brown hyaenas, black-backed jackal, honey badgers, large-spotted genets, porcupines, and warthogs, all of which have been documented in fossil cave assemblages from the Cradle of Humankind (Maguire *et al.*, 1980; Brain, 1981; Turner, 1990; Cruz-Uribe, 1991; Pickering, 2002; Pickering, 2004a; de Ruiter *et al.*, 2008, 2009; O'Regan & Menter, 2009; O'Regan & Reynolds, 2009; Dirks *et al.*, 2011).

1.16 Synopsis of Chapters

Chapter 2- Study Area

The Malapa Nature Reserve, where this study has taken place, is described. Past and present species that have been found in fossil accumulations in the Cradle of Humankind are noted. The habitat, vegetation, climate, and geology have also been described as well as the four caves where cameras were located.

Chapter 3- Results

This chapter has laid out the results of this study from each cave observed, including what was done at the cave: entering, exiting, loitering, or inside. Tables of animal occurrences at each cave individually from June 2010 to December 2011 have been added here, as well as a table of the combined results from all four caves.

Chapter 4- Discussion

Data from L. Berger & B. Kuhn (unpublished, 2008-2010) has been added at the beginning of the discussion to give a better record of cave use. The results of this study, and the previous work, have been discussed in detail in Chapter 4. Information from the background studies has also been included as reference points for discussion topics.

Chapter 5- Conclusion

In the conclusion the two hypotheses and questions mentioned above have been revisited and answered. Implications, final thoughts, and future works are stated at the end.

CHAPTER 2: STUDY AREA

2.1 Area

This study was conducted at the Malapa Nature Reserve (formerly the John Nash Reserve) in the Cradle of Humankind, Gauteng, South Africa. The reserve is located 45 kilometers Northwest of Johannesburg on the border of the Gauteng and the North West Provinces (See Figure 2.1). The Cradle of Humankind is a UNESCO (United Nations Educational, Scientific and Cultural Organization) World Heritage site compromised of 47,000 hectares of mostly private owned land (Hilton-Barber & Berger, 2002) and is the location of many well-known fossil sites in South Africa.

Figure 2.1: Map of the Cradle of Humankind

http://www.en.wikipedia.org/wiki/Cradle_of_Humankind

http://www.sa-venues.com/mapsgauteng_cradle_of_humankind.htm

The Malapa Nature Reserve, which is located within the Cradle of Humankind, is home to well-known fossil accumulations such as Gladysvale Cave (Berger, 1993; Berger & Tobias, 1994; Fleminger, 2006), Malapa, where the *Australopithecus sediba* fossils were recently discovered, (Berger *et al.*, 2010; Dirks *et al.,* 2010: Kuhn *et al.*, 2011a), and the Late Stone Age and Iron Age site of Uitkomst Cave (Mason, 1962; Hilton Barber & Berger, 2002). The reserve is comprised of approximately 9500 hectares of privately owned land (de Ruiter & Berger, 2000), which is not accessible to the general public.

2.2 Wildlife

Table 2.1: Species identified at the Malapa Nature Reserve and their association with caves

FAMILY	COMMON NAME	LATIN NAME	INSIDE CAVE	AT CAVE ENTRANCE	NEAR CAVE ENTRANCE
Cercopithecidae	Chacma Baboon	*Papio hamadryas ursinus*			X
	Vervet monkey	*Cercopithecus pygerythus*			X
Felidae	Leopard	*Panthera pardus*		X	
	Serval	*Leptailurus serval*			
	Caracal	*Caracal caracal*			
Viverridae	Small spotted genet	*Genetta genetta*			
	Large-spotted genet	*Genetta tigrina*			
	Civet*	*Civettictus civetta*			
Herpestidae	Slender Mongoose	*Galerella sanguinea*			
Hyaenidae	Brown hyaena	*Parahyaena brunnea*	X	X	
Canidae	Black-backed jackal	*Canis mesomelas*	X		
Mustelidae	Honey Badger or Ratel	*Mellivora capensis*		X	
	African Clawless Otter	*Aonyx capensis*			
Equidae	Zebra	*Equus quagga*			
Procaviidae	Rock hyrax	*Procavia capensis*			
Suidae	Warthog	*Phacochoerus africanus*	X	X	
Giraffidae	Giraffe	*Giraffa camelopardalis*			
Bovidae	Sable	*Hippotragus niger*			X
	Eland	*Tragelaphus oryx*			
	Impala	*Aepyceros melampus*			
	Blesbok	*Damaliscus pygargus phillipsi*			
	Greater Kudu	*Tragelaphus strepsiceros*			
	Gemsbok	*Oryx gazella*			
	Wildebeast (Blue)	*Connochaetes taurinus*			
	Mountain Reed Buck	*Redunca fulvorufula*			
	Red hartebeast	*Alcelaphus buselaphus*			
	Steenbok	*Raphicerus campestris*			
Hystricidae	Porcupine	*Hystrix africaeaustralis*	X	X	
Numididae	Helmeted Guinea Fowl	*Numida meleagris*	X		
Sagittariidae	Secretary Bird	*Sagittarius serpentarius*			
Struthionidae	Ostrich	*Struthio camelus*			

*Civet is from de Ruiter & Berger, 2000

2.2.1 Extant carnivores from fossil accumulations

The Cradle of Humankind has long been home to a wide range of animals including hominids. Evidence of this can been seen in the many fossil sites located within the UNESCO site, which include: Swartkrans, Sterkfontein, Malapa, Makapansgat, Gladysvale, Cooper's Cave, Plovers Lake, Drimolen, Kromdraai, Motsetse, Gondolin, Wondercave, and Bolts Farm (Harris & White, 1979; Hilton-Barber & Berger, 2002; Avery, 2001; Berger *et al.*, 2003; Brophy *et al.*, 2006; Fleminger, 2006; de Ruiter *et al.*, 2008; O'Regan & Menter, 2009; O'Regan & Reynolds, 2009; Werdelin & Peigné, 2010; Kuhn *et al.*, 2011a). In these fossil accumulations evidence of both extinct and extant predators is found, and prey animals that inhabit(ed) the region, both of which have given significant scientific contributions to assist in the interpretations of fossil assemblages and associated palaeoenvironments. The modern existence of a large number of animals found in fossil accumulations is highly advantageous to the study of said accumulations, as it presents the opportunity to study and observe these animals and their relevant behaviour in life. Studying extant species may also be of use to infer past behaviour of the same or similar species.

The list above includes extant animals that have been found in fossil accumulations in the Cradle of Humankind that are still living in Africa today, however not all of the listed species still occur within the Cradle of Humankind. Some of the carnivores that can be found in the Cradle of Humankind today occur only at places like The Rhino & Lion Nature Reserve. The carnivore species found at The Rhino & Lion Nature Reserve are not free ranging, but are fed (do not hunt) and are caged thus not appropriate for a study of this nature. Animals listed below that no longer occur in the wild within the Cradle of Humankind include the striped hyaena (*Hyaena hyaena*), lion (*Panthera leo*), cheetah (*Acinonyx jubatus*), spotted hyaena, (*Crocuta crocuta*), black-footed cat (*Felis nigripes*), and the wild dog (*Lycaon pictus*).

Table 2.2: Extant carnivores from fossil accumulations in Africa

FAMILY	COMMON NAME	LATIN NAME	AGE
Felidae	Lion	*Panthera leo* *^[#]	from 3.5 Mya[#]
	Leopard	*Panthera pardus* *^[#]	from 3.5 Mya[#]
	Cheetah	*Acinonyx jubatus* *^[#]	from 3.5 Mya[#]
	Wild cat	*Felis silvestris* *	
	Caracal	*Caracal caracal* *[#]	from 5 Mya[#]
	Serval	*Leptailurus serval* *[#]	from 5 Mya[#]
	Black-footed cat	*Felis nigripes*[æ]	from 1.977 Mya[æ]
Hyaenidae	Brown hyaena	*Parahyaena brunnea* *^[#]	from 2.5 Mya[#]
	Striped hyaena	*Hyaena hyaena* *[#]	from 3 Mya[#]
	Spotted hyaena	*Crocuta crocuta* *^[#]	from 3.5 Mya[#]
	Aardwolf	*Proteles cristatus* *^	
Canidae	African wild dog	*Lycaon pictus* *[#]	from 1 Mya[#]
	Black-backed jackal	*Canis mesomelas* ^[#]	From 2.75 Mya[#]
	Cape Fox	*Vulpes chama* *	
	Bat-eared fox	*Otocyon sp.**	

^ de Ruiter *et al.*, 2009 from Cooper's Cave D
* O'Regan & Reynolds, 2009 from various Cradle sites
[#] Turner, 1990 dates from various African deposits
[æ] Kuhn *et al.*, 2011a from Malapa

2.2.2 Carnivore guild of the past

Africa had a greater number of carnivore species during the Plio-Pleistocene compared to modern day Africa (Turner, 1990; O'Regan & Reynolds, 2009), with a minimum of 10 carnivore species having become extinct in the last 1 to 2 million years (Turner, 1990; O'Regan & Reynolds, 2009; Kuhn, *et al*., 2011a). It has been theorized that the extinction of many of the large carnivores played a significant role in giving early hominids a chance to expand their dietary niche (Lewis, 1996). This expansion was have been possible because hominids had less competition and this would have given them the chance to expand their hunting area.

Table 2.3: Extinct carnivores from fossil accumulations in Africa

FAMILY	COMMON NAME	LATIN NAME	AGE
Felidae	False saber-tooth cat	*Dinofelis piveteaui** [#]	between 1-2 Mya[#]
	False saber-tooth cat	*Dinofelis barlowi** [#]	between 2-5 Mya[#]
	Saber-tooth cat	*Homotherium latidens **	
	Saber-tooth cat	*Megantereon whitei **	
Hyaenidae	Giant hyaena	*Pachycrocuta brevirostris** [#]	between 1.5-3 Mya[#]
	Hunting hyaena	*Chasmaporthetes nitidula** [#]	between 1-4 Mya[#]
	Hunting hyaena	*Chasmaporthetes silberbergi** [#]	between 1.5-3.2 Mya[#]
	Extinct aardwolf	*Proteles amplidenta**	
	Extinct striped hyaena	*Hyaena makapani*[Δ]	
Canidae	Extinct fox	*Vulpes skinneri* [¥]	

^ de Ruiter *et al.*, 2009 from Cooper's Cave D
* O'Regan & Reynolds, 2009 from various Cradle sites
[#] Turner, 1990 dates from various African deposits
[¥] Kuhn, unpublished
[æ] Kuhn *et al.*, 2011a from Malapa
[Δ] Maguire *et al.*, 1980 from Makapansgat

Above is a list of carnivores that have been found in fossil accumulations within the Cradle of Humankind and are now extinct. These animals occur within accumulations that also have extant animals, showing that they once lived on this landscape together.

Table 2.4: Extant vs. extinct (in relation to Malapa Nature Reserve)

FAMILY	COMMON NAME	LATIN NAME	EXTINCT	EXTANT AND NOT KNOWN TO OCCUR AT MALAPA NATURE RESERVE	OCCURING AT MALAPA NATURE RESERVE TODAY
Felidae	Lion	*Panthera leo* *^[#]		X	
	Leopard	*Panthera pardus* *^[#æ]			X
	Cheetah	*Acinonyx jubatus* *^[#]		X	
	Wild cat	*Felis silvestris **		X	
	Black-footed cat	*Felis nigripes*[æ]		X	
	Caracal	*Caracal caracal** [#]			X
	Serval	*Leptailurus serval** [#]			X
	False saber-tooth cat	*Dinofelis piveteaui** [#]	X		
	False saber-tooth cat	*Dinofelis barlowi** [#æ]	X		
	Saber-tooth cat	*Homotherium latidens **	X		
	Saber-tooth cat	*Megantereon whitei **	X		
Hyaenidae	Brown hyaena	*Parahyaena brunnea* *^[#æ]			X
	Striped	*Hyaena hyaena** [#]		X	

	hyaena				
	Spotted hyaena	*Crocuta crocuta* *^[#]		X	
	Extinct striped hyaena	*Hyaena makapani*[Δ]	X		
	Giant hyaena	*Pachycrocuta brevirostris** [#]	X		
	Hunting hyaena	*Chasmaporthetes nitidula** [#]	X		
	Hunting hyaena	*Chasmaporthetes silberbergi** [#]	X		
	Extinct aardwolf	*Proteles amplidenta**	X		
	Aardwolf	*Proteles cristatus* *^		X	
Canidae	African wild dog	*Lycaon pictus* *[#]		X	
	Black-backed jackal	*Canis mesomelas* ^[#]			X
	Cape Fox	*Vulpes chama* *		X	
	Bat-eared fox	*Otocyon sp.**		X	
	Extint fox	*Vulpes skinneri*[¥]	X		

^ de Ruiter *et al.*, 2009 from Cooper's Cave D

* O'Regan & Reynolds, 2009 various Cradle sites

[#] Turner, 1990

[æ] Kuhn *et al.*, 2011a

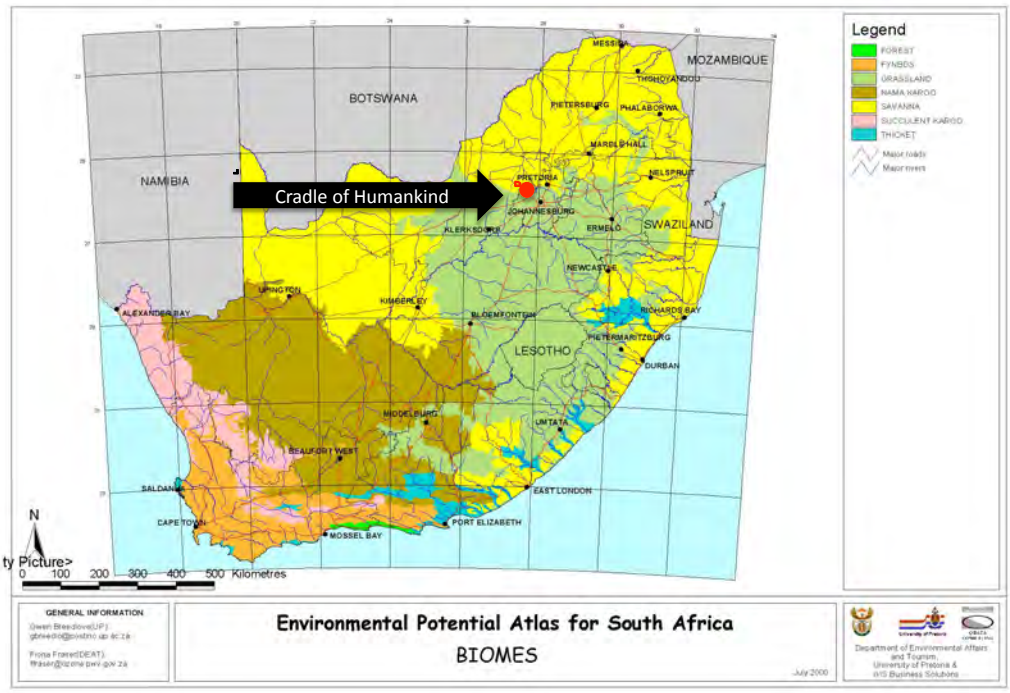
[¥] Kuhn, unpublished

[Δ] Maguire *et al.*, 1980 from Makapansgat

- Some of the carnivores that no longer occur in the Cradle of Humankind (as natural predators) are not extinct, but rather have been controlled for by modern humans.

2.3 Habitat & vegetation

Figure 2.2: Map of biomes in South Africa



http://www.southafricaholiday.org.uk/images/biome_map.jpg

The landscape of the Malapa Nature Reserve has many physical characteristics, including rolling hills (Plate 2) and valleys (Plate 3), open veld, rocky outcrops (Plate 4 and Plate 5), caves (Plates 6, 7, 8, and 9), and a rare tufa formation (Plate 10). There are also a number of springs and streams (Plate 11) that run through the reserve year round supplying water to plants and animals alike. The diversity in habitat offered at the Malapa Nature Reserve makes it an ideal place for a variety of animals to live.

The rolling hills and valleys were made by fluvial action causing erosion on the original African Surface (Martini & Keyser, 1989; McCarthy, pers. comm., 2011). It was this same erosion of the surface that opened and closed many of the caves (McCarthy, pers. comm., 2011) that have provided science with a great deal of data on the palaeo-landscape. Some of the valleys on the reserve are small and filled with dolomite stones (see Plate 12).

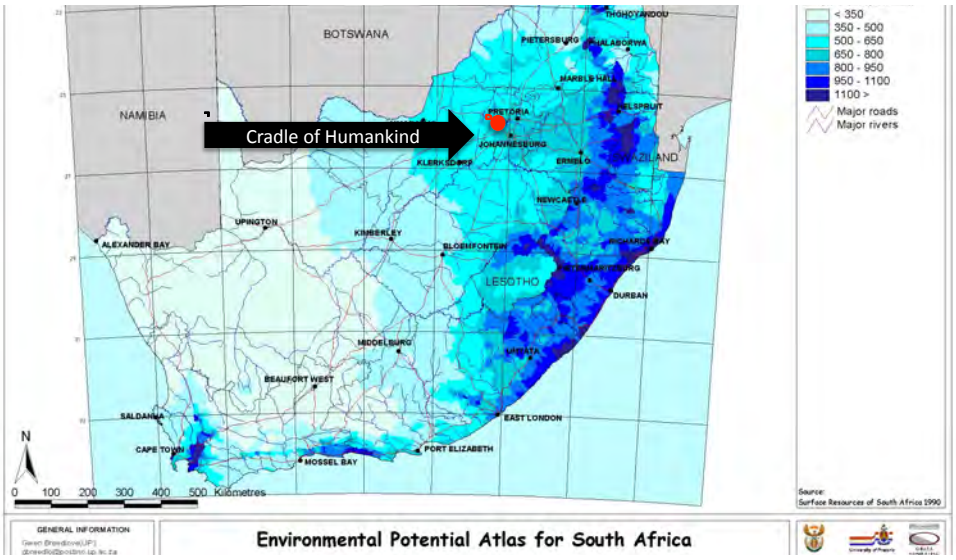
The rocky outcrops on the reserve are an ideal habitat for animals like the rock hyrax (*Procavia capensis*), and occur throughout the property. There are many caves that have formed by dissolution of water within the dolomite that runs through the reserve (Martini & Kavalieris, 1976; Martini & Keyser, 1989; Martini *et al.*, 2003). The cave structures themselves are often closed off to the outside elements; the reason for caves being open and closed over time is due to the nature of dolomite, they open by erosion and close by rock collapse, and this can occur many times in a caves history (McCarthy, pers. comm., 2011).

The open veld vegetation can be attributed to the annual rainfall, about 600-800mm, and climate of the region (Palmer & Ainslie, 2005). The dominant dry grasses that occur throughout the reserve and are only slightly interrupted by water or small groves of trees, often these are the white stinkwood (*Celtis africana*) and wild olive (*Olea europaea africana*) trees that are indicative of cave entrances (Fleminger, 2006; Berger, pers. comm.)

The Cradle of Humankind straddles two biomes, savanna and grassland (Fleminger, 2006; Bamford *et al.*, 2010). The savanna region supports both grazers and browsers that live on the landscape and in return these animals help to maintain the landscape (Owen-Smith & Danckwerts, 1997; Scholes, 1997). Savanna regions have more trees than grassland regions supporting many trees from the genus *Acacia*, which are seen throughout the reserve. The large numbers of herbivores that live and feed within this biome supply a food resource to the carnivores of this region as well. The grassland region is an ideal habitat for grazers (O'Connor & Bredenkamp, 1997), and supports the high amount of grazers found at the Malapa Nature Reserve. It is these two landscapes combined that form the savanna-grassland complex that allows for such a high amount of diversity within the reserve and the Cradle of Humankind. The fires that happen every year at the reserve are also helpful in maintaining these vegetations (O'Connor & Bredenkamp, 1997; Scholes, 1997)

2.4 Climate

Figure 2.3: Map of rainfall means in South Africa



http://www.environment.gov.za/enviro-info/nat/images/rain.jpg

The temperature range in this region of South Africa ranges from ~0˚C on winter nights to ~34˚C on summer days (Palmer & Ainslie, 2005) and the rainfall pattern is typically dry in winters and wet in summers, with an average annual rainfall of 600 mm (Palmer & Ainslie, 2005). Typical for a region that experiences summer rainfall, C_4 plants mostly dominate the vegetation (Pickering R., 2004) and a C_4 heavy region would include plants that are mostly grasses and have an open landscape (Ségalen *et al.*, 2007). It is likely that southern Africa became a C_4 biome during the Miocene or Pliocene (Ségalen *et al.*, 2007) and this type of vegetation can be seen at the Malapa Nature Reserve today where grasses and an open landscape dominate the area. C_3 plants have occurred throughout South Africa for tens of thousands of years (Carto *et al.*, 2009), but the vegetation in the Cradle of Humankind has been mostly C_4 due to the seasonal conditions of that area (Pickering, R., 2004). Recent research based at Gladysvale has shown that this regions temperature and flora will determine the type of sedimentation that occurs in caves, with flowstone layers representing 60% C_3 plant coverage and breccia layers representing 50-80% C_4 plant coverage (Pickering R., 2004). These

interpretations are based on $\delta^{13}C$ signals taken from the breccia and flowstones of Gladysvale Cave, at the Malapa Nature Reserve, which show breccia being formed during glacial periods and flowstones forming during the warmer interglacials (Pickering, R., 2004).

2.5 Geology

The dolomite of the Malapa Nature Reserve was formed in Malmani Subgroup (Martini & Kavalieris, 1976; Berger *et al.*, 2009; Dirks *et al.*, 2010), which is part of the Transvaal Supergroup (Eriksson *et al.*, 1995; Pickering, R., 2004; Leyland *et al.*, 2008; Berger *et al.*, 2009). The geology of the area can be used to examine the caves observed in this study and search for any similarities or differences between them. Certain soils and dolomitic terrain can allow for fossilization to occur at higher frequencies (Lyman, 1994a), which explains such a high rate of fossil finds within the Cradle of Humankind, including the Malapa Nature Reserve.

Dolomite outcrops like Plate 4 and Plate 5 occur sporadically on the reserve, breaking up the dominating dry grasses of the open veld. Although dolomite rocky outcrops are a distinct feature of the landscape there are many other contributing features to the geology of the Malapa Nature Reserve including dolomite caves and a locally rare tufa formation.

The caves located in the Malapa Nature Reserve are most often made from dissolution of dolomite, and are common on the reserve (Martini & Kavalieris, 1976; Brain, 1981; Hilton-Barber & Berger, 2002; Martini *et al.*, 2003; Leyland *et al.*, 2008; International Association of Hydrologists, 2011). There is also a tufa formation on the reserve that is the home to two caves observed in this study. “The term tufa is used to describe all cool water deposits of highly porous or "spongy" freshwater carbonate rich in microphytic and macrophytic growths, leaves and woody tissue.”(Pedley, 1990, p. 143) and by this definition tufa deposits are also karst sediment, made by water depositing minerals that have been collected by rock dissolution (Marker, 1973). The difference between a speleothem and a tufa is that tufa deposits are usually made on the surface while speleothems occur within a cave (Marker, 1973). Tufa caves will not form by dissolution, as do dolomitic caves (McCarthy, pers. comm., 2011). Tufa caves form when a waterfall flows off of a ledge where it slowly develops a wall of calcium carbonate which over time will turn into a tunnel or tufa cave (Pedley, 1990). Due to the multi-leveled landscape, and flowing stream where this tufa formation is located it is possible that the tufa caves on the reserve formed in this manor as well. Evidence of other tufa caves formed in this manor can be seen at the Tonto National Monument in Arizona (Encyclopedia Britannica, 2011), and the Taung fossil site in South Africa a well-known site that according to previous interpretations was formed in a tufa cave (Kuhn, *et al.*, 2011b).

2.5.1 Karst topography

Karstification in its simplest definition refers to the process of rock dissolution by groundwater (Leyland *et al.*, 2008). According to Wray (2003) karst is more of a process then a characteristic restricted to limestone, and that the term should, and can, be used to describe any system where the principle agent is rock dissolution by water. Karst landscapes are typically known to have major systems of underground caves (Martini *et al.*, 2003), which can be seen in cave systems such as Sterkfontein and Gladysvale. In the Cradle of Humankind karst systems occur mainly within the dolomitic rock, and as the water table drops and water flows through it dissolves the rock leaving behind residual layers called calcite flowstone, or limestone (Brain, 1981; Martini *et al.*, 2003; Fairchild *et al.*, 2006; Dirks *et al.*, 2010). However before this can happen the caves must be formed, which is done by the dissolution of rock beneath the surface (Brain, 1981; Dirks *et al*, 2010).

Dolomite cave systems are karst systems created by the dissolution of rock underneath the water table causing an underground cavern to appear (Martini & Kavalieris, 1976; Brain, 1981; Wray, 2003; Hilton-Barber & Berger, 2002; Martini *et al.*, 2003; Leyland *et al.*, 2008; International Association of Hydrologists, 2011). Eventually these caverns, made by the dissolution of dolomite, will be exposed either by roof collapse or possibly the opening up the cave by slow erosion of the old African Surface by river systems (Martini *et al.*, 2003, McCarthy, pers. comm., 2011). Once the cave is opened it can be used by animals or become a death trap.

The limestone within these caves was used to smelt gold and thus limestone mining became a very profitable business in southern Africa (Brain, 1981; Berger & Tobias, 1994; Pickering, R., 2004). Limestone is still being used today as a binding agent in products from toothpaste to fertilizer (Berger & Tobias, 1994), but the mining industry is today is a fraction of what it once was and has led to many mines being shut down (ex. Buxton-Norlim Limeworks associated with the Taung site). Fossils were discovered soon after limestone mining began and thus began the intertwined relationship between miners and palaeontologists. Lime miners used explosives to gain access to the limestone often destroying numerous fossil deposits while simultaneously exposing the fossils that would be studied so in depth by palaeoanthropologists for years to come (Martini *et al.*, 2003; Pickering, R., 2004). The Taung child, found at the Buxton-Norlim Limeworks Quarry near Taung, was recognized as a new species by Dart in 1925, and 22 years later another australopithecine was

found at the Makapansgat Limeworks (Mason, 1962; Fleminger, 2006) showing how closely these two fields have worked together.

The Cradle of Humankind has had a long history of science and mining before becoming a UNESCO World Heritage Site in 1999 (Fleminger, 2006). Archaeological scientific research in southern Africa was first documented in the 19th century when Robert Moffat wrote about the Iron Age peoples then living in the Transvaal (Mason, 1962). Later finds of fossil remains in the early 20th century began a long history of palaeontology in southern Africa including work by Dart, Broom, and van Riet Lowe (Mason, 1962). Although the limestone mining business has destroyed many remnants of the past, it has also been part of a symbiotic relationship with palaeontology from early on; Martini *et al.* (2003) referring to Sterkfontein- "During the 1920s the cave was exploited for calcite flowstone by the Glencairn Limestone Company. The operations were managed by Mr. G.W. Barlow, who sent specimens of fossils recovered to various scientists." (p. 47) and "Shortly before World War II in 1939 mining of calcite was curtailed at Sterkfontein due to a drop in the price of lime and with that the paleontological work also came to an end for the duration of the war." (p. 47). Funding within the field of palaeontology has often been problematic yet while there was limestone mining occurring caves were being exposed to scientists at the cost of the miners (Martini *et al.,* 2003). The mining industry in southern Africa is still a productive business, and the majority of fossil locations in South Africa today owe their discovery to the mining industry.

2.6 Caves in this study

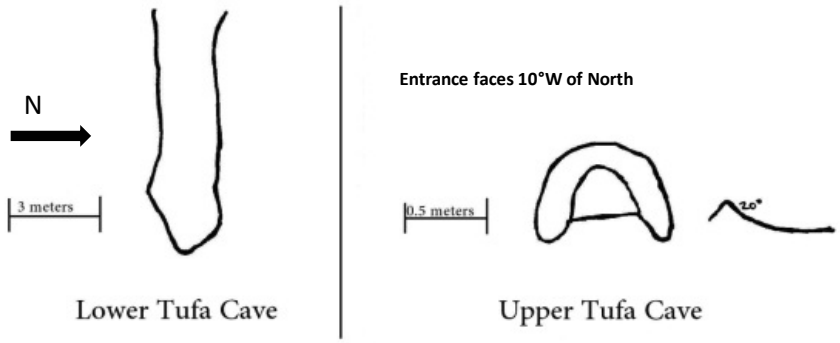
Below the four different caves that were observed in this research are described, with the entrance type interpreted by the researcher. The first two caves were formed in a tufa formation and second two caves were formed in dolomite, for a total of four different caves with two distinctly different geologies.

2.6.1 Upper Tufa Cave

Figure 2.4: Google Earth map of Upper Tufa Cave & Lower Tufa Cave

This cave entrance is located on the upper part of a tufa formation (see Plate 9) and consists of a very small opening with a steep slope above and a steep slope below on its North side and a flat ground entrance on the West side (see Plate 10). This cave is too dangerous to enter and map therefore interpretations are based on direct observations and knowledge of tufa cave formations. What can be recorded are the measurements at the cave opening and a rough estimate of the depth of the cave before it disappears out of sight due to darkness caused by the shape of the cave. This rough estimate puts the depth of this cave at approximately 2.2 meters, this was determined by placing a branch inside the cave entrance and then measuring the branch from the end where is hit the back wall of the cave and the part that was at the entrance. The entrance to Upper Tufa Cave faces 10 degrees West of North towards the stream and inside the entrance there is a 20-degree downward slope.

Figure 2.5: Map of Upper Tufa Cave and Lower Tufa Cave



2.6.2 Lower Tufa Cave

See Figure 2.4 for Google Earth map of Lower Tufa Cave

Lower Tufa Entrance

The entrance to Lower Tufa Cave site is a small cavern type entrance with a height of about 1.5 meters (see Plate 7), due to the positioning of the cave within the tufa formation and the surrounding vegetation this cave goes from light zone to dark zone rather quickly. Lower Tufa Cave goes straight back and does not have any turns or curves, the roof is approximately 1-1.5 meters high, and due to it only having one entrance would most likely not be used by carnivores for denning purposes as they tend to prefer multiple entrances and exits (Kuhn, pers. comm., 2010). The length of the Lower Tufa Cave is approximately 7 meters before the roof descends and meets the floor. The width of this cave fluctuates between 1.6-2 meters across from front to back and has a West facing entrance.

See Figure 2.5 for map of Lower Tufa Cave

This cave is located at the upper portion of the western edge of the tufa formation that occurs along one of the year-round streams found at the Malapa Nature Reserve. This tufa formation is the only formation known of in the region and houses two of the four caves observed in this research. The Upper Tufa Cave and Lower Tufa Cave entrances both appear on the western facing side of the tufa formation, with the Upper Tufa Cave appearing about 2.5 meters above the entrance to the Lower Tufa Cave and 3.5 meters to the South. There is a stream running approximately 5 meters from the front entrances of both tufa caves, and the elevation differences between the two caves causes the water in the stream to flow down a small waterfall.

2.6.3 Porcupine Cave

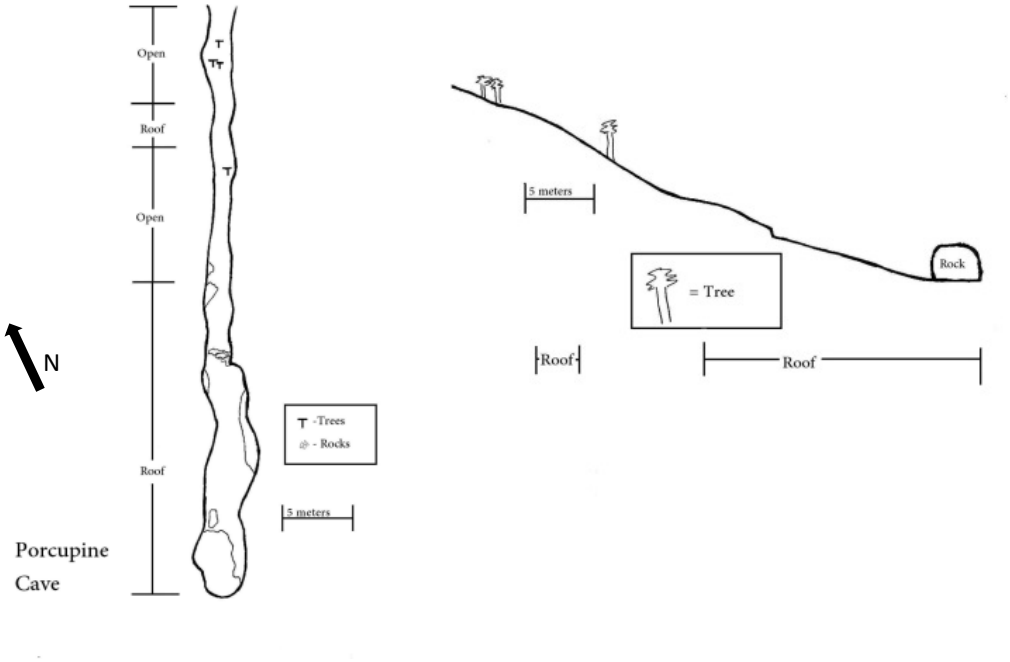
Figure 2.6: Google Earth map of Porcupine Cave

Porcupine Cave was named such due to it being the first cave that porcupines were recorded using on the Malapa Nature Reserve, from earlier research by Berger & Kuhn (2008-2010). Porcupines however have been known to be cave users for many years (Maguire *et al.*, 1980; Brain, 1981), thus porcupine occurrences at this cave are not unfounded. Porcupine Cave is located near to a variety of dolomite fissure caves, including Malapa, which is aged at 1.977 Mya (Kuhn *et al.*, 2011a; Pickering *et al.*, 2011). It is not to say that this cave holds the same age as Malapa, but is only mentioned to give an idea of the age of exposure in this area. The vegetation surrounding Porcupine Cave is mostly dry grass with sporadic tree cover, white stinkwood and wild olive mainly, along the fault line (see Plate 8).

The opening of this cave faces 26 degrees East of North and the total length is ~38.5 meters, of which 15 meters has been exposed by roof collapse, and is roofed for the remaining ~23.5 meters. The roofing covers the cave from the rear for 20.5 meters towards the entrance, with the remaining 3 meters of roof occurring between 6 and 9 meters from the cave entrance. The Porcupine Cave gives opportunity for more than one entrance/exit for more agile animals as it is unroofed for more than one third of it's length, this use can be seen by the large spotted genet leaving from the unroofed section and not the entrance that warthog and

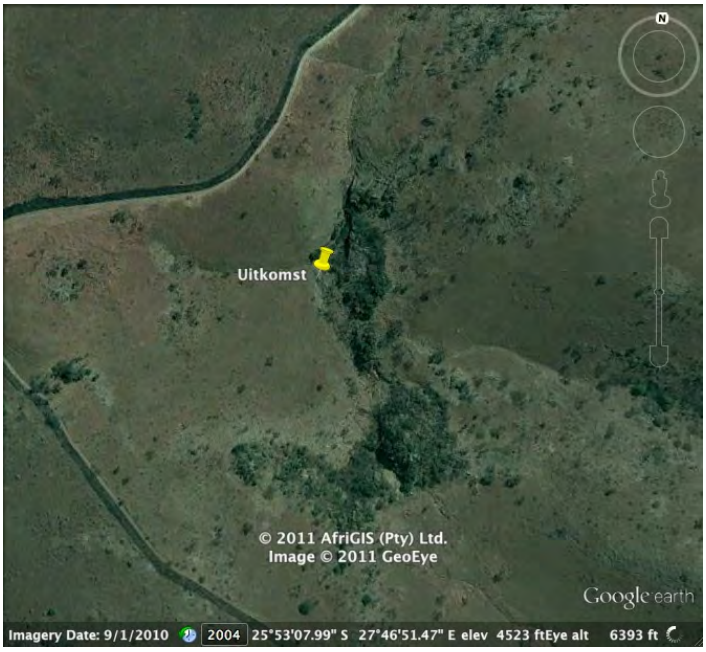
porcupine use. There are many rock clusters located within the cave, and trees occurring where the cave is exposed.

Figure 2.7: Map of Porcupine Cave



2.6.4 Uitkomst Cave

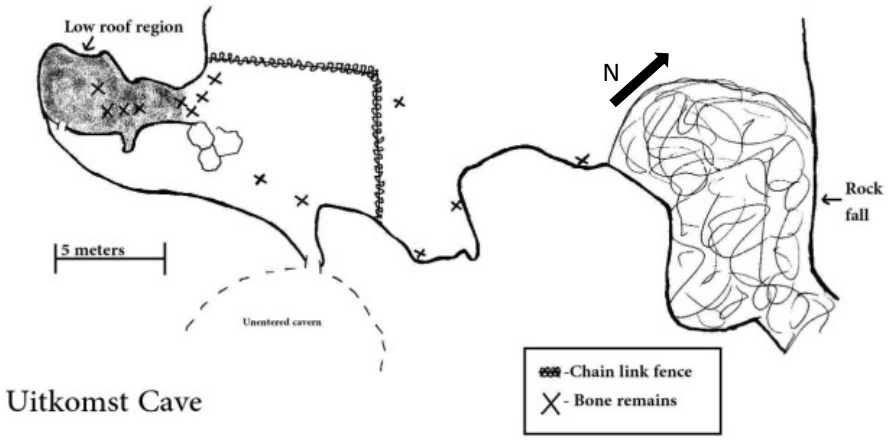
Figure 2.8: Google Earth map of Uitkomst Cave



Stone Age and Iron Age peoples had previously used this cave and these findings were by Revil Mason in the 1960's (Mason, 1962; Hilton-Barber & Berger, 2002). From the previous research there is a fence set-up inside partitioning off half of the cave. This dolomite cave has a large opening on one side and many crevices and rock piles on the opposing side of the cave (see Plate 9). The opposing side, or back portion of the cave, appears ideal for carnivores as it has multiple entry/exit ways. Dry grasses surround this cave with shrub trees occurring in the valley that runs along the front entrance of the cave and larger trees occurring on the top portion.

This cave is located in a valley and just above a small valley that runs through the bottom of the valley. The main entrance to Uitkomst Cave faces 20 degrees North of West. This cave was not approached from the back entrance; therefore it is not possible to describe the back entrance/exit in detail. When seen from the Google Earth image we can see the heavy tree cover in the direct region of the cave, both at the front and the back entrances.

Figure 2.9: Map of Uitkomst Cave



CHAPTER 3: RESULTS

The results are shown as occurrences at caves, including the categories of: entering (Plate 13), above (Plate 14), exiting (Plate 15), guarding (Plate 16), inside (Plate 17), and loitering (Plate 18). The first and third are exactly what they say; entering is when the animal is seen entering the cave, and exiting is when the animals is seen exiting the cave. Above is seen with a baboon that is sitting above the open roofed section of Porcupine Cave. The next one is not as self explanatory, guarding is only seen in the case of the warthog when it will exit a cave and look around or just sit inside of the entrance looking out. Inside occurs mainly at Uitkomst Cave, where all photos are taken from within the cave thus all animals are inside of the cave. Every occurrence at Porcupine Cave also takes place inside, but when possible is recorded as entering or exiting, when Chacma baboons are seen on the trees growing in the exposed region of the cave it is recorded as inside (Plate 19), inside includes enter and exit. Loitering is often referring to animals that neither enter nor exit, but spend a period of time outside of the cave, yet still within the range of the motion sensor camera. A sighting of an animal is when any animal is recorded via the camera trap; regardless of number of animals, to see the number of animals refer to the tables for each cave.

3.1 Camera results

3.1.1 Upper Tufa Cave

Table 3.1: Upper Tufa Cave results

Animal	Scientific name	# of animals	Date	Time	Action
Vervet monkey	*Cercopithecus pygerythus*	1	14-Jun-10	1:24 PM	LOITER
Kudu	*Tragelaphus strepsiceros*	1	19-Jun-10	11:16 PM	LOITER
Leopard*	*Panthera pardus*	1	29-Jun-10	12:02 AM	LOITER
Vervet monkey	*Cercopithecus pygerythus*	1	14-Jul-10	11:44 AM	LOITER
Vervet monkey	*Cercopithecus pygerythus*	1	18-Jul-10	12:02 PM	LOITER
Chacma baboon	*Papio hamadryas ursinus*	1	25-Jul-10	2:26 PM	LOITER
Kudu	*Tragelaphus strepsiceros*	1	28-Jul-10	12:43 PM	LOITER
Chacma baboon	*Papio hamadryas ursinus*	1	4-Aug-10	1:36 PM	LOITER
Vervet monkey	*Cercopithecus pygerythus*	1	7-Aug-10	12:37 PM	LOITER
Warthog	*Phacochoerus africanus*	1	3-Oct-10	12:49 PM	EXIT
Porcupine	*Hystrix africaeaustralis*	2	5-Oct-10	1:13 AM	ENTER
Porcupine	*Hystrix africaeaustralis*	1	15-Oct-10	1:43 AM	EXIT
Warthog	*Phacochoerus africanus*	2	16-Oct-10	5:25 PM	ENTER
Warthog	*Phacochoerus africanus*	1	16-Oct-10	6:04 PM	GUARD
Honey badger*	*Mellivora capensis*	1	16-Oct-10	10:29 PM	LOITER
Warthog	*Phacochoerus africanus*	1	17-Oct-10	9:34 AM	GUARD
Warthog	*Phacochoerus africanus*	1	17-Oct-10	5:51 PM	ENTER
Warthog	*Phacochoerus africanus*	1	17-Oct-10	5:51 PM	GUARD
Warthog	*Phacochoerus africanus*	1	17-Oct-10	6:00 PM	ENTER
Warthog	*Phacochoerus africanus*	1	17-Oct-10	6:06 PM	ENTER
Warthog	*Phacochoerus africanus*	1	18-Oct-10	7:08 AM	ENTER
Warthog	*Phacochoerus africanus*	2	18-Oct-10	8:27 AM	EXIT
Warthog	*Phacochoerus africanus*	3	18-Oct-10	6:02 PM	ENTER
Warthog	*Phacochoerus africanus*	4	20-Oct-10	6:13 PM	ENTER
Warthog	*Phacochoerus africanus*	1	21-Oct-10	7:19 AM	ENTER
Warthog	*Phacochoerus africanus*	1	21-Oct-10	7:26 AM	EXIT
Warthog	*Phacochoerus africanus*	1	21-Oct-10	7:33 AM	EXIT
Warthog	*Phacochoerus africanus*	3	22-Oct-10	6:36 PM	ENTER
Warthog	*Phacochoerus africanus*	2	23-Oct-10	6:36 AM	ENTER
Warthog	*Phacochoerus africanus*	3	29-Oct-10	6:19 PM	ENTER
Warthog	*Phacochoerus africanus*	3	29-Oct-10	6:19 PM	EXIT
Porcupine	*Hystrix africaeaustralis*	1	2-Nov-10	2:11 AM	EXIT
Vervet monkey	*Cercopithecus pygerythus*	1	7-Nov-10	6:27 AM	LOITER
Warthog	*Phacochoerus africanus*	3	10-Nov-10	5:56 PM	ENTER
Warthog	*Phacochoerus africanus*	1	10-Nov-10	7:54 PM	EXIT
Warthog	*Phacochoerus africanus*	1	10-Nov-10	8:37 PM	EXIT

Warthog	*Phacochoerus africanus*	2	10-Nov-10	8:43 PM	EXIT
Honey badger*	*Mellivora capensis*	1	15-Nov-10	5:59 PM	LOITER
Warthog	*Phacochoerus africanus*	1	19-Nov-10	5:50 PM	EXIT
Warthog	*Phacochoerus africanus*	1	24-Nov-10	8:45 PM	ENTER
Warthog	*Phacochoerus africanus*	3	14-Dec-10	12:13 PM	ENTER

*Animals at cave entrance looking in.
12-Jan-11, 12-Mar-11, 16-Mar-11 there are blown out shots, they are mentioned to show that animals' activity carried on into 2011 and there was most likely a problem with the camera.

Upper Tufa Cave has seven different species recorded at the cave including vervet monkey (*Cercopithecus pygerythus*) (Plate 20), kudu (*Tragelaphus strepsiceros*) (Plate 21), leopard (*Panthera pardus*) (Plate 22), Chacma baboon (*Papio hamadryas ursinus*) (Plate 23), warthog (*Phacochoerus africanus*) (Plate 24), porcupine (*Hystrix africaeaustralis*) (Plate 25), and the honey badger (*Mellivora capensis*) (Plate 26). Upper Tufa Cave, along with Porcupine Cave, was the most frequented cave with forty-one animal occurrences.

3.1.2 Lower Tufa Cave

Table 3.2: Lower Tufa Cave results

Animal	Scientific name	# of animals	Date	Time	Action
Kudu*	*Tragelaphus strepsiceros*	3	2-Sep-11	2:24 PM	LOITER
Sable	*Hippotragus niger*	1	10-Sep-11	3:23 PM	LOITER
Warthog	*Phacochoerus africanus*	1	1-Oct-11	5:03 PM	ENTER
Warthog	*Phacochoerus africanus*	2	1-Oct-11	5:37 PM	EXIT
Warthog	*Phacochoerus africanus*	2	1-Oct-11	5:53 PM	EXIT
Warthog	*Phacochoerus africanus*	2	1-Oct-11	6:01 PM	EXIT
Warthog	*Phacochoerus africanus*	1	1-Oct-11	6:33 PM	EXIT
Warthog	*Phacochoerus africanus*	1	2-Oct-11	11:19 AM	EXIT
Warthog	*Phacochoerus africanus*	1	3-Oct-11	8:02 AM	ENTER
Warthog	*Phacochoerus africanus*	1	3-Oct-11	5:59 PM	EXIT

*Group of Kudu, never more than 2 in shot at once.
The photos taken at this cave were occasionally over exposed making animal counts difficult.

Lower Tufa Cave has three different species recorded at the cave entrance including kudu (*Tragelaphus strepsiceros*) (Plate 27), sable (*Hippotragus niger*) (Plate 28), and warthog (*Phacochoerus africanus*) (Plate 29). The warthog is the only animal that is recorded entering or exiting the cave, with the two bovids only seen loitering at the caves entrance. Lower Tufa Cave was the least frequented cave with only ten animal occurrences.

3.1.3 Porcupine Cave

Table 3.3: Porcupine Cave results

Animal	Scientific name	# of animals	Date	Time	Action
Warthog	*Phacochoerus africanus*	1	19-Apr-11	9:02 AM	ENTER
Porcupine	*Hystrix africaeaustralis*	2	9-May-11	6:43 PM	ENTER
Warthog	*Phacochoerus africanus*	1	14-May-11	8:27 AM	ENTER
Warthog	*Phacochoerus africanus*	1	14-May-11	8:28 AM	ENTER
Warthog	*Phacochoerus africanus*	3	14-May-11	8:40 AM	EXIT
Warthog	*Phacochoerus africanus*	1	7-Jun-11	8:55 AM	ENTER
Warthog	*Phacochoerus africanus*	1	7-Jun-11	8:56 AM	EXIT
Large-spotted genet	*Genetta tigrina*	1	26-Jun-11	11:40 PM	EXIT
Warthog	*Phacochoerus africanus*	1	5-Jul-11	10:24 AM	ENTER
Warthog	*Phacochoerus africanus*	1	5-Jul-11	10:27 AM	EXIT
Warthog	*Phacochoerus africanus*	2	10-Jul-11	8:36 AM	ENTER
Warthog	*Phacochoerus africanus*	1	10-Jul-11	8:39 AM	ENTER
Warthog	*Phacochoerus africanus*	4	10-Jul-11	8:45 AM	EXIT
Porcupine	*Hystrix africaeaustralis*	1	17-Jul-11	6:58 PM	EXIT
Brown hyaena	*Parahyaena brunnea*	1	30-Aug-11	7:52 AM	ENTER
Warthog	*Phacochoerus africanus*	1	3-Sep-11	8:49 AM	ENTER
Warthog	*Phacochoerus africanus*	1	3-Sep-11	8:50 AM	EXIT
Warthog	*Phacochoerus africanus*	1	3-Sep-11	12:08 PM	ENTER
Warthog	*Phacochoerus africanus*	1	7-Oct-11	9:41 AM	EXIT
Warthog	*Phacochoerus africanus*	1	11-Oct-11	12:19 PM	EXIT
Chacma baboon	*Papio hamadryas ursinus*	1	28-Oct-11	2:30 PM	LOITER
Chacma baboon	*Papio hamadryas ursinus*	2	28-Oct-11	2:34 PM	LOITER
Warthog	*Phacochoerus africanus*	1	31-Oct-11	9:27 AM	ENTER
Warthog	*Phacochoerus africanus*	1	31-Oct-11	9:29 AM	ENTER
Warthog	*Phacochoerus africanus*	1	28-Nov-11	11:31 AM	ENTER
Warthog	*Phacochoerus africanus*	1	4-Dec-11	8:37 AM	ENTER
Warthog	*Phacochoerus africanus*	1	4-Dec-11	8:56 AM	ENTER
Warthog	*Phacochoerus africanus*	1	13-Dec-11	2:25 PM	ENTER
Black- backed jackal	*Canis mesomelas*	1	13-Dec-11	2:28 PM	ENTER
Warthog	*Phacochoerus africanus*	2	13-Dec-11	2:41 PM	EXIT
Black-backed jackal	*Canis mesomelas*	1	13-Dec-11	3:04 PM	ENTER
Chacma baboon	*Papio hamadryas ursinus*	1	15-Dec-11	1:11 PM	ABOVE
Warthog	*Phacochoerus africanus*	1	19-Dec-11	7:36 AM	ENTER
Warthog	*Phacochoerus africanus*	1	19-Dec-11	12:22 PM	EXIT
Porcupine	*Hystrix africaeaustralis*	1	11-Jan-12	8:28 PM	EXIT

Warthog	*Phacochoerus africanus*	1	11-Jan-12	8:52 AM	ENTER
Warthog	*Phacochoerus africanus*	5	11-Jan-12	9:27 AM	EXIT
Warthog	*Phacochoerus africanus*	1	20-Jan-12	10:59 AM	ENTER
Warthog	*Phacochoerus africanus*	2	20-Jan-12	11:13 AM	EXIT
Porcupine	*Hystrix africaeaustralis*	2	28-Jan-12	7:33 PM	EXIT
Porcupine	*Hystrix africaeaustralis*	1	31-Jan-12	4:46 PM	ENTER

Porcupine Cave has six different species recorded within the cave including warthog (*Phacochoerus africanus*) (Plate 30), porcupine (*Hystrix africaeaustralis*) (Plate 31), large-spotted genet (*Genetta tigrina*) (Plate 1), brown hyaena (*Parahyaena brunnea*) (Plate 32), black-backed jackal (*Canis mesomelas*) (Plate 33), and Chacma baboon (*Papio hamadryas ursinus*) (Plate 19). These six species make for a total of forty-one occurrences between June 2010 and January 2012.

3.1.4 Uitkomst Cave

Table 3.4: Uitkomst Cave results

Animal	Scientific name	# of animals	Date	Time	Action
Warthog	*Phacochoerus africanus*	1	9-Jul-11	1:35 PM	INSIDE
Brown hyaena	*Parahyaena brunnea*	1	17-Jul-11	9:58 PM	INSIDE
Warthog	*Phacochoerus africanus*	1	5-Nov-11	1:24 PM	INSIDE
Warthog	*Phacochoerus africanus*	1	8-Nov-11	5:56 PM	INSIDE
Warthog	*Phacochoerus africanus*	1	8-Nov-11	6:03 PM	INSIDE
Warthog	*Phacochoerus africanus*	1	9-Nov-11	5:45 AM	INSIDE
Warthog	*Phacochoerus africanus*	1	14-Nov-11	8:20 AM	INSIDE
Warthog	*Phacochoerus africanus*	1	14-Nov-11	10:33 AM	INSIDE
Warthog	*Phacochoerus africanus*	2	15-Nov-11	12:40 PM	INSIDE
Warthog	*Phacochoerus africanus*	1	15-Nov-11	1:23 PM	INSIDE
Warthog	*Phacochoerus africanus*	5	16-Nov-11	12:41 PM	INSIDE
Warthog	*Phacochoerus africanus*	1	16-Nov-11	12:45 PM	INSIDE
Warthog	*Phacochoerus africanus*	1	26-Nov-11	10:14 AM	INSIDE
Warthog	*Phacochoerus africanus*	2	3-Dec-11	10:59 AM	INSIDE
Warthog	*Phacochoerus africanus*	1	3-Dec-11	11:33 AM	INSIDE
Warthog	*Phacochoerus africanus*	2	3-Dec-11	11:39 AM	INSIDE
Warthog	*Phacochoerus africanus*	1	3-Dec-11	11:42 AM	INSIDE
Warthog	*Phacochoerus africanus*	1	7-Dec-11	9:46 AM	INSIDE
Warthog	*Phacochoerus africanus*	1	7-Dec-11	12:18 PM	INSIDE
Warthog	*Phacochoerus africanus*	2	7-Dec-11	12:19 PM	INSIDE
Warthog	*Phacochoerus africanus*	2	7-Dec-11	12:25 PM	INSIDE

Uitkomst Cave has two different species recorded within the cave including warthog (*Phacochoerus africanus*) (Plate 34), and brown hyaena (*Parahyaena brunnea*) (Plate 17). This cave has the least amount of species seen with only two, but does not have the least appearances with warthogs seen inside the cave twenty times and the brown hyaena one time for a total of twenty-one appearances. There is a large amount of evidence, quills and scat; implying porcupine has also been using this cave (Plate 35).

3.1.5 Upper Tufa Cave, Lower Tufa Cave, Porcupine Cave, and Uitkomst Cave

Table 3.5: Combined cave results

Animal ACTION	Lower Tufa	Porcupine	Uitkomst	Upper Tufa	Grand Total
Warthog	**8**	**29**	**20**	**26**	**83**
ENTER	2	18		14	**34**
EXIT	6	11		8	**25**
GUARD				4	**4**
INSIDE			20		**20**
Vervet monkey				**5**	**5**
LOITER				5	**5**
Sable	**1**				**1**
LOITER	1				**1**
Porcupine		**5**		**3**	**8**
ENTER		2		1	**3**
EXIT		3		2	**5**
Leopard*				**1**	**1**
LOITER				1	**1**
Large-spotted genet		**1**			**1**
EXIT		1			**1**
Kudu	**1**			**2**	**3**
LOITER	1			2	**3**
Honey badger*				**2**	**2**
LOITER				2	**2**
Chacma baboon		**3**		**2**	**5**
INSIDE		2			**2**
LOITER				2	**2**
ABOVE		1			**1**
Brown hyaena		**1**	**1**		**2**
ENTER		1			**1**
INSIDE			1		**1**
Black-backed jackal		**2**			**2**

ENTER		2			**2**
Grand Total	**10**	**41**	**21**	**41**	**113**

*Honey badgers and leopard we recorded looking into the cave.

As can be seen in Table 3.5 there are 113 occurrences of animals at cave entrances that were recorded during this project from June 2010 to January 2012, a period of 20 months.

CHAPTER 4: DISCUSSION

Additional data has been given by L. Berger & B. Kuhn (unpublished 2008-2010) and has been added to the results with the hopes of giving a better record of cave usage on the Malapa Nature Reserve. This data consists of 25 cave occurrences taking place at Porcupine Cave, Upper Tufa Cave, and Lower Tufa cave prior to the commencement of this study in June 2010.

Table 4.1: Additional data (pre-June 2010)

Animal	Scientific Name	#	Date	Time	Action	Cave
Warthog	*Phacochoerus africanus*	1	12-Dec-09	2:31 PM	ENTER	Lower Tufa
Warthog	*Phacochoerus africanus*	2	12-Dec-09	2:32 PM	ENTER	Lower Tufa
Warthog	*Phacochoerus africanus*	3	16-Dec-09	1:29 PM	ENTER	Lower Tufa
Warthog	*Phacochoerus africanus*	1	16-Dec-09	1:35 PM	EXIT	Lower Tufa
Warthog	*Phacochoerus africanus*	1	2-Jan-10	12:36 PM	GUARD	Lower Tufa
Warthog	*Phacochoerus africanus*	3	22-Feb-10	12:02 PM	ENTER	Lower Tufa
Sable	*Hippotragus niger*	2	15-Mar-10	3:17 PM	LOITER	Lower Tufa
Warthog	*Phacochoerus africanus*	1	9-Jan-08	9:18 AM	EXIT	Upper Tufa
Kudu	*Tragelaphus strepsiceros*	1	9-Jan-08	3:18 PM	LOITER	Upper Tufa
Warthog	*Phacochoerus africanus*	1	7-Feb-08	3:09 PM	EXIT	Upper Tufa
Warthog	*Phacochoerus africanus*	1	9-Feb-08	5:50 PM	ENTER	Upper Tufa
Warthog	*Phacochoerus africanus*	4	8-Apr-10	5:20 PM	ENTER	Upper Tufa
Warthog	*Phacochoerus africanus*	2	9-Apr-10	8:42 AM	EXIT	Upper Tufa
Warthog	*Phacochoerus africanus*	1	9-Apr-10	9:36 AM	LOITER	Upper Tufa
Warthog	*Phacochoerus africanus*	1	9-Apr-10	1:14 PM	GUARD	Upper Tufa
Porcupine	*Hystrix africaeaustralis*	1	10-Jul-09	4:04 AM	ENTER	Porcupine
Porcupine	*Hystrix africaeaustralis*	1	8-Sep-09	6:28 PM	EXIT	Porcupine
Porcupine	*Hystrix africaeaustralis*	1	11-Sep-09	4:47 AM	ENTER	Porcupine
Porcupine	*Hystrix africaeaustralis*	1	11-Sep-09	6:44 PM	EXIT	Porcupine
Porcupine	*Hystrix africaeaustralis*	1	12-Sep-09	5:03 AM	ENTER	Porcupine
Porcupine	*Hystrix africaeaustralis*	1	15-Sep-09	3:20 AM	ENTER	Porcupine
Porcupine	*Hystrix africaeaustralis*	1	15-Sep-09	4:52 AM	EXIT	Porcupine
Porcupine	*Hystrix africaeaustralis*	1	15-Sep-09	5:02 AM	ENTER	Porcupine
Porcupine	*Hystrix africaeaustralis*	1	18-Sep-09	6:30 PM	EXIT	Porcupine
Porcupine	*Hystrix africaeaustralis*	1	19-Sep-09	6:39 PM	EXIT	Porcupine

Represents number of animals

Table 4.2: Study results including pre-June 2010 photos

Animal ACTION	Lower Tufa	Porcupine	Uitkomst	Upper Tufa	Grand Total
Warthog	**14**	**29**	**20**	**33**	**96**
ENTER	6	18		16	40
EXIT	7	11		11	29
GUARD	1			5	6
INSIDE			20		20
LOITER				1	1
Vervet monkey				**5**	**5**
LOITER				5	5
Sable	**2**				**2**
LOITER	2				2
Porcupine		**15**		**3**	**18**
ENTER		7		1	8
EXIT		8		2	10
Leopard*				**1**	**1**
LOITER				1	1
Large-spotted genet		**1**			**1**
EXIT		1			1
Kudu	**1**			**3**	**4**
LOITER	1			3	4
Black-backed jackal		**2**			**2**
ENTER		2			2
Honey badger*				**2**	**2**
LOITER				2	2
Chacma baboon		**3**		**2**	**5**
INSIDE		2			2
LOITER				2	2
ABOVE		1			1
Brown hyaena		**1**	**1**		**2**
ENTER		1			1
INSIDE			1		1
Grand Total	**17**	**51**	**21**	**49**	**138**

4.1 Interpretations

4.1.1 Upper Tufa Cave

Camera coordinates- S 25.52.473' EO 27.46.808'
Date of camera placement/removal- Moultre® Game Camera M50: March 25th, 2010-May 6th, 2011; Bushnell® Trail Sentry: April 12th, 2011-May 6th, 2011, for a total of 17 months.

Table 4.3: Upper Tufa Cave pre-June 2010

Animal	Species	# Of animals	Date	Time	Action
Warthog	*Phacochoerus africanus*	1	9-Jan-08	9:18 AM	EXIT
Kudu	*Tragelaphus strepsiceros*	1	9-Jan-08	3:18 PM	LOITER
Warthog	*Phacochoerus africanus*	1	7-Feb-08	3:09 PM	EXIT
Warthog	*Phacochoerus africanus*	1	9-Feb-08	5:50 PM	ENTER
Warthog	*Phacochoerus africanus*	4	8-Apr-10	5:20 PM	ENTER
Warthog	*Phacochoerus africanus*	2	9-Apr-10	8:42 AM	EXIT
Warthog	*Phacochoerus africanus*	1	9-Apr-10	9:36 AM	LOITER
Warthog	*Phacochoerus africanus*	1	9-Apr-10	1:14 PM	GUARD

L. Berger & B. Kuhn, unpublished data, 2008-2010

Upper Tufa Cave was the most frequented cave in this study with 41 out of 113 post-June 2010 and 49 total animal occurrences at the entrance out of 138 total occurrences of animals at all cave entrances observed, 36.3% and 35.5% respectively. From here on the occurrences mentioned will include all data from this study and the previous study run at these caves, the majority of these occurrences at Upper Tufa Cave were of warthogs with 33 occurrences followed by vervet monkey and porcupine with three occurrences of each. The results have shown that seven species of mammal appear at Upper Tufa Cave: leopard (one occurrence), Chacma baboon (two occurrences), honey badger (two occurrences), porcupine (three occurrences), kudu (three occurrences), vervet monkey (five occurrences), and warthog (33 occurrences).

The results from the motion sensor cameras show that there is not a high percentage of predator activity at Upper Tufa Cave, having only sporadically recorded predator species at this location such as leopard and honey badger, in addition to primates such as Chacma baboon, and vervet monkey. The evidence suggests that predators most often stayed outside of the cave, however leopard and honey badger did appear to inspect the entrance for possible indications of prey within.

The only recorded occurrence of leopard was on June 29th, 2010 at Upper Tufa Cave, and motion sensor cameras do not record any animal inside of the cave for two months and three weeks prior (warthog on April 9th, 2010) and for three months and four days after (warthog on October 3rd, 2010). There were kudu, vervet monkey, and Chacma baboon (June 19th, 2010, June 14th, 2010, and July 25th, 2010 respectively) appearing closer to the occurrence of leopard, but they did not enter the cave. The only other carnivore recorded at Upper Tufa Cave was honey badger on two separate occasions. One honey badger was photographed on October 16th, 2010 at 10:29 pm with warthogs recorded about four hours previously at 6:04 pm and the following day at 9:34 am. The second occurrence of honey badger was on November 15th, 2010 at 5:59 am with warthogs recorded previously on November 10th, 2010 at 8:43 pm and after on November 19th, 2010 at 5:50 pm. It appears that leopard and honey badger are looking into the entrance of Upper Tufa Cave, possibly attempting to locate food. There is not any photographic evidence of animals being inside the cave on June 29th or November 15th, 2010 however it is possible given the recorded entrances and exits of warthog that they were inside the cave on the 16th of October 2010 the first occurrence of the honey badger. Despite evidence showing that warthogs were inside the cave on the 16th of October there is no evidence that the honey badger outside of the entrance acquired any food on this day.

Although not carnivores Chacma baboons are omnivores and thus are potential taphonomic agents, baboons have been photographed at Upper Tufa Cave entrance on two separate occasions; July 25th, 2010 at 2:26 pm and August 4th, 2010 at 1:36 pm, both occurrences taking place in the early afternoon. In the time period between the two instances of Chacma baboon the only animal recorded was a kudu on the 28th of July 2010 at 12:43 pm. Previous to the occurrence of Chacma baboon there were two occurrences of vervet monkey on the 14th and 18th of July at 11:44 am and 12:02 pm respectively, the results shows the next animals to be a vervet monkey as well on August 7th, 2010 at 12:37 pm. After this there were no animals recorded at Upper Tufa Cave for nearly two months between the vervet monkey on August 7th, 2010 and when a warthog was recorded on October 3rd, 2010 at 12:49 pm. On November 7th, 2010 at 6:27 am there is a primate recorded outside of the entrance to Upper Tufa Cave, the photograph is blown out from the sun however due to the size it is thought to be a vervet monkey.

In the time period from March 15th, 2010 to May 6th, 2011 (nearly 15 months) while cameras were functioning at Upper Tufa Cave, there was

no evidence of warthogs occurring at Upper Tufa Cave during the colder months (April 2010 to October 2010). There were technical problems with the camera during 2011, and only a few photos were taken and these were very over exposed, with animals not identifiable, so these results are difficult to interpret. The last occurrence of warthog before it did not appear again for almost six months at Upper Tufa Cave was on April 9th, 2010 at 1:14 pm. The next occurrence of warthog at Upper Tufa Cave was not until October 3rd, 2010 at 12:49 pm. The warthogs were most often recorded at the cave in the evening and morning hours and were only seen during mid-day on three occasions. On April 9th, 2010 at 1:14 pm there was a warthog in the entrance to the cave neither exiting or entering, but appearing to guard and check the surrounding area. The next mid-day appearance was at 12:49 pm on October 3rd, 2010 and this warthog appeared to be leaving the cave, although there is no photograph of it having entered. The last occurrence of a warthog mid-day was on December 14th, 2010 at 12:13 pm with clear evidence of warthog entering the cave, and a blur right after, possibly the warthog darting away. All other warthogs entered the cave between the hours of 5:25 pm and 8:45 pm, and most often exited in the early morning between 6:36 am and 8:27 am. On October 29th, 2010 at 6:19 pm three warthogs approached the cave and entering partially only to immediately leave the cave. Only four times did warthog exit the cave in the evening and three of the four occurrences were from the same day and within one hour, implying a possible anomaly. Warthogs tend to avoid rain (Cumming, 1975) and this behaviour could have been an instance of that type of avoidance. Warthog guarding has also been seen at all times of the day, and often involves letting other warthogs into or out of the cave. Some instances of what the researcher calls guarding are believed to be the warthog backing into the cave on its front leg joint, as has been previously observed by Cumming (1975).

In some occurrences warthogs were recorded doing more than one thing within a short period of time, often entering the cave and loitering inside (seen on October 16th, 2010) the entrance, or entering and exiting almost immediately (seen on October 29th, 2010). It is probable that while warthogs are loitering, or guarding, inside the cave entrance they are actually on the look out for potential predators in the area. Warthogs reversing into holes has been observed and described by Cumming (1975). Cumming (1975) has observed the behaviour of a warthog leaving its hole on two occasions and on both of these occasions the warthogs slowly emerged from the hole, at first only its head, it thought to be sniffing and looking around for predators (Cumming, 1975). Cumming (1975) has

also observed that the warthog has on occasion been seen bursting out of its hole at a very quick speed only to slow down once it has cleared the area. In the study conducted at the Malapa Nature Reserve carnivores were observed waiting outside of warthog holes (at Upper Tufa Cave), so it is possible that this behaviour is to avoid predation.

There were juvenile warthogs recorded at this cave.

Time spent within Upper Tufa Cave ranges from less than one minute (by warthogs) on October 29th, 2010, entering at 6:19 pm and exiting at 6:19 pm, to 15 hours and 22 minutes (by warthog) entering April 8th, 2009 at 5:20 pm and leaving April 9th, 2009 at 8:42 am.

4.1.2 Lower Tufa Cave

Camera coordinates- S25.52.480' EO 27.46.808'
Date of camera placement/removal- Moultre® Game Camera M50: December 2nd, 2009-March 15th, 2010; Bushnell® Trail Sentry: July 22nd, 2010-August 19th, 2010; Bushnell® Trail Sentry (different than previous Bushnell®): September 29th, 2011- October 13th, 2011 (pulled for repairs), for a total of eight months.

Table 4.4: Lower Tufa Cave pre June 2010 findings

Animal	Scientific name	# Of animals	Date	Time	Action
Warthog	*Phacochoerus africanus*	1	12-Dec-09	2:31 PM	ENTER
Warthog	*Phacochoerus africanus*	2	12-Dec-09	2:32 PM	ENTER
Warthog	*Phacochoerus africanus*	3	16-Dec-09	1:29 PM	ENTER
Warthog	*Phacochoerus africanus*	1	16-Dec-09	1:35 PM	EXIT
Warthog	*Phacochoerus africanus*	1	2-Jan-10	12:36 PM	GUARD
Warthog	*Phacochoerus africanus*	3	22-Feb-10	12:02 PM	ENTER
Sable	*Hippotragus niger*	2	15-Mar-10	3:17 PM	LOITER

L. Berger & B. Kuhn, unpublished data, 2008-2010

Lower Tufa Cave was the least active cave with two bovids, sable and kudu, loitering at the cave entrance and only one species recorded, the warthog, entering and exiting the cave. Lower Tufa Cave had ten post-June 2010 occurrences, and 17 total occurrences of animals at the entrance, 14 warthog, two sables and one kudu. Both the sable and the kudu were only seen loitering outside of the cave entrance. The sable was seen March 15th, 2010 at 3:17 pm and again on September 10th, 2011 at 3:23 pm. The kudu was seen September 2nd, 2011 at 2:24 pm. There was one occurrence of warthog entering the Lower Tufa Cave at 8:02 am on

October 3rd, 2011 and not leaving until 5:59 pm the same day, which seems to be the opposite of the warthog's normal diurnal behaviour and is the longest time that a warthog was recorded at Lower Tufa Cave during this research. Most of the occurrences of the warthog entering Lower Tufa Cave are in the early afternoon between 12:02 pm and 2:32 pm, with the exceptions being October 1st, 2011 at 5:03 pm and October 3rd, 2011 at 8:02 am. Warthogs were most often seen exiting Lower Tufa Cave in the early evening hours between 5:37 pm and 6:33 pm, with the exceptions being December 16th, 2009 at 1:35 pm and October 2nd, 2011 at 11:19 am. This is also of interest because four of the five total occurrences of warthogs leaving in the early evening take place on the same day, and it appeared to be the same two warthogs repeatedly come out to check the area surrounding the cave entrance.

There were very small juvenile warthogs recorded at this cave.

Time spent within Lower Tufa Cave ranges from six minutes (by warthog) on December 16th, 2009, entering at 1:29 pm and exiting at 1:35 pm, to nine hours and 57 minutes (by warthog) on October 3rd, 2011, entering at 8:02 am and exiting at 5:59 pm.

4.1.3 Porcupine Cave

Camera coordinates- S 25.53.779' EO 27.48.108'
Date of camera placement/removal- Moultre® Game Camera M50: June 10th, 2009- September 26th, 2009; Lynx Optics® Ranger Trail Camera: April 12th, 2011-January 31st, 2012, for a total of 15 months.

Table 4.5: Porcupine Cave pre June 2010 findings

Animal	Scientific name	# Of animals	Date	Time	Action
Porcupine	*Hystrix africaeaustralis*	1	10-Jul-09	4:04 AM	ENTER
Porcupine	*Hystrix africaeaustralis*	1	8-Sep-09	6:28 PM	EXIT
Porcupine	*Hystrix africaeaustralis*	1	11-Sep-09	4:47 AM	ENTER
Porcupine	*Hystrix africaeaustralis*	1	11-Sep-09	6:44 PM	EXIT
Porcupine	*Hystrix africaeaustralis*	1	12-Sep-09	5:03 AM	ENTER
Porcupine	*Hystrix africaeaustralis*	1	15-Sep-09	3:20 AM	ENTER
Porcupine	*Hystrix africaeaustralis*	1	15-Sep-09	4:52 AM	EXIT
Porcupine	*Hystrix africaeaustralis*	1	15-Sep-09	5:02 AM	ENTER
Porcupine	*Hystrix africaeaustralis*	1	18-Sep-09	6:30 PM	EXIT
Porcupine	*Hystrix africaeaustralis*	1	19-Sep-09	6:39 PM	EXIT

L. Berger & B. Kuhn, unpublished data, 2008-2010

The Porcupine Cave had 41 post-June 2010 occurrences, and 51 total occurrences with the remaining ten occurrences taking place pre-June 2010. From July 10th, 2009 to September 19th, 2009 of the ten instances of porcupines in this cave, nine are from only the month of September. In 2011 there were only two instances of porcupine at this cave early in the year, once on May 9th at 6:43 pm, and again on July 17th at 6:58 pm. In 2012 three porcupines were seen in January; once January 1st, 2012 at 8:28 pm, again on January 28th, 2012 at 7:33pm, and finally on January 31st, 2012 at 4:46 pm. Of the 15 total instances of porcupine at this cave nine were between the hours of 4:46 pm and 8:28 pm and the remaining six occurred between 3:20 am and 5:03 am. The aim of this research was not to determine what these animals were doing inside of these caves, yet it is interesting that the occurrences appear to happen at specific time periods, pre-dawn and sun down. The porcupines most often entered the cave in the early pre-dawn hours and left in the evening hours, this aligns with porcupines being a nocturnal species.

There were three carnivores that occurred at Porcupine Cave over the course of this study. The first recorded carnivore occurrence at Porcupine Cave was of a large-spotted genet photographed exiting the cave via the wall portion of a deroofed section June 26th, 2011 at 11:40 pm.

The second recorded occurrence of a carnivore at Porcupine Cave was a brown hyaena, and took place on August 30th, 2011 at 7:52 am. The brown hyaena was seen entering the cave at this time, but was not seen exiting. Warthog was however seen entering the cave only four days after this occurrence of brown hyaena, on September 3rd, 2011 at 8:49 am, and exiting quickly after at 8:50 am. Then at 12:08 pm the same day (September 3rd, 2011) there was another occurrence of warthog entering, and was not recorded leaving.

On December 13th, 2011 a third carnivore, the black-backed jackal was seen entering Porcupine Cave only three minutes after a juvenile warthog was seen entering. Thirteen minutes later, at 2:41 pm, one adult and one juvenile warthog were seen fleeing the cave. Another jackal was seen at 3:04 pm on the same day entering Porcupine Cave.

Warthogs occur at Porcupine Cave a total of 29 times, once again being the most common animal at a cave. The first occurrence of a warthog at Porcupine Cave was April 19th, 2011 entering the cave at 9:02 am. The last occurrence of warthog was January 20th, 2012 at 11:13 am. In between these dates the warthog occurred at least one time per month

except for the month of August. Of the 29 occurrences of warthog, 79.3% appear to have taken place in the morning hours, with 20.7% of warthog occurrences after 12 pm. These after 12 pm occurrences range from between 12:08 pm to 2:41 pm. Warthogs spent between one minute to four hours and 46 minutes inside of Porcupine Cave, which was different than what was seen at the Upper Tufa Cave where warthog were seen spending over fifteen hours inside of the cave.

There were juvenile warthog and porcupine recorded at this cave.

Time spent within Porcupine Cave ranges from one minute (by porcupine) on June 7th, 2011, entering at 8:55 am and exiting at 8:56 am (also on September 3rd, 2011 entering at 8:49 am and exiting at 8:50 am), to 13 hours and 57 minutes (by porcupine) September 11th, 2009, entering at 4:47 am and exiting at 6:44 pm.

4.1.4 Uitkomst Cave

Camera coordinates- S 25.53.100' EO 27.46.845'
Date of camera placement/removal- Lynx Optics® Ranger Trail Camera: June 29th, 2011-December 8th, 2011, for a total of seven months.

Animal presence at Uitkomst was less common and consists only of brown hyaena and warthog; the brown hyaena was photographed on July 17th, 2011 in the evening with photos being taken between 9:57 pm and 9:58 pm and was the only sighting of this species at this cave. Previous to the arrival of the brown hyaena there was a warthog documented on July 9th, 2011 at 1:35 pm in the afternoon. For many months following the brown hyaena occurrence the motion sensor camera inside this cave remained inactive. It was not until November that this cave became active again when on November 5th, 2011 at 1:24 pm there was a photograph of a warthog in the cave. From November 5th, 2011 to December 7th, 2011 warthog occurred every 3-10 days for a total of 20 occurrences of warthogs at Uitkomst Cave. The group size of warthogs occurring at Uitkomst Cave ranged from a single warthog to a group of up to five warthogs per photo, however most occurrences were of a single warthog. The group of five occurred on November 16th, 2011 at 12:41 pm and was a single adult warthog accompanied by four very small juveniles (see Plate 36).

On two occasions two warthogs were observed fighting each other, which can be seen in Plate 37. It is not clear if these are the same two warthogs

involved in both of the occurrences, as they take place on two separate days, one on December 3rd, 2011 at 11:39 am and the next on December 7th, 2011 at 12:19 pm.

The 19 occurrences of warthog in Uitkomst Cave are divided into three time periods, eight occurrences before noon, nine at midday, and two in the evening, showing no apparent pattern at this cave.

As this camera is located inside the cave it is difficult to speculate time spent within the cave. When there is a pair of photos close together it is the belief of the researcher that the first is the "entrance" and the second the "exit" and example would be on November 16th, 2011 at 12:41 pm there is the first occurrence of a group of warthogs (1 adult and 4 juveniles) and they are photographed sporadically until 12:45 pm when the photographs stop.

4.1.5 Types of caves used

Results have shown that animals today are using caves at a rate that is crucial to acknowledge when taking into account the examination of faunal accumulations. In addition, regarding non-carnivores, the type of cave being used appears to not be of great importance. Warthogs, with a total of 96 occurrences, and porcupines, with a total of 18 occurrences, were the most observed animals using caves, making up 114 of the 138 observed animal occurrences**.** Both warthog and porcupine were also both seen in at least two of the four caves.

Warthog was recorded at all four caves observed in this study and appeared to have had no preference with regard to cave type/structure. This was also seen with porcupine given that porcupines were recorded at both Porcupine Cave and Upper Tufa Cave, and there was significant evidence (quills and scat) of porcupines at Uitkomst Cave. It is interesting that the type of cave does not appear to hold the same significance for all animals at all times, for example porcupines and warthogs do not seem to have strong preferences to cave type or structure, however when long periods of time were spent within the cave the warthog seemed to prefer Upper Tufa Cave. Of all the animals recorded at caves in this study carnivores appeared to be the most preferential in cave choice. It has been recognized that carnivores prefer using caves that have multiple entrances, and it is thought they are preferred so that they can escape if necessary (Owens & Owens, 1979; Skinner *et al.*, 1986; East *et al.*, 1989; Kuhn, pers. comm., 2010).

Guarding is a term used by the researcher to describe warthog behaviour at the Upper Tufa Cave entrance, often coming to the entrance and standing outside while other warthogs enter the cave and again coming and standing at the exit when they leave. Warthog was also observed inside the entrance looking outside for extended periods of time (see Plate 16).

It was originally believed by the researcher that warthogs were not using the Upper Tufa Cave in the colder winter months, April to October, a period of nearly six months. Further examination shows that the period of warthogs not occurring at Upper Tufa Cave also correlates with the occurrence of the leopard in June. In this study warthog were not seen for four months after the occurrence of a leopard at Upper Tufa Cave. This was the only time in this study when warthog were not recorded at this cave for a period longer than three weeks, November 24th, 2010 to December 14th, 2010. It is possible that this absence had to do with the occurrence of the leopard, however as this occurrence of leopard was rare it cannot be used to determine a pattern at this time.

As observed through this research, porcupines have been recorded at two of the four caves (one dolomite and one tufa), and evidence of porcupines (large amounts of quills and scat) was seen at a third cave (dolomite). All three of the caves in question (Porcupine Cave, Upper Tufa Cave, and Uitkomst Cave respectively) are completely different in structure, size, geology, and surrounding vegetation. Porcupine Cave is long, narrow, and a mostly deroofed cave that exists in a dolomite environment and thus does not have as many grasses as other areas on the reserve. Porcupine Cave does however have the distinct clustering of wild olive and white stinkwood trees that indicate caves, fissures, or faultlines (Fleminger, 2006; Steininger *et al.*, 2008; Berger, pers. comm., 2011). Both Upper Tufa Cave and Lower Tufa Cave are within very close proximity to running water as such these two caves have the most diverse vegetation. Uitkomst Cave has a large open entrance facing the road, while the opposite side of the cave is a rock collapse on one side and cavern on the other. There is at least one additional exit amongst the rock collapse section of the cave. The main vegetation that occurs outside of Uitkomst Cave is comprised of dense shrubs at the entrance in the valley with short dry grasses on the hillside, and trees above the cave (see Plate 12).

4.2 Valuable animals not seen at caves during this study

There are a number of other small carnivores that occur at the Malapa Nature Reserve including, African clawless otter (Plate 38), slender mongoose (Plate 39), civet (from previous research there are no photographs of the civet on the Malapa Nature Reserve), serval (Plate 40), caracal (Plate 41), and small spotted genet (Plate 42) that are not seen at caves. Of the greatest significance of these carnivores is the caracal. Although less than 20 kg, the caracal has been known to kill prey up to 60 kg (Mills & Harvey, 2001). Given the caracals prey size it could very well be an animal that a black-backed jackal or brown hyaena may scavenge from. Caracals also use caves as birthing dens (Sunquist & Sunquist, 2002), which may have implications for accumulations.

4.3 Taphonomy revisited

If seven animals can be at one cave entrance within a period of just over four months (as seen at Upper Tufa Cave, with all seven species occurring between June 14, 2010 and October 16, 2010) there is no way to know how many animals could come in contact with a cave throughout the time it may take for a fossil faunal assemblage to accumulate. It must also be taken into consideration that more than one of the same agent may possibly come in contact with a given accumulation over the years it takes to form, for example: if there is a brown hyaena den containing an accumulation of bone it is possible that many years after those hyaenas left the cave another separate group of hyaenas, not necessarily the same species, may inhabit the same cave and in some way alter or add to the bones. This has been seen before when Skinner & van Aarde (1991) recorded members from two different clans of brown hyaenas using the same two dens in the Namib Desert, Namibia, and each den with decades of accumulations thought to be from previous brown hyaena use as well.

It is not a simple process to examine an accumulation of fossils by looking at marks that remain, such as gnaw marks, cut marks, and tooth pits. Determining the animal responsible for accumulating and/or modifying bones is extremely complicated as shown by the results of the studies by Dominguez-Rodrigo & Piqueras (2003) and Pickering *et al*. (2004b). Instead of looking at accumulations with one or two possible accumulators at different periods of time, accumulations must now be examined with the knowledge that there were likely many simultaneous taphonomic agents. There is no set time it takes for a bone to become a fossil, and fossilization can happen by a multitude of processes from minerals in the surrounding soil replacing the bone by filling the empty spaces, to sediment forming a hollow cast of the original specimen (Lyman, 1994a; Hilton-Barber & Berger, 2002). It is crucial to acknowledge that the accumulator of a site is not always the modifier and that both are taphonomic agents regardless. It is with this in mind that research recognizes that bones can be modified by more than one animal over a short period of time, and also that bones can be modified first outside of a cave by one animal and be brought in by a different animal at a later time.

Although this study was focused on multiple accumulators there was evidence of cave use by single species as well, however it was not always documented with certainty whether other animals entered said caves. In this research the only animal that was seen inside of the Lower Tufa Cave was warthog, with both sable and kudu seen outside of the entrance.

Evidence has also been seen of a cave that was hypothesized as having been used solely by a leopard on the Malapa Nature Reserve (de Ruiter & Berger, 2000). At this time however there was no motion sensor camera evidence at the cave entrances. The evidence that exists is that leopards cached food in the recesses of the caves and there is no indication that this cached food had undergone subsequent gnawing (de Ruiter & Berger, 2000). We see this evidence three more times two with porcupine lairs in South Africa, and a group of several lairs in Kenya. The Hartebeesthoek porcupine lair researched by Maguire (1976) was an isolated porcupine lair and had no other taphonomic agents using it at the time of research. The second instance is at the Nossob porcupine lair that R. Hughes first visited in 1956 and was subsequently investigated by Brain in 1968 and 1969, again this lair appeared to be used solely by porcupines (Brain, 1981). The third instance occurs in Kenya, where eight porcupine dens were investigated for scavenged items used for the honing of teeth (Kibii, 2009). Brain (1981) also suggests that the percentage of gnawed bones within a porcupine assemblage will often reflect the availability of bone; i.e. when there is more bone available in the area the percentage of gnaw marks will decrease and when bone is not as easy to attain the percentage of bones with gnaw marks will increase. Porcupines are known to collect bones regardless of need for honing teeth; it has been suggested by Brian (1981) that this is a possible compulsion.

Once the origin of an accumulation has been determined, if it can be determined, there is then a starting place to examine more in depth about the environment at the time that the accumulation was made. This is relevant because the more that is known about the animal or animals responsible for accumulating and/or modifying the more accurate information can be extrapolated about the past; including animal behaviour, landscape and climate. The less that is known about which animal is responsible for creating and affecting an accumulation the more difficult it becomes to extrapolate accurate knowledge of the past landscape. One way that researchers try and determine animals responsible for marks on bones is by examining tooth pits (Blumenschine *et al.*, 1996; Dominguez-Rodrigo & Piqueras, 2003; Pickering *et al.*, 2004b; Njau & Blumenschine, 2006; Delany-Rivera *et al.*, 2009).

It has been established through research that often only the relative size of the carnivore responsible for a tooth pit can often be determined by tooth pit marks, but it cannot be determined with certainty which species was responsible (Dominguez-Rodrigo & Piqueras, 2003; Pickering *et al.*, 2004b), nor does a tooth pit show what animal is responsible for the

accumulation only what size animal has acted on the bone. Tooth pit lengths on cancellous bone are split up into the categories of small (under 4 mm): jackals, leopards and cheetahs; medium (between 4-6 mm): baboon, dog and bear; and large (greater than 6mm): hyaenas and lions (Dominguez-Rodrigo & Piqueras, 2003). The situation become more complicated when tooth pit marks in cortical bone are examined, as marks under 2 mm long most often belong to small carnivores such as mid-sized felids or jackals, and marks larger than 2 mm could belong to any of the remaining carnivores (Dominguez-Rodrigo & Piqueras, 2003). A question that the Dominguez-Rodrigo & Piqueras (2003) study does not address is that of young individuals, which can be problematic because they will also be present as taphonomic agents in accumulations. The research from the Dominguez-Rodrigo & Piqueras (2003) study can help in determining the most likely size of a carnivorous agent (without taking age into account). However even determining the size of the taphonomic agent will not in the end get the researcher what they are looking for, which is the actual collecting and/or modifying agent. This is even more complicated when dealing with animals that are extinct; as their bite force and specific feeding habits have not and cannot be observed. It becomes increasingly difficult to determine the accumulators of the past if we cannot analyze known tooth pit marks of all possible accumulators.

Generally sites are assigned accumulators and modifiers based on probabilities and information learned from actualistic investigations, however the landscape and fauna are different now compared to how they once were which makes this process much more complicated. For example we can know what a leopard mark on bone may look like because leopards still exist today, but there is no way to know with out a doubt what a saber tooth cat mark may look like since these cats have been extinct for at least 1 million years (Turner, 1990). There are fair amounts of species that are potential taphonomic agents, but not enough research has been conducted to say with certainty. These animals, which have been observed at caves in this study, include warthog and honey badger. The possibility of there being additional taphonomic species to consider will make assigning a taphonomic agent to an accumulation much more complicated than previously thought as it represents more unknown variables the researcher must contend with.

The animals that have been observed in this research are extant; however as mentioned above there are at least ten carnivores, which are now extinct, and many others, which have been controlled for by humans, that previously lived in the Cradle of Humankind, and would have had the

opportunity to accumulate and/or modify bones. There is no way that it can be known precisely what the extinct taxa were doing to bones, and information can only be extrapolated from what can be seen with current taphonomic identification research done on the modern counterparts of extinct taxa. The best way to accomplish this is to examine the skeletal anatomy of a similar living animal, which is helpful but cannot give as much accurate information as observing an animals behaviour in it's natural environment.

Carnivores are not the only animals that affect and accumulate bones; omnivores such as baboons (Dominguez-Rodrigo & Piqueras, 2003) and herbivores such as porcupines (Brian, 1981) and most likely warthogs (Cumming, 1975) will also affect bones. The animal that was seen using caves most often in this research was warthog, although this animal is not a confirmed taphonomic agent previous research done on warthogs (Cumming, 1975) and other suids (Galdikas, 1978; Dominguez-Solera & Dominguez-Rodrigo, 2009) has shown that warthogs are likely taphonomic agents. Warthogs are the only animal that were recorded with photographic evidence at all four caves, followed by the porcupine which was photographed at two caves with evidence of the porcupine observed at Uitkomst Cave (a third cave) by the researcher. Although not seen by the motion sensor camera at Uitkomst Cave there are a large number of porcupine quills as well as porcupine scat in this location, implying that porcupines may also be responsible for a portion of the accumulation and subsequent gnawing.

Research has shown that porcupine caves are often shared with other animals, or in other words that porcupines will use the caves of other animals (Diedrich, 2009; Kerbis Peterhans & Singer, 2006). This study has shown porcupines using caves with the same short time period as other animals, and in the case of Porcupine Cave and Uitkomst Cave sharing caves with carnivores. With at least three bone-collecting agents using Porcupine Cave, and two at Uitkomst Cave, it is difficult to know which animal was responsible for the collection and modification. If a cave was occupied first by porcupines and then by carnivores it suggests that it is possible that of all the remains left by porcupines only a small percentage would survive. This implies it is possible that when that accumulation is discovered there may only be minimal bones left with porcupine gnaw marks. What is a necessity to remember is that even with only a small amount of bones showing signs of porcupine gnawing in an accumulation, porcupines were still present and/or occupied the cave site.

4.3.1 Accumulations in the Cradle of Humankind

The Cradle of Humankind has long been home to various animals that have and do use caves to their advantage (Maguire *et al.*, 1980; Brain, 1981; de Ruiter & Berger, 2000; Pickering *et al.*, 2000; Avery *et al.*, 2001; Crawford *et al.*, 2004; Pickering *et al.*, 2004a; 2004b; Pickering, R., 2007; Backwell & d'Errico, 2008; de Ruiter *et al.*, 2008; Backwell *et al.*, 2009; Berger *et al.*, 2009; O'Regan & Menter, 2009; O'Regan & Reynolds, 2009; Avery *et al.*, 2010), and also on occasion fallen to their death when those caves were opened up to the surface and became death traps such as can be seen at Malapa Cave (Dirks *et al.*, 2010). Aside from death traps, accumulations will also form when animals are actively using caves. Some cave sites mentioned previously that occur within the Cradle of Humankind include: Gladysvale, Plovers Lake, Kromdraai, Makapansgat, Swartkrans, and Sterkfontein (Maguire *et al.*, 1980; Brain, 1981; Berger & Tobias, 1994; Avery, 2001; Lacruz *et al.*, 2002; Berger *et al.*, 2003; Crawford *et al.*, 2004; de Ruiter *et al.*, 2008; Steininger *et al.*, 2008; de Ruiter *et al.*, 2009). These cave sites mentioned above have been assigned accumulators or modifiers based on evidence found within the accumulation; i.e. carnivore/ungulate ratios, carnivore damage, live weight of remains, coprolites, and cut marks.

Carnivores have been suggested as accumulators or modifiers of bone at all of the sites mentioned above based on different aspects of what was found within the accumulation. Often times it seems that accumulators are only specified to the family level, and in those situations it is most likely an educated guess. When accumulators or modifiers are often specified as carnivores, or to family level as hyaenids, or felids, and although helpful none of these classifications are specific enough to clearly understand an accumulation as a whole. Given that there are many differences between members of the modern hyaenidae family (Kuhn, *et al.*, 2009; Kuhn, 2011), to speculate that there would not be between hyaenas, extinct or extant, on the palaeo-landscape as well is remiss. To say that a carnivore was responsible for some part of accumulations does little to understand said accumulation, and as we have seen in the past there were at least twenty-five carnivores living in South Africa (see Table 2.4).

The accumulation at the Gladysvale External Deposits was reportedly made and modified by both carnivores and porcupines based on bone modification (Lacruz, 2002; Lacruz *et al.*, 2002). At Plovers Lake brown hyaena is thought to be the main accumulator, based on coprolites and animal remains left behind (de Ruiter *et al.*, 2008). The difference with the

Plovers Lake site is that it is a more recent accumulation made within the past 100 ka, and has evidence left by Middle Stone Age humans as well (de Ruiter *et al.*, 2008). The Grey Breccia of Makapansgat is thought by Maguire *et al.* (1980) to be the work of fossil carnivores and mainly hyaenas based on carnivore damage apparent on fossilized remains, Maguire *et al.* (1980) goes on to state that other carnivores and hominids were likely also involved in this accumulation. The accumulations found at Kromdraai A and Swartkrans Member 1 have been assumed to be due to the actions of both hyaenids and felids based on live weight of remains, and carnivore/ungulate ratios, while Swartkrans Member 2 is thought to be made from human hunters and brown hyaenas based on Acheulean tools, and small carnivore remains, respectively (Brain, 1981). Brain (1981) and Vrba (1975; 1976) suggest that a large felid is responsible for the Member 4 assemblage at Sterkfontein, again based on live weight of the remains, and carnivore/ungulate ratios (Brain, 1981), although Pickering *et al.* (2004a) states that there is not enough evidence to know the accumulator. This pattern of assigning such broad categories as accumulators or modifiers of bones does little to aid in the understanding of the palaeolandscape.

It is accepted that extinct larger felids; such as saber tooth cats (*Homotherium latidens*, and *Megantereon whitei*) and false saber tooth cats (*Dinofelis piveteaui*, and *Dinofelis barlowi*) that existed in the Plio-Pleistocene were also taphonomic agents (Lewis, 1996). It is likely that extinct hyaenas such as the fossil striped hyaena (*Hyaena makapani*) and the giant hyaena (*Pachycrocuta brevirostris*) were also taphonomic agents. However, often within cave sites these extinct species are rarely named as specific accumulators unless under the blanket of carnivore, felid, or hyaenid (Lewis, 1996). Once it can be seen that carnivores contributed to an accumulation it is most often predicted that it is one of two main bone-collecting carnivore families, either the hyaenids or the felids. For example; two sites that are thought to be hyaenid and felid accumulations are Kromdraai A and Swartkrans Member 1 (Brain, 1981). Given how little is known about the past it is difficult to assign an accumulator or modifier to a fossil site when such sites were made in a different time with different fauna existing. This holds especially true for sites pre-dating 1 mya as there were still many carnivores on the landscape at that time that are now extinct, yet this is also relevant for remains at sites younger than 1 mya given that many animals that once lived in the Cradle of Humankind no longer live here although are not extinct.

At present there are at least ten carnivores that are now extinct and had once occurred in the area of the Cradle of Humankind during the Plio-Pleistocene (Turner, 1990; de Ruiter *et al.*, 2009; O'Regan & Reynolds, 2009), when many well-known fossil faunal collections were accumulated. Fossil sites that have at least one of the now extinct taxa within the accumulation include Sterkfontein, Swartkrans, Drimolen, Cooper's Cave, Kromdraai, and Malapa (Maguire *et al.*, 1980; Brain, 1981; Turner, 1990; Lewis, 1996; de Ruiter & Berger, 2000; Pickering *et al.*, 2004a; Pickering *et al.*, 2004b; O'Regan & Menter, 2009; O'Regan & Reynolds, 2009; Dirks *et al.*, 2010; Kuhn *et al.,* 2011). These extinct taxa are also thought to be bone accumulators (Lewis, 1996) and thus must be considered when examining accumulations predating their extinction. With many carnivore species lost either by extinction or habitat relocation and with many ungulates intentionally placed upon the landscape (Kuhn, pers. comm., 2011), it is essential to keep in mind that the animals living in the Cradle of Humankind today are living in a very different ecological system than the one that once existed.

4.3.2 Extinct carnivores vs. extant carnivores

Some of the carnivores that no longer occur in the Cradle of Humankind (as natural predators) are not extinct, but rather have been controlled for by modern humans. This can be seen in Table 2.4 that there are now at least 20 less carnivores living in the Cradle of Humankind today.

There are additional factors, aside from the extinction of certain carnivore competition, which can affect modern carnivore activity such as roads, game fences, and specialized electric fences. Some of these can affect the wild animal population in the Cradle of Humankind more than others by cutting through natural habitats. Animals can cross the roads, however they risk being hit by a passing car, in which case man becomes a mode of death to wild animals. We can see via photographs from a project being run simultaneously at the Malapa Nature Reserve that hyaenas, baboons, honey badgers, and gemsbok are moving between the reserve and the adjacent property despite the game fence. Instances where it is not possible to cross fences include the Rhino & Lion Nature Reserve where animals like lion, cheetah, and wild dog are kept, but specialized electric fences are used that prevent these animals from getting out of their enclosures. Although these animals can be studied here, as has been mentioned previously studying animals that are not existing in their natural habitat does not give a clear picture of their natural behaviour.

It is not only free ranging and caged animals that are living in this landscape today, there are also humans living in the Cradle of Humankind. Humans have and will do what they can to keep their livestock safe and have thus turned to removing specific carnivores from the region via shooting, translocation, poisoning, and trapping (Mills & Harvey, 2001; Fleminger, 2006). These carnivores, specifically lions and spotted hyaenas, are aggressive and social hunters (Mills & Harvey, 2001), which makes them more dangerous to the farmer's livestock. Leopard and brown hyaena however, which are still found free ranging in the Cradle of Humankind today, are extremely adaptable and inconspicuous (Skinner & van Aarde, 1991; de Ruiter & Berger, 2000; Mills & Harvey, 2001; Fleminger, 2006; Hayward *et al.*, 2006; Kuhn, pers. comm., 2010) and it is this adaptability that has given them the edge as humans have attempted to control the landscape.

Today the two largest wild carnivores inhabiting the Malapa Nature Reserve are leopard and brown hyaena followed by an array of smaller carnivore species including (in no particular order): black-backed jackal, caracal, civet, large-spotted genet, small-spotted genet, honey badger, serval, slender mongoose, and African clawless otter (de Ruiter & Berger, 2000; data from this study). Brown hyaenas are typically scavengers, often scavenging from the kills of larger carnivores (Owens & Owens, 1996) and not known to be successful hunters (Kruuk, 1976; Wiesel, 2006). However due to the lack of other large predators on the Malapa Nature Reserve brown hyaena is likely to become an apex predator along with leopard (van der Merwe *et al.*, 2009). As observed by de Ruiter & Berger (2000) leopards will cache many of their larger kills in the caves of the region and it appears that the kills remain un-scavenged.

The reason for the caching of food by leopards is thought to be to prevent scavengers from gaining access to it (de Ruiter & Berger, 2000) and for many years it was the belief of researchers that leopards cached their food mainly in trees (Brain, 1981). The theory then being that these carcasses would fall from the trees, which often occur outside of cave entrances (Fleminger, 2006; Berger, pers. comm., 2011), and would be transported into the caves (Brain, 1981; de Ruiter & Berger, 2000). More current research has shown that leopards living on the Malapa Nature Reserve will cache food remains in the back of the caves located within the reserve (de Ruiter & Berger, 2000). Leopards do cache food in trees (Hayward *et al.*, 2006) but given that leopards are now known to use caves for caching food it is likely that these felids may have had a larger role in cave accumulations than previously understood (de Ruiter & Berger, 2000).

4.4 Summary

Although it is known that many animals are cave users (Dart, 1954; Sutcliffe, 1970; Kruuk, 1972a; Kruuk, 1972b; Winkler & Adams, 1972; Cumming, 1975; Vrba, 1975; Kruuk, 1976; Maguire, 1976; Vrba, 1976; Klein, 1978; Mills & Mills, 1978; Owens & Owens, 1979; Maguire *et al.*, 1980; Skinner *et al.*, 1980; Brain, 1981; Mills, 1982a; Mills, 1982b; Straus, 1982; Skinner *et al.*, 1986; East *at al.*, 1989; Skinner & van Aarde, 1991; Berger, 1993; Doncaster & Woodroffe, 1993; Berger, 1994; Berger *et al.*, 1995; Stiner *et al.*, 1996; Jagnow, 1998; Skinner *et al.*, 1998; Latham, 1999; de Ruiter & Berger, 2000; Pickering *et al.*, 2000; Avery *et al.*, 2001; Begg, 2001; Berger *et al.*, 2002; Hilton-Barber & Berger, 2002; Lacruz, 2002; Lacruz *et al.*, 2002; Pickering, 2002; d'Errico & Backwell, 2003; Berger *et al.*, 2003; Barrett *et al.*, 2004; Pickering *et al.*, 2004a; Pickering *et al.*, 2004b; Kuhn, 2005; Lacruz & Maude, 2005; Rohland *et al.*, 2005; Skinner & Chimimba, 2005; Strong & Goodbar, 2005; Boydston *et al.*, 2006; Skinner, 2006; Fleminger, 2006; Kerbis Peterhans & Singer, 2006; Wiesel, 2006; Pickering *et al.*, 2007; Pokines & Kerbis Peterhans, 2007; Pruetz, 2007; Backwell & d'Errico, 2008; de Ruiter *et al.*, 2008; Kuhn *et al.*, 2008; Steininger *et al.*, 2008; Backwell *et al.*, 2009; Berger *et al.*, 2009; de Ruiter *et al.*, 2009; Diedrich, 2009; Herries *et al.*, 2009; Kibii, 2009; Kuhn *et al.*, 2009; O'Regan & Menter, 2009; O'Regan & Reynolds, 2009; Avery *et al.*, 2010; Kuhn *et al.*, 2010; Wiesel, 2010; Kuhn, 2011; Kuhn *et al.*, 2011a; Pickering *et al.*, 2011; Val *et al.*, 2011; Villaluenga *et al.*, 2011) it is also poignant to remember that the Malapa Nature Reserve has numerous caves, and that all animals on the reserve, and especially the animals observed as cave users during this study, have access to them all. Confirmed taphonomic agents are found at three of the four caves (Upper Tufa Cave, Porcupine Cave, and Uitkomst Cave) yet there are only two caves (Porcupine Cave, and Uitkomst Cave) that have evidence of bone remains. The implications are that although collectors and/or modifiers are using a cave it may not necessarily mean that those caves are collecting bones which leads to the possibilities of different caves being used for different reasons. There is not enough evidence to confirm this theory as Upper Tufa Cave was not entered during this study, so it is unknown if there are remains inside the cave, although upon external examination none were present. Uitkomst was a Late Stone Age to Late Bronze Age site discovered in the early sixties by Revil Mason (Hilton-Barber & Berger, 2002), however was first recognized by Brain (1981) as a brown hyaena den in 1955. Uitkomst Cave today still shows evidence of carnivore occupation from what is most likely a current occupation, and could also include bones from a previous occupation, as this was a known hyaena

den (Brain, 1981). It is not known from photos how the cave is currently being used. There are 14 visible remains located inside Uitkomst Cave and of these most are modified. These remains occur throughout the cave, but are most concentrated at the southern end of the cave in the enclosure that was built during previous excavations in the 20th century. The bones consist of two left bovid humeri, two left bovid femurs, one unknown sided bovid femur, two bovid metacarpals, one bovid radius-ulna, one small cat humerus, one warthog skull, one warthog humerus, one vertebra, some isolated teeth, and a bone shaft fragment (see Plates 43-46).

The two caves that have bone remains are the same two caves that have evidence of brown hyaena, however brown hyaena was only recorded at each cave one time (once at Porcupine Cave and once at Uitkomst Cave). So even when remains are seen within caves carnivores are not often seen at these caves, implying that non-carnivores may have a greater influence on accumulations than previously thought. Porcupine and black-backed jackal were also recorded at one of these two caves (Porcupine Cave) and evidence was seen of porcupine at Uitkomst Cave. Porcupines were seen at the Upper Tufa Cave three times, but it was not safe to enter Upper Tufa Cave and look for possible remains. The fourth cave, Lower Tufa Cave, has only seen evidence of potential bone collectors (warthogs) inside the cave. There are many possible reasons that animals are using caves other than feeding or gnawing on bones some of these reasons include using them for resting sites, thermoregulation, places to consume mineral nutrients, or protection.

4.4.1 Rest

If these caves are being used as places to stop and rest, it is not occurring in all of them equally. Time spent inside caves ranges from less than one minute to more than 15 hours (both occurrences by warthog at Upper Tufa Cave), showing that although animals may use caves for extended time periods they will also often just enter and exit within a very short time period. It does appear that warthogs are using the Upper Tufa Cave for sleeping, with most entrance times occurring around sun down and many exit times occurring in the early morning, often the morning after the sun down entering. Evidence of warthogs sleeping at the other three caves is not as apparent, with the longest occurrence being nine hours and fifty-seven minutes at Lower Tufa Cave on October 3rd, 2011, entering at 8:02 am and exiting at 5:59 pm (opposite of the warthogs typical diurnal sleep cycle). Evidence of a porcupine inside Porcupine Cave for almost 14 hours in one day (September 11th, 2009 a porcupine is inside of the cave for 13

hours and 57 minutes from 4:47 am to 6:44 pm) could imply using the cave for rest, and coincides with porcupines being nocturnal foragers (Grubb *et al.*, 2008).

4.4.2 Thermoregulation

Thermoregulation is another viable option for cave use, yet data from this research shows that caves are used at all temperatures (range of 2°C to 33°C degrees Celsius), with over half of all cave occurrences happen when temperatures were above 20°C, when the temperature was recorded. In addition to this more than half of all warthog occurrences happened when the temperature was above 20°C and involve Upper Tufa Cave, Lower Tufa Cave, and Uitkomst Cave. There were only three recorded occurrences of warthog at Upper Tufa Cave when the temperature was below 20°C, once when the temperature was 14°C and twice when the temperature was 18°C. Interestingly the opposite is seen at Porcupine Cave where warthog occurrences were more typical when the temperature is below 20°C, the reason for this is not clear. Warthogs tended to be more active at caves during the warmer months while porcupines were more active at caves during the colder months.

All occurrences, when the temperature was recorded, inside of Lower Tufa Cave occurred when the temperature was above 25°C. When the temperature was not recorded correlating temperatures at the Upper Tufa Cave during the same month the previous year show the temperature during these times was at a minimum 20°C. Upper Tufa Cave and Lower Tufa Cave appear to have been used more often during the warmer months, especially by warthog, with all unknown temperatures taking place in September and October of 2011 (which are generally warmer months in the Cradle of Humankind). It would appear the Upper Tufa Cave and Lower Tufa Cave, are used by the warthog for thermoregulation of some kind. These two caves are also very close to a water source, which may be a reason they are used more often when the temperatures are higher. The water source also creates more vegetation, as the warmer months are also the rainy months in this region.

Uitkomst Cave and Porcupine Cave appeared to have no significant temperature ranges where they were more active, with overall temperatures ranging from 3°C to 25°C and 2°C to 27°C respectively. All occurrences of warthog at Uitkomst Cave were seen when the temperature ranged between 11°C and 24°C. Occurrences of warthog at Porcupine Cave ranged from 4°C to 26°C, and occurrences of porcupine

at Porcupine Cave ranged from 7°C to 27°C. At the time of this study, and given the aim of this study these temperatures show no specific significance.

Carnivores seem to not have any pattern with regards to temperature and cave use. Leopard was seen when the temperature was 11°C and brown hyaena were seen at 13°C, and 3°C. The honey badger was seen once when the ambient temperature is 15°C and once more when the ambient temperature was 20°C. Lastly the black-backed jackal was seen at both 24°C and 25°C.

4.4.3 Protection

Protection from predators may be another reason for cave use, as can be seen from the results of this work there are times when predators occur outside of the Upper Tufa Cave. There was however no evidence that any animals at the Upper Tufa Cave were ever taken by predator, however these photos may imply that the cave is a place that predators know to look for prey. What is known is that a solitary predators going into the cave to obtain prey might be unwise due to the risk involved, so if the predators were to occur outside of the cave while an animal was inside it may just turn into a waiting game between the two species. Evidence from this study also shows caves being turned into traps for animals, as opposed to places for protection.

A brown hyaena is seen inside of Porcupine Cave with no other animals known to be inside. Results of this study also show a juvenile warthog attempted to escape from a jackal by running into Porcupine Cave, which may imply that caves can also be traps for animals that are chased in. Brown hyaena was also seen inside of Uitkomst Cave.

4.4.4 Bias

As research is often met with bias, assigning taphonomic agents, which is key in understanding the past environments, is also met with bias (Soligo & Andrews, 2005). When all there is to examine is bits and pieces of the full picture it becomes difficult to know what is in front of you.

CHAPTER 5: CONCLUSION

There has been a great deal of work done on the extant cave using fauna of southern Africa (Cumming, 1975; Mills & Mills, 1978; Brain, 1981; Mills, 1982a; Mills; 1982b; Ferguson *et al.*, 1983; Mills; 1984; Skinner & van Aarde, 1991; de Ruiter & Berger, 2000; Begg, 2001; Burgener & Gusset, 2003; Wiesel, 2006; Kuhn *et al.*, 2008; Wiesel, 2010; Kuhn, 2011), however little has been done that examines animal cave usage as a whole. The aim of this study has been to gain a better understanding of modern cave usage by a variety of mammals in the Cradle of Humankind, South Africa. The focus was on the Malapa Nature Reserve, and the implications of multiple taphonomic agents use of said caves over a short period of time. Given that fossil accumulations are often found within caves located in the Cradle of Humankind it becomes extremely relevant to understand how fauna existing on the landscape today are using these caves. The information gleaned from this study will give future researchers a broader knowledge base to interpret accumulations previously found and yet to be discovered.

5.1 Questions

Do animals utilize caves?

Yes, at very high frequencies. In the 20 month period of this study, with ten additional months of previous work included, there were a total of 138 occurrences of at least 11 different mammals (leopard, brown hyaena, large-spotted genet, black-backed jackal, honey badger, porcupine, warthog, Chacma baboon, vervet monkey, kudu, and sable) at cave entrances or inside of caves. Warthog was seen at caves a total of 96 times, which is 69.6% of all animal occurrences. Porcupine was seen 18 times, or 13.0% of all occurrences, and the remaining 17.4% of occurrences were five times or less for brown hyaena, large-spotted genet, leopard, kudu, sable, Chacma baboon, vervet monkey, and honey badger (see Table 4.2: Study results including pre-June 2010 photos).

Is there a preferred time of year for cave use?

October appeared to have the highest frequency of occurrences, with 22 occurrences in October 2010, and 14 in October 2011 for 36 total occurrences in the month of October, out of 138 occurrences, this shows that 26.1% of all recorded cave occurrences took place during the month of October. While 93, or 67.4%, of all occurrences took place between the months of September and December. These results indicate the last four months of the year are the most active months for cave usage at the four caves observed at the Malapa Nature Reserve having 93.5% of all occurrences.

In the warmer months of September thru April warthogs were often seen at Upper Tufa Cave and Lower Tufa Cave, the reason for this is not known, but it is believed by the researcher to be due to these caves close proximity to water.

Porcupines on the other hand are seen at caves during the coldest months of June and July through to the warmer months of September and November, and are also seen in January at Porcupine Cave. The length of this study was too brief to properly understand the porcupines' behaviour.

Which animals are using caves today at the Malapa Nature Reserve?

A total of 11 mammals were recorded at four cave sites located at the Malapa Nature Reserve. There were six species seen inside of caves:

warthog, porcupine, brown hyaena, black-backed jackal, Chacma baboon, and large-spotted genet, and an additional five species seen either at cave entrances, or at a very close proximity to entrances but with no direct photographic evidence of them entering said caves, including: leopard, honey badger, vervet monkey, kudu, and sable. Of the five animals that were seen at entrances, but not inside caves, two of them, the leopard and the honey badger, are known cave users (de Ruiter & Berger, 2000; Begg, 2001; Skinner & Chimimba, 2005). L. Berger & B. Kuhn observed Buck spoor inside of Gladysvale Cave in 2008, evidence that buck will also enter caves.

Do the selected study animals prefer one cave type to another?

Warthogs and porcupines, the two most seen animals occurring 114 times (or 82.6%), appear to have no general preferred cave type although these two animals did appear at different caves during different times of the year. This could have more to do with these species normal behaviour of changing the caves that they are using than the temperature; it is not clear from the scope of this study. It appears that cave type does not have a specific relevance, although proximity to water may be influential in cave choice.

Are there any specific factors that appear in any or all of the caves that could be said are a proxy for the cave being used by specific animals?

None found in this research. Of all 138 occurrences, 51 (37.0%) occurrences were at Porcupine Cave, 49 (35.5%) occurrences were at Upper Tufa Cave, 21 (15.2%) occurrences were at Uitkomst Cave, and 17 (12.3%) occurrences were at Lower Tufa Cave. Upper Tufa Cave and Porcupine Cave are the two most frequented caves in this study and given that one is in a tufa formation and the other is a dolomite cave, respectively, it is seen that type of cave appears to have no influence on usage.

What animals use the same cave more than once and which only appear sporadically?

Frequencies of cave use (including data from L. Berger and B. Kuhn, unpublished, 2008-2010) by animals observed are as follows: warthog and porcupine have the highest percent of occurrences at all four caves

monitored in this study, 69.6% and 13.0% respectively, totaling 82.6%. This shows that these two species are using caves more than any other species recorded.

Chacma baboon and vervet monkey were seen a total of ten times, or about 7.2% of all occurrences. Of these ten primate occurrences only two are inside of a cave, when two Chacma baboons were recorded in a tree in Porcupine Cave.

Cave usage by carnivores was not documented as often as non-carnivores in this study with five carnivore species appearing at caves a total of eight times (leopard, brown hyaena, honey badger, black-backed jackal, and large-spotted genet) making up only 5.8% of all occurrences at caves. Of the eight occurrences, five of them were of carnivores seen inside of caves (brown hyaena at Uitkomst Cave and Porcupine Cave, large-spotted genet at Porcupine Cave, and the black-backed jackal twice at Porcupine Cave). The remaining three occurrences are of leopard seen once, and honey badger seen twice outside of Upper Tufa Cave.

The remaining 4.3% of occurrences are either kudu or sable, both of which are recorded outside of Lower Tufa Cave and Upper Tufa Cave, but near to entrances and as previously mentioned buck spoor has been identified inside of caves.

Are the animals of the Malapa Nature Reserve using the same caves within short period of time?

Yes, the same caves are being used by more than one species over a short period of time. Porcupine Cave is used exclusively by porcupines during the previous study run by L. Berger and B. Kuhn (unpublished work from 2008-2010), and is used mainly by warthogs during the time of this study (June 2010-January 2012). During the time that warthogs are using Porcupine Cave there are at least five other mammals seen inside the cave including porcupine, Chacma baboon, large-spotted genet, black-backed jackal, and brown hyaena. It appears that during the earlier study that Porcupine Cave was an active porcupine den, and that during the time of this study warthog mainly used Porcupine Cave, with only five occurrences of porcupine. This demonstrates Porcupine Cave initially being used primarily by porcupines, and later being used primarily by warthogs.

Upper Tufa Cave had evidence of both warthog and porcupine inside of the cave during the time of this study although warthog were more often recorded, with 26 warthogs and only three porcupines. In previous work by L. Berger and B. Kuhn (unpublished, 2008-2010) there were ten warthogs seen, five entering and five exiting Upper Tufa Cave, and one occurrence of a kudu outside of the cave.

At Uitkomst Cave brown hyaena and warthog have both been recorded inside of the cave. Brown hyaena appeared only one time, and warthog occurred at Uitkomst Cave 20 times. It is likely that there are also porcupine using this cave given the high amount of quills and scat located within.

How many individuals are using the caves within short period of time?

What is seen from the results of this study is that in a period of 20 months there were 113 occurrences, of 11 different species, recorded at four caves. With the additional ten months of work by L. Berger & B. Kuhn (unpublished, 2008-2010) the total number of animal occurrences recorded increases to 138.

5.2 Hypotheses

A) More than one species uses the same caves within a relatively short period of time.

All four of the caves in this study have shown multiple species at caves within a short period of time. This hypothesis has been shown to be true given that in a period of four months (June 14th, 2010 to October 16th, 2010) the Upper Tufa Cave was visited by at least seven species. While in 2011 during the month of July, Uitkomst Cave saw two different species inside. In June and July 2011, and again in December and January 2012, Porcupine Cave had at least three different species. In September and October 2011 Lower Tufa Cave had warthog inside and both kudu and sable seen outside the entrance. The implications for fossil accumulations is that if multiple known or possible taphonomic agents are seen at a cave entrance within 20 months than it would be difficult to speculate how many animals appear in caves where faunal accumulations are forming over a period of 10,000 years or more.

B) Animals prefer certain cave types.

Of the two most active caves, one was formed in a tufa and the other was formed in dolomite, Upper Tufa Cave and Porcupine Cave respectively. There is not enough evidence to support this hypothesis either way although it appears that non-carnivores are not as scrupulous in terms of cave choice, and will use any cave that is accessible to them. There are a very few number of carnivores seen at caves in this study, compared to non-carnivores, and thus it becomes difficult to deduce their particular cave type preference.

5.3 Collector vs. modifier

The distinction between collector and modifier is important. It is true that collector and modifier can be the same animal and if this is the case it makes the work of the researcher that much easier. However it is also possible that these animals are different: for example if the collector was a hyaena, but the modifier was a porcupine. This complicates the work of the researcher, if it is even possible to see the distinction between which animal was responsible for which action. There are numerous examples listed to explain the difficultly in distinguishing between collector and modifier. First this can happen where both animals are the collectors and modifiers; if a brown hyaena collects and modifies, and then a porcupine collects and modifies in the same cave. The next scenario would be to imagine that a brown hyaena scavenges on the kill of a leopard, and then vultures and possibly other scavengers come and finish the work. After this the bones remain in the sun, exposed and weathering, until a porcupine comes and collects said bones and takes them to a cave. In this example the bones would have seen the action of no less than four animals: one collector (porcupine) and three modifiers (leopard, brown hyaena, and vulture), and the porcupine can also be a modifier. This can happen in the reverse as well, if a carnivore makes an assemblage that is later modified by a porcupine or another carnivore. Once an animal has made an accumulation and left it behind it is now exposed to any other animal that comes in contact with it. The cave is also left to possibly have another animal accumulate or modify different material inside, and can be seen within a species when Skinner & van Aarde (1991) observed two brown hyaena dens and saw that each one was used by members of two different clans over the course of their study.

Brain (1981), while speaking of Swartkrans Member 1, states that only one bone of 2,366 (0.04%) shows porcupine gnaw marks, yet in at least three of the four caves observed in this study we see evidence of porcupines present. It seems more reasonable to say that of the remains that have survived in the Swartkrans Member 1 assemblage there is only one bone that shows clear evidence of porcupine gnawing. It has been observed that although porcupines may be present in a den there may be no evidence of gnawing by porcupines found on bones (Skinner *et al.*, 1998). This suggests that although porcupines may be present at a den they may only be the collectors and not the modifiers, or they may just be using the cave without leaving any taphonomic indications. Skinner *et al.* (1986) observed that although porcupines are present in three spotted hyaena

dens examined at Kruger National Park the percentage of porcupine gnawed bones in these dens is only 1.3%, 13.6%, and 15%.

If more than one taphonomic agent is using a cave, and said agents are both accumulators and modifiers, than it cannot be known which animal is responsible for each bone present in the cave.

5.4 Assigning an agent

What has been seen repeatedly is that discovering the accumulator becomes more important that accepting than it cannot be said with certainty what it might have been. For example Sterkfontein Member 4 is placed at an age of 2.16-2.58 mya (Herries & Shaw, 2011) meaning that the Member 4 accumulation could have possibly been collecting for 420,000 years. Although this is a short amount of time when one considers the concept of geological time, it is quite a long time for an accumulation to form. When taken into consideration that in this study, over a period of 20 months (plus an additional ten months of evidence from previous camera traps), and at least 11 species have been seen in that time, it becomes inconceivable to suggest an accumulator for something that has been accruing for over 420,000 years. As has been seen previously Pickering *et al*. (2004a) concluded that the Sterkfontein Member 4 assemblage was most likely made with carnivore involvement, but results are inconclusive as to which carnivore, showing that scientific research is moving towards a place of realization that accumulators cannot always be determined, and that there is still far to go.

Accumulations throughout the Cradle of Humankind have been made over extended periods of time, and with different accumulation theories as well. This is to say that given the time it takes accumulations to accrue determining what animal/s were responsible becomes virtually impossible.

Cooper's Cave D was deposited between 1.4 and 1.5 mya (de Ruiter *et al.*, 2009), a possible accumulation time of 100,000 years. In 2009 de Ruiter *et al.* proposed, based on carnivore/ungulate ratios and high amounts of small carnivores, that Cooper's Cave D was most likely made by a hyaena. Although likely that hyaenas' had a large part in the accumulation and modification at Cooper's it is also likely that there were many under recognized animals responsible as well.

Another site that was accumulated for an even longer time period was Drimolen, which was deposited between 1.5 and 2.0 mya (Backwell & d'Errico, 2008; O'Regan & Menter, 2009), an accumulation time of 500,000 years. It has been hypothesized that Drimolen was collected by felids due to the wide range of felid remains found at the site (O'Regan & Menter, 2009). Seeing how many animals use caves within 20 months, it seems difficult to say that in a period more than 300,000 times as long that a researcher would be able to speculate the collector and/or modifier.

The Makapansgat Limeworks Grey Breccia was most likely accumulated by “fossil carnivores” which would likely have been the fossil striped hyaena (*Hyaena makapani*), or the giant hyaena (*Hyaena brevirostris*) (Maguire *et al.*, 1980). This is interesting because it can only be pure speculation since both of these hyaenids are extinct. Using skeletal anatomy, particularly dentition, it is possible to hypothesize what these hyaena ancestors would have been able to do to bone, however conjecture and best guesses are not the goal of science and will not attain the answers that science seeks. When attributing an accumulation to an extinct species we also run into the problem of not knowing the behaviour of that species and again must hypothesize the diet and pattern of predation.

It is clear that different animals have different dietary niches, with the possibility of overlap in niches as well. The specific diet of carnivores is important to researchers and is why research attempts the greatest amount of accuracy when determining accumulators and/or modifiers of fossil assemblages. For example certain carnivores eat what is most available to them and thus an accumulation made by said carnivore will be more inclusive of the inhabitants (prey) of the region, while other carnivores may choose a specific prey item and thus an accumulation made by one of these carnivores would not necessarily reflect the landscape. If the agent responsible for an accumulation can be determined then it may help researchers put together a more accurate picture of the palaeolandscape. Determining the accumulator becomes far more complicated when there are for example four taphonomic agents at Porcupine Cave: porcupine, brown hyaena, large-spotted genet, and black-backed jackal; with at least two possible taphonomic agents; warthog, and Chacma baboon. With so many agents or possible agents seen at one cave in a period of 20 months it becomes difficult to say that an accumulation spanning hundreds of thousands of years could be made by just one or two agents as has been suggested for many South African fossil sites.

5.5 Implications

The implications of these finds are critical when looking at the fossil record. As accumulations are examined one of the first things that researchers try to determine is the collector and/or modifier (when these two are different) that are responsible for said accumulations. Once the collector and/or modifier of a cave accumulation has been identified, researchers can then look at the specific way that particular animal collects and modifies bones, especially when there is a modern analogue. The difficulty, as has been seen in this study, is that any number of animals can access and use any given cave over a very short period of time. What has also been seen through earlier research is that carnivore patterns are not always predictable (Kruuk, 1972; Brain, 1981; de Ruiter & Berger, 2000; Mills & Harvey, 2001; Burgener & Gusset, 2003; Dominguez-Rodrigo & Piqueras, 2003; Faith, 2007; Kuhn *et al.*, 2009; Kuhn, 2011), so using an accumulation to determine the carnivore responsible is not always viable.

Aside from the difficulty in determining exact accumulators it is also difficult to say that an accumulation was made by any certain number of animals. Fish Hoek Lair for example is thought to have been a brown hyaena den that became a porcupine lair, as well as a leopard den after the porcupine left (Kerbis Peterhans & Singer, 2006). So although it has been acknowledged that more than one species will use the same den (Wiesel, 2006; Kerbis Peterhans & Singer, 2006; Pokines & Kerbis Peterhans, 2007; Diedrich, 2009), what is seen with this research is that this cave usage can and often does occur simultaneously. When dealing with the possibility of multiple animals responsible for an accumulation it becomes increasingly difficult to separate taphonomic marks left behind and it is possible that the research can be misinterpreted due to the bias of the researcher. This study has shown that the idea of having many species using a single cave within a short period of time is not an outrageous thought.

This study has illustrated that many species will use the same cave in a very short period of time and that cave type appears to be irrelevant. Given the length of time it can take for a fossil accumulation to be made makes it extremely difficult to assign any specific actions or species as the sole cause of the accumulation, because most likely many different agents have affected remains in an accumulation that has been exposed for so long. The amount of species using caves in such a short length of time has vast implications when examining the fossil record with regards to cave

use, as many animals are seen to be using caves, as crediting certain species and not all possible agents is remiss.

5.6 Final Thoughts

Actualistic studies that are done to aid in deciphering the past become very complicated because, despite researchers best efforts, the past cannot be recreated. To match the identical scenarios that would have taken place while these fossil accumulations were made is nearly impossible. If this kind of study were to be attempted starting from today, science would have to wait millions of years for the results, and to run a study while controlling all the variables would be nearly impossible. What is seen by this research is that it takes much more than what had previously been thought to determine the accumulator and/or modifier of any given fossil accumulation, and that it may not yet be possible to do so accurately. It is also crucial to remember that the accumulator is not always the same species as the modifier and there does not appear to be a way to distinguish which one is which within a fossil accumulation.

5.6.1 Future Research

This study has brought to light many things that need to be researched further to have a better understanding of the taphonomy is the caves of this region. Future research should be conducted to determine the taphonomic signatures of species such as the warthog and honey badger. Since these animals both occur in modern caves and in fossil cave accumulations it is crucial to understand their possible involvement. Future research should also be done on the large-spotted genet as a taphonomic agent and as a cave user.

Further studies regarding cave use in this area would be helpful to better understand how and why animals are using caves in the Cradle of Humankind and to find more distinct patterns of cave use. These studies should include work on seasonal cave usage, by observing entrances for long time periods and with greater variation in caves paying close attention to proximity to a water source.

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Plate 1: Large-spotted genet (*Genetta tigrina)* at Porcupine Cave

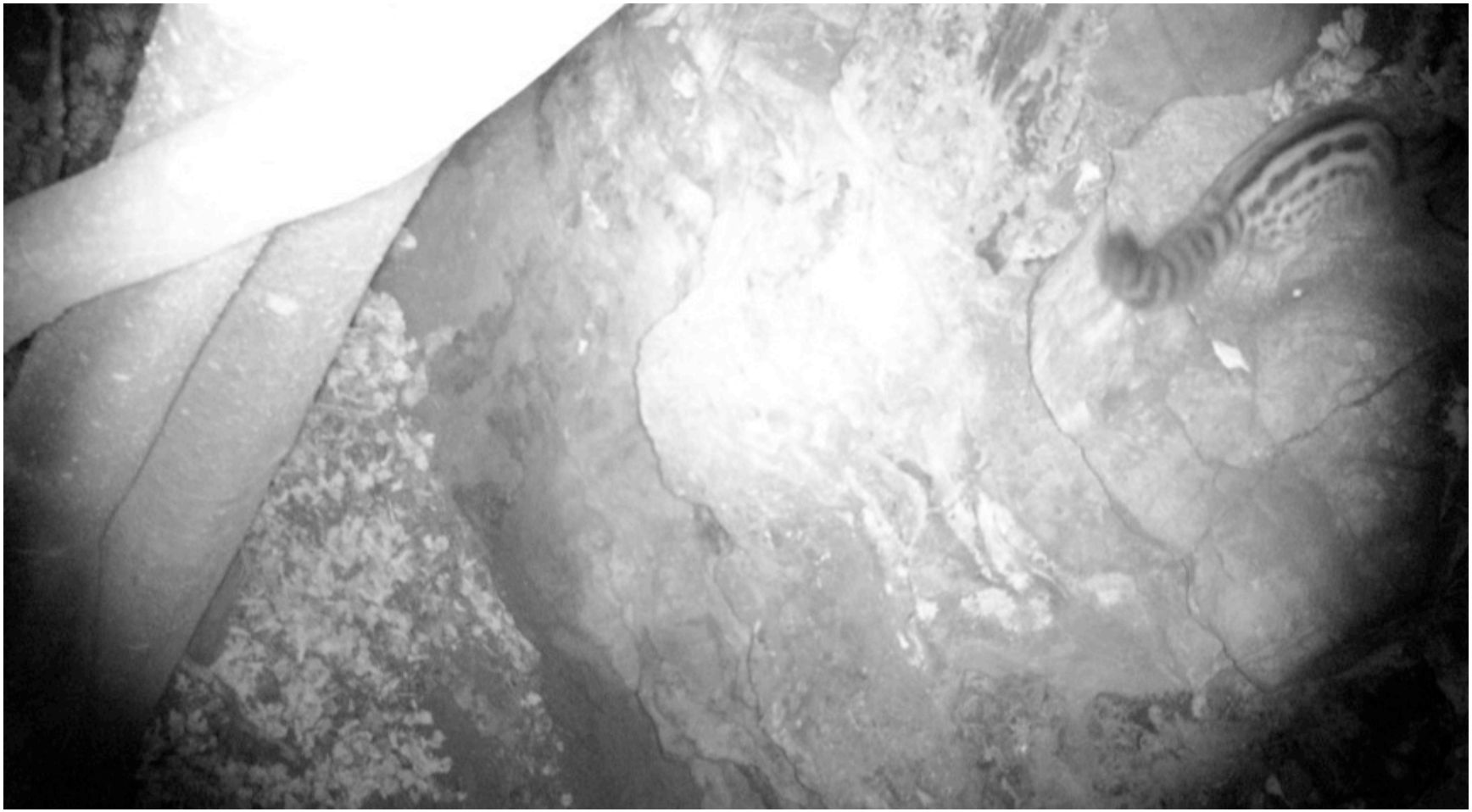

Plate 2: Malapa Nature Reserve during the dry months

Plate 3: Malapa Nature Reserve during the wet months

Plate 4: Dolomite outcrops on the Malapa Nature Reserve

Plate 5: Dolomite outcrops on the Malapa Nature Reserve

Plate 6: Upper Tufa Cave entrance

Plate 7: Lower Tufa Cave entrance

Plate 8: Porcupine Cave entrance

Plate 9: Uitkomst Cave entrance

Plate 10: Tufa formation

Plate 11: A natural spring on the Malapa Nature Reserve

Plate 12: Small valley with dolomite stone

Plate 13: Warthog (*Phacochoerus africanus*) entering

Plate 14: Chacma baboon (*Papio hamadryas ursinus*) above

Plate 15: Porcupine (*Hystrix africaeaustralis*) exiting

Plate 16: Warthog (*Phacochoerus africanus*) guarding

Plate 17: Brown hyaena (*Parahyaena brunnea*) inside

Plate 18: Kudu (*Tragelaphus strepsiceros*) loitering

Plate 19: Chacma baboon (*Papio hamadryas ursinus*) inside

Plate 20: Vervet monkey (*Cercopithecus pygerythus*) at Upper Tufa Cave

Plate 21: Kudu (*Tragelaphus strepsiceros*) at Upper Tufa Cave

Plate 22: Leopard (*Panthera pardus*) at Upper Tufa Cave

Plate 23: Chacma baboon (*Papio hamadryas ursinus*) at Upper Tufa Cave

Plate 24: Warthog (*Phacochoerus africanus*) at Upper Tufa Cave

Plate 25: Porcupine (*Hystrix africaeaustralis*) at Upper Tufa Cave

Plate 27: Honey badger (*Mellivora capensis*) at Upper Tufa Cave

Plate 27: Kudu (*Tragelaphus strepsiceros*) at Lower Tufa Cave

Plate 28: Sable (*Hippotragus niger*) at Lower Tufa Cave

Plate 29: Warthog (*Phacochoerus africanus*) at Lower Tufa Cave

Plate 30: Warthog (*Phacochoerus africanus*) at Porcupine Cave

Plate 31: Porcupine (*Hystrix africaeustralis*) at Porcupine Cave

Plate 32: Brown hyaena (*Parahyaena brunnea*) at Porcupine Cave

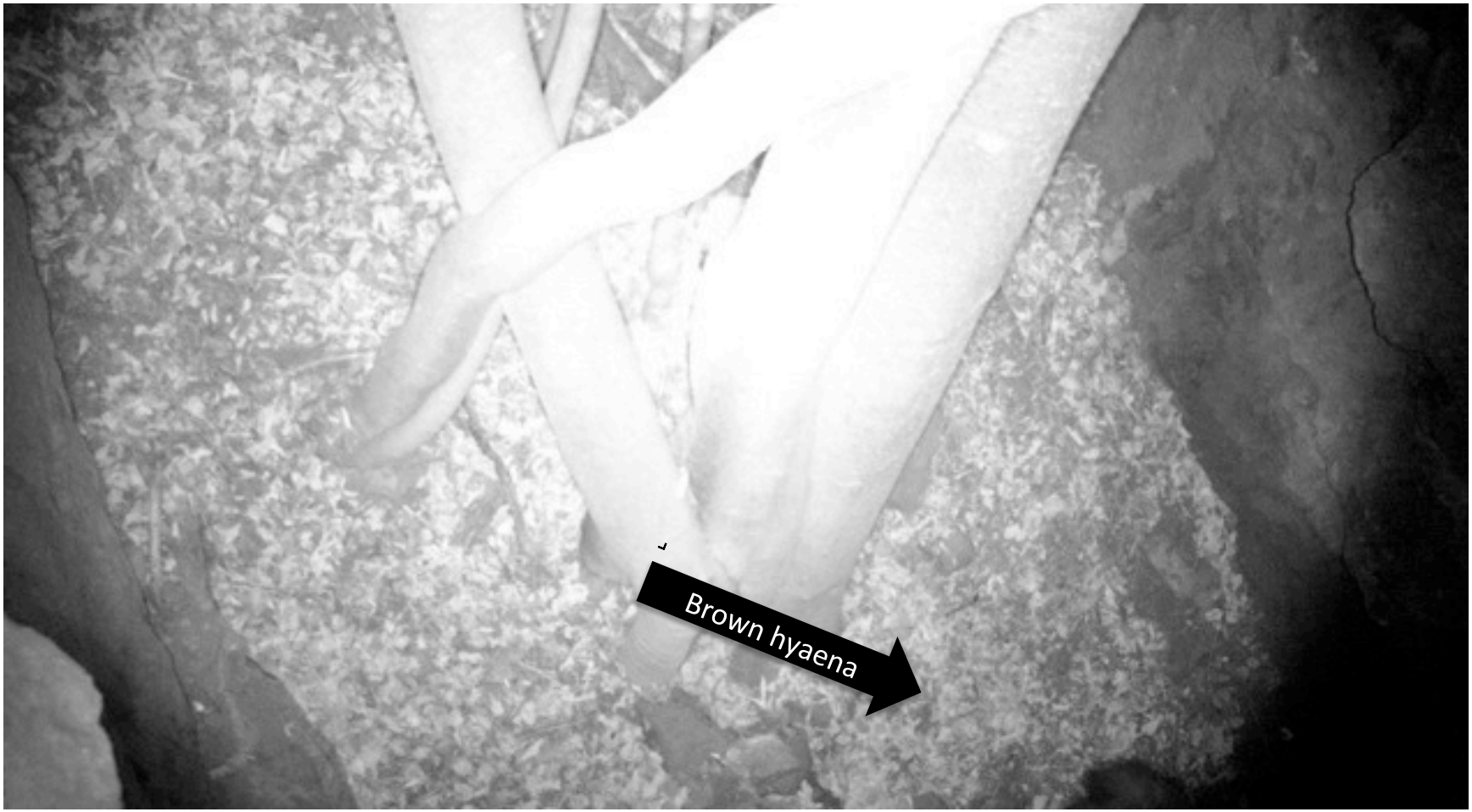

Plate 33: Black-backed jackal (*Canis mesomelas*) at Porcupine Cave

Plate 34: Warthog (*Phacochoerus africanus*) at Uitkomst Cave

Plate 35: Porcupine quills at Uitkomst Cave

Plate 36: Warthog and four juveniles at Uitkomst Cave

Plate 37: Warthogs fighting at Uitkomst Cave

Plate 38: African clawless otter (*Aonyx capensis*) on the Malapa Nature Reserve

Plate 39: Slender mongoose (*Galerella sanquinea*) on the Malapa Nature Reserve

Plate 40: Serval (*Leptailurus serval*) on the Malapa Nature Reserve

Plate 41: Caracal (*Caracal caracal*) on the Malapa Nature Reserve

Plate 42: Small-spotted genet (*Genetta genetta*) on the Malapa Nature Reserve

Plate 43: Bovid metacarpal inside Uitkomst Cave

Plate 44: Bone shaft inside Uitkomst Cave

Plate 45: Bovid femur inside Uitkomst Cave

Plate 46: Suid humerus inside Uitkomst Cave