

Accumulation Behaviours and Taphonomic Signatures for Extant Verreaux's Eagle Nests, *Aquila verreauxii*, in Southern Africa

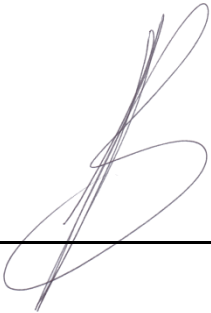
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A Dissertation submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Master of Science.

April, 2013

DECLARATION

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



Stephanie Edwards Baker

On this the 22nd day of April, 2013 at Johannesburg

ABSTRACT

Recognising the mechanisms that led to the deposition of the Plio-Pleistocene caves of South Africa provide an irreplaceable window into the environment at the time. Differentiating between various accumulating agents based on the markings and accumulation variances has become an integral part of palaeontological research. Large birds of prey have been investigated for their connection to the *Australopithecus africanus* type specimen, commonly, the Taung Child. The verreaux's eagle, *Aquila verreauxii*, was investigated in this study to establish whether it produced a taphonomic signature that would be distinguishable from other similarly sized raptors and small mammalian carnivores. Prey remains were collected from 11 nesting-sites in the Gauteng and Northwest Provinces as well as nesting-sites from across the Northern and Western Cape Provinces. The objective was to illustrate how prey selection was directly influenced by the immediate environmental stresses.

Prey was analysed in terms of prey choice, skeletal part representation and the markings that the skeletal elements bore. Of the total of 886 specimens that were collected, rock hyrax (*Procavia capensis*), hares (*Lepus* sp.), Smith's red rock rabbit (*Pronolagus rupestris*) and helmeted guineafowl (*Numida meleagris*) were the most common. The skeletal part representation directly mirrors the feeding behaviour of Verreaux's eagles: body parts with larger muscle attachments and skeletal elements covering choice meat options were most often targeted and damaged. Finally, ten damage types were recorded as well as the combinations thereof, of which chewed and crenulated edges, V-nicks, removal of bone and punctures featured prominently. The results showed that verreaux's eagles do leave a characteristic taphonomic signature in terms of the assemblage composition as well as the markings on bone surfaces.

*In every conceivable manner, the family is the link to our past and the
bridge to our future*

*I dedicate this work to my family who have resolutely supported me,
regardless of the avenue*

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LIST OF ABBREVIATIONS

SITES:

KANP- Klipriviersberg Artificial Nesting Platform

WSBG- Walter Sisulu Botanical Gardens

UTM- Upper Tonquani, Magaliesberg

GVE- Gladysvale

KP- Kameelpoort

GH- Groblershoop

GK- Gifkloof

TK- Tafelkop

PZ- Phillipstown, Zwagershoek

LV- Lockview

DAQ- De Aar Quarry

DAMAGE:

Chewed Edge- CE

Crenulated Edge- CREN

V- Nick- VN

Notch- NT

Scratch- SC

Removal- REM

Puncture- PUNC

Keyhole Puncture- KHP

Acid Etching- AE

NUMERAL

mm- Millimetres

cm- Centimetres

m- Metre

kg- Kilogramme

NOMENCLATURE

Accumulation- The skeletal assemblage that remains as a result of the activities of an accumulator.

Accumulator- The agent, either biotic or abiotic, that collects skeletal and plant remains in accumulations that subsequently fossilize. Also known as a taphonomic agent.

Coprolite- Fossilized faeces.

Diurnal- Active during the daylight hours, opposite of nocturnal.

Minimum Number of Individuals- The fewest possible number of Individuals within an assemblage. Using the example above, MNI= 10. Abbreviated at MNI.

Number of Identified Specimens Presents- The count of bone specimens present in an assemblage where each fragment is counted. The total of these is used as an estimate of individuals present at a site. E.g. if there are five left humeri and ten left femurs identified from an assemblage, NISP= 15. It is often used in concert with Minimum Number of Individuals (See below). Abbreviated as NISP.

Raptor- The avian orders of Falconiformes and Strigiformes which are comprised of carnivorous birds with hooked beaks and talons.

Taphonomy- The study of the processes that act upon animal and plant remains before, during and after fossilization. These processes include (amongst numerous others) decay, scavenging, burial, disturbance and excavation.

Accumulation Behaviours and Taphonomic
Signatures for Extant Verreaux's Eagle
Nests, *Aquila verreauxii*, in Southern Africa

Stephanie Edwards Baker

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CHAPTER 1

INTRODUCTION

1.1. Background

“The analysis and interpretation of complete bone assemblages and representative samples of them has come to be known as taphonomy”

-Brain, 1981, pg. 7.

The term ‘Taphonomy’ was first coined in 1940 by Efremov when he introduced the new discipline within palaeontology (Efremov, 1940). The field entails the study of a fossil or archaeological assemblage as whole rather than studying individual elements. In doing so, one is able to interpret the burial processes that have taken place on the resulting assemblage we see today (Efremov, 1940; Brain, 1981; Klein & Cruz-Urbe, 1984; Andrews, 1990; Lyman, 1994). Taphonomic agents and their individual characteristic features has been the subject of discussion for over two centuries (Buckland, 1822, 1823). The range of species, markings and variations of characteristic taphonomic features have been discussed in length in fossil and archaeological assemblages the world over (Buckland, 1822; Buckland, 1823; Broom, 1934; Washburn, 1957; Dart, 1958; Davis, 1959; Voorhies, 1969; Behrensmeyer, 1975; Mayhew, 1977; Mills & Mills, 1977; Dodson & Wexlar, 1979; Henschel *et al.*, 1979; Boshoff & Palmer, 1980; Maguire *et al.*, 1980; Binford, 1981; Brain, 1981; Scott & Klein, 1981; Wolff, 1981; Bunn, 1983; Klein & Cruz-Urbe, 1984; Potts, 1988; Hill, 1989; Andrews, 1990; Kusmer, 1990; Cruz-Urbe, 1991; Skinner & van Aarde, 1991; Stiner, 1991a, 1991b; Lam, 1992; Lyman, 1994; McKee & Tobias, 1994; Berger & Clarke, 1995; Marean & Ehrhardt, 1995; Villa & Bartham, 1996; Brugal *et al.*, 1997; Bochenâski & Tomek, 1997; Arribas & Palmqvist, 1998; Skinner *et al.*, 1998; Kuhn, 2001; Pickering, 2002; Robert & Vigne, 2002a, 2002b; Pickering *et al.*, 2004; Terry,

2004; Kuhn, 2005; Reed, 2005; Berger, 2006; Kuhn, 2006; McGraw *et al.*, 2006; Berger & McGraw, 2007; de Ruiter *et al.*, 2008; Kuhn *et al.*, 2008; Berger *et al.*, 2009; Domínguez-Solera & Domínguez-Rodrigo, 2009; Gilbert *et al.*, 2009; Kuhn *et al.*, 2009; Reeves, 2009; de Ruiter *et al.*, 2010; Kuhn *et al.*, 2010; McKee, 2010; Kuhn, 2011; Marín Arroyo & Margalida, 2011; Fernández *et al.*, 2012; Krajcarz & Krajcarz, 2012; Kuhn, 2012; Spradely *et al.*, 2012). As such, taphonomic studies have become specialised in focus in terms of differentiating between mammalian (Leopard, hyaenid, hominin, foxes, etc.), reptilian (crocodile- see Njau & Blumenschine, 2006) and avian fauna's as well as abiotic accumulating agents (such as wind and water wash- Voorhies, 1969; Behrensmeyer, 1975; Maguire *et al.*, 1980; Brain, 1981; Klein & Cruz-Urbe, 1984).

Raptor taphonomy in Africa originated as an explanation for the abundance of microfauna remains within fossil assemblages; specifically in relation to owl accumulating behaviours (see Mayhew, 1977; Brain, 1981; Andrews, 1990; Lyman, 1994). The common barn owl (*Tyto alba*) has been studied extensively for its prolific bone collecting capabilities as a result of its affinity for nesting in the twilight zone of cave openings (Duke *et al.*, 1975; Mayhew, 1977; Dodson & Wexlar, 1979; Brain, 1981; Klein & Cruz-Urbe, 1984; Mendelsohn, 1989; Andrews, 1990; Kusmer, 1990; Taylor, 1994; Martínez & Zuberogitia, 2004; Terry, 2004; Reed, 2005; Ortego, 2007; Fernández *et al.*, 2012). Owls have been observed to cast up to three pellets a night (Brain, 1981), which can increase the microfauna component to a fossil assemblage substantially, considering most cave systems are open for thousands of years (Brain, 1981; Mendelsohn, 1989; Martínez & Zuberogitia, 2004; Ortego, 2007). These microfauna have aided in determining the environment during deposition of fossil accumulations as these small mammals are environmentally sensitive (Andrews, 1990).

The discovery of the *Australopithecus africanus* type specimen from the fossil site of Taung, Northwest Province, in 1924 sparked widespread debate regarding the mechanism of accumulation and the palaeo-environment associated with the

hominin child (Dart, 1925; Hrdlička, 1925; Dart, 1929; Broom, 1934; Peabody, 1954; Washburn, 1957; Cipriani, 1928; Binford, 1981; Butzer, 1974; Partridge *et al.*, 1991; McKee, 2010). By analysing taphonomic features on the type skull itself along with those of the hypothetically associated fauna from the Dart Pinnacle (particularly the primate remains), Berger and Clarke (1995) suggested that the accumulating agent responsible for the hominin-bearing assemblage at Taung was a large raptor. Three extant species were suggested as potential analogs for a hypothesized Plio-Pleistocene bird of prey based on their size and ability to carry such large prey items: Verreaux's eagle (*Aquila verreauxii*); Crowned eagle (*Stephanoaetus coronatus*); and Martial eagle (*Polemaetus bellicosus*).

From the assemblage they observed six distinct characteristics that they suggested could be attributed to an eagle's involvement in an accumulation. These features were expanded by subsequent work on fossil Crowned eagle assemblages in both Angola's Humpata Plateau and the modern assemblages of the Ivory Coasts' Tai forest habitats (McGraw *et al.*, 2006; Berger & McGraw, 2007; Gilbert *et al.*, 2009; de Ruiter *et al.*, 2010). The six criteria were: 1) Homogeneous body sizes of prey items having adult live weights of below 20kg; 2) Primate crania were fairly complete with mandibles attached; 3) The presence of tortoise carapaces with very little carnivore damage, if any; 4) The presence of large eggshells; 5) The lack of additional hominin prey items other than the Taung Child; 6) The presence of a cave infill below a large escarpment plateau or high cliff face (Berger & Clarke, 1995). Dart (1925) in his description of the Taung faunal assemblage coined four types of damage which he attributed to the hunting habits of early Australopithecines. These were depressed fractures and punctures, basi-cranium removal, cranium crushing and mandible distortion¹, and finally V-shaped nicks. Berger and Clarke (1995) recognised that these were in fact characteristic of eagle activity on a skeleton.

¹ This appears contradictory to the second criteria listed above as one implies substantial damage whilst the other implies very little damage. Kerbis Peterhans (Pers. comm., 2013) explains that this is often a function of the age of the primate individual. Younger individuals with looser basicranial sutures will most likely appear heavily damaged compared to adults.

The Verreaux's eagle (*Aquila verreauxii*) has long been studied in terms of its unique hunting and nesting behaviour along the cliff faces of southern Africa (Gargett, 1971; Gargett, 1975; Brain, 1981; Frere, 1982; Jubb, 1983; Jenkins, 1984; Allan, 1988b; Gargett, 1990; Davies, 1994; Zinner & Paláez, 1999; Chiweshe, 2007). Verreaux's eagles are capable of carrying prey as large as small Bovidae (such as klipspringer (*Oreotragus oreotragus*), bushbuck (*Tragelaphus scriptus*), common duiker (*Sylvicapra grimmia*), rhebuck (*Pelea capreolus*), damara dik-dik (*Madoqua damarensis*)) and chacma baboons (*Papio hamadryas ursinus*) (Letley, 1962; Visser, 1963; Grobler & Wilson, 1972; Steyn, 1982; Gargett, 1990; Zinner & Paláez, 1999; Chiweshe, 2007). This prey range coupled with their nesting habit of cliff faces and rock facies - possibly above cave openings - makes them a prime example of a raptor that could potentially add a substantial number of individuals to a fossil assemblage (as first noted by Brain, 1981). Understanding the characteristic taphonomic signature created by Verreaux's eagles, and how it differs from mammalian carnivores and other large raptors, is essential to the accurate interpretation of Plio-Pleistocene fossil assemblages as well as the implications an additional carnivore has on the hominin-environmental pressure interactions that so critically drive hominin evolution.

1.2. Raptor taphonomy work done to date

1.2.1. Owls

Owls (Order: Strigiformes) have been the most widely focused upon raptor order when investigating the taphonomic signature in fossil assemblages. The order of Strigiformes dates back to as far as Cretaceous (approximately 60 Mya) with the common barn owl (*Tyto alba*) becoming quite prolific some 25 million years ago (Olsen, 1985; Mortimer, 2004). A number of studies have highlighted the significance of recognizing owl pellets and digestive acid etching in fossil assemblages (Mayhew, 1977; Dodson & Wexlar, 1979; Brain, 1981; Andrews, 1990; Kusmer, 1990; Lyman, 1994; Terry, 2004; Reed, 2005; Fernández *et al.*, 2012). Barn owls often roost in cave mouths or openings and as such collect a large variety of small mammalian and reptilian fauna from the landscape and unintentionally deposit them into the cave system (Dodson & Wexlar, 1979; Brain, 1981; Andrews, 1990; Kusmer, 1990; Lyman, 1994; Terry, 2004; Reed, 2005).

Barn owl pellets are formed when a feeding owl recasts or regurgitates indigestible components of a prey item, namely the denser skeletal elements (such as long bones and skulls), hair and teeth (e.g. Andrews, 1990; Brain, 1981; Lyman, 1994). These are ejected as articulated skeletons, however over time they disperse within the fossil assemblage (Duke *et al.*, 1975; Mayhew, 1977; Brain, 1981; Lyman, 1994; Terry, 2004; Fernández *et al.*, 2012). Brain explained that the common barn owl has been known to collect prey weighing up to approximately 60 grams with up to ten individuals in a night (Brain, 1981, pg. 124-125; Kusmer, 1990; Taylor, 1994). These microfauna make up the bulk of many a fossil assemblage within the dolomitic caves sites throughout the UNESCO 'Fossil Hominid Sites of Sterkfontein, Swartkrans, Kromdraai, and Environs' World Heritage Area, such as Sterkfontein, Swartkrans, Plovers Lake, Kromdraai, Bolts Farm and Makapansgat (Davis, 1959; Brain, 1981; de Ruiter *et al.*, 2008). This ability to add so significantly to the microfauna component of an

assemblage is due to the preferential nesting behaviour of Barn owls to roost within cave mouths in predominantly undisturbed grassland environments (Brain, 1981; Mendelsohn, 1989; Martínez & Zuberogitia, 2004; Ortego, 2007).

Mayhew (1977) was the first to categorically describe the skeletal representation for both diurnal and nocturnal raptor prey items. He described in depth how the pellets of nocturnal raptors, such as owls, preserved larger quantities of undamaged bone material since they swallow complete skeletons (with the exception of the occasional shrew skull and cervical vertebrae) whilst the prey of diurnal raptors, such as Kestrels (*Falco tinnunculus*) are dismembered before feeding and the resulting skeletal representation becomes fragmentary. Furthermore, he illustrated how the digestive acid of diurnal raptors alters the enamel on prey teeth to appear dull and eroded. The opposite is true for dentition recovered from owl pellets- the dental enamel remains intact.

1.2.2.Vultures

Not many studies have been done on vulture taphonomy in conjunction with cave deposits (Robert & Vigne, 2002a, b; Marín Arroyo *et al.*, 2009), however a number have been done in relation to the forensic sciences (Reeves, 2009; Pokines & Baker, 2013). Recognising the patterns that remain on human carcasses that have been accessible to avian scavengers is of paramount importance in order to differentiate between the marks left by scavengers and those potentially related to the cause of death. Vultures are capable of producing large pellets (Kelly *et al.*, 2007) which lead to characteristic acid-etched edges on carrion skeletal remains (Margalida & Bertran, 2001; Margalida, 2008; Reeves, 2009). Furthermore, whilst capable of dispersing skeletal elements over large areas while feeding (over an area of 83.6m², Spradley *et al.*, 2012), they have been shown to be capable of transporting skeletal elements up to 100mm in their beaks (Stolen, 2003). A potential reason for transporting of skeletal elements long distances could be to bring calcium-rich food back to the

nest for chicks (Mundy & Ledger, 1976; Plug, 1978). As a large number of vulture taxa roost in communities (e.g. Cape Griffon (*Gyps coprotheres*) Robertson, 1986), thus these accumulations can become fairly concentrated (Plug, 1978; Thomaides *et al.*, 1989; Yahner *et al.*, 1990).

1.2.3. Eagles

Southern African eagle taphonomy was first investigated in 1981 by Brain in *Hunters or the Hunted?: an introduction to African cave taphonomy* where the nesting behaviour and size of Verreaux's eagles were factors that contributed to its feasibility as an accumulator of fossil assemblages. Since the Verreaux's eagle is one of the largest (by mass) of the southern African eagles its carrying capacity and its ability to carry prey items over larger distances is higher than that of other raptors in the region - for example Letley (1962) observed a Verreaux's eagle attacking and killing a subadult grey rhebuck which weighs approximately 13.5 kg. The rock hyrax (*Procavia capensis*- live weight of approximately 5 kg (Brown *et al.*, 1982)) is reported to be the most commonly selected prey item for Verreaux's eagle throughout the Matopos National Park in Zimbabwe (Brain, 1981; Jenkins, 1984; Gargett, 1990). South African Verreaux's eagles appear to be more diverse with their prey choice, but still uphold a large hyrax component to their diet (Letley, 1962; Visser, 1963; Steyn, 1982). Verreaux's eagles will be discussed in greater detail in a following chapter as they are the focus of the current study.

Berger and Clarke (1995) took the concept of eagle taphonomy further in relation to the deposition of the young *Australopithecus africanus* skull from the Greater Taung Fossil site in the North West Province of South Africa. The skull unfortunately lacks concrete provenience but is loosely associated with either the Dart or Hrdlička Pinnacle sites within the Thabaseek tufa of the Norlim-Buxton Limeworks (Dart, 1925; Hrdlička, 1925; Cipriani, 1928; Dart, 1929; Broom, 1934; Peabody, 1954; McKee & Tobias, 1990; Pickford *et al.*, 1990; Partridge *et al.*, 1991; McKee, 1994; McKee & Tobias, 1994). Using the six criteria proposed by

Berger and Clarke (1995), the work done along the Humpata Plateau focused on comparing both fossil primates from the plateau and those of the Taung assemblages to extant primates killed in the Ivory Coast's Tai Forest (McGraw *et al.*, 2006; Berger & McGraw, 2007; Gilbert *et al.*, 2009). They found that the size distribution, faunal composition and damage types were reminiscent of those outlined by Berger and Clarke (1995). Additionally, modern Crowned eagle nests in Ngogo, Kibale National Park (Uganda) showed similar results to those first introduced by Berger and Clarke in that crania were mostly complete with attached mandibles (Sanders *et al.*, 2003). They did however find that hindlimb elements with minimal damage dominated the postcranial remains whilst scapulae were heavily raked by the eagle's talons during feeding (Sanders *et al.*, 2003). They also recognised the presence of damage types classified as nicks, punctures and 'can-opener' (triangular punctures) perforations (Sanders *et al.*, 2003).

The features that are now associated with eagle predation, and specifically Crowned eagles, are mostly focused on the primate prey items that Crowned eagles are known to preferentially select. These include a maximum prey live body weight of approximately 20 kilograms with an average of 8- 10 kg and no items of less than 2kg mean body weight (Daneel, 1979; Brown *et al.*, 1982; Berger and Clarke, 1995; Gilbert *et al.*, 2009). The remains from larger prey species are found as isolated elements, which adhere to the practice of decapitating and dismembering skeletons prior to transporting them back to the nest (Berger and Clarke, 1995). Berger and Clarke (1995) suggested that relatively complete skulls with articulated mandibles were typical for eagle accumulations however Gilbert *et al.* (2009) showed that the cranial remains from the Ivory Coast nests were fragmentary (sometimes crushed) with unattached mandibles. Tortoise carapaces made up a large percentage of the Taung fauna and were also listed as a potential character of a raptor signature. Fourth, Berger and Clarke list the presence of eggshell as an indicator for raptor involvement; however eggshell has never been noted at any of the Crowned eagle sites subsequently studied.

The fifth characteristic noted by Berger and Clarke (1995) was the absence of any further hominin remains within the Dart and Hrdlička assemblages. The presence of a single, juvenile individual is consistent with the presence of the large numbers of baboon. The infant australopithecine would most likely have been similar in appearance and size of other terrestrial primates on the landscape at the time of deposition. Additionally, that there is only a skull with an attached mandible of this individual led Berger and Clarke to argue its accumulator was in all probability a large raptor. Subsequent publications have shown how there are markings on the skull and mandible that are consistent with those of Crowned eagle predation (Berger, 2006; Berger & McGraw, 2007; Gilbert *et al.*, 2009). This damage is described as crania with holes in both the orbits and vaults, often the occipital is damaged or removed altogether; there are scratches randomly placed across the skulls; there are what are described as V-shaped punctures (due to the beak breaking through the bone) as well as depressions (where a break through the bone leads to fractured and indented bone fragments).

Escarpment nesting is recognized as the final feature of Verreaux's eagle behaviour that adds to the possibility of skeletal elements collecting below a nesting site, either to be fossilized there or washed further downstream into a cavity (Brain, 1981). Recent work by McKee (2010) has suggested that the fossil assemblages of the Dart and Hrdlička Pinnacles at Taung were the result of waterwash, which does not eliminate the involvement of raptors in the accumulation but rather adds a second taphonomic agent in the process to final fossilization. Berger and Clarke (1995) addressed this hypothesis in two ways: firstly, the skeletal elements are neither water polished, nor are they weathered. Secondly, there are no water-worn pebbles or river pebbles in the assemblage. Either of these features would validate McKee's hypothesis of a water-borne assemblage during a dry phase of tufa deposition, the absence thereof suggests an alternative accumulation mechanism. Berger and Clarke suggest that the cavity was in all likelihood below the nesting platform (be it ledge, tree or overhanging rock shelter) of the large bird of prey. This is commonly observed for

Verreaux's eagles, Golden eagles (*Aquila chrysaetos*), Martial eagles and Crowned eagles (Steyn, 1982; Ginn *et al.*, 1989; Gargett, 1990).

An alternative study done on African eagle taphonomy by Stewart and colleagues (1999) focused on the fish-accumulating raptor, the fish eagle (*Haliaeetus vocifer*) at Lake Turkana, Kenya. Fish eagles were first studied for their taphonomic significance by Whitfield and Blaber at Lake St. Lucia, South Africa (1978). Stewart *et al.* (1999) found that fish dominated the assemblage with over 80% of the total prey remains. They also found that prey items were small (limited to <400g for fish and <100g for mammals and birds) and represented a diverse, ecologically restricted selection for the area, including small mammals, aquatic birds, inshore fish, nocturnal mammals and small reptiles (snakes and monitor lizards). They recognised that the nocturnal mammals were probably the result of another raptor feeding whilst the reptiles may have been opportunistic prey items and caught whilst trying to scavenge at the roost (Stewart *et al.*, 1999). Poor skeletal element survivalship was found for fish and bird cranial elements and axial bones, in addition mammalian and reptilian fore- and hindlimb foot elements also survived poorly (Whitfield & Blaber, 1978). However, fish spines, bird longbone elements, as well as mammalian and reptilian cranial and hindlimb elements, survived well. The authors found that the fracture profiles of the bones were similar to those of other diurnal accumulators, albeit that they had proportionally fewer complete bones than other raptor assemblages (Whitfield & Blaber, 1978). They found that the smaller skeletal elements of all prey types survived best whilst long bone mammalian elements exhibited acid corrosion, similar to that observed in other diurnal raptor assemblages, such as Pel's fishing owl (*Scotopelia peli*) (Whitfield & Blaber, 1978).

On another note, the Golden eagle is one of the Verreaux's eagle's closest relatives (Brown, 1970) and has also been studied for its taphonomic importance (Schmitt, 1995; Hocket, 1996). The Golden eagle is similar in size, if not slightly larger than the Verreaux's eagle but its range extends across North America,

Eurasia and parts of northern Africa (Ferguson-Lees & Christie, 2001; Watson, 2010). A large number of studies have been done on the prey items selected for by Golden eagles (Olendorff, 1976; Johns, 1977; Steenhof & Kochert, 1988; Phillips *et al.*, 1996; Mason, 2000) as well as the taphonomic signature (Bramwell *et al.*, 1987; Hoffman, 1988; Hockett, 1989; Hockett, 1995; Schmitt, 1995; Hockett, 1996). Hockett focused predominantly on the skeletal remains found within pellets and observed that they mimicked the corrosion, thinning and polished effects seen in mammalian scat remains (Schmitt & Juell, 1994). Both Hockett (1996) and Schmitt (1995) found that the predominant prey type in Golden eagle prey accumulations were leporid bones. Schmitt noted (1995), having studied Golden eagle assemblages from the Cathedral Roost in Utah, that the high representation of these leporid remains characterised Golden eagle accumulations compared to those of mammalian carnivores, including humans. Furthermore, he noted the high percentage of hind limb elements (specifically tibia and hindfoot bones) with a very low representation of skulls, scapulae and forelimbs. Recorded damage types included jagged, transverse breaks as well as a number of extensively acid-etched remains (however these were not definitively associated with Golden eagle pellets and could have been from coyote scats- Schmitt, 1995; pg. 243). Hare crania showed similar breakage patterns to those collected by Crowned eagles in that the occipital regions and mandibular rami were removed and broken respectively. A very low frequency of punctures was recorded for the Cathedral Roost Golden eagle accumulation, an exception to this was found on multiple tibias.

By combining the broader based damage types (such as removing criteria like the specialised high fish content for the fish eagle, as these are unique to a species), it is possible to tabulate a number of criteria that characterize eagle damage from studies done previously (Brain, 1981; Berger & Clarke, 1995; Schmitt, 1995; Berger, 2006; Berger and McGraw, 2007; Gilbert *et al.*, 2009). In doing so, a model for large raptor taphonomy characteristics is presented (Table 1).

Table 1: A collated list of the previously presented criteria for eagle assemblage recognition. This has been divided into two categories: assemblage characteristics and specific damage characteristics.

Criteria	Author
<i>Assemblage characteristics</i>	
Prey body is size below 20 Kilograms in adult live weight.	Berger & Clarke (1995)
Crania have occipitals removed; and mandibular ramus damage, often the two are unhinged.	Dart (1925) Berger & Clarke (1995) McGraw <i>et al.</i> (2006) Gilbert <i>et al.</i> (2009)
The presence of tortoise carapace with minimal to zero carnivore damage.	Berger & Clarke (1995)
The presence of large eggshell fragment.	Berger & Clarke (1995)
The absence of adult hominins.	Berger & Clarke (1995) Gilbert <i>et al.</i> (2009)
<i>Damage characteristics</i>	
Depressed fractures	Dart (1925) Berger & Clarke (1995)
Punctures	Dart (1925) Berger & Clarke (1995) Sanders <i>et al.</i> (2003)
Crushed skulls	Berger & Clarke (1995)
V-shaped nicks	Dart (1925) Berger & Clarke (1995) Sanders <i>et al.</i> (2003)
‘Can-opener’ perforations	Sanders <i>et al.</i> (2003)
Acid-etching	Schmitt (1995) Hockett (1996) Whitfield & Blaber (1978)

1.3. Mammalian carnivore taphonomy

In order to truly recognise the characteristics of raptor taphonomy fully one needs to investigate how it differs from that of mammalian carnivores. Mammalian carnivores have been studied in far greater detail over a wider scope of palaeontological and archaeological depositional scenarios. The most prolifically studied within the South African context are the hyaena and leopard populations as these are considered the more habitual cave-users and bone collectors.

1.3.1. Small carnivores

Possibly the most relevant bone accumulator and modifier in terms of comparisons to eagles are the small mammalian carnivores. These carnivores are collecting prey items within similar size ranges as eagles, and with their smaller dentition and lesser bite force, could potentially leave taphonomic marks similar to those left by eagles during the feeding process (Bothma, 1971; Stuart, 1981; Hawks, 1987; Kok, 1996; Virgós *et al.*, 1999; Rosalina & Santo-Reis, 2002; Fredriani *et al.*, 2000). These small mammalian carnivores are in the families of Mustelidae (otters, badgers, weasels, polecats and minks), Canidae (dogs, wolves, jackals, foxes and coyotes), Viverridae (genets and civets) and Herpestidae (mongoose and meerkats). Of these, the smaller canid and the larger mustelid and viverrid groups are of interest.

1.3.1.1. Foxes

The fox (Tribe: Vulpini) is a small, omnivorous canid present on nearly every continent (Lloyd, 1981). Their diet consists of small mammals, small birds, amphibians, reptiles, invertebrates, berries, fruits and eggs (Fredriani *et al.*, 2000). Southern African fox species (such as the Cape fox (*Vulpes chama*)) have never been studied for their bone accumulating capabilities but the European red fox (*Vulpes vulpes*) has (Krajcarz & Krajcarz, 2012). This study focused on the

skeletal remains found within an abandoned underground millstone mine passage in southeastern Poland that had been inhabited by a pair of red foxes. They uncovered 602 bones in 16 clusters throughout the den and found that these varied in number of bones per cluster. The prey species found included five species of bird (domestic chicken (*Gallus gallus domesticus*), pheasant (*Phasianus colchicus*), domestic geese (*Anser anser* f. *domestica*), hooded crow (*Corvus cornix*), and common kestrel (*Falco tinnunculus*)) and eight species of mammals (red fox, domestic cat (*Felis silvestris* f. *catus*), wild cat (*Felis silvestris silvestris*), European badger (*Meles meles*), European hare (*Lepus europaeus*), domestic rabbit (*Oryctolagus cuniculus* f. *domestica*), European roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), domestic pig (*Sus scrofa* f. *domestica*), and a species of bat, Chiroptera).

Damage patterns left by red foxes were collated into three typical types (Krajcarz & Krajcarz, 2012): 1) canine punctures that formed oval holes of over 4mm across, these are found mainly on “flat bones” (like the sternum), aves skulls and pelvic girdles; 2) medium sized punctures found on all bone types measuring 1-2mm across; 3) also found on all bone types were the small punctures (attributed to juvenile red fox gnawing), measuring >0.5mm.

1.3.1.2. Jackals

Black-backed jackals (*Canis mesomelas*) fall within the medium-sized range of the Canidae family in southern Africa and are omnivorous (Walton & Joly, 2003). Their diet consists of small Bovidae, carrion, hares and rabbits, invertebrates and rodents (Bothma 1971; Stuart 1981; Kok 1996). Pitting and markings left by jackals have been investigated to examine their potential role as taphonomic markings and, whilst not distinctively unique to other predators, they do leave tooth scores and pits (Domínguez-Rodrigo & Piqueras, 2003; Walton & Joly, 2003; Delaney-Rivera *et al.*, 2009). Individual jackals do hunt, however, and both Begg (2001) and Wiesel (2006) high-lighted that they also tend to scavenge from other carnivores such as honey badgers and hyaenas, respectively. This could

lead to a mixed deposit and make it difficult to differentiate one carnivore activity from another.

1.3.1.3. *Badgers*

Badgers (Mustelidae) are carnivorous cave-users that have been observed to feed on the bulk of their food items below ground to avoid scavenging from larger carnivores (Kruuk & Mills, 1983; Begg, 2001; Begg *et al.*, 2005a; Begg *et al.*, 2005b; Skinner & Chimimba, 2005; Bountalis, 2012). Furthermore, they have been known to use both caverns and burrows to store food and even to bury their food for later consumption (Smith & Reichman, 1984; Reichman & Smith, 1990). Although no studies have been done to date on the taphonomic signature of the African honey badger (*Mellivora capensis*), the possibility that they are accumulating and modifying skeletal remains is high and warrants attention.

1.3.1.4. *Large-spotted genets*

Genets in general have not been recorded as a taphonomic agent, but as with the badger, there is a potential for them to hoard bone. Large-spotted genets (*Genetta tigrina*) have a carnivorous-insectivorous diet that includes small mammals, invertebrates, amphibians, birds, reptiles and rodents (Hawks, 1987; Virgós *et al.*, 1999; Rosalina & Santo-Reis, 2002).

1.3.2. Large Carnivores

1.3.2.1. *Hyaenids*

There are three extant carnivorous hyaena species on the African landscape today: spotted hyaena (*Crocuta crocuta*); brown hyaena (*Parahyaena brunnea*) and the striped hyaena (*Hyaena hyaena*) with an additional member of the family Hyaenidae being *Proteles cristatus*, the aardwolf, which is a specialised termite hunter (Mills, 1982; Rieger, 1981). Of these three species the most prolifically studied is the spotted hyaena, primarily due to its larger size (Kruuk,

1972; Skinner & Smithers, 1990; Skinner & Chimimba, 2005; Pokines & Kerbis Peterhans, 2007). In the early stages of taphonomic interpretation of bone accumulations in caves in southern Africa, hyaenas were discredited as bone hoarders (Dart, 1956). One of the earliest studies into hyaena taphonomy was that of Buckland (1822, 1823) which explored the possibility of a cave system in England, Kirkdale, being the result of hyaena activity. He reasoned that the reputed bone-hoarding ability of hyaenas (specifically those of the spotted hyaena) and presence of coprolites in the assemblage made them the most likely candidate to have accumulated the deposit (1822). His work was largely undisputed until Professor Raymond Dart adamantly opposed this view in light of his “Osteodontokeratic Culture” hypothesis of 1955. Dart’s investigation into the large bodied assemblage associated with the *Australopithecus prometheus* remains of The Makapansgat Valley Deposits (1957) led him to conclude that the assemblage was the result of early hominin hunting and feeding behaviour rather than that of a large carnivore.

The Osteodontokeratic Culture was subsequently disproved (Hughes, 1954, 1958; Simons, 1966; Sutcliffe, 1970), which prompted a host of other researchers to begin re-examining carnivore involvement in cave system accumulations (Hughes, 1954, 1958; Simons, 1966; Sutcliffe, 1970; Klein, 1978; Shipman & Phillips-Conroy, 1977; Henschel *et al.*, 1979; Haynes, 1980; Klein *et al.*, 1991; Kerbis Peterhans & Horwitz, 1992; Villa & Bartham, 1996; Arribas & Palmqvist, 1998; Pokines & Kerbis Peterhans, 2007). As a result, a large contingent of taphonomic research began to examine the hoarding capabilities and specific features representative of hyaena activity and how to dissociate them from those of both early hominins and other large-bodied carnivores, such as the leopard (*Panthera pardus*) (Hughes, 1954; Washburn, 1957; Simons, 1966; Brain, 1969; Shipman & Phillips-Conroy, 1977; Scott & Klein, 1981; Bunn, 1983; Klein & Cruz-Urbe, 1984; Potts, 1988; Hill, 1989; Cruz-Urbe, 1991; Marean & Ehrhardt, 1995; Pickering, 2002; Pickering *et al.*, 2004; Kuhn *et al.*, 2008; Berger *et al.*, 2009; Kuhn *et al.*, 2009; Kuhn *et al.*, 2010; Kuhn 2011; Kuhn, 2012).

To date a range of different features have been presented to extricate hyaena activity such as those listed first by Cruz-Uribe (1991) and later discussed by Stiner (1991a), Pickering (2002) and Kuhn *et al.* (2010). The comparisons between seven fossil hyaena dens, five archaeological dens, nine modern brown hyaena dens, one striped hyaena den and eight spotted hyaena dens resulted in six criteria for distinguishing between hyaenid and hominin activity (Cruz-Uribe, 1991). These are as follows: 1) A high percentage of carnivore remains within the assemblage (also put forth as a Carnivore-Ungulate ratio of >20% MNI), 2) hyaena damage on the bone surfaces (described as “striations, pitting, grooves, scooping and acid etching”- Cruz-Uribe, 1991), 3) a high percentage of long bone shafts with removed epiphyses, 4) the inverted relationship between cranial-postcranial remains and ungulate size (meaning that with an increase in body size of ungulates, the cranial to postcranial ratio decreases), 5) the lack of small, compacted bones, and 6) attritional age-profiles. To these, Stiner (1991a) added an additional criterion stating that an excess of horn or antler remains were common in hyaena-accumulated assemblages.

Pickering (2002) re-evaluated these criteria in light of modern observational studies of hyaena behaviour (both his own and those of Bearder, 1977; Mills & Mills, 1977; Henschel *et al.*, 1979; Binford, 1981; Brain, 1981; Bunn, 1983; Hill, 1989; Lam, 1992) and based on these observations rejected three of the criteria presented by Cruz-Uribe (1991) as well as the horn abundance criterion posed by Stiner (1991a). He found that the observations of a high carnivore-ungulate ratio, a high proportion of limb shafts with missing epiphyses and the presence of hyaena-inflicted bone surface damage along long bone shafts were valid criteria. More importantly though a new criterion to distinguishing hyaena involvement in an accumulation was introduced- the presence of juvenile hyaena bones (Stiner, 1991b; Brugal *et al.*, 1997; Pickering, 1999) as well as an amendment to the criterion of bone modification (2002): the presence of acid-etched pieces of bone in addition to the presence of coprolites within the assemblage.

More recently all of the retained criteria argued by Pickering (2002) were disproved by Kuhn *et al.* (2010), based on observations from an extensive collection of research projects done on the three extant hyaenid species from both Africa and the Middle East (Kuhn, 2001; Kuhn, 2005; Kuhn, 2006; Kuhn *et al.*, 2008; Kuhn *et al.*, 2009; Kuhn *et al.*, 2010; Kuhn, 2011; Kuhn 2012). Active striped hyaena den contents from the eastern desert of Jordan (Kuhn, 2001; 2005) were collected. Remains from spotted hyaena dens were collected from the Mashatu Game Reserve in Botswana and from the Namib-Naukluft Park, Namibia, while those of brown hyaenas came from the South African sites of Rietvlei Nature Reserve and the John Nash Reserve as well as the Namibian sites around Diamond Area Number 1 (Kuhn, 2006). Additional brown hyaena material was previously collected from along the Namibian coast line by Skinner (Skinner & van Aarde, 1991; Skinner *et al.*, 1998). By accessing in excess of 23 den sites, over 27 000 bone elements were recovered. Based on the findings from this research, Kuhn *et al.* (2010) rejected all of the criteria previously introduced and maintained that only the presence of juvenile hyaena bones and coprolites definitively implicated hyaena activity in an assemblage.

1.3.2.2. *Leopards*

Leopards (*Panthera pardus*) were first introduced as taphonomic agents when Brain described how when feeding, leopards would drag carcasses of their prey up trees in order to avoid larger carnivores stealing their meal, and connected this phenomenon to how the trees – specifically the common acacia (*Acacia caffra*) and wild olives (*Olea europaea* subsp. *africana*) – grow on the outskirts of dolomitic outcrops in the Cradle of Humankind (Brain, 1981). The theory is that once the leopard has finished eating, the prey item is dropped or falls from the tree and lands in a cave below. Alternatively, leopards have been known to use caves for denning and rearing young, which could explain leopard modified carcasses accumulating directly in cave systems (Brain, 1981; de Ruiter & Berger, 2000; Pickering *et al.*, 2004; Skinner & Chimimba, 2005; Bountalis, 2012).

Leopards deflesh bone rather than crush like hyaenids, and as such the bulk of their tooth to bone contact is made by the anterior dentition (Pickering *et al.*, 2004). The pitting damage left by carnivores in experimental comparison-based research showed that leopards fell into the smaller group of mark length and breadth damage (Domínguez-Rodrigo & Piqueras, 2003). Leopards left marks of lengths <4mm and breadths of <2mm with an average range of between <2mm in length and <1.5mm in breadth for pitting on epiphyses (Domínguez-Rodrigo & Piqueras, 2003). Furthermore, it has been shown that leopards' preferred prey size range is within the size two and three classes (as per Brain's classification, 1981) which have live weights of 4.5-104kg (Kruuk & Turner, 1967; Pienaar, 1969; Brain, 1981; Wilson, 1981; Bertram, 1982; Scott, 1985; Bailey, 1993; Cavallo, 1997).

1.4. Non-carnivoran taphonomy

1.4.1. Porcupines

Porcupines (*Hystrix africaeaustralis*) have been extensively investigated for their bone accumulating and modifying behaviours in relation to caves for many years (Dart, 1958; Maguire, 1976; Brain, 1981; Wolff, 1981; Kerbis Peterhans & Singer, 2006). Porcupines, like all rodents, have aradicular incisor growth (open ended incisor roots which leads to continual tooth growth) and thus hoard bones in order to gnaw on the hard surfaces so as to wear their teeth down (Wiggs and Lobprise, 1997; Capello & Gracis, 2005). The upper and lower incisors are circular in cross section which leads to the characteristic parallel semi-circular gnaw marks (Figure 1). These are concentrated along long bone shafts and along broken edges (Brain, 1981; Kerbis Peterhans & Singer, 2006). Consecutive cave usage can result in composite carnivore and porcupine damage within a single cave assemblage, as observed by Kerbis Peterhans and Singer (2006) in an abandoned lair near the hominin site of Fish Hoek Cave, Western Cape. They found that the lair had been occupied by both porcupine and leopard consecutively. They found that the role of porcupines in the dens had led to a substantial component of the assemblage being large axial elements from a large taxon, which mimics the results found by Brain (1980) at a porcupine den in the Nossob valley.



Figure 1: Porcupine damage results in two parallel striations that are circular in cross section. Image from O'Regan *et al.*, 2011.

1.4.2. Warthogs

Suids are a common find in fossil assemblages throughout palaeontological sites in southern Africa and Europe (Klein, 1978; Harris & White, 1979; Harris, 1983; Sáez-Royuela, 1987; Cruz-Urbe, 1991; de Ruiter *et al.*, 2008; Herries *et al.*, 2009). Their bone modifying ability has recently been explored by Domínguez-Solera and Domínguez-Rodrigo (2009), with a specific focus on domestic pig as well as wild and hybrid boars in Spain. They found that suids were capable of modifying both complete and broken bones. The suids in their study were capable of reducing a mammal carcass of approximately 50kg to a collection of fragmentary bone shafts and epiphyseal ends; however larger carcasses were not depleted as industriously. Any remaining fragments - regardless of the initial carcass size - over 2cm had tooth scores and marks on them.

These tooth-marks are broad and shallow as a result of suid incisor-use for stripping flesh off the bone, rather than molars and premolars as seen in canids and hyaenids (Capaldo, 1995). Punctures and pitting was also observed, in particular an L-shaped pit mark was noted to appear on skeletal elements modified by suids that was not present in carnivore scavenging.

1.4.3. Abiotic accumulators (gravity, water, wind)

Natural forces act upon bone accumulations in conjunction with the biotic influences all the time. These include forces such as fluvial movement (in the form of rainfall, flashfloods, waterwash, etc.), aeolian deposits, and geographical shifts (earthquakes, tremors, sinkholes, etc.). Each of these natural systems will perform a similar sorting mechanism upon an assemblage. Long bone shafts for example will all be oriented parallel to the flow of the force, in order to become a less resistant surface (Hanson, 1980). Also, small elements will be moved further down the path of the force whilst larger, heavier elements will form lag deposits (Voorhies, 1969; Behrensmeyer, 1975, Hanson, 1980).

The most studied of these forces is water or fluvial transport, which was first experimentally tested by Michael Voorhies (1969) on sheep and coyote bones in a flume (Table 2). By running water through the system he found that certain bones were more susceptible to movement than others. Behrensmeyer (1975) extended this study to accommodate variation in bone density, as well as the size and shape of different skeletal elements. Skeletal elements have been found to be naturally sorted into three major groups with two intermediate groups which are now called "Voorhies groups" (Table 2).

Table 2: The mammalian skeletal element groups that are sorted by water velocity described by Voorhies (1969) and Behrensmeyer (1975). (Table adapted from Lyman, 1994).

Group I	I & II	Group II	II & III	Group III
Immediately removed (float or bounce)		Gradually removed, always in contact with bottom		Forms a lag deposit
Sacrum	Scapula	Femur	Mandibular ramus	Skull
Sternum	Phalanx	Tibia		Complete mandible
Ribs	Ulna	Humerus		
Vertebrae		Metapodials		
		Pelvis		
		Radius		

Fluvial accumulations leave a characteristic polished effect along the bone surfaces (Figure 2). This polish is the result of millions of sediment particles in the water making micro-abrasions along the surface of the bone; in the same manner that hydro-blasting or water blasting is used today in industry to remove the outer layer off a surface without damaging it, leaving it smooth and polished (Ross *et al.*, 2003). The presence of fluvial processes has been noted for the Makapansgat fossil material as described by Maguire *et al.* (1980) and Latham *et al.* (2002). The water polished effect on the bone surfaces can be seen in the fossil material excavated at this site, as seen in Figure 2.



Figure 2: Water polished bone from the Makapansgat Valley Fossil Site, Limpopo Province, South Africa.

1.5. Verreaux's eagles

As previously mentioned, the Verreaux's eagle is one of the largest eagle species in southern Africa, along with the Crowned eagle and Martial eagle (Ferguson-Lees & Christie, 2001). Verreaux's eagles consistently select for steep cliff face nesting sites, whether they be on a rocky outcrop or a tree (Brain, 1981; Gargett, 1990). These nesting platforms are also predominantly above a seasonal or permanent water source which acts as a cleaning mechanism for bone debris below a given nesting site. Oft times this water source is responsible for the hollowing out of cavities in the host rock that become cave sites and facilitate the fossilisation of Verreaux's eagle prey remains as well as a number of other skeletal elements that may have been washed downstream (Brain, 1981; Gargett, 1990; McKee, 2010).

1.5.1. Appearance and Size

The Verreaux's eagle (the largest of the *Aquila* genus) is described as "the finest of the genus *Aquila*" (Brown, 1970, pg. 36) with a plumage that appears completely black (moulted feathers reveal that they are in fact a very dark brown), except for the pure white rump and back. When an adult's wings are closed, only the white 'V' is visible on their back. Juveniles are born pure white and progressively moult into darker brown plumage until adult plumage is reached at maturity around four and a half years (Gargett, 1990). As a member the "true" or "booted" eagles the tarsi are entirely covered in feathers to the toes. The head is small with a tapering neck line that is capable of turning almost three quarters of a full rotation. The female of the species is typically larger than the male, both of which range from 75 to 96cm long. Males weigh 3 to 4.2 kg while females range in weight from 3.1 up to 5.8 kg (Gargett, 1990). The characteristic leaf shaped wing with a broad middle and tapered tip has an

average total wingspan length of 1.81 to 2.2 m (Brown, 1970; Gargett, 1990; Ferguson-Lees and Christie, 2001).

In flight, differentiating between a male and female can be done by observing the angle of the primary feathers as well as the degree of fanning in the tail. Female's primary feathers are relatively parallel with the length of the wing whilst male primaries bend upwards, at an angle of up to approximately 60° (Gargett, 1990). The tail feathers in flight can also be used if one has a good view- the female tail tends to fan out to create a wedge-shape while the male holds his tail feathers straight to give a more rectangular view (Gargett, 1990).

Talons are typically between one to four centimetres in length. The first digit is the longest averaging between three and four centimetres, with a shorter fourth digit of approximately 1.5 to two centimetres (Figure 3). The hooked beak is black, and a yellow cere (Figure 4). Overall length shortens with age but averages at approximately four and a half centimetres from the cere to the tip. In cross section the talons are circular and the beak is a rounded triangle that widens medial-laterally towards the head.

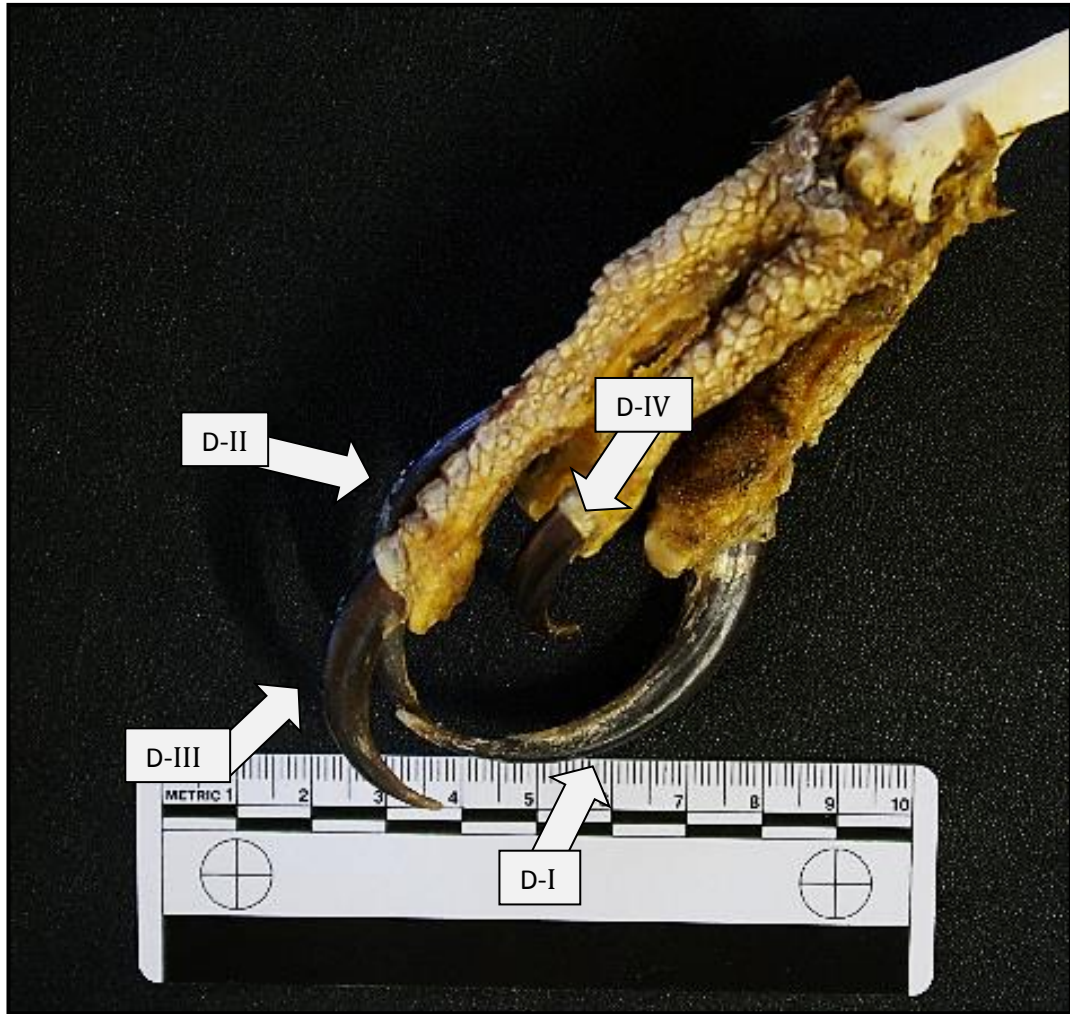


Figure 3: A photo of the talon shape and size for a young adult Verreaux's eagle specimen housed in the Bulawayo Natural History Museum. The digits are marked with individual arrows and the associated digit number. Note: D: digit; D-I is otherwise known as the hallux.



Figure 4: A photo to illustrate the hooked beak shape and yellow colouration of an adult Verreaux's eagle housed at the Bulawayo Natural History Museum, Zimbabwe.

The overall size of this species allows the birds to be formidable opportunistic hunters along the rocky outcrops and steep inclines found in their home ranges. The broad wingspan and powerful uplift allow for larger carrying capacities, which coupled with the effortless ability to utilise natural airstreams, also allow for longer hunting ranges (from which they can return carrying heavy prey). This is particularly useful during brooding and nesting periods when food needs to be continually brought back to a chick.

1.5.2.Distribution

Verreaux's eagles are limited to cliff outcrops and rocky escarpment plateaux across southern and eastern Africa. They are also recorded as straying into Arabia and Israel; with up to 60 established breeding pairs recorded in Arabia (Gargett, 1990; Jennings, 2010). Due to trends for cliff-face housing developments a number of nesting sites have become urbanised, especially within Gauteng province (Bird *et al.*, 1996). In the Plio-Pleistocene however distribution would assumedly have been far reaching into Central and Northern Africa as well as denser along southern Africa (Harrison, 1980).

Currently, a small number of nests occur at the southern border of Namibia, Botswana and South Africa, with no recorded nesting in northern Namibia. There are high occurrences in South Africa as well as localized high densities in Zimbabwe. The range then continues directly north along the Rift Valley, with populations in Kenya, Ethiopia, north central Tanzania, eastern Egypt and eastern Sudan. Small isolated populations occur in both the central Democratic Republic of the Congo as well as Chad. Within South Africa, population groups are scattered across a variety of altitudes and biomes, from the Cape Province at sea level to the Drakensberg range at 3,482 metres above sea level (Brain, 1981; Gargett, 1990; Sycholt, 2002). The Magaliesberg range, which spans the provincial border between Northwest Province and Gauteng, is also densely populated with approximately one pair per 35km² to 65km² (Brown *et al.*, 1982; Steyn, 1982; Allan, 1988b; Gargett, 1990; Davies, 1994).

1.5.3.Territories

The ability of Verreaux's eagle nesting pairs to limit territories to relatively small areas allows for higher densities over smaller landscape areas (Gargett, 1990). Both Brain and Gargett describe the territories of Verreaux's eagles being an "inverted truncated cone" resulting in a small terrestrial area with a larger aerial component for each nesting pair (see Gargett, 1990, Figure 28, pg. 84). Whilst the areas around the boundary that are closer to the ground are heavily maintained and defended, those higher up tend to overlap into a mutual space and these shared territory areas are rarely defended.

Territory boundaries between neighbours are maintained by mated pairs through complex aerial display flights, conspicuous perch choices and vocalisations (Gargett, 1975; 1990). Territories have no set shape or design but rather are a direct result of the environment below the aerial territory. The land surface needs to comprise both rocky outcrops and areas of open grassland (Gargett, 1990).

The Ghaap Plateau Escarpment (which borders the Taung Fossil sites) along the Kalahari Desert has a low density of Verreaux's eagle despite the higher levels of eagle population in relatively close areas, such as the Nuweveld Mountains in the Karoo (Davies, 1994; Anderson & Hohne, 2007). The escarpment extends approximately 280km from Vryburg to Douglas (Butzer, 1974; Anderson & Hohne, 2007). Anderson and Hohne (2007) have argued that the low density is due to the lack of fault lines and fissures within the limestone tufa, which would provide natural nesting platforms for the eagles as well as crevices for the rock hyrax.

1.5.4. Prey selection and distribution

The most commonly selected prey item is the hyrax or Dassie, of which there are four extant species within the order Hyracoidea: Rock hyrax (*Procavia capensis*); Western tree hyrax (*Dendrohyrax dorsalis*); Yellow spotted rock hyrax (*Heterohyrax brucei*); and Southern tree hyrax (*Dendrohyrax arboreus*) (Jones, 1978; Olds and Shoshani, 1982; Barry and Shoshani, 2000). Due to the cliff face habitat selected for by Verreaux's eagles, the rock hyrax and yellow spotted rock hyrax are the most common prey items. In Sub-Saharan Africa, the yellow spotted rock hyrax's range does not extend further down into South Africa past the northern tip of the Limpopo Province so the Rock Hyrax makes up the largest component of the Verreaux's eagle reported diet (Figure 5) (Brain, 1981; Davies, 1994).

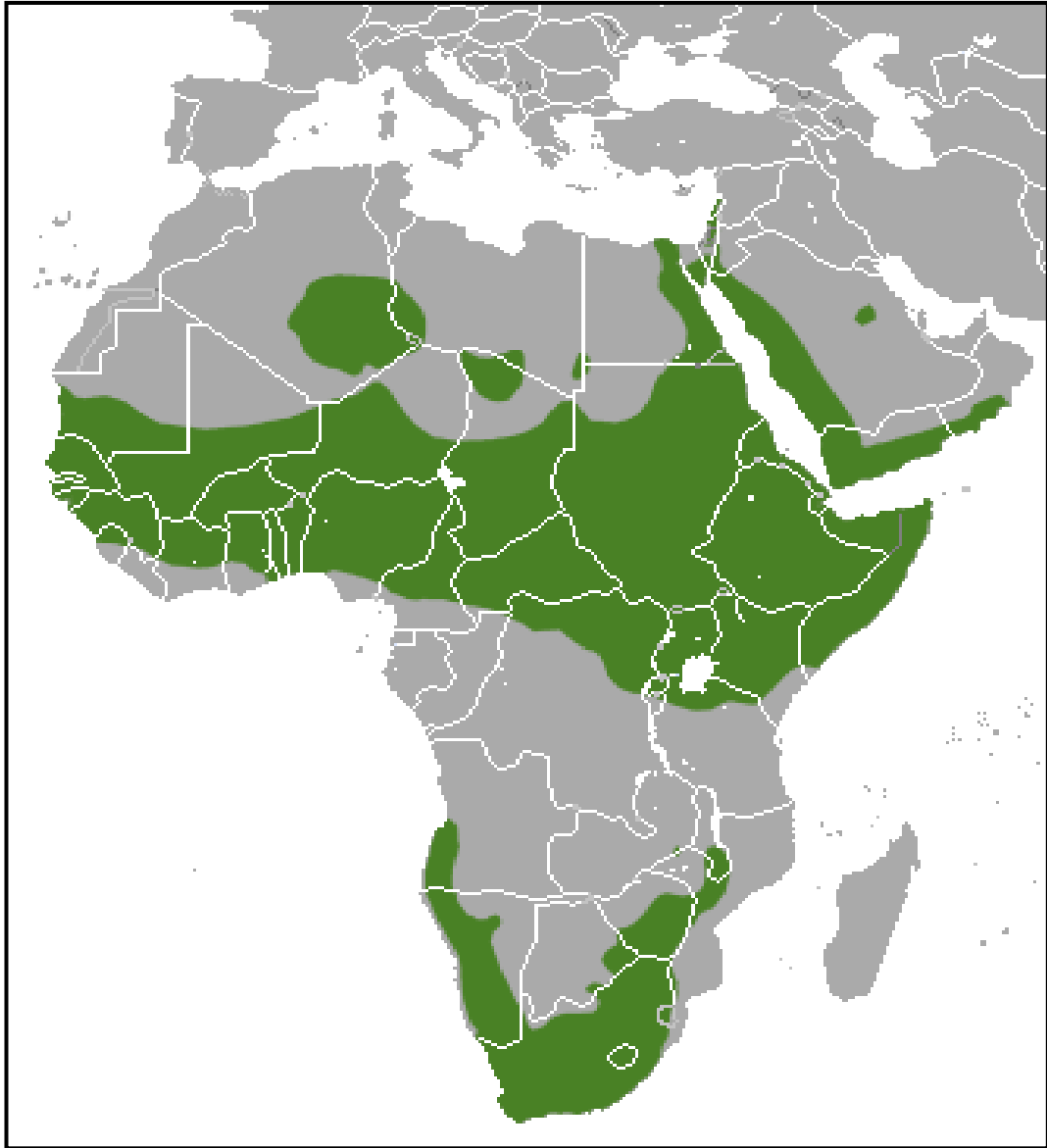


Figure 5: The distribution of the Rock Hyrax, *Procavia capensis*, throughout Africa. Note that the majority of South Africa has rock hyrax population with the exception of small areas along the southern Botswana border and the eastern border to Mozambique. (Image from IUCN Red Data List- accessed on the 21/6/2012).

Other mammalian prey items from across the Verreaux's eagle distribution range (a number of these prey items are endemic to a very small portion of the overall range) include Smith's red rock hare (*Pronolagus rupestris*), scrubhare (*Lepus saxatilis*), slender mongoose (*Galerella sanguinea*), vervet monkey (*Chlorocebus pygerythrus*), young chacma baboons, bushbabies (*Galago moholi*), klipspringer (*Oreotragus oreotragus*), bushbuck (*Tragelaphus scriptus*), common duiker (*Sylvicapra grimmia*), rhebuck (*Pelea capreolus*), damara dik-dik (*Madoqua damarensis*), black-backed jackals (*Canis mesomelas*) and genets (*Genetta* spp.) (Chiweshe, 2007; Gargett, 1990; Grobler & Wilson, 1972; Letley, 1962; Steyn, 1982; Visser, 1963; Zinner & Paláez, 1999). Avian prey items are dominated by helmeted guineafowl (*Numida meleagris*) and francolins (*Francolinus* spp.), with the occasional rock pigeon (*Columba guinea*), goose (Anatidae spp.) and cape griffon chick (*Gyps coprotheres*) (Rowe, 1947; Pitman, 1960; Bowen, 1970; Steyn, 1982; Mundy *et al.*, 1986; Gargett, 1990). Reptilian prey items are rarer choices but are occasionally hunted. These include leguaan (Varanidae spp.), plated lizards (Gerrhosauridae spp.), tortoises (Testudinidae spp.), puff adders (*Bitis arietans*) and cape cobras (*Naja nivea*) (Jubb, 1983; Gargett, 1990). Verreaux's eagles are opportunistic hunters and are always ready when any prey item presents itself, including occasionally feeding on carrion. However they have never been recorded bringing carrion back to a nest (Gargett, 1971; Frere, 1982; Steyn 1982; Gargett, 1990).

1.5.5. Feeding behaviours

Feeding is rarely observed as these birds tend to eat where they make a kill, the exception being during the nesting period where they will return prey items to the nest for the chick. It is this material that is returned to a set feeding perch or the nest that presumably collects below the nest or is washed into cave openings to form fossil assemblages. Understanding the hunting behaviours as well as

feeding habits will provide an explanation for the taphonomic markings on skeletal elements within these assemblages.

1.5.5.1. Hunting behaviours

As previously mentioned the Verreaux's eagle is an opportunistic hunter and is always on the alert for new prey items. That being said there is no definitive proof that partners of a pair collaborate together to 'plan' an attack. Both Bowen (1970) and Porter (1984) have recorded instances that appear to be teamwork or collaborative hunting among a mated pair, but as Gargett (1990) discussed, these are isolated and since Verreaux's eagle partners spend up to 95% of their time together, could be misinterpretations. Partners hunt either together or separately and have an equally good chance of being successful either way. Gargett explains how there are no distinct flight patterns associated with hunting, as there are with other behaviours such as territory defence flights or courtship, but rather a number of flying techniques. Sudden vertical stoops, twists, angled descents and vertical drops are all characteristic of prey being spotted from a gliding or perched position (Gargett, 1990).

Prey items do not appear to be selected for based on sex, age or species - prey choice appears rather to be solely based on availability. This then challenges the hypothesis of Verreaux's eagles being specialist hyrax hunters, when it is most likely a reflection of the species' composition and densities within a given area. Furthermore, these observations are based on the long term observation project in the Rhodes Matopos National Park, which has a distinctly unique environment with large clusters of weathered boulders that form huge stacks with small grassland areas between stacks (Figure 6). This unusual environment is what facilitates both large densities of Verreaux's eagles and hyraxes. Verreaux's eagles observed outside of the Matopos have what is described as a far more "catholic" diet (Gargett, 1990, pp. 64), assumedly due to the larger variety of prey species available.

When hunting, prey is often basking out on the rocky outcrops within an eagle pair's territory where it is ambushed and killed. The body is then carried in both feet, with the exception of smaller individuals which are carried in only one foot whilst the other folds back towards to the tail. Should much larger items be hunted and killed and the eagles are unable to transport them back to the nest, they are decapitated or eviscerated before being returned to the nest.

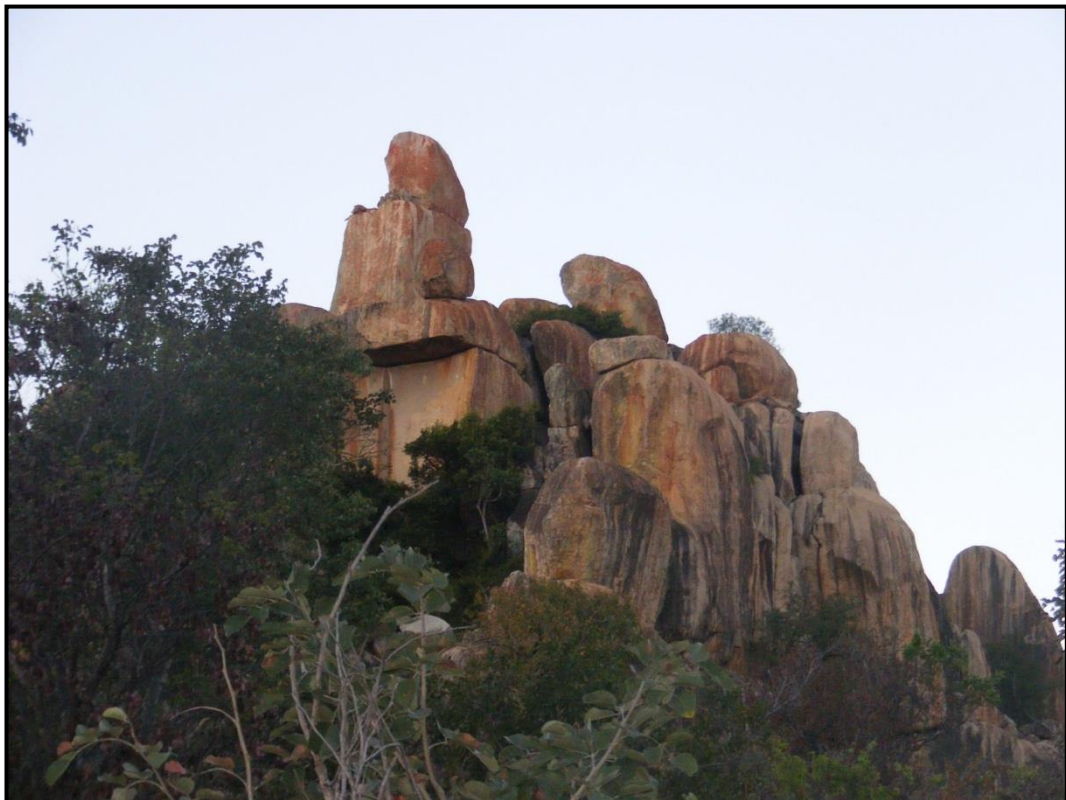


Figure 6: The characteristic “bread boulder weathering” that is unique to the Matopos area and leads to the stacked inaccessible peaks that Verreaux’s eagles prefer for nesting.

1.5.5.2. *Feeding behaviour of adult birds*

During her extensive study on Verreaux's eagles, Gargett (1990) observed that when feeding, there appears to be a set routine of consumption, especially with regards to hyrax prey items. First the caeca are removed and discarded. The skull is then processed- eyes and tongue are eaten out before detaching the mandible in order to gain access (via the palatine bone) to the cranial cavity and the brain is then consumed. The scalp is then removed along with the skin and fur of the face and neck (including ears). This is often fed to younger birds. The head is then removed by twisting the cervical vertebrae and eating the vertebral discs. The spinal cord and bone marrow is pulled out in strips and eaten, along with the heart, liver and lungs. Occasionally the ribs, legs and feet are consumed as well. Prey remains found in the nest after feeding have been recorded as being limited to skulls, the pelvic girdle and sections of articulated vertebrae (Gargett, 1990). These prey remains are also occasionally carried off the nest for hygienic purposes in the bill, especially during the nesting period and deposited some arbitrary distance away (Gargett, 1990).

1.5.6. Nesting

Verreaux's eagles nest along rocky outcrops and mountainous escarpments in fissures and cracks that provide a secure inaccessible crevice safe from wind and predators (Figure 7). Nest sites are almost never placed within a tree, however a few have been recorded (see Perrett, 1976; Dick & Fenton, 1979; Mavros, 1988). Four factors appear to influence the placement for the nest site (Gargett, 1990). The size of the shelf and its ability to house quite a large nest along with the stability of the shelf base play essential roles. The most crucial factor however seems to be the head room: whether or not there is an overhang above the shelf which might impede either the eagles themselves or nest growth. Nests can

grow to quite great heights over numerous years of usage. The highest ever recorded nest was in the Soutpansberg in South Africa and measured 4.1 metres tall (Tarboton & Allan, 1984). This is coupled with the sheltered aspect to the nesting platform- young chicks are susceptible to the elements because of their sparse downy feathers.



Figure 7: A number of examples of Verreaux's eagle nests throughout the Drakensberg range. Note the natural rock crevices and inaccessibility for

each nest. The lowermost photo clearly illustrates the severity and steepness of the escarpment wall selected for by Verreaux's eagles (The nests are marked by the arrows).

1.6. Aims and Objectives

This project aims to add to the current understanding of Verreaux's eagle accumulation behaviours and hopefully aid in dissecting potential variations in the accumulation behaviours between raptor species as well as within a species geographically. By sampling nest sites of the Verreaux's eagle from across two distinctly different geographical biomes one can establish whether the greater environmental variations impact on the hunting and subsequent accumulations of a single species of raptor.

It should be noted that the species Verreaux's eagle, while present in the Plio-Pleistocene, is not the sole raptor collector of prey items in cave systems and one should be apprehensive when aligning a site to one specific raptor species without also investigating the taphonomic characteristics of both the Crowned and Martial eagles. That being said, this study will hopefully spawn a similar intensive investigation into the accumulation behaviours and signatures of other large raptors.

This study was conducted to potentially introduce a new accumulating agent to those typically considered when analysing fossil assemblages as well as provide the basis for such a consideration. Furthermore, it aims to add to previous hypotheses and understandings on the bird of prey hypothesis prevalent at the Taung fossil sites of the Dart and Hrdlička Pinnacles. It is well understood that by understanding the environmental stressors and pressures active on a species, one can begin to analyse the potential reasons for evolutionary advances, especially those in the unusually rapid hominin lineage.

Some of the earlier questions asked were along the lines of: Do Verreaux's eagles preferentially seek out hyrax as a prey item? If not, what were the constraints that influence prey selection? Were all prey species disarticulated in the same manner, and how was this disarticulation reflected on the skeletal remains?

Collating these questions together resulted in three succinct hypotheses on which this project was based.

1.7. Hypotheses

A. Verreaux's eagles produce a unique taphonomic signature

Verreaux's eagles are distinct in terms of both their morphological appearance as well as their hunting strategies compared to other large raptors such as the Crowned eagle and Martial eagle. Furthermore, they occupy niches that are environmentally different to those occupied by these other large raptors, which implies that they come into contact with prey items that are unique to those niches.

B. The taphonomic signature reflects this uniqueness with regards to prey choice selection, skeletal part-representation and taphonomic marking distribution across the skeletal elements

The ability of the Verreaux's eagle to live in small territory range over a large variation of biome types have led to them being a successful raptor species. Within these variable habitats, the range of small mammal species will alter based on the availability of key factors in their landscape preferences. As such the Verreaux's eagle is introduced to a suite of prey choice selections far exceeding those originally described by Gargett (1990) in the Rhodes Matopos National Park. I then hypothesise that the prey choice is wider than initially described.

Furthermore, different prey items will have different body morphs. These will similarly have different positions for the vital organs, some of which are more desirable for the eagles from a nutritional stand point. Accessing these organs on a range of prey species will leave characteristic marks on the surrounding skeletal elements, which are not necessarily the same across taxa. An example is the placement of the heart in both a rock hyrax (*Procavia capensis*) and a

helmeted guineafowl (*Numida meleagris*). In the hyrax, the scapula and associated thoracic vertebrae are likely to be removed to access the heart while in the bird it would be the keel (avian equivalent of a mammalian sternum) that exhibits the greatest damage. The placement of these taphonomic marks, such as punctures, v-shaped nicks and scratches, should be distributed across skeletal elements in respect of the prey species.

Certain elements, such as the smaller limb bones will undoubtedly be swallowed and digested, as described by Gargett (1990), or at least appear heavily acid-etched, while the longer limb bones and more robust carpals and tarsals will be discarded. The skeletal element representation that one would encounter below a modern Verreaux's eagle nest, and in theory a fossil cave deposit, should then reflect the eating preferences unique for this species.

C. This taphonomic signature is a direct response to the environment

Verreaux's eagle prey choice has been structured chiefly on observations based in the Rhodes Matopos National Park, Zimbabwe (Gargett, 1990). The variation in prey choice, whilst mentioned in the Matopos study, has not been further explored to make allowances for their entire geographical range. As Kuhn (2011) illustrated (using the three bone-collecting species of hyaenid), mammalian carnivore feeding behaviour is a direct response to the environmental pressures exerted from the climate, landscape and interspecific competitions for resources. Considering the impact that the climate has on the biome, which in turn has knock-on effects on the species distribution in an area, I hypothesise that the Verreaux's eagle entire taphonomic signature, especially in terms of prey selection, will change with a shift in the geographical location of a nesting pair.

1.8. Materials and methods

1.8.1. Nest site selection

The area in which nest sites were located was based on the predominant biome structure for that area. A comparison of two areas with contrasting rainfall patterns was ideal and as such the Highveld/Magaliesberg area around Johannesburg provided a summer rainfall biome compared to the drier Succulent and Nama-Karoo biomes.

Subsequently, a number of the nesting sites were located through the help of a range of foundations, such as the Endangered Wildlife Trust (through the Birds of Prey Programme), The Walter Sisulu Botanical Gardens and the Mountain Club of South Africa, to which Dr Brett Gardner of the Johannesburg Zoo is a member. The nesting sites include Klipriviersberg Nature Reserve, Upper Tonquani Site (Magaliesberg), Walter Sisulu Botanical Gardens as well as a number of sites on privately owned farms within the Western Cape and Northern Cape Provinces.

Furthermore, material initially collected by Professor Lee Berger from the John Nash Nature Reserve in The Cradle of Humankind was included as it was collected over a number of years and as such allows for an indication of annual accumulation growth.

1.8.2. Data collection

The prey material from the Magaliesberg nesting sites was collected by means of abseiling directly into the nest, with the help of Dr Brett Gardner (the Upper Tonquani and Walter Sisulu Botanical Gardens samples were collected like this) or by climbing up the artificial nesting platform as with the Klipriviersberg nest. In all cases, the ground below the nest was surveyed and prey items that had been dropped from the nest were also collected. This was done at very specific

times of the year- directly before the mating season and again after the chicks have fledged, ensuring that there is neither direct animal contact, nor any disturbance to the mated pair and its' chick. This time period also provided the highest number of skeletal remains for data as more prey remains were brought to the nest for the chick.

The prey material that was collected in the Karoo area was done so by Eskom and Vodacom employees. In conjunction with the Endangered Wildlife Trust's Bird of Prey Programme, these companies have provided artificial nesting platforms for large raptors in an attempt to stop them from nesting on pylons and receptor towers. The employees clean the prey remains from the base of the nest every few weeks to keep them as neat as possible. These remains were then stored for me, rather than destroyed as usual. Since I was unable to attend any of these collections, a data sheet was sent through to the cleaners with all the relevant information required for each collection (see Appendix A).

1.8.2.1. Excel database

All the prey items that were collected were catalogued in a Windows 7 Excel spreadsheet. Each specimen was given its own accession number with a code that represented the site that it came from (Table 3). Each specimen was then catalogued in terms of element, orientation or siding, taxon identification (if possible) and all taphonomic markings were recorded.

Table 3: A list of the site names and the respective codes for each. The top four sites are in the Highveld whilst the following seven are in the Northern Cape.

Site name	Site code
Klipriviersberg Artificial Nesting Platform	KANP
Walter Sisulu Botanical Gardens, Roodepoort	WSBG
Upper Tonquani, Magaliesberg	UTM
Gladysvale, Magaliesberg	GVE
Philipstown, Zwagershoek	PZ
De Aar Quarry	DAQ
Tafelkop	TK
Lockview	LV
Gifkloof	GK
Grobbershoop	GH
Kameelpoort	KP

1.8.3.Dismemberment- data collection and analysis

Gargett (1990) provided in-depth descriptions of feeding practices by Verreaux's eagles in the Rhodes Matopos National Park, Zimbabwe. The prey remains collected from below the nesting sites were reviewed in light of these descriptions to see if there were consistencies between the dismemberment process and the skeletal part representations in remaining prey items. These skeletal elements were also assessed for taphonomic markings that can be a direct result from dismemberment and feeding practices and unique to Verreaux's eagles. No elements were collected from downstream of the nest.

1.8.4. Taphonomic interpretation

Specimens were brought back to the modern comparative collection housed at the Palaeosciences Centre, University of the Witwatersrand for identification. Additional resources for identification included *A guide to post-cranial bones of East African mammals* by Walker (1985) and the Ditsong Natural History Museum in Pretoria.

Any markings, such as scratches and puncture marks on bone material were collated and photographed so as to ascertain whether there is an identifiable, repeated taphonomic signature for Verreaux's eagles. These markings were compared to the four taphonomic markings as well as the six raptor accumulation characteristics outlined by Berger and Clarke (1995).

1.8.5. Limitations

When working with either the environment or live animals, one will always encounter a limitation to the accessibility of data. Working according to the weather patterns and the Verreaux's eagle breeding cycle imposed a number of time constraints as well as access restrictions. One of the largest issues was timing collections relevant to the heavy rainfall season on the Highveld. Accessing material was both hindered by rainfall and a large component of the assemblage was undoubtedly swept away by the seasonal or permanent water sources that flank these nesting sites. This however, rather than be a hindrance, proved to be an invaluable note towards the taphonomic signature of Verreaux's eagles and their nesting patterns. By comparing material accessed before and after heavy rainfall periods, I was able to observe the natural sorting process active on skeletal-part representations that would lead to either a fossil assemblage downstream or a lag deposit below the nest.

Additionally, the majority of the prey species selected for by Verreaux's eagles are smaller mammals and reptiles. Separating these out to species level identifications becomes increasingly difficult when dealing with individual and isolated elements. Furthermore, the reference collection housed at the University of Witwatersrand does not house all of the variations within families such as the Hyracoid (four species) and Leporidae (seven indigenous species and one invasive species, the European rabbit (*Oryctolagus cuniculus*)). Based on the distribution of species within these families one can begin to narrow down the possibilities but in cases where identifications were uncertain elements were aligned within a family rather than species. For the Hyracoid, the most likely species in all cases is the rock hyrax (*Procavia capensis*), as it inhabits the rocky outcrops typical of Verreaux's eagle nesting (see chapter 1.5). The hares and rabbits have been divided into *Lepus* spp. and *Pronolagus* spp., respectively, unless a positive identification could be made. Reptiles have all been classified as Reptilia.

1.9. Brief overview

This study was an actualistic approach to investigating the taphonomic characteristics of Verreaux's eagles' prey remains. By accessing nesting sites and collecting the skeletal elements of the prey items from the source, this study was able to categorically outline the taphonomic signature of Verreaux's eagles in terms of prey selection, skeletal part representation and the taphonomic markings left on skeletal elements. To date there has been very little done in the way of analysing Verreaux's eagle damage: the bulk of the research has been focused on Crowned eagle and owl damage (Davis, 1959; Mayhew, 1977; Daneel, 1979; Dodson & Wexlar, 1979; Brain, 1981; Andrews, 1990; Taylor, 1994; Berger & Clarke, 1995; Bochenński & Tomek, 1997; Terry, 2004; Reed, 2005; Berger, 2006; McGraw *et al.*, 2006; Berger & McGraw, 2007; Gilbert *et al.*, 2009; de Ruiter *et al.*, 2010), with exception of the studies done on the identity of the prey-remains of Verreaux's eagles (Boshoff *et al.*, 1991), Martial eagles (Boshoff & Palmer, 1980) and Crowned eagles (Boshoff *et al.*, 1994). The aim of the present study has been to introduce a new set of taphonomic markings to be aware of when assessing the accumulation mechanism of fossil sites and archaeological sites the world over.

1.10. Synopsis of chapters

Chapter 2: Study areas

The nesting sites that were collected from are described in terms of the biome type, dominant vegetation type and nest description. Nesting sites are divided into two main categories- those on the Highveld of South Africa and those in the greater Karoo area.

Chapter 3: Results

The results of all of the nesting sites outlined in chapter two are presented here. These include a list of the prey items found at each nesting site as well as the skeletal elements that each of these prey types is represented by. Also a categorization of the taphonomic markings found on bone surfaces is provided along with images of each mark. The damage from each region, individual site and each prey species is also documented.

Chapter 4: Discussion

Interpretations of the results are discussed and those that are unique to Verreux's eagles are emphasised. How these then impact on future taphonomy work on raptors are then discussed. Finally, Verreux's eagle taphonomy is summarized.

Chapter 5: Conclusion

Here, the hypotheses from chapter 1.7 are revisited and answered in light of the results found. The original criteria introduced by Berger and Clarke (1995) as well

as the damage types they assigned to eagle activity on a carcass are revisited and assessed for Verreault's eagle taphonomy. The potential environmental impacts on the taphonomic signature are discussed as well as final thoughts and potential future research avenues.

CHAPTER 2

STUDY SITES

South Africa is divided into seven distinct greater biomes (Figure 8- Low & Rebelo, 1996; Rutherford, 1997). The biomes of interest for the sites around the Gauteng/ Northwest Province are Savanna (Gladysvale and Upper Tonquani) and Grassland (Klipriviersberg Artificial Nesting Platform and Walter Sisulu Botanical Gardens). The sites in the Northern Cape fall into three different biomes: Nama-Karoo (Philipstown, De Aar Quarry, Tafelkop, Lockview and Kameelpoort); Savannah (Groblershoop); and Succulent-Karoo (Gifkloof). These groups of nesting sites have been divided into Highveld Nest Sites and Karoo Nest Sites respectively (Figure 8). The Taung Verreaux's eagle Nesting Site was listed on the figure too, however no remains were found from this site and it has not been described further.

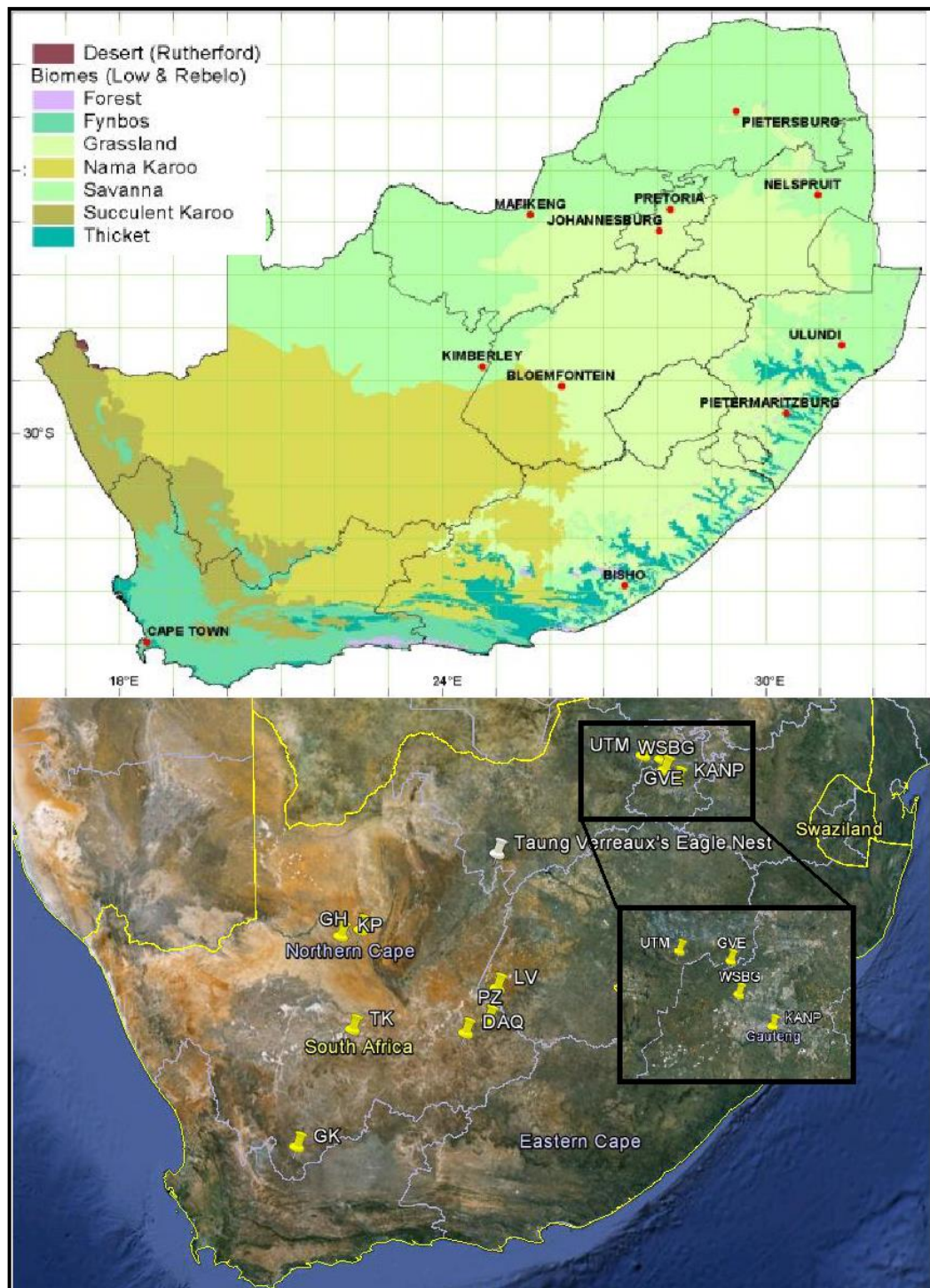


Figure 8: The major South African biomes, as outlined by Low and Rebelo (1996), Mucina and Rutherford (1996) and Rutherford (1997) as well as the placement of all of the nesting sites used in this study across South

Africa. Note that the Highveld Nesting Sites are shown close up in a second window and the Taung Verreaux's eagle nesting site is marked by a white pin.

2.1 Highveld Nesting Sites

2.1.1 Klipriviersberg Artificial Nesting Platform (KANP)

The Klipriviersberg Artificial Nesting Platform was constructed by Siyavaya Highway Construction JV in conjunction with the Rural & Agricultural Raptor Projects initiative as an alternative nesting site for the Verreaux's eagle pair nesting alongside the Reading Interchange (Alberton, Johannesburg) as the original pylon nest was destroyed. The nesting platform was erected in 2008 and stands 16 metres high (Figure 9). The nest is situated on the privately owned Meyers Farm in the south of Johannesburg (26°16'17.59"S; 28°5'2.31"E).



Figure 9: The Klipriviersberg Artificial nesting platform erected in 2008 on Meyers Farm, Alberton.

The dominant vegetation type for the area is Andesite Mountain Bushveld (Code SVcb11- Mucina & Rutherford, 2006). Vegetation features include dense,

medium to tall thorny bushveld trees and shrubs with well-developed grass-layered hill slopes (Mucina & Rutherford, 2006). There is a mean annual precipitation (MAP) of 650mm during the summer months with very dry winters (Mucina & Rutherford, 2006).

2.1.2 Walter Sisulu Botanical Gardens (WSBG)

This active nesting site consists of two nests adjacent to the Witpoortjie Waterfall in Roodepoort's Walter Sisulu Botanical Gardens (26°5'32.04"S; 27°50'24.68"E). The nest has been actively used for nesting since the late 1940's and has seen in the order of four generations of Verreaux's eagle (Woodcock, pers. comm, 2011). The two nests are approximately 40 metres above the ground and both are on rock ledges. Due to the rapid urbanisation around the Botanical Gardens, especially the development of housing on the plateau above and behind cliff face, the rock hyrax population has diminished significantly.

Mucina and Rutherford describe the area for this nesting site as Egoli Granite Grassland (Gm10 (2006)). This biome is described as an undulating plain with low hills dominated by tall grasses and some woody species on rocky outcrops or along rock sheets. The woody species are typically scattered shrub or solitary trees (Mucina & Rutherford, 2006). As with all highveld biome types, there is a strong seasonality with summer rainfall range of 620-800mm and very dry winters.

2.1.3 Upper Tonquani Nest Site (UTM)

This active nesting site is within a ravine on property owned by the Mountain Club of South Africa (MCSA), in the Magliesberg, Northwest Province. There are two nests located on the southern face of the ravine (25°50'57.09"S; 27°25'0.09"E).

The landscape above the ravine is Gold Reef Mountain Bushveld (SVcb 9) with the area in the ravine Northern Afrotemperate Forest (FOz 2). The Bushveld complex is characterized by rocky hills with dense woody vegetation along the south-facing slopes and an even grass cover elsewhere (Mucina & Rutherford, 2006). The forested environment has a canopy of over 20m with poor species diversity (Mucina & Rutherford, 2006). Again, the rainfall is highest during the summer months with an annual precipitation range of 600-750mm (Mucina & Rutherford, 2006).

2.1.4 Gladysvale (GVE)

The Gladysvale Nesting Site falls within the John Nash Nature Reserve in the Cradle of Humankind. The nest site lies within a kloof riverine near the fossil cave site of Gladysvale (25°53'48.77"S; 27°46'39.09"E). Gladysvale falls within the Gauteng Shale Mountain Bushveld (SVcb 10) and is described as short, semi-arid thicket with a variety of woody species (including *Acacia caffra*- Common hook thorn). Annual precipitation ranges between 600-750mm (Mucina & Rutherford, 2006).

2.2 Karoo Nesting Sites

2.2.1 Philipstown (PZ)

An alternative 50 metre tall nesting platform was erected for Verreaux's eagles on the privately owned farm of Zwagershoek, near Philipstown, Northern Cape (30°27'58.32"S; 24°28'26.34"E). This nesting site straddles the two biomes of Northern Upper Karoo (NKu 3) and Besemkaree Koppies Shrubland (Gh 4). Both biomes are dominated by dwarf karoo shrubs, grasses and the occasional low tree (Mucina & Rutherford, 2006). The annual precipitation (AP) ranges from between 190mm and 400mm (Mucina & Rutherford, 2006). This nesting site was collected from twice- first in July and again in August of 2011. These two collections have been divided and are presented as PZ1 and PZ2.

2.2.2 De Aar Quarry (DAQ)

Not much is known about this 55 metre high nesting site, other than that it is along a man-made cliff face in an abandoned stone quarry outside of the town of De Aar, Northern Cape (30°40'49.97"S; 24°1'25.56"E). The town of De Aar falls into the biome classification of Eastern Upper Karoo (NKu 4). As such the vegetation is made up of dwarf microphyllous (small-leaved) shrubs and 'white' grasses (Mucina & Rutherford, 2006). Rainfall is concentrated around the summer months and the AP ranges from 190 to 400mm (Mucina & Rutherford, 2006).

2.2.3 Tafelkop (TK)

The Tafelkop Nesting Site (near Vanwyksvlei) is an artificial nesting platform approximately 50 metres tall (30°36'0.49"S; 21°46'59.62"E). According to Mucina and Rutherford (2006) this site is classified as Upper Karoo Hardveld (NKu 2) and

comprises steep slopes with large boulders and sparse dwarf karoo shrubs and grasses. Rainfall ranges from 150mm to 320mm (Mucina & Rutherford, 2006).

2.2.4 Lockview (LV)

This nesting site is a Vodacom tower that the eagles are utilising. It is approximately 50 metres tall (29°55'7.95"S; 24°38'38.70"E). This nesting site falls within the Besemkaree Koppies Shrubland (Gh 4), as described above for Philipstown (Mucina & Rutherford, 2006). Rainfall ranges from 300mm to 400mm.

2.2.5 Gifkloof (GK)

The Gifkloof nesting platform is artificial and only stands 20 metres high (32°35'13.66"S; 20°34'59.54"E). The dominant vegetation for this region is Tanqua Escarpment Shrubland (SKv 4) which is a succulent shrubland of medium height (Mucina & Rutherford, 2006). Annual precipitation ranges between 200mm to 300mm.

2.2.6 Groblershoop (GH)

The Groblershoop nesting platform is artificial and stands 45 metres high (28°54'6.07"S; 21°58'58.49"E). This region is characterised by Bushmanland Arid Grasslands (Nkb 3). The AP ranges from 70mm to 200mm leads to sparsely vegetated grasses (Mucina & Rutherford, 2006).

2.2.7 Kameelpoort (KP)

The Kameelpoort nesting platform is artificial and stands 40 metres high (29°0'0.75"S; 21°35'0.02"E). The nesting platform is within the Gordonia Duneveld (SVkd 1) which is characterised by open shrubland on parallel dunes

above grassy plains (Mucina & Rutherford, 2006). The annual rainfall ranges from between 150 to 200mm.

CHAPTER 3

RESULTS

3.1. Prey selection

A total of 886 specimens were collected with the majority coming from the Highveld sites (N= 468 specimens, Table 4; Figure 10) (See Appendix B for a full list of prey items found (669) and analysed. Note that the number of prey items found is less than the number of specimens as a number of items were articulated specimens. These were extrapolated out into the individual elements for analyses, making the total number of specimens larger). Prey species found from the Highveld Nesting Sites (Table 5) included rock hyrax, Smith's red rock rabbit, scrubhare, hare (*Lepus* spp.), bovid (size class 1 and 2- as per Brain, 1981), klipspringer, steenbok, jackal, baboon, vervet monkey, small birds (*Aves* spp.), helmeted guineafowl, duck (*Anas* spp.) and owl (cf. *Tyto alba*). The Karoo sites (Table 6) yielded more variability with respect to species than those of the Highveld, despite being a smaller collection (N= 418). Species identified from the Karoo sites included rock hyrax, rodents, hare, bovid size class 1 and 2, impala, a juvenile sheep (*Ovis* spp.), mongoose (*Herpestidae*), suricate (*Suricata suricatta*), *Felidae* spp., domestic dog (*Canis familiaris*), aves (small and large), tortoise (*testudine*) and lizards (*Varanus*-sized). Groblershoop Nesting Site yielded no identifiable fauna, and has therefore been left off of Table 4 and Table 6.

Hyrax formed the largest number of prey items with a total of 390 specimens recovered from all of the nesting sites combined (Figure 10). It was also the only species present at every site (Table 4). The second most common were rabbits (cf. Smith's red rock rabbit) followed by hares and helmeted guineafowl, respectively (Figure 10).

Table 4: The species representation displayed in terms of a percentage of the total collection at each nest site. The actual specimen numbers are provided in Tables 5 and 6. The majority species for each site assemblage is in bold. For a full list of the nesting site abbreviations see chapter two.

		KANP	UTM1	UTM2	WSBG	GVE-92	GVE-95	GVE-00		PZ1	PZ2	DAQ	TK	LV	GK	KP
BOVIDAE	<i>Oreotragus oreotragus</i>		6													
	<i>Aepyceros melampus</i>											2				
	<i>Raphicerus campestris</i>				3											
	BOVID SIZE CLASS 1						4					53		10		
	BOVID SIZE CLASS 2						1							14		
	Ovis spp.													5		
PRIMATES	<i>Cercopithecus aethiopicus</i>							5								
	<i>Papio hamadryas ursinus</i>					1	1									
CARNIVORA	FELIDAE										10					
	<i>Canis familiaris</i>									1		4				
	<i>Canis mesomelas</i>						2									
	<i>Cynictis penicillata</i>									2			2			
	<i>Suricata suricatta</i>											4				
RODENTIA											1		2		54	
HYRACOIDEA	<i>Procavia capensis</i>	89	83	97	14	27	32	24		19	47	27	67	67	46	54

LAGOMORPHA	LEPORIDAE		11		15	39	49	52			2	9			46
	<i>Pronolagus rupestris</i>	2							75	29	8	13	5		
	<i>Lepus saxatilis</i>				1										
AVES	<i>Anas</i> spp.				1										
	cf. <i>Tyto alba</i>				1										
	<i>Numida meleagris</i>	9		3	64	1		19		1					
	AVES small				2	31	10		1	1					
	AVES large								2			4			
REPTILIA	LIZARD Small									5					
	TESTUDINE								1	5		2			

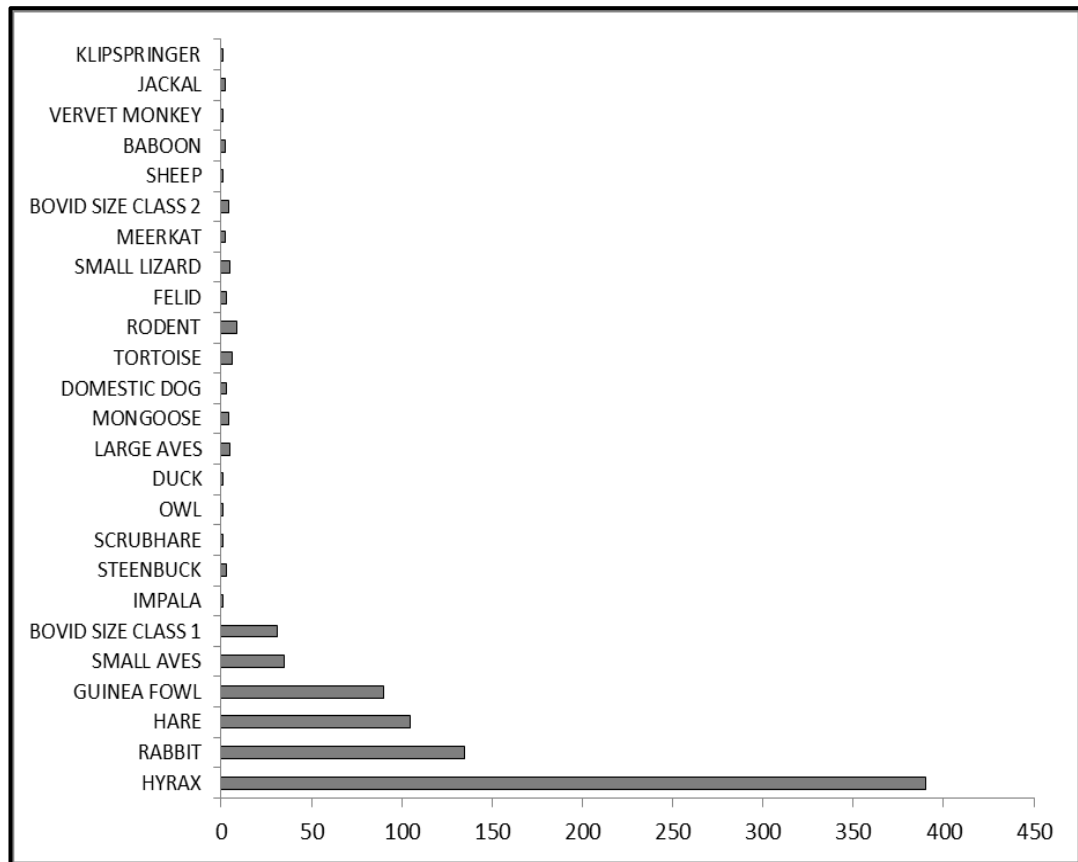


Figure 10: A comparison of the total Number of Identified Specimens Present (NISP) for all sites combined.

Table 5: Number of Identified Specimens Present (NISP)¹ and Minimum Number of Individuals (MNI)² at the Highveld Nesting Sites. The actualistic totals (NISP/MNI) are provided: those for each species on the left and each site below.

		KANP		UTM1		UTM2		WSBG		GVE92		GVE95		GVE00		TOTAL	
		NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
BOVIDAE	<i>Oreotragus oreotragus</i>			2	1											2	1
	<i>Raphicerus campestris</i>							3	1							3	1
	BOVID SIZE CLASS 1											3	1			3	1
	BOVID SIZE CLASS 2											1	1			1	1
PRIMATES	<i>Cercopithecus aethiopicus</i>													1	1	1	1
	<i>Papio hamadryas ursinus</i>									1	1	1	1			2	2
CARNIVORA	<i>Canis mesomelas</i>											2	2			2	2
HYRACOIDEA	<i>Procavia capensis</i>	91	26	29	8	37	15	17	2	20	7	26	8	5	2	225	68
LAGOMORPHA	LEPORIDAE			4	1			18	5	29	3	40	9	11	3	102	21
	<i>Pronolagus rupestris</i>	2	1													2	1
	<i>Lepus saxatilis</i>							1	1							1	1
AVES	<i>Anas</i> spp.							1	1							1	1
	cf. <i>Tyto alba</i>							1	1							1	1
	<i>Numida meleagris</i>	9	2			1	1	75	13	1	1			4	3	90	20
	AVES small							1	1	23	3	8	1			32	5
TOTAL	NISP	102		35		38		117		74		81		21		468	
	MNI		29		10		16		25		15		23		9		127

¹ NISP refers to the total count of specimens within a collection.

² MNI is defined as the fewest possible individuals within a collection.

Table 6: Number of Identified Specimens Present (NISP) and Minimum Number of Individuals (MNI) at the Karoo Nesting Sites.

		PZ1		PZ2		DAQ		TK		LV		GK		KP		TOTAL	
		NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
BOVIDAE	<i>Aepyceros melampus</i>					1	1									1	1
	BOVID SIZE CLASS 1					26	3			2	1					28	4
	BOVID SIZE CLASS 2									3	1					3	1
	<i>Ovis</i> sp.									1	1					1	1
CARNIVORA	FELIDAE			8	1											8	1
	<i>Canis familiaris</i>	1	1			2	2									3	3
	<i>Cynictis penicillata</i>	3	2					1	1							4	3
	<i>Suricata suricatta</i>					2	2									2	2
RODENTIA				1	1			1	1			25	1			27	3
HYRACOIDEA	<i>Procavia capensis</i>	25	8	37	4	13	2	30	10	14	1	21	1	25	1	165	27
LAGOMORPHA	LEPORIDAE					1	1	4	2					21	1	26	4
	<i>Pronolagus rupestris</i>	99	3	23	1	4	1	6	1	1	1					133	7
AVES	<i>Numida meleagris</i>			1	1											1	1
	AVES small	1	1	1	1											2	2
	AVES large	2	1					2	2							4	3
REPTILIA	LIZARD Small			4	1											4	1
	TESTUDINE	1	1	4	1			1	1							6	3
TOTAL	NISP	132		79		49		45		21		46		46		418	
	MNI		17		11		12		18		5		2		2		67

3.2. Skeletal part representations

An important pattern to observe is with the skeletal part representation for all species is that, regardless of the biome or nesting site, the ratio of NISP: MNI is constantly above 3:1. On average the ratio is 5:1 but at times it is as high as 33:1 (Philipstown Nesting Site Smith's red rock rabbit remains- Table 6) and 25:1 (Kameelpoort Nesting Site hyrax- Table 6).

The skeletal representation for hyrax was dominated by cranial elements (skulls, maxilla fragments and mandibles) and pelvises (Figure 11). No clear preference for either hind- or forelimb was shown; however there was a higher representation of limb bones from the Karoo Nesting Site accumulations than those of the Highveld Nesting Sites. Only vertebrae were repeatedly found in articulation and these were mostly lumbar vertebrae.

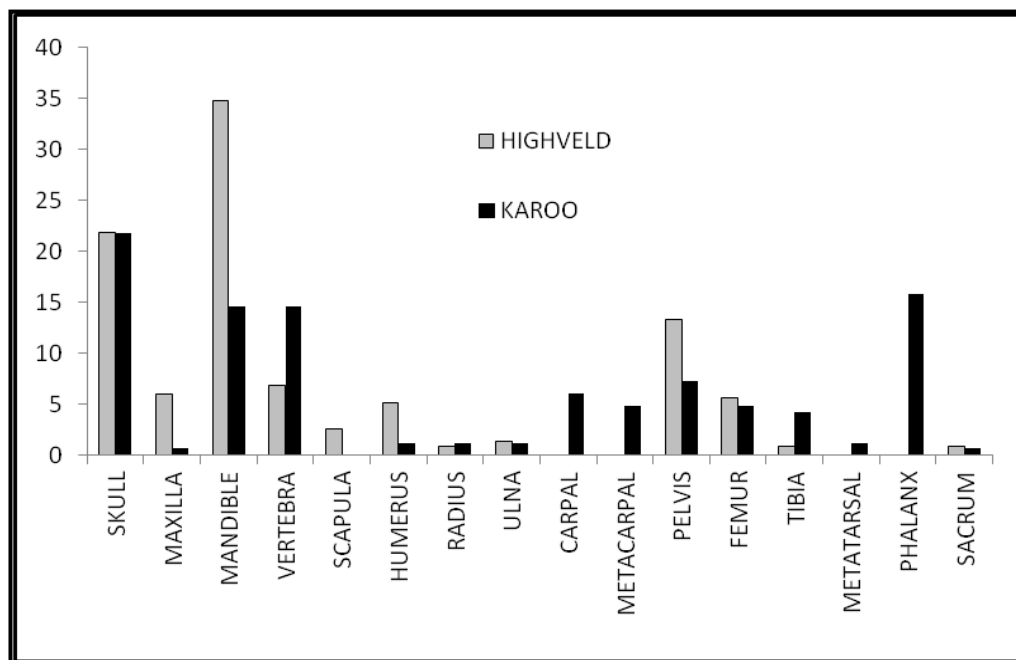


Figure 11: A comparison of the Hyrax skeletal part representation (Number of Individual Specimens Present). The vertical axis represents the actual NISP for each element.

Rabbits were represented mostly by hindlimb elements, particularly articulated feet which led to the high incidence of tarsals, metatarsals and phalanges (Figure 12). Only two rabbit elements were recovered from the Klipriviersberg Artificial Nesting Platform (KANP- Highveld Nesting Site) which interestingly are also hindlimb elements (a femur and a pelvis, both lefts). Very few forelimb elements were recovered from rabbit. Vertebrae were commonly found in articulation, and often attached to the sacrum and pelvis. Only a single rabbit skull was found (from Lockview), and a mandible (from Philipstown, Zwagershoek), both Karoo nest sites. Both of these elements were heavily damaged (Appendix B).

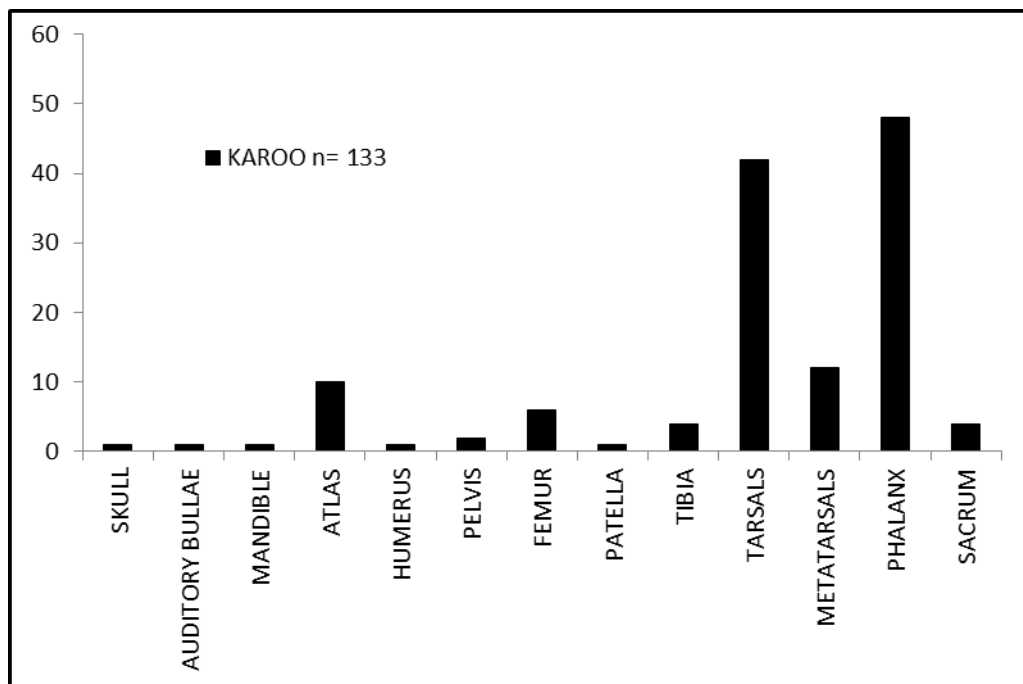


Figure 12: A comparison of the Smith's red rock rabbit skeletal part representation (Number of Individual Specimens Present). The vertical axis represents the total NISP for each element. Note that only Karoo Smith's red rock rabbit material was presented as the Highveld collection had only two specimens.

Hares were found from both biomes, with the bulk having come from the Highveld (Figure 13). The skeletal part representation mimics that of rabbits, with a high density of hindlimb elements and very few cranial elements. Articulated hindlimbs were common, one even included both hind limbs, from the lumbar vertebrae down to the keratin sheaths on the distal phalanx. Again, only one heavily damaged cranium was found, from the Highveld site of Gladysvale (collected in 1992).

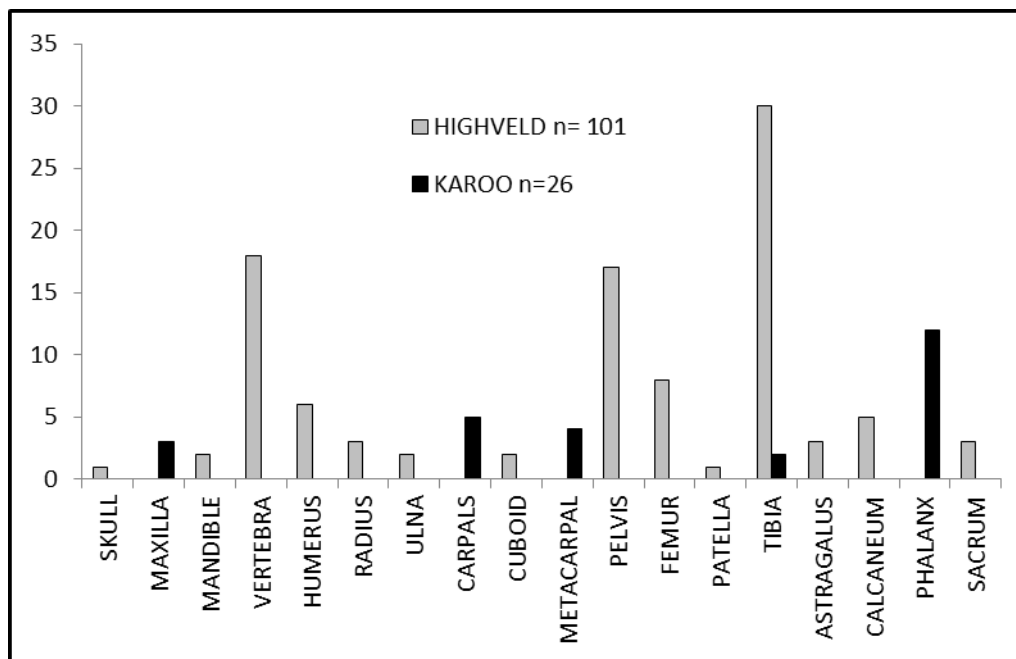


Figure 13: A comparison of the hare skeletal part representation (Number of Individual Specimens Present). The vertical axis represents the total NISP for each element.

Helmeted guineafowl remains were common throughout the Highveld sites, however only a single skeletal element was recovered from the Karoo Nesting Sites. Both helmeted guineafowl (Figure 14A) and aves spp. (Figure 14B) showed a high occurrence of humeri and sterna. Similar elements were repeatedly found within both accumulations in lower percentages, such as femurs, tarsometatarsi and vertebrae. Guinea fowl had an overall higher frequency of limb bones (such as tibiotarsi and tarsometatarsi) than those of the other aves spp. found, which had a higher frequency of forelimb or wing elements (humeri and ulnae).

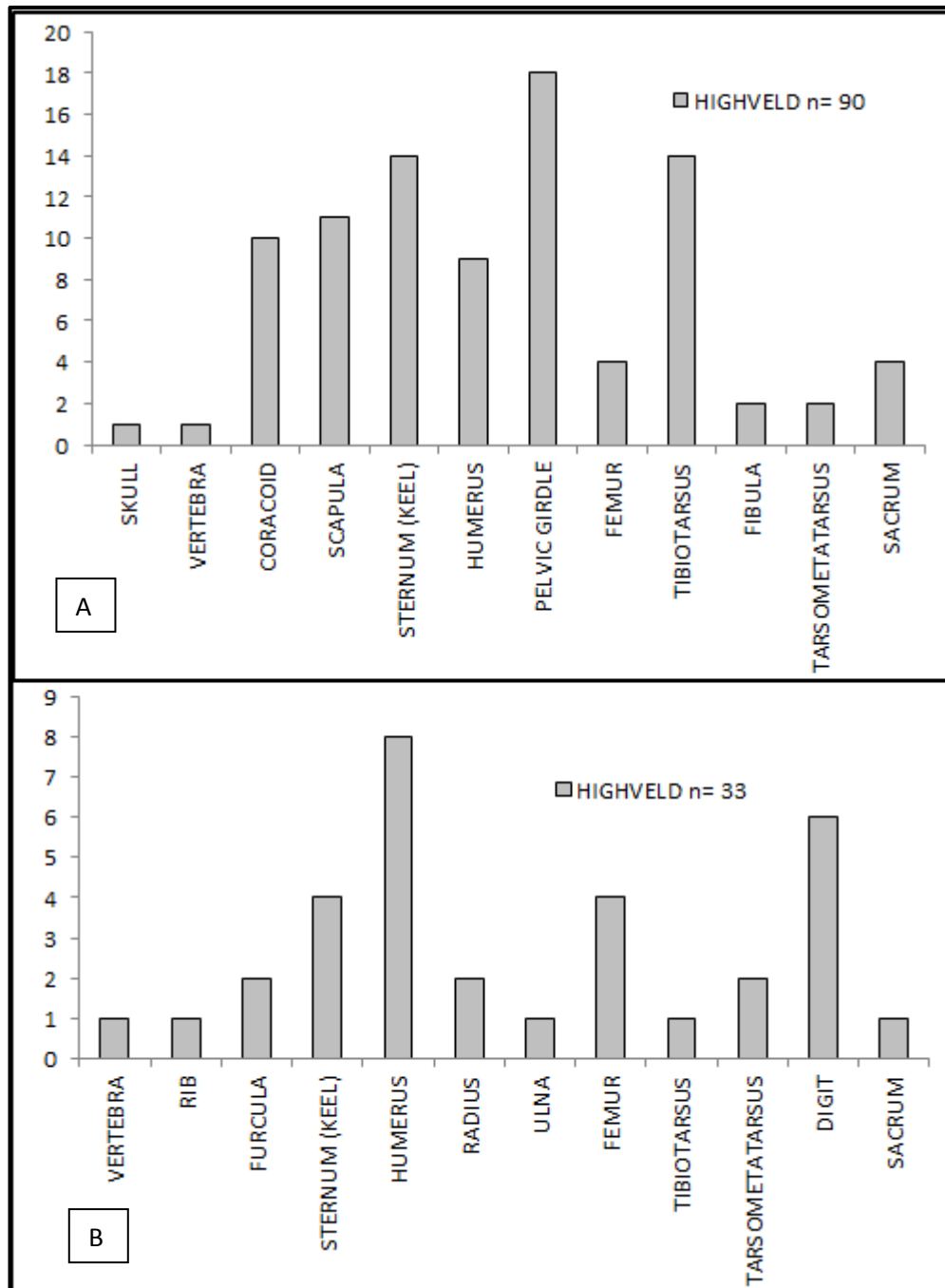


Figure 14: A comparison of A: helmeted guineafowl and B: aves spp. NISP. The only guineafowl remains from Karoo Nesting Sites were feathers with the distinctive grey and black mottled pattern of guineafowl found at Philipstown, Zwagershoek.

3.3. Taphonomy

A wide variety of taphonomic markings were found from across all nesting sites, which were repetitive and conformed to a distinct pattern (Table 7), illustrated in figures 14 to 22. The presence or absence, type and placement of the markings directly correlated with the type of prey species and skeletal element on which they occurred (Figures 24 to 37).

Four of these damage types have been previously noted and described by both Dart (1926) and Berger and Clarke (1995). These were summarized by Berger and Clarke as:

1. “depression fractures” and “puncture marks” in skulls (as a result of talon damage);
2. removal of the basicranium in order to access the brain;
3. cranium crushing and fracturing with distorted maxillae and mandibles;
4. V-shaped nicks from beak damage.

These four damage types have been refined and presented here with new damage types in a fully defined list as well as a description of the typical areas on the skeleton where these respective damage types occur. Damage types, such as punctures, have been broadened to include multiple, clearly defined variants.

As an additional note, large quantities of pellets were recovered from the Karoo Nesting Sites while no pellets were recovered from the Highveld nest sites (Figure 24). These were opened and the bone material, if any, was analysed. All of the remains were heavily acid etched and very few were identifiable (Figure 23).

Table 7: Verreaux's eagle characteristic damage types and descriptions.

Damage type	Definition	Typical placement
Chewed Edge (First described by Dart, 1926; amended by Berger & Clarke, 1995) See Figure 15	Uneven, sharp zig-zagged edges that show distinctly small v-nicks along the edge. Also there are no fractures running perpendicular to the chewed edge, causing the plane of the bone surface to dip	Edges of cortical bone that have been broken off in pieces/chunks
Crenulated Edge See Figure 16	Similar to chewed edges but show no small v-nicks characteristic of chewing. Distortion causing the bone surface to flake away from the natural plane of the bone edge, also fractures running perpendicular to the bone edge	Found along edges where bone removal has occurred in large chunks and no subsequent chewing has taken place. Long bone shafts and skull caps exhibit this type of damage typically
V- nick (Term coined by Dart, 1926) See Figure 17	A distinctive v-shaped nick along an area that has been chewed (see below) which clearly implicates beak involvement	Often in the same areas as both crenulated edges and chewed edges. Sometimes found along edges where removal has taken place
Notch See Figure 18	A small incidence of a single bone removal event, no defined shape	Found in areas where removal takes place but was halted mid-dismemberment
Scratch See Figure 19	Small, grouped and unparallelled grooves along the bone surface, do not puncture into the medullary cavity	Near areas where bone removal have taken place (see below); Around orbits
Removal (First coined by Dart, 1926; expanded on by	Portions of cortical bone that have been purposefully removed	Areas where thin bone has muscle attachments that shield choice meat options: e.g. zygomatic

Berger & Clarke, 1995) See Figure 20		arches (eye), pubis-ischium bridge (caeca), etc.
Coarse Puncture (First noted by Dart, 1926; expanded by Berger & Clarke, 1995) See Figure 21	An amorphous hole through cortical bone	Found along surfaces of thin cortical bone where possible circular punctures (see below) ripped further
Circular Puncture See Figure 21	Punctures that implicate talon usage in dismemberment	Oft times through long bone shafts and in orbits, possibly as a result of handling during feeding and hunting, respectively
Keyhole Puncture See Figure 22	Punctures that are triangular, implicate beak usage in dismemberment	Thin cortical bone where large muscle attachments occur (e.g. scapula blades and acromion process)
Acid Etching See Figure 23	Small pitting and overall thinning of the outer cortex due to gastric juices digesting prey items in the stomach (as described in chapter 1.2)	Found on smaller prey items, often in association with pellets.



Figure 15: Chewed edge showing a v-nick along the parietal of a hyrax skull. The occipital and right zygomatic have been removed. Note also the v-nick (arrow).



Figure 16: Crenulated edges along the mandibular rami of three hyrax hemi-mandibles.



Figure 17: A characteristic V-nick (arrow) on the iliac blade of a hyrax pelvis.



Figure 18: A left hyrax mandible showing notching (arrows) along the ramus.

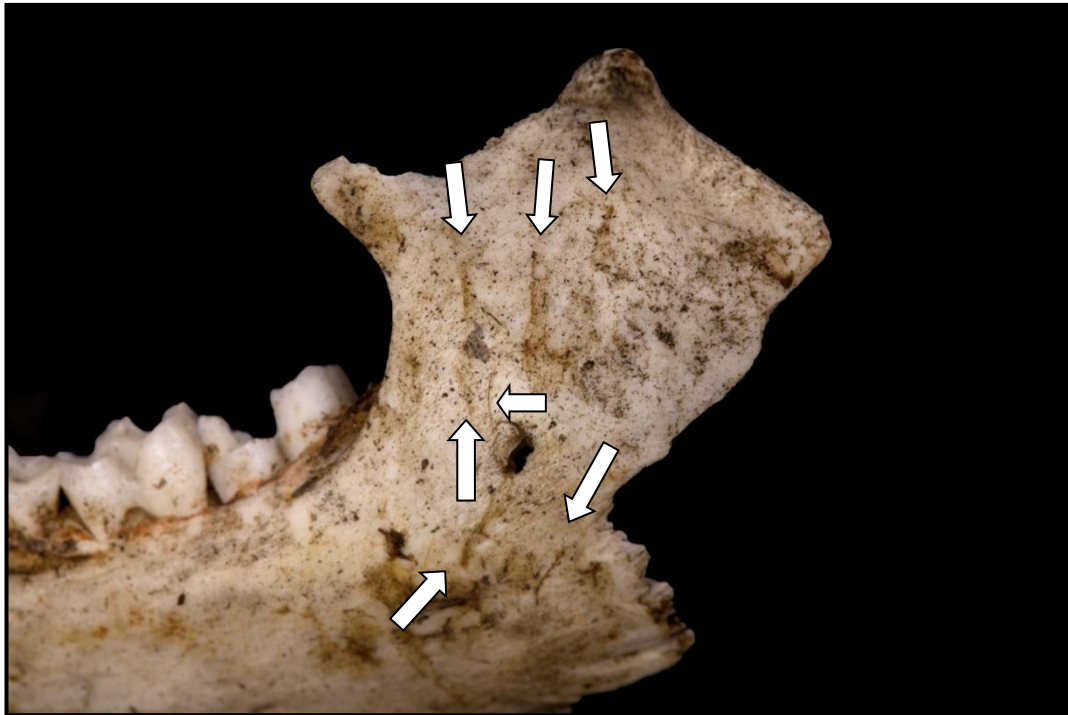


Figure 19: A number of scratches on the same mandible as illustrated in Figure 18.

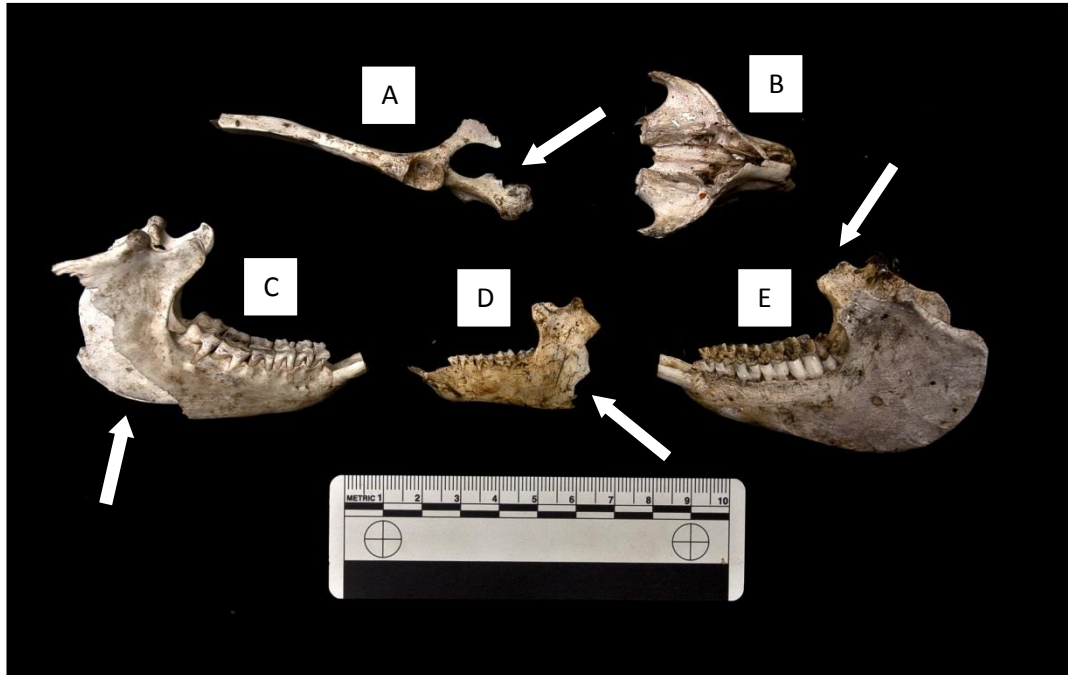


Figure 20: A range of various examples of bone removals. From top left: A: The removal of the ischium-pubis bridge (hyrax hemi-pelvis); B: a hyrax skull with the complete removal of the occipital, parietal and frontal bones resulting in only a muzzle remaining; C: complete hyrax mandible showing the removal of chunks of the ramus; D: left juvenile hyrax mandible with the partial removal of the ramus; E: complete hyrax mandible with the removal of the coronoid process.



Figure 21: A close up of orbit damage (hyrax skull) that exhibits examples of both coarse and circular punctures, illustrated by the black and white arrows, respectively.



Figure 22: Keyhole puncture on a helmeted guineafowl humerus.

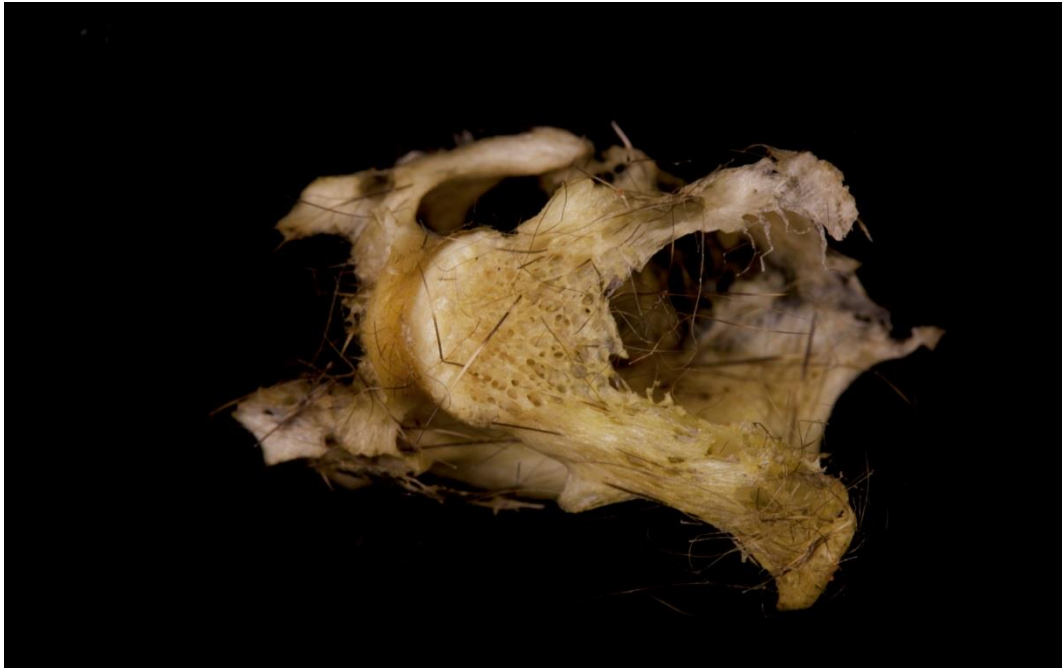


Figure 23: Acid etching on a vertebra, caused by partial digestion in the eagle's stomach prior to the pellet being regurgitated.



Figure 24: A range of the pellets retrieved from Karoo Nesting Sites. Note the variation in both colouration and size.

The previously discussed damage types as well as a further 26 combinations of these damage types were found in all of the sites studied (Table 8). Of these damage types, removal of bone material, crenulated edges and chewed edges were the most common (Figure 25). In terms of the combinations of damage observed, removal with associated punctures was placed highest with 5% of the total damage types observed.

The Highveld Nesting Sites mirror the patterns exhibited by the overall nesting site damage types in Figure 25 with high counts of removal, crenulated and chewed edges (Figure 26). Combinations of damage that featured most prominently were removal and punctures, as well as chewed edges with notching and V-nicks.

The Karoo Nesting Sites showed a higher percentage of crenulated edges, followed by acid etching and then removals (Figure 27). Chewed edges were also quite frequent, but not so much so as in the Highveld Nesting Site damage types. Again, removals with associated punctures placed high in the combination damage types along with chewed edges and removals.

Table 8: A list of the damage type combinations observed throughout the collections.

Combination number	Combination damage	Abbreviation for figures
1	Chewed edges; removal	CE/REM
2	Chewed edges; punctures	CE/PUNC
3	Chewed edges; notching	CE/NT
4	Chewed edges; keyhole punctures	CE/KHP
5	Chewed edges; crenulated edges	CE/CREN
6	Chewed edges; acid etching	CE/AE
7	Chewed edges; removal; notching	CE/REM/NT
8	Chewed edges; notching; V-nicks	CE/NT/VN
9	Chewed edges; notching; keyhole punctures	CE/NT/KHP
10	Chewed edges; notching; punctures	CE/NT/PUNC
11	Chewed edges; punctures; notching; crenulated edges	CE/PUNC/NT/CREN
12	Chewed edges; scratches; punctures; notching; keyhole	CE/SC/PUNC/NT/KHP/CREN

	punctures; crenulated edges	
13	Scratches; punctures	SC/PUNC
14	Scratches; removal; punctures	SC/REM/PUNC
15	Scratches; removal; punctures; crenulated edges	SC/REM/PUNC/CREN
16	Removal; punctures	REM/PUNC
17	Removal; notching	REM/NT
18	Removal; crenulated edges	REM/CREN
19	Removal; punctures; crenulated edges	REM/PUNC/REN
20	Punctures; notching	PUNC/NT
21	Punctures; V-nicks	PUNC/VN
22	Punctures; crenulated edges	PUNC/CREN
23	V-nicks; keyhole punctures	VN/KHP
24	V-nicks; crenulated edges	VN/CREN
25	V-nicks; keyhole punctures; crenulated edges	VN/KHP/CREN
26	Keyhole punctures; crenulated edges	KHP/CREN

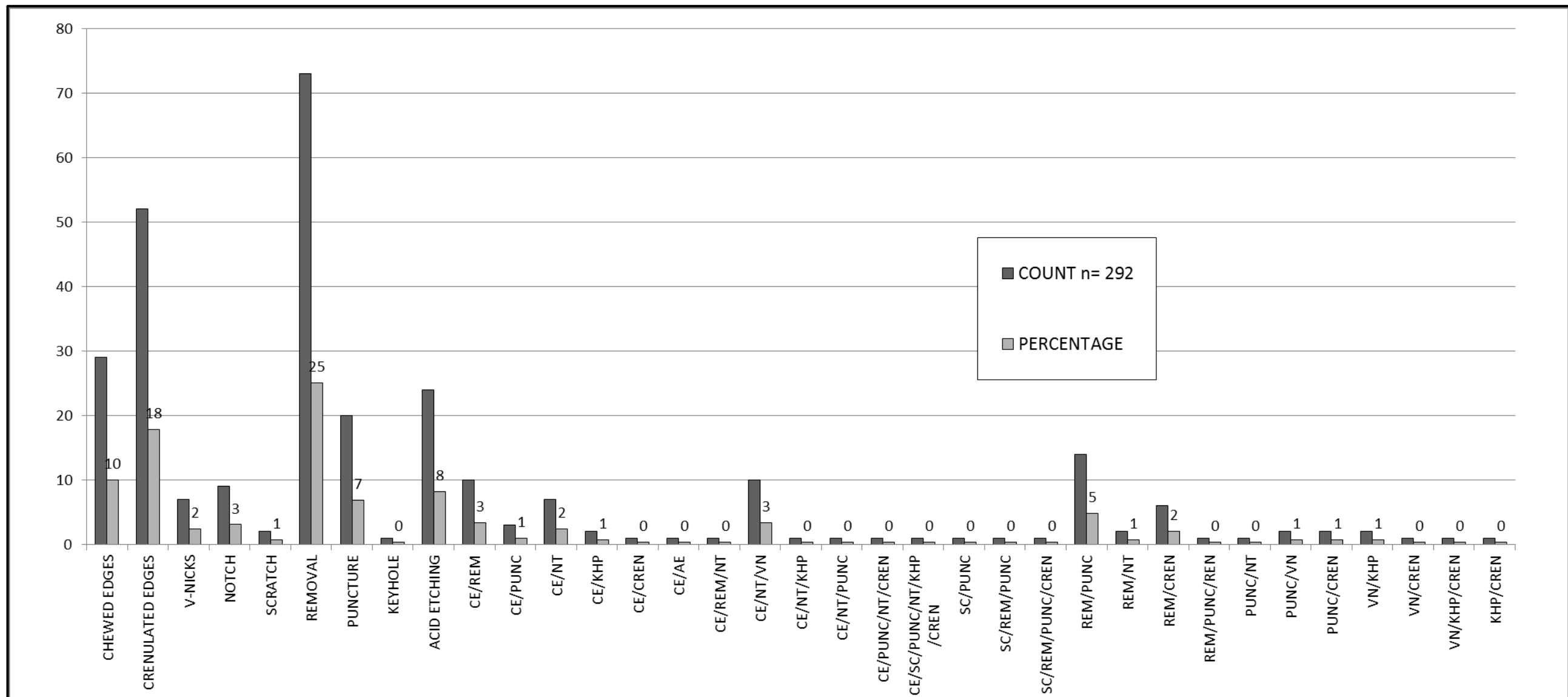


Figure 25: A histogram showing all the different damage types discussed above in Table 7, along with the 26 combinations outlined in Table 8 above for all of the specimens recovered.

Note that the percentage data are listed above the individual grey bars.

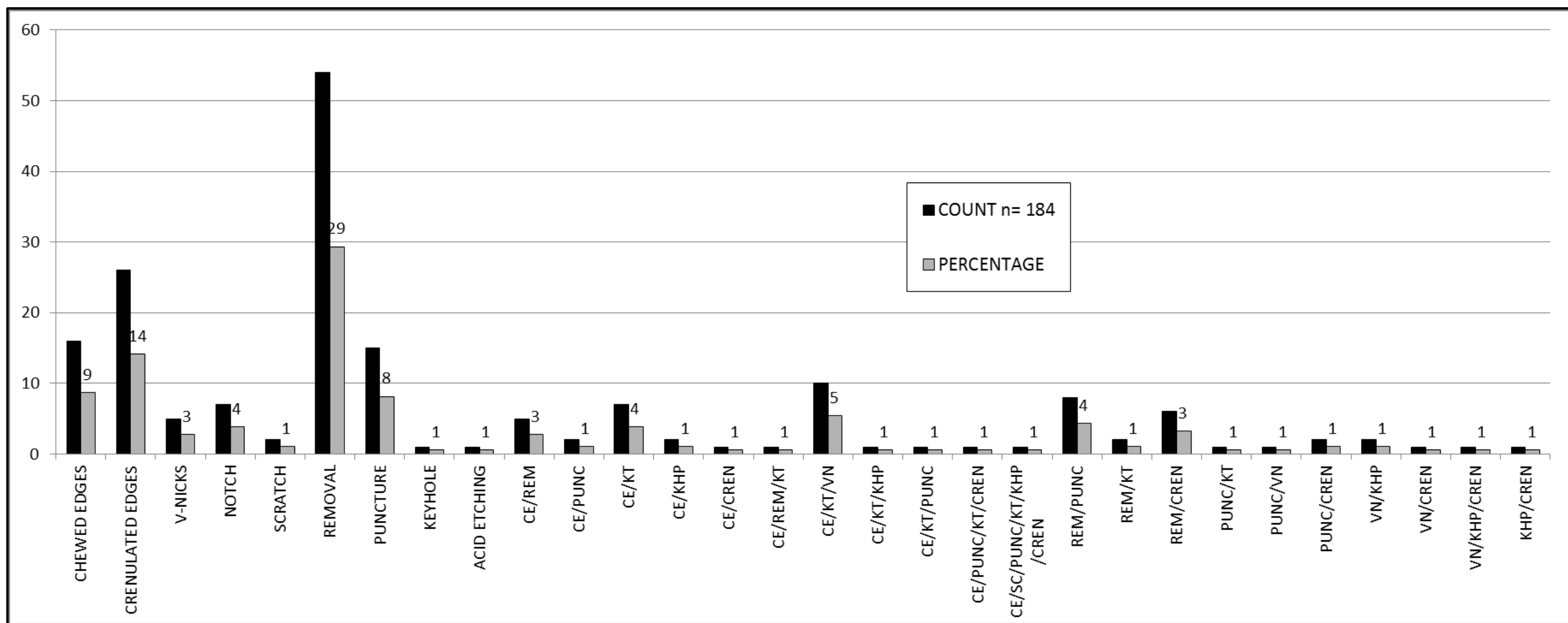


Figure 26: A composite of all the damage for the Highveld Nesting Sites remains as well as all (21) of the combinations observed.

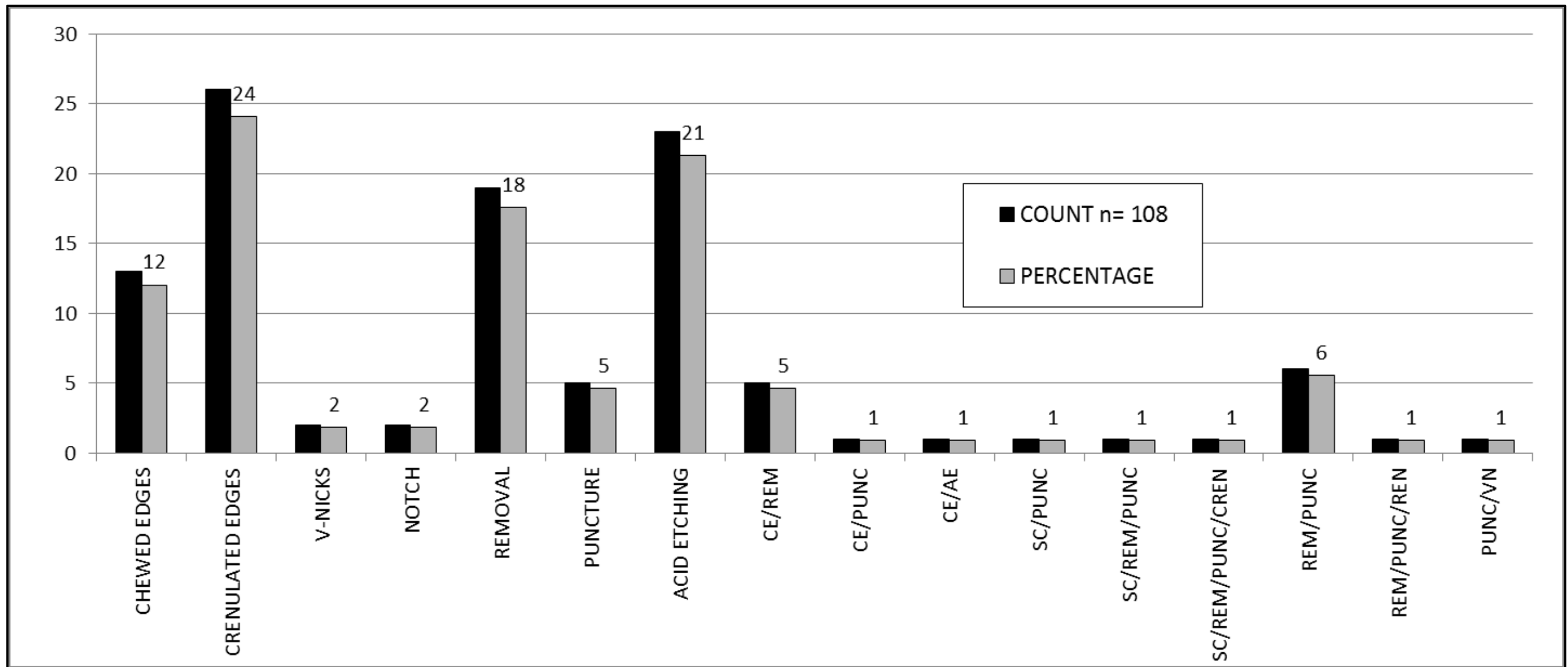


Figure 27: A composite of all the damage for the Karoo Nesting Sites remains as well as all (9) of the combinations observed.

There was a total count of 13 damage occurrences observed from Klipriviersberg Artificial Nesting Platform. The damage on skeletal remains was dominated by six counts of removal followed by 2 counts of notching (Figure 28). Both combinations include one or the other of these types of damage. The majority of the damage is distributed across hyrax remains as they form the bulk of the collection from this nesting site (see Table 4).

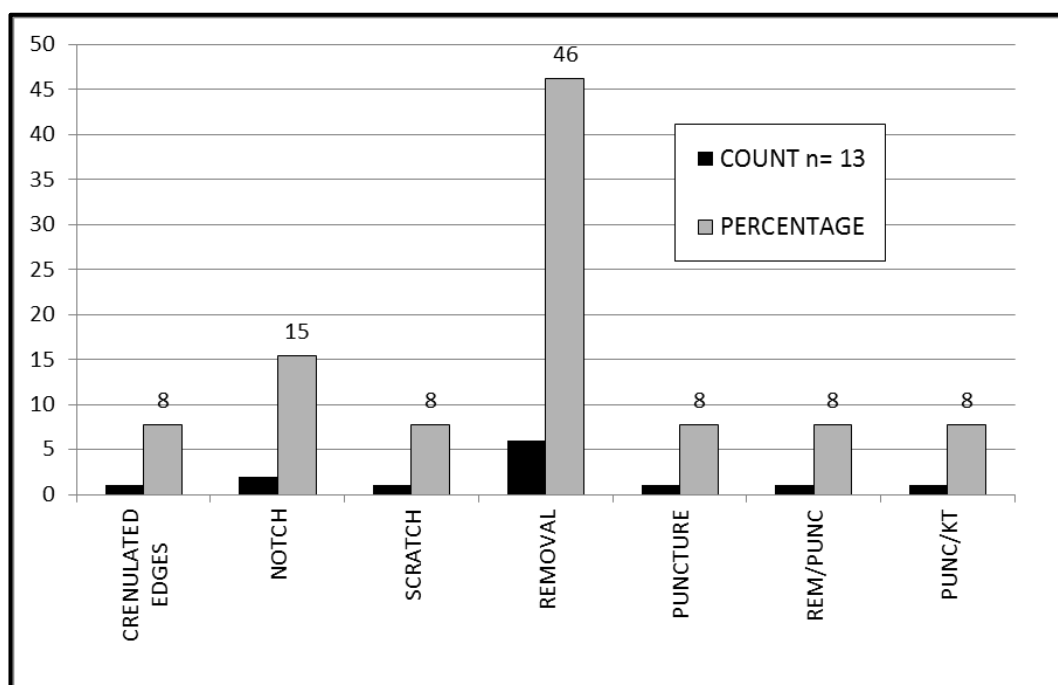


Figure 28: The damage found on skeletal remains from the Klipriviersberg Artificial Nesting Platform.

Removals were highest (42%) of the damage types observed for the Walter Sisulu Botanical Gardens Nesting Site (Figure 29). The combination of chewed edges, scratches, punctures, notching, keyhole punctures and crenulated edges (14%) as well as observations of isolated chewing damage (13%) were the following highest damage types.

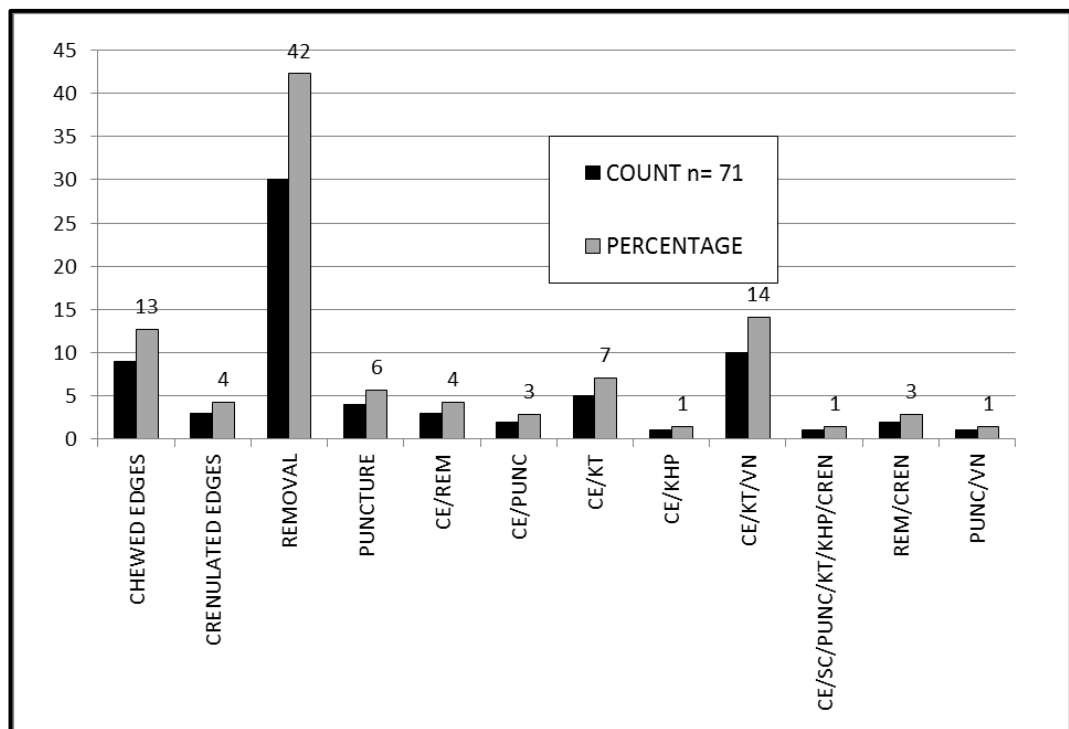


Figure 29: The damage found on skeletal remains from the Walter Sisulu Botanical Gardens Nesting Site.

Again, removal was the most common damage type for the Upper Tonquani Nesting Site followed closely by crenulated edges (Figure 30). Removals with associated punctures were the highest combination of damage observed.

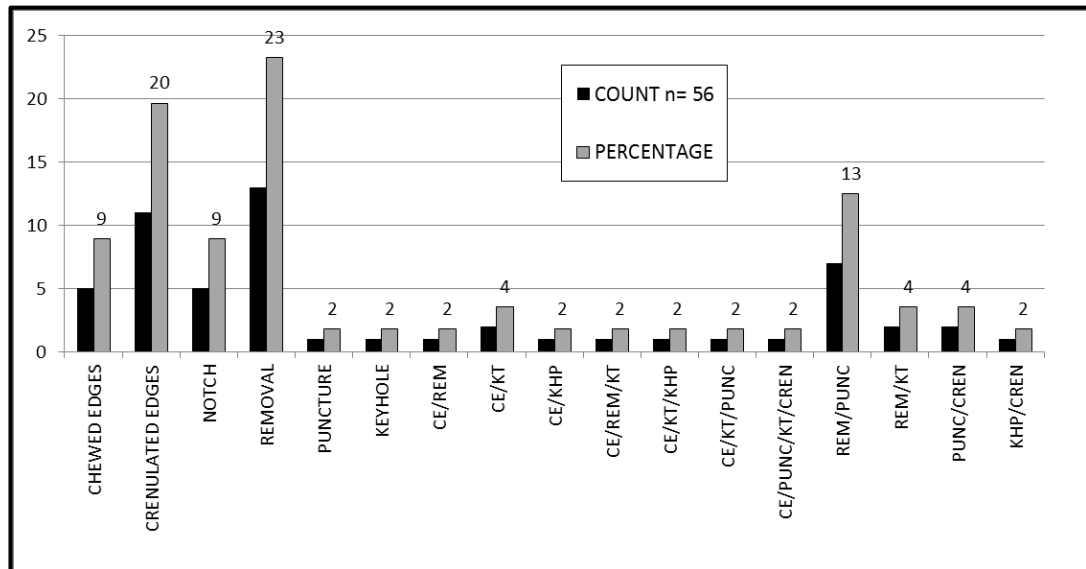


Figure 30: The damage found on skeletal remains from the Upper Tonquani Nesting Site in Magaliesberg.

At the Gladysvale Nesting Site, the most regularly occurring damage type observed was crenulated edges, followed by punctures and then removals (Figure 31). The composite of removals and crenulated edges featured as the most common of the combination damage types. This was the only site on the Highveld that showed evidence of acid damage, albeit on a single element.

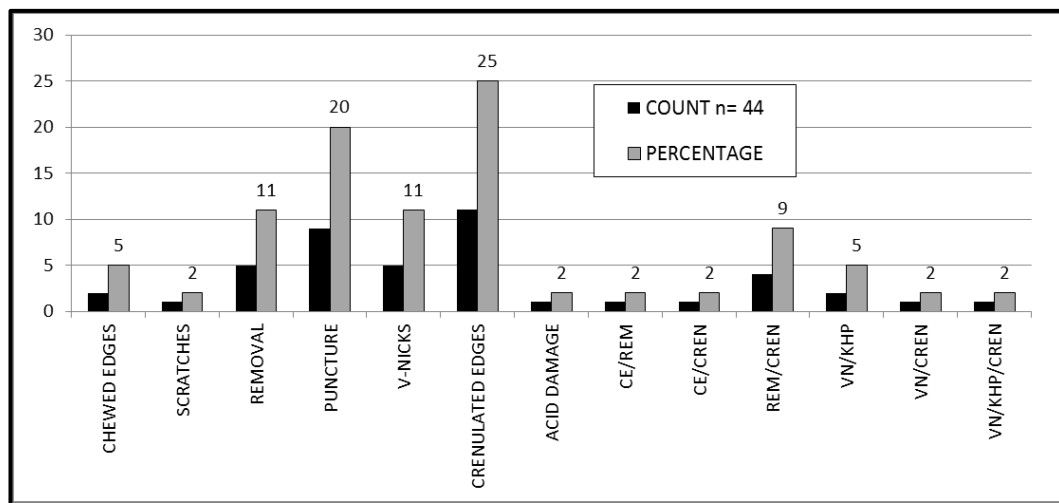


Figure 31: The damage found on skeletal remains from the Gladysvale Nesting Site.

The Karoo Nesting Sites exhibited less damage counts than did those of the Highveld Nesting Sites (Figures 36 and 37). As such only three of the sites had enough damage to warrant similar figures as the others. Groblershoop, Gifkloof, Kameelpoort and Lockview had fewer than ten counts of damage each. Groblershoop had acid etching on all fifteen elements in its collection. The three specimens from Gifkloof Nesting Site had no damage; however two of the specimens were an articulated front paw of a rock hyrax and an articulated fore-limb of a rodent. Only a single rock hyrax skull from Kameelpoort exhibited chewed edges. The Kameelpoort fauna also, interestingly, had three articulated

specimens: a forelimb of a rock hyrax; a hindfoot of a hare; and a string of three lumbar vertebrae (taxon unidentifiable). Lockview had acid etching on seven (all of which were rock hyrax skeletal elements) of its 18 specimens. This site also had three articulated vertebrae of unknown taxon and a partial articulated hindfoot of a rock hyrax.

The Philipstown Nesting site exhibited high counts of crenulated edges along bone surfaces along with high acid damage and removal occurrences (Figure 32). Seven articulated hindlimb specimens were recovered, four of which were Smith's red rock rabbit and the remaining three were from rock hyrax. One of the articulated specimens (Smith's red rock rabbit) was the complete back half of the animal, from the final lumbar vertebra, with both limbs and tail.

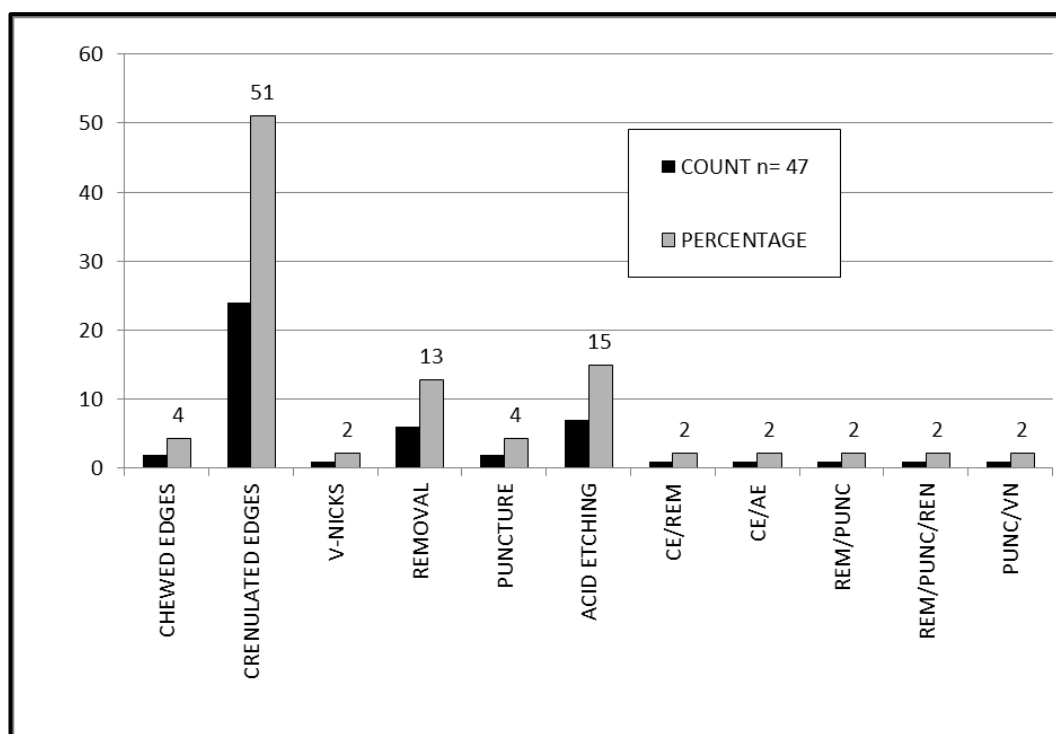


Figure 32: The damage found on skeletal remains from the Philipstown, Zwagershoek Nesting Site.

Chewed edges, removals and removals with associated punctures dominated the De Aar Quarry Nesting Site assemblage (Figure 33). At this site there were two articulated specimens, both bovid size class one hindlimbs. Both exhibited chewed areas on the most proximal exposed element (a femur and tibia, respectively).

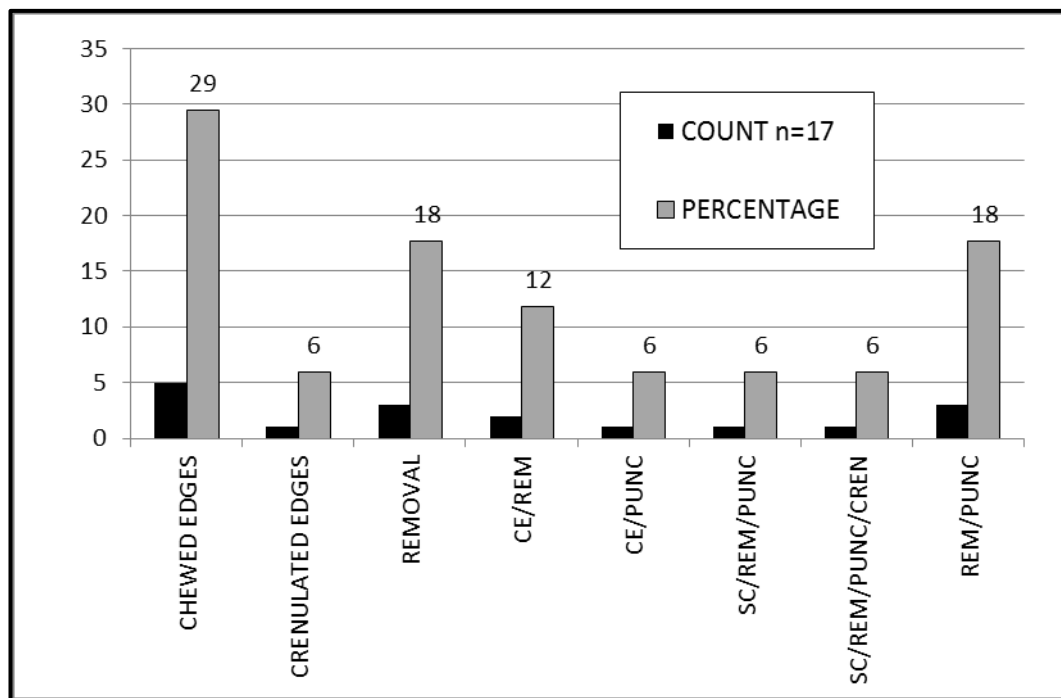


Figure 33: The damage found on skeletal remains from the De Aar Quarry Nesting Site.

A third of the damage from the Tafelkop Nesting Site specimens showed removal of skeletal material, along with chewed edges and punctures making up another third (Figure 34). Two lengths of articulated lumbar vertebrae (rock hyrax and Smith's red rock rabbit) were recovered.

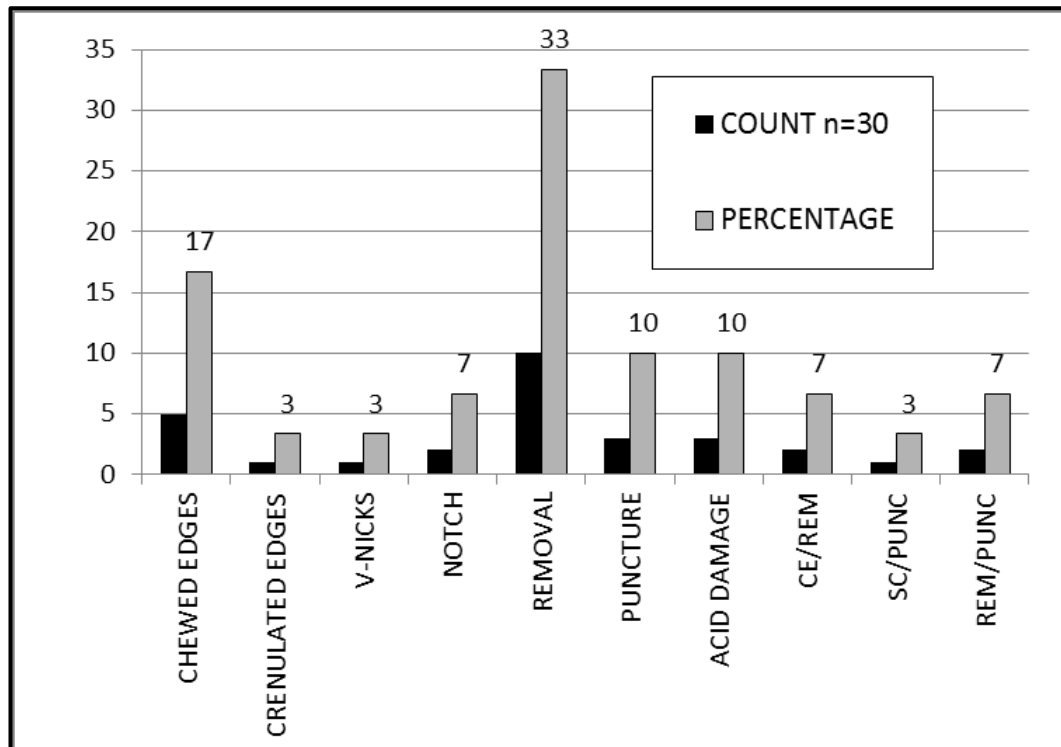


Figure 34: The damage found on skeletal remains from the Tafelkop Nesting Site.

Rock hyrax, whilst the most commonly found prey item from all of the sites, also exhibited the highest occurrence of damage (Figure 35). Nearly equal proportions of removal and crenulated edges dominate the damage types, but were only the second highest type of damage to occur in combination. The most common damage to occur in combination was removal with associated punctures. Furthermore, the rock hyrax exhibited the greatest range of damage

with 25 types of damage out of a possible 36 (10 isolated damage types and 26 combinations).

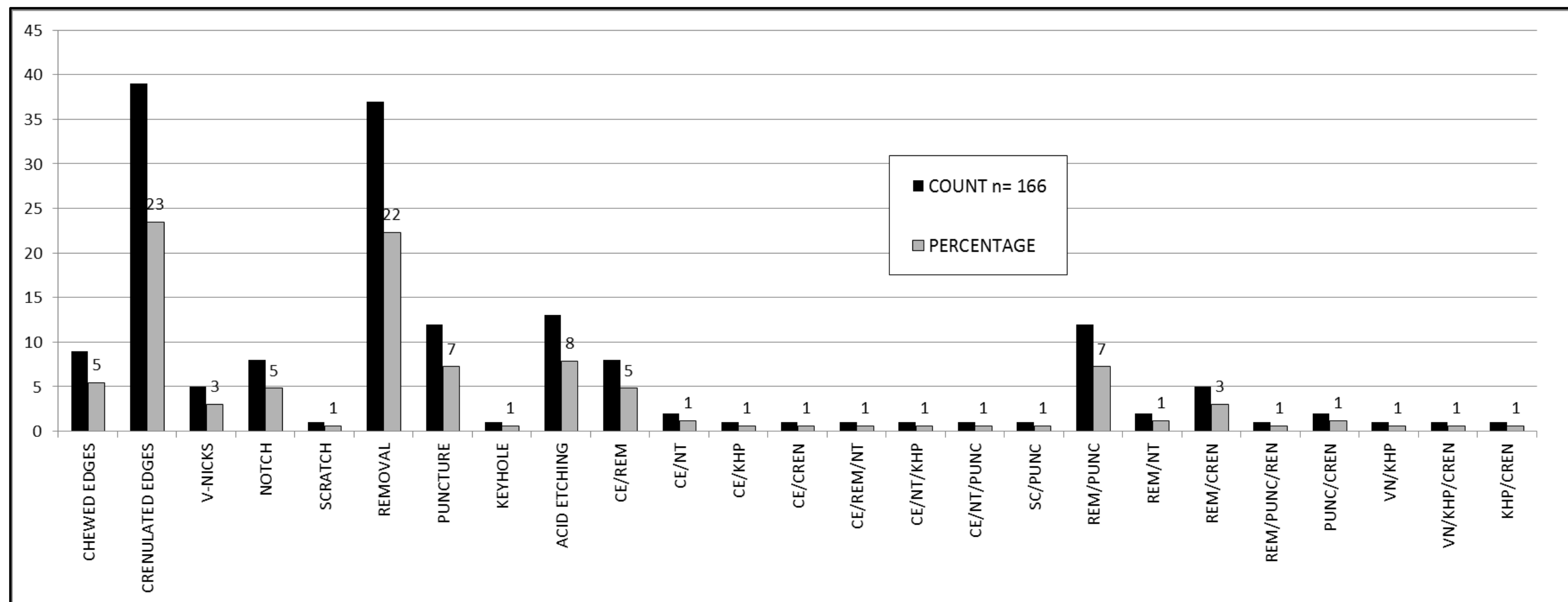


Figure 35: The damage patterns found on rock hyrax skeletal remains from all of the nesting sites combined.

Hare remains had high frequencies of chewed and crenulated edges with very few instances of composite damage (one occurrence: a left pelvis with both chewed edges and a puncture mark from Walter Sisulu Botanical Gardens) (Figure 36). It is also the only other taxon (in addition to rock hyrax) to have specimen with V-nicks.

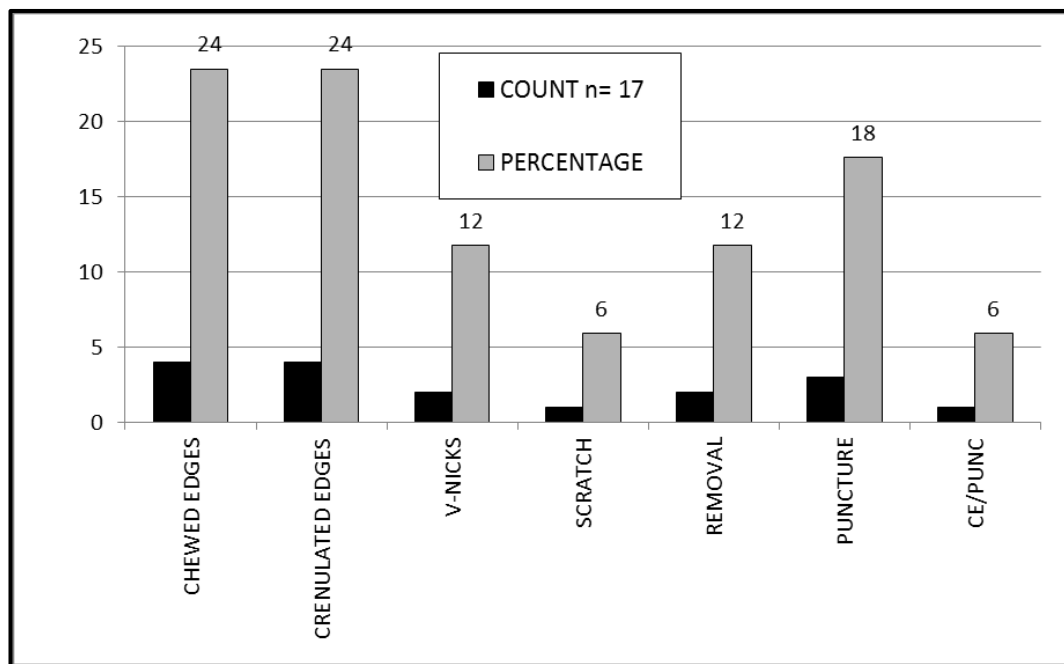


Figure 36: The damage patterns found on hare skeletal remains from all of the nesting sites combined.

Smith's red rock rabbit had damage on only 16 of the total of 135 specimens collected (Figure 37). Removals were the most common form of damage on its skeletal remains. Single occurrences of chewed edges, notching, acid damage, chewed edges/removal and punctures/V-nick were represented. This was the only taxon, other than rock hyrax, to exhibit acid etching on a specimen (humerus).

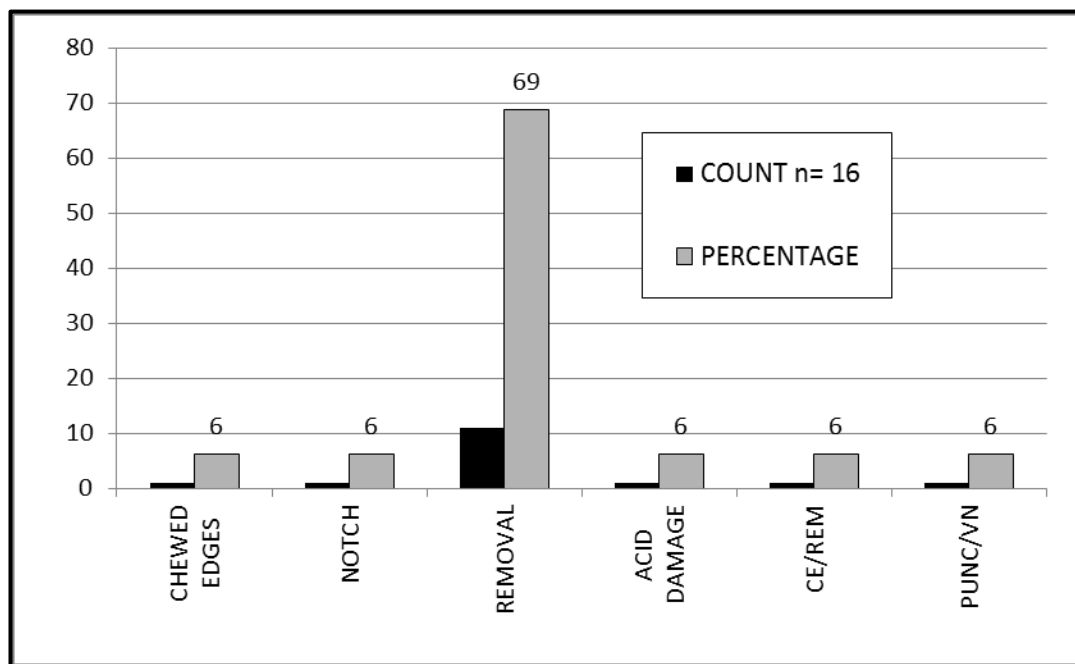


Figure 37: The damage patterns found on Smith's red rock rabbit skeletal remains from all of the nesting sites combined.

Helmeted guineafowl had high representations of removal as well as chewed edges (Figure 38). The combination of chewed edges, notching and V-nicks was also high. This taxon showed the highest number of combinations (8) after rock hyrax (16).

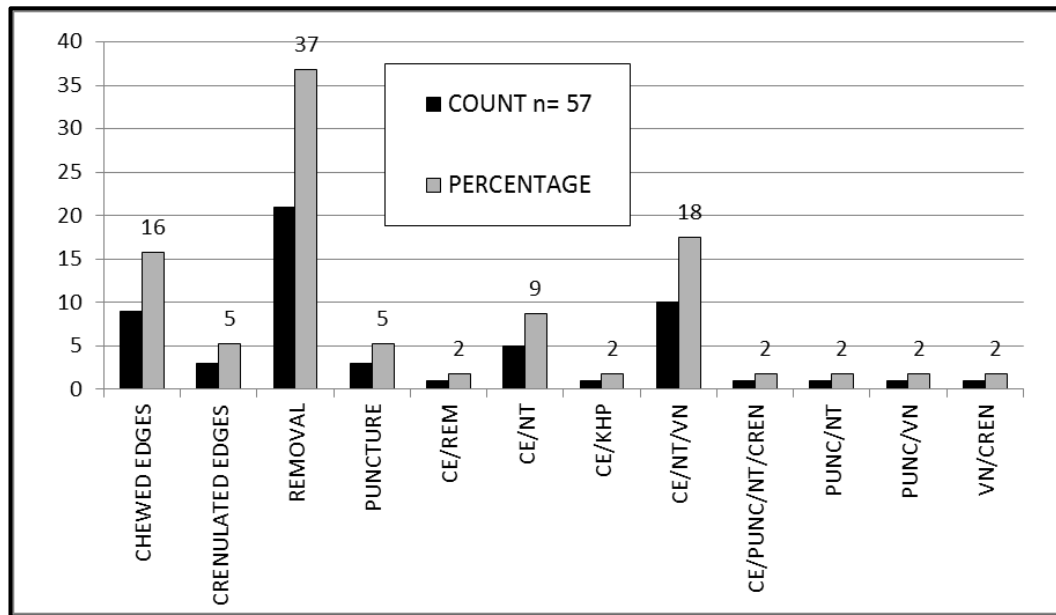


Figure 38: The damage patterns found on helmeted guineafowl skeletal remains from all of the nesting sites combined.

The two other taxa that had higher numbers of individual specimens present, the small aves and size class one bovids, had very low damage counts. The small aves group had only seven counts of damage: notching (a humerus and a keel); removal (humerus); crenulated edges (keel and bone fragments), acid etching (femur); and a combination of chewed edges and a puncture (articulated vertebrae). The size class one bovids exhibited only three counts of damage: chewed edges on a femur; crenulated edges on a tibia; and a combination of chewed edges and a puncture on a tibia. Only four other taxa had damage types and these are listed below in Table 9.

Table 9: A list of the remaining damage types found on poorly represented taxa.

SPECIES	ELEMENT	SITE	DAMAGE TYPE
<i>Canis familiaris</i>	Femur	DAQ	Chewed edges
	Femur	DAQ	Scratches, removal, punctures and crenulated edges
<i>Canis mesomelas</i>	Skull cap	GVE 95	V-nicks and keyhole punctures
<i>Papio hamadryas ursinus</i>	Skull cap	GVE 92	Crenulated edges
Herpestidae	Mandible	PZ 1	Crenulated edges
	Frontal	PZ 1	Chewed edges
	Skull	TK	Chewed edges and acid etching

CHAPTER 4

DISCUSSION

4.1. Interpretations

4.1.1. Prey selection

Hyrax was certainly the most common prey item recovered when one views the collection holistically, however it was not necessarily always the most common for each of the individual sites. For example, Walter Sisulu Botanical Gardens Nesting Sites had a far higher representation of helmeted guineafowl (64%), and the Gladysvale Nesting Sites showed a markedly higher percentage of leporidae across the three different years (1992- 39%, 1995- 49%, 2000- 52%). Both of these results are interesting in that there were definitely a far greater variety of small mammal prey options in these areas, some of which had been selected for at other nesting sites (see Table 10 for the small mammal species found at the Walter Sisulu Botanical Gardens as listed by South African National Biodiversity Institute).

As previously mentioned the hyrax population at the botanical gardens has dwindled over the years due to the increasing urbanisation, but not so much so that the small mammal population is reflected in Verreaux's eagle prey selection (Kruger, 2010). Hyrax still form the largest contingent of the Walter Sisulu Botanical Gardens Verreaux's eagles prey selection despite the diminishing population in the area. Although not observed in this study, this particular nesting pair has expanded its prey selection to include domesticated dogs and cats, which are subsequently removed from the nest (there is a surveillance camera positioned on the nest to record the eagles activities, which is accessible to the public, and as such domesticated pets are removed for sensitivity purposes- B. Gardner, pers. comm. 2011).

Table 10: A list of the mammalian species found at the Walter Sisulu Botanical Gardens (listed by the South African National Biodiversity Institute). Those species selected by Verreaux's eagles in this study are in boldface.

Common Name	Latin name
South African Hedgehog	<i>Atelerix frontalis</i>
Chacma Baboon	<i>Papio hamadryas ursinus</i>
Vervet monkey	<i>Cercopithecus aethiops</i>
Scrub hare	<i>Lepus saxatilis</i>
Cape Porcupine	<i>Hystrix africaeaustralis</i>
Greater canerat	<i>Thryonomys swinderianus</i>
Red veld rat	<i>Aethomys chrysophilus</i>
Caracal	<i>Felis caracal</i>
Black-backed Jackal	<i>Canis mesomelas</i>
Cape clawless otter	<i>Aonyx capensis</i>
Honey badger	<i>Mellivora capensis</i>
Small-spotted Genet	<i>Genetta genetta</i>
Yellow mongoose	<i>Cynictus penicillata</i>
Slender mongoose	<i>Galerella sanguinea</i>
Water mongoose	<i>Atilax paludinosus</i>
Antbear (aardvark)	<i>Orycteropus afer</i>
Rock hyrax	<i>Procavia capensis</i>
Common duiker	<i>Sylvicapra grimmia</i>

With the exception of the Klipriviersberg Artificial Nesting Platform, the remaining Highveld Nesting Sites are all surrounded with naturally occurring vegetation and prey species with minimal impact from human encroachment (Table 11). Only Klipriviersberg and Upper Tonquani had rock hyrax as the most common prey item whilst Gladysvale had a higher representation of leporids. The area surrounding the Gladysvale Nesting Site is not as rocky as that of Klipriviersberg and Upper Tonquani but rather a sheer cliff with surrounding grasslands (Figure 39), short thicket and wooded species (Mucina & Rutherford, 2006), which could account for the lower representation of rock hyrax.



Figure 39: The cliff on which the Gladysvale Verreaux's eagle pair nests, high-lighting the ill-suited vegetation and lack of rocky outcrops for high numbers of rock hyrax.

Table 11: The small mammal species found on the Meyer's Farm property where the Klipriviersberg Artificial Nesting Platform is located (listed by the South African National Biodiversity Institute). Those species selected by Verreaux's eagles in this study are in boldface.

Common name	Latin name
South African Hedgehog	<i>Atelerix frontalis</i>
Scrub Hare	<i>Lepus saxatilis</i>
Smith's red rock rabbit	<i>Pronolagus capensis</i>
Cape Porcupine	<i>Hystrix africaeaustralis</i>
Slender Mongoose	<i>Galerella sanguinea</i>
Yellow Mongoose	<i>Cynictus penicillata</i>
Small-spotted genet	<i>Genetta genetta</i>
Grey Duiker	<i>Sylvicapra grimmia</i>
Black-backed Jackal	<i>Canis mesomelas</i>
Cape fox	<i>Vulpes chama</i>
African Civet	<i>Civettictis civetta</i>
Spotted-necked Otter	<i>Lutra maculicollis</i>
Cape clawless Otter	<i>Aonyx capensis</i>
Rock hyrax	<i>Procavia capensis</i>
Springbok	<i>Antidorcas marsupialis</i>

The majority of the mammalian prey items had live weights that fall within size class I category (<23kg- Brain, 1981; see Table 12). Those species, such as *Papio hamadryas ursinus* and *Aepyceros melampus*, which have large live weights over

25kg, are individual elements and juveniles, respectively. In the case of the baboon remains, both elements are crania which substantiate the observations made by Berger and Clarke, amongst others, who noted that large prey species are decapitated before the skull is transported back to the nest (Brain, 1981; Berger & Clarke, 1995; McGraw *et al.*, 2006; Gilbert *et al.*, 2009).

Table 12: Live Adult weights of the prey items identified in this study.

Those species marked with an asterisk are representatives of Family taxon (such as Rodentia). All mammalian weights are from Skinner and Smithers (1990) and Brain (1981); avian weights are taken from Brown *et al.* (1982).

Male (M) and female (F) weights are provided where available.

Common name	Average adult live weights (kilogrammes)
Common duiker	15
Impala	M= 60; F= 45
Steenbok	7- 16
Bovid size class 1	<23
Bovid size class 2	24- 84
Sheep	Variable
Vervet monkey	5.5
Chacma baboon	M= 32; F= 15.5
Felidae (domestic cat)	Variable
Domestic dog	Variable

Black-backed jackal	10
Yellow mongoose	0.5
Suricate	0.9
Rodentia (cane rat*)	3.6- 4.5
Rock hyrax	3.0- 3.5
Leporids	>4
Smith's red rock rabbit	2.5
Scrub hare	3.5
Duck*	Very variable
Barn owl*	0.4- 0.5
Helmeted guineafowl	1.3
Tortoises	Variable

4.1.2.Skeletal part representation

In the Highveld Nesting Sites, the rock hyrax was dominated by cranial elements (skull, maxilla and mandible) which collectively made up over 60% of the total hyrax skeletal part representation. The rock hyrax post cranial remains are from the shoulder (scapula and humerus) and hip joints (pelvis and femur). This implies a preference for the distal extremities, particularly the feet, which would therefore be removed from the assemblage via ingestion. Vertebrae are also poorly represented, and if present were articulated in two or more vertebrae. All of these skeletal part representations corroborate the observations made by Gargett for the Verreaux's eagle feeding behaviour in the Rhodes Matopos National Park. Skulls are processed for the eyes, tongue and brain first and then the head is removed by severing the cervical vertebrae. Internal organs such as the heart, liver and lungs are then eaten, which would impact on the scapula and

rib representation. Hyrax ribs are completely absent from the collection in this study. Gargett notes that the ribs, legs and feet are occasionally consumed. The remains from this study indicate that they are almost always consumed. Alternatively, the Verreaux's eagles could be targeting the portions of the skeleton that have the most muscle attachments such as hindlimbs in lagomorphs, hyrax and guineafowl.

In the Karoo Nesting Sites there was less of a focus on the cranial elements (which collectively made up 37% of the collection) or shoulder joint elements but rather a higher representation of hindlimb elements and feet. Skulls and mandibles were present but in fewer numbers. This implies that the eagles in this region are processing the forelimb region of the carcass more competently than that of the hindlimb. Also, they appear not to be feeding on the feet in contrast to the Highveld eagle pairs as both isolated elements and articulated feet were recovered.

Smith's red rock rabbit remains seem to be the inverse of rock hyrax as they are represented by mostly hindlimb elements; only 2 cranial and a single forelimb element (humerus) were identified. The Karoo Nesting Sites had almost all of the rabbit remains while the Klipriviersberg Artificial Nesting Platform was the only site in the Highveld to have rabbit identified. It would appear that the eagles in the Karoo Nesting Sites are consuming the bulk of the upper half of the rabbit remains, including the skull, since the cranial remains that had been recovered were heavily damaged and reduced to maxilla fragments. Rabbit skulls are both porous and heavily muscled (see Figure 40) which could explain the low frequency of skulls in a Verreaux's eagle assemblage since they would be choice regions to focus on dismembering (Rafferty *et al.*, 2012). The remaining hindlimb elements are often preserved in articulation which suggests that the hindlimbs are discarded. Rabbit internal morphology is arranged such that organs can be accessed by removing the ribcage and vertebral column and not having to break through the pelvis or sacrum (see Figure 41).



Figure 40: A domestic rabbit skull in comparison to a rabbit brain, showing the intricate lobations and extensions, which could explain the intensive damage patterns observed on rabbit crania in this study. Also note the thin cortical bone on the cranium. Figure adapted from <http://animaldiversity.ummz.umich.edu/> and Brainmuseum.org.

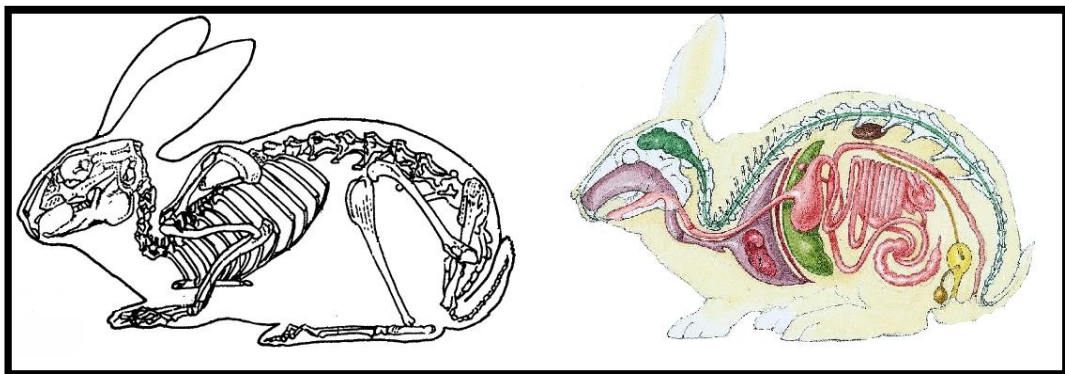


Figure 41: Lagomorph internal anatomy high-lighting the position of the scapulae/rib cage and pelvic girdle relevant to the internal cavity. Image from <http://www.ucmp.berkeley.edu> (accessed 26/10/2012).

The scrub hare remains are similar to those of the Smith's red rock rabbit in that the Highveld Nesting Sites had predominantly hindlimb elements and only a single heavily damaged cranial fragment. The Karoo Nesting Sites interestingly did not follow this pattern as there were a high number of maxillary fragments as well as only fore-foot elements, which suggests a different feeding pattern in more arid climates. In the Karoo, the environment is more arid with scarcer diurnal mammalian prey options. Carnivores in these environments are subject to higher instances of inter- and intraspecific competition for prey resources and tend to utilise the carcass to its fullest potential which could explain the lower abundance of the heavily muscled scrubhare limb elements in the collections (Kruuk & Turner, 1967; Bertram, 1978; Smuts, 1978; Sunquist & Sunquist, 1989).

Avian prey remains showed no clear preference for either fore- or hindlimb elements, but large surface area bones, namely the keel and pelvic girdle were highly represented and heavily damaged. The positions of these two elements in the body of a fowl form the main structural support for their bipedal lifestyle (Figure 42). The keel supports the abdominal cavity, cradling the lungs and gizzard, both choice nutritional organs. The pelvic girdle shields the kidneys, ovaries and greater intestine. By removing the large muscle attachments on both of these elements and breaking through the thin bone, the Verreaux's eagle is capable of accessing the entire organ system of a bird. Avian remains were only recovered from the Highveld Nesting Sites, which were all well stocked with small mammal prey options, which could explain the inconsistent skeletal part representation of avian remains for this collection.

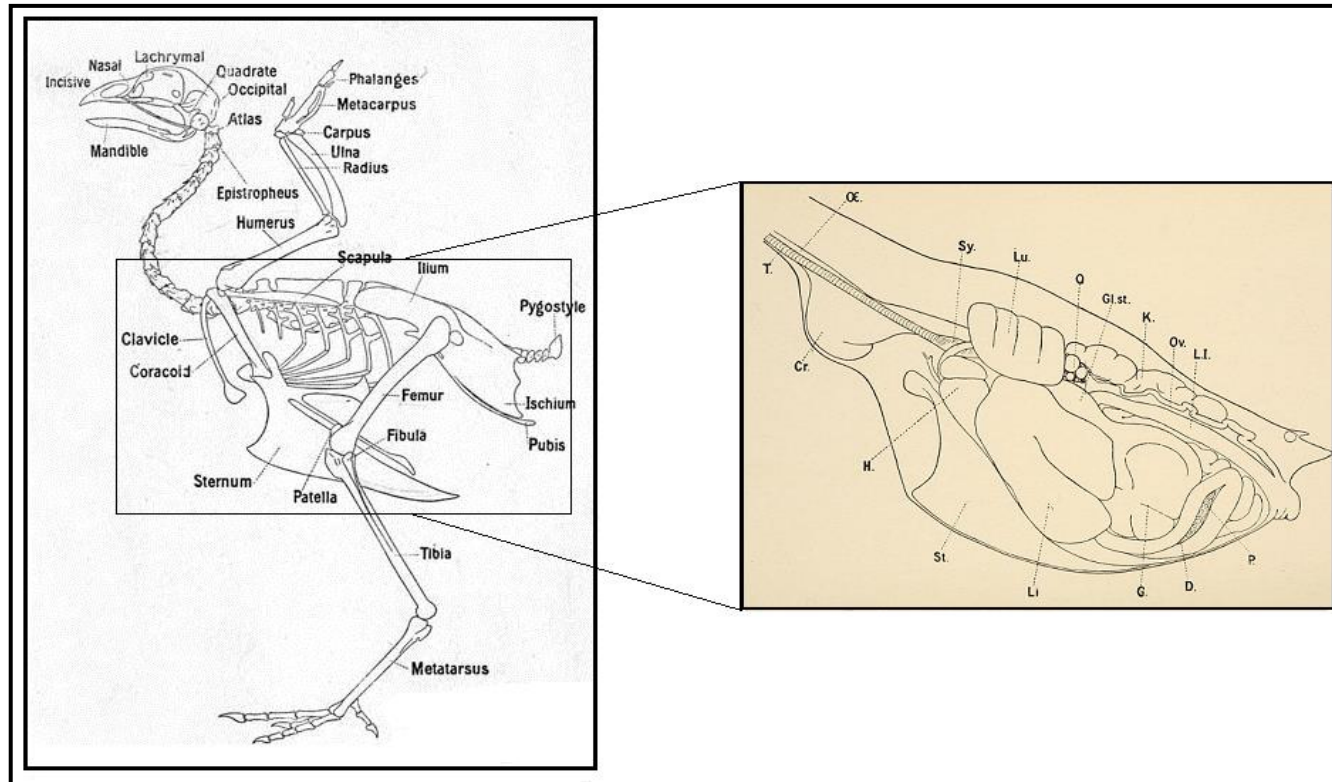


Figure 42: The anatomy of a fowl, used as a proxy for the anatomy of helmeted guineafowl. Image adapted: Bradley, 1915.

OE.: oesophagus; T.: trachea; Cr.: crop; Sy.: syrinx; Lu.: lung; H.: heart; O.: ovary; Gl.st.: glandular stomach; K.: kidney; Ov.: oviduct; L.I.: large intestine; St.: sternum (keel); Li.: liver; G. gizzard; D.: duodenum; P. pancreas.

Another interesting observation with the skeletal part representation is the constant ratio of Number of Identified Specimens (NISP) to the Minimum Number of Individuals (MNI). This implies that, on average, a very low proportion of the skeletal remains from a single prey item are swallowed or removed from the assemblage. This differs from the feeding practices of mammalian carnivores where swallowing small skeletal elements, such as carpals and phalanges, is not so challenging. Due to the avian digestive system, even though smaller elements may be swallowed, they may be returned to the assemblage in the form of pellets and then bear characteristic acid etching damage.

4.1.3. Taphonomic Markings

When prey opportunities are low, predators tend to utilise more of a single carcass as the next meal is uncertain. Damage patterns are likely to be more spread over the carcass with higher occurrences of acid etching as swallowing small elements and portions would result in a higher nutritional intake. In areas such as the Highveld however, which are covered in long grasses and denser mid-height vegetation, prey is more readily available. In these areas the Verreaux's eagles need to consume only those choice organs, concentrating damage on the adjacent skeletal elements only. Removal of sections of bone, chewed and crenulated edges are the most common damage type.

Berger and Clarke (1995) were the first to introduce four specific damage types that were the result of large raptor involvement in an assemblage. They described the first of these as depressed fractures in combination with punctures on primate skulls as a result of talon use in the manipulation of the skull while feeding. They also noted the removal of the basicranium, using the beak, in order to access the brain and possibly the tongue. When feeding on the skulls, damage to the cranium, in the form of crushing and fracturing, was also noted- especially in relation to the distortion of maxilla and mandibles, possibly also due to the manipulation of the prey whilst feeding. Lastly, as a result of extensive beak

usage in feeding, a number of v-shaped nicks were common along the surface of broken areas of bone, made by the beak removing sections of bone and the upper beak leaving a cross-section impression in the remaining bone surface.

The present study has allowed for an amendment to these four damage criteria in relation to Verreaux's eagle feeding behaviours as well as the introduction of a further six damage features. These ten distinctive macroscopic taphonomic markings, as well as 26 combinations thereof, were observed in relation to the skeletal part representations in this collection.

1. Chewed edges were defined as uneven, sharp zig-zagged edges that show distinctly small v-nicks along the edge of a cortical bone, typically along a surface of bone that has had a section removed (see damage type six "Removal" below). Also there are no fractures running perpendicular to the chewed edge, causing the bone surface to dip below or above the natural plane.

This damage type was the third most common damage type to be found in isolation but the most frequent in combination with other damage types (12 combinations). There was an equivalent representation of this damage from both the Highveld and Karoo Nesting Sites of approximately 10% but interestingly it was absent from the Klipriviersberg Artificial Nesting Platform. Chewed edges most often accompanied removal events. Breaking into the internal organ cavity or the cranium required both removals of larger areas of cortical bone followed by chewing to further expand the hole and to remove the sinew and muscle attachments that could hinder feeding. In something as curved as the cranial vault chewing away excess bone casing can be in order to access deeper recesses, such as the extended temporal lobes that lengthen anteriorly between the eye sockets or the brain stem as the base of the cranial vault (Figure 43).

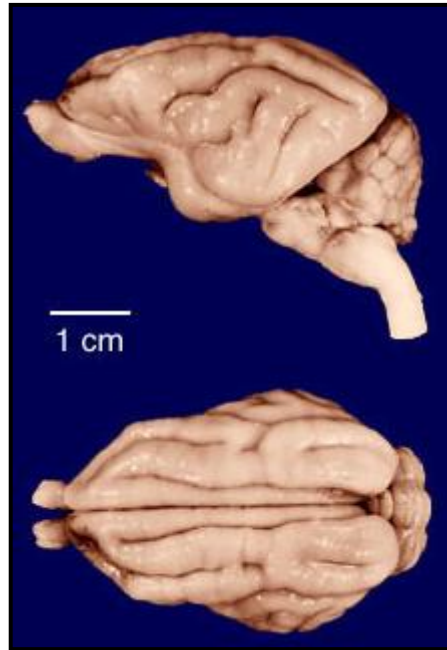


Figure 43: The rock hyrax brain, high-lighting the morphology of the extended temporal lobes and the elongated brain stem. Figure adapted from Brainmuseum.org.

Scrub hare skeletal remains were heavily chewed. Scapulae, pelvises and the ends of long bone shafts were most commonly chewed. As previously discussed, Smith's red rock rabbit skulls were rarely present but if they were they exhibited heavy chewing damage and crenulated edges around the skull cap until only a maxillary fragment remained. Rabbit skulls are anteriorly-posteriorly elongated which, in conjunction with a porous and fragile skull (Figure 40), resulted in high levels of damage (Figure 37). These elements showed low occurrences of chewing as not much force would have to be applied to break into the cranial vault other than the initial removal event.

Guineafowl remains and the bones of other small aves were heavily chewed, especially along the keel and pelvic girdle flat surfaces. This coincides with the anatomical position of these two elements encapsulating choice organs as

discussed above (Figure 42). As with hyrax skulls, removal of larger portions of the cortical bone took place, followed by chewing to further expand on the exposed areas making access to the internal organs easier.

2. Similar to chewed edges, crenulated edges are roughly edged cortical bone but show no small v-nicks characteristic of chewing. Distortion causing the bone surface to flake away from the natural plane of the bone edge occurs as well as fractures running perpendicular to the bone edge. This is the result of large removal instances with no subsequent chewing activity and subsequent weathering has taken place, causing the distortion.

Occurrences of these damage types mimic those of areas for different species where chewed edges occur. This is most probably due to the removal of a large surface that was sufficient and did not require further chewing.

3. V-nicks, as described by Berger and Clarke (1995), are upper beak impressions along chewed areas of cortical bone. This damage type is most often found in combination with chewed edges, crenulated edges and removals. These v-nicks are potentially the result of a keyhole puncture along the edges of long bone surfaces that lead to the removal of the thin outer stretch of bone. Whilst not frequently observed in isolation, they are commonly found in conjunction with chewed edges.

4. A notch is similar to a v-nick in that it is an area where there has been removal of cortical bone, however it does not conform to any particular shape. This is the result of a large area of removal in a ripping action (probably the removal of a muscle attachment where the attaching bone surface was also removed). Notching is present whenever there is chewing activity.

5. Scratches are shallow, semi-parallel grooves along the bone surface. Scratches never puncture into the medullary cavity. This damage type only occurred three times in isolation but always occurred in combination with removals and punctures. Scratches from talons are the result of manipulation of prey remains

during feeding. They are seemingly unintentional and serve no obvious purpose in terms of disarticulation or flesh removal but rather a by-product of these feeding behaviours.

6. Removal in this study is an extension of the definition given by Berger and Clarke (1995). Bone surface removal categorises damage made from purposefully removing chunks of cortical bone and occurred in areas where thin bone covered a choice meat option. Hyrax skulls nearly always had the occipital removed (sometimes the entire skull cap was removed until only a muzzle remained- Figure 20B), as well as one or both of the zygomatic arches (Figure 15). Berger and Clarke (1995) originally stated that the skulls and mandibles of eagle primate prey remains were always found in articulation; however Gilbert *et al.* (2009) stated that this was not the case but rather that they were forcibly separated. Hyrax mandibles often had one or both of the coronoid processes removed or broken in order to unhinge the jaw and access the tongue, as described by Gargett (1990)(Figure 20E). In doing so the Verreaux's eagle is also granted easier access to the occipital base, which is removed. Removal along the pelvis and scapula was also very common, in addition to removal of a portion of the long bones (humerus, ulna, femur, tibia, and so forth) in mammals; whilst in birds removal of large segments of the keel and pelvic girdle was frequent.

7. Berger and Clarke (1995) never truly defined the dimensions of puncture marks so here they have been divided into three distinct variants. The coarse puncture is an amorphous puncture through the cortical bone into the medullary cavity. These are possibly circular or keyhole punctures (see below) that were ripped further. Punctures are not purposefully made and serve no function in the disarticulation of prey items but are rather made during the hunting and killing activities (see "circular punctures" below for a full explanation).

8. A circular puncture describes simply a puncture that has preserved the circular cross section of the talon in the cortical bone. These punctures are often in the orbital floors (see Figure 21) as a result of hunting where the eagle swooped and

grabbed the prey item by the head, driving its front talons into the orbit floors and the hallux into the base of the neck (Gargett, 1990). Alternatively, prey items are collected by grabbing the body with both talons, leading to puncture wounds through either the pelvis or the scapula. Circular punctures are then logically very frequently on these two elements and skulls. In skulls they are always positioned around the orbits and occasionally further back in the parietals (Figure 21). Infrequently there are circular punctures on long bones, as a result of excessive force whilst handling the remains causing the talon to puncture the outer bone cortex.

9. The final puncture damage type is described as a keyhole puncture and is attributed to the involvement of the upper beak piercing through the cortical bone and preserving the triangular cross sectional shape of the beak. This damage type is visible across all skeletal elements. The true purpose of such a marking is unclear as there is no true advantage to having a small triangular puncture through the cortical bone. As such it would be safe to assume that this damage type is simply a byproduct of feeding.

10. Acid etching has been seen as a characteristic in many raptors investigated for their taphonomic abilities. Whilst feeding, raptors will swallow smaller prey portions and these portions will be stored in the crop where strong digestive acids dissolve skin, muscle, ligament and other organs (Proctor & Lynch, 1993). Those elements that are indigestible are expelled from the stomach and show evidence of etching in the form of small pits and thinning of the outer bone cortex. Even though it is found in Verreaux's eagle collections, it is not a common damage type in the Highveld and almost solely found in the Karoo Nesting Sites' accumulations. Prey remains are utilised for far more of their nutritional value in the Karoo, where the resources are less frequently available than those of the more abundant Highveld regions. Avian prey remains together with reptile and rodent bones repeatedly had acid etching on their surfaces, conceivably due to their already thin cortex making them easier to digest.

These damage types differ from those made by mammalian carnivores in a variety of ways. Larger carnivores such as hyaenids and leopards collect far larger prey items. Furthermore the punctures made by the canines of these carnivores are much larger in cross section and deeper overall than those made by Verreaux's eagles (Pickering *et al.*, 2004). Hyaenids are known to typically leave only long bone shafts in an assemblage and remove the epiphyseal ends whilst leopards are the reverse (Buckland, 1822, 1823; Brain, 1981; Cruz-Urbe, 1991; Pickering, 1999; de Ruiter & Berger, 2000; Pickering *et al.*, 2004; Skinner & Chimimba, 2005; Kuhn *et al.*, 2010). Neither of these patterns was observed for Verreaux's eagle prey remains. Based on the characteristics posed by Kuhn *et al.* (2010) that typify hyaenid involvement in an assemblage are the presence of coprolites and juvenile hyaenid remains- obviously neither of these were present in Verreaux's eagle prey accumulations. Neither was there a high proportion of primate remains nor bovid size classes two and three prey items that dominate the assemblages of leopards (Kruuk & Turner, 1967; Pienaar, 1969; Brain, 1981; Wilson, 1981; Bertram, 1982; Scott, 1985; Bailey, 1993; Cavallo, 1997). It must be noted that crenulated edges are recorded in mammalian carnivore assemblages (Binford, 1981; Brain, 1981; Cruz-Urbe, 1991; Lyman, 1994; Pickering & Wallis, 1997; Pickering *et al.*, 2004; Kuhn, 2006), however when reviewing a fossil assemblage all the damage types should be taken in conjunction with one another. Therefore, crenulated edges alone do not typify a Verreaux's eagle assemblage but in conjunction with the other ten damage types listed here, they do.

Small mammalian carnivores all had very similar diets as observed for Verreaux's eagles in this study: which included hares, fowls, small birds, small bovids, small canids and small felids (Bothma 1971; Stuart 1981; Kruuk & Mills, 1983; Hawks, 1987; Kok 1996; Virgós *et al.*, 1999; Fredriani *et al.*, 2000; Begg, 2001; Rosalina & Santo-Reis, 2002; Begg *et al.*, 2005a; Begg *et al.*, 2005b; Skinner & Chimimba, 2005; Krajcarz & Krajcarz, 2012). Foxes and jackals both exhibited tooth scores and pitting of approximately 4mm in length (Domínguez-Rodrigo & Piqueras,

2003; Walton & Joly, 2003; Delaney-Rivera *et al.*, 2009; Krajcarz & Krajcarz, 2012). But these are nondescript damages, and whilst potentially overlapping with Verreaux's eagles, are not present in conjunction with the ten damage types explained above (pp. 113- 117).

4.2. Environmental impacts

The Karoo Nesting Sites, with the exception of De Aar Quarry, are all man-made structures. These were erected in an attempt to encourage the breeding success of the Verreaux's eagle in southern Africa. The nesting sites of Walter Sisulu Botanical Gardens and Klipriviersberg on the Highveld have a large human involvement factor, in the form of being heavily monitored (with additional food resources supplied in times of low prey abundance- Kruger, 2010) and an artificial nesting platform, respectively. From a zoological perspective the results of this study are positive in that Verreaux's eagles are obviously adaptable to differing climates as well as encroaching urbanisation (Symes & Kruger, 2012). Even at sites where artificial nesting platforms have been erected, there have been successful cases of breeding and fledging (Boshoff & Fabricius, 1986; Ledger *et al.*, 1987; Allan, 1988a; Ledger *et al.*, 1993).

The biggest indication of a change in biome was that of the prey selection. Prey choice appears more variable in areas where resources are low, forcing higher levels of intra- and interspecific competition. Both the Nama- and Succulent Karoo have a wide variety of small mammal fauna, however as these biomes are listed as semi-arid desert climates small mammals have developed a number of survival strategies that limit interaction with predators, as well as maximise access to food resources (Owen, 1988; Kerley *et al.*, 1990; Kerley, 1992). One of the most common defences is to be active during hours that predators are less active, most commonly at night. This also reduces thermal regulation requirements as well as allows them to inhabit areas of low vegetation abundance (Hoeck 1982, 1989; Haveron, 2008). Verreaux's eagles in these arid environments are less likely to cross paths with small mammal prey items because of these defences.

The palaeontological record in southern Africa has posed numerous challenges to researchers regarding the environment at the time of deposition. By studying

modern taxa, researchers are able to infer the climate based on the presence or absence of certain keystone species (Klein, 1980; Andrews, 1990; Hopley *et al.*, 2006). Small mammals are sensitive to both rainfall and climate fluctuations and as such the presence of a particular small mammal species will provide a clue as to what those climatic parameters may have been during cave deposition (Simonetti, 1989; Erasmus, *et al.*, 2002; Blois *et al.*, 2010; Rubidge *et al.*, 2010). Broader scale climate speculation as well as the level of interspecific predator competition could possibly be made by pairing the presence of particular prey species with the amount of damage that appears on the remaining prey skeletal elements in an assemblage. This study shows how the environment impacts on the intensity of feeding and prey utilization could potentially be used to infer the stresses active in the immediate area of a cave opening for the period of deposition. That is not to say though that an assemblage is that simplistic; South African cave assemblages – with the exception of the Malapa hominin site – are thought to possibly be time-averaged assemblages and are subject to a variety of potential accumulating agents with natural fluctuations in atmospheric climate (Dirks *et al.*, 2010; Bountalis, 2012). Identifying Verreaux's eagle involvement in a fossil assemblage would only aid in stating what the environment may have been like at one point in time, based on the damage intensity and prey variability.

Berger and Clarke (1995) introduced the possibility that the *Australopithecus africanus* type specimen from the Taung fossil site was collected by a large bird of prey. Knowing which raptor species were active during the Plio-Pleistocene of southern Africa is problematic for a number of reasons. Firstly, birds, specifically raptors, that are not ground-dwelling rarely occur in cave systems (with the exception of owls), which are the most common fossil deposit type that we have in southern Africa. Large raptors are apex predators and thus do not enter cave systems as the result of predation by another cave-using carnivore, nor do they fall into cave-systems accidentally as some mammals do (see Worthy & Holdaway, 1993; Clarke, 2006; Berger *et al.*, 2010). Additionally, raptors have the capacity to travel extensive distances over comparatively small time periods

which means easier expansion into new areas when climate fluctuations and environment biomes shift (Bildstein & Zalles, 2005). As such, understanding the taphonomic signatures of large extant raptors such as the Golden, Bald (*Haliaeetus leucocephalus*), Martial, Crowned and Verreaux's eagles will provide a greater understanding of variations within raptor taphonomy since the ecological range of these species may well have extended into the southern hemisphere during the Plio-Pleistocene.

4.3. Summary: Characteristics of Verreaux's eagles

Here proposed is an amended set of criteria to those six bird of prey characteristics introduced by Berger and Clarke (1995) that are specific to Verreaux's eagles.

1. Rock hyraxes were always present in high numbers, but are not always necessarily the most dominant species. This enforces the observation made by Gargett, amongst others, that rock hyrax is the most sought after prey item for Verreaux's eagle. However it does imply that when an area is not conducive for high population densities of rock hyrax, other prey items will be sought (Brain, 1981; Jenkins, 1984; Gargett, 1990).
2. Prey items are always below an average adult live weight of 20 kg. Prey items are selected for according to weight and availability. Larger adult prey species are selected for rarely, and are often disarticulated and only a portion of the skeleton is returned to the nesting site. Alternatively, juveniles of larger species are collected, minimising the total weight that would need to be carried. The actualistic weight of the items within the prey range is more likely to be around 6kg's as the items are made up of isolated elements from larger prey items or from juveniles. From a palaeontological perspective however, it helps to recognise that the prey assemblage will be made up of species within the 2- 20 kg live weight range.
3. There is always a NISP to MNI ratio of at least 3:1, regardless of the biome or prey species. This interesting ratio is observed from all of the nesting sites across both of the biomes. The ratio of 3:1 is a minimum, with the average being closer to 5:1 with some sites showing extremely high ratios of skeletal remains to individuals, such as Philipstown Nesting Site Smith's red rock rabbit remains (Table 6) and Kameelpoort Nesting sites rock hyrax ratio of 25:1 (Table 6).

4. Assemblages comprised 11 different taphonomic markings as well as a multitude of combinations thereof. Verreaux's eagles' feeding habits have resulted in 11 recognisable and repeated damage markings. The distribution of these marks across skeletal elements is based upon the environmental pressures exerted in terms of prey availability, visibility and density.
5. Natural nesting platforms on cliff faces or rock crevices are always above either seasonal or permanent water sources. Smaller skeletal elements are then susceptible to short distance water wash, especially during periods of heavy rainfall. Because of the natural inclination to nest on cliff faces and in areas where there are high levels of rocky outcrops, the presence of cave systems is increased. This increases the likelihood of a fossil assemblage accumulating with the remains collected by a Verreaux's eagle pair.
6. The absence of eggshell in the assemblages. Berger and Clarke (1995) noted the presence of large eggshell fragments in the Taung hominin deposit and suggested that they were evidence of a large raptor nesting in the area. No eggshells were recovered from any of the Verreaux's eagle nesting sites, not even from the nests themselves, despite a number of the collections having taken place after breeding and fledging had occurred (Verreaux's eagles breed and roost from late April and fledging occurs from around September of the same year- Brown, 1970; Steyn, 1982; Gargett, 1990).
7. The presence of very few tortoise carapaces in the assemblage, always undamaged. Berger and Clarke (1995) indicated that there was the presence of tortoise carapaces in significant numbers from the Taung assemblage, with no signs of carnivore damage. In this study only Karoo Nesting Sites had tortoise remains and none of the elements exhibited damage. One carapace was completely undamaged with the exception of the scutes having naturally flaked off from weathering (Figure 44).



Figure 44: The tortoise carapace from the Philipstown, Zwagershoek Nesting Site showing how complete and undamaged the tortoise carapace remains were in this study.

The Taung Child skull, as well as the associated baboon material from the Taung assemblage, have been shown to bear the characteristic damage types described as typical to raptors (Berger & Clarke, 1995; Berger, 2006; Berger & McGraw, 2007). These include punctures to the orbits (Berger, 2006; Figure 45), scratches along the forehead region and other areas of the skull as well as braincase punctures (Berger & McGraw, 2007). All of these damage types are present on the prey items recovered from Verreaux's eagles in this study. I am inclined to agree with Berger and Clarke (1995) in that it would be foolish to presume the exact species of eagle responsible for the collection of the Taung hominin. It is unlikely though that the Taung Child was collected by a Verreaux's eagle since primates make up a very small part of the typical diet nor is the cranium of the Taung Child as heavily damaged as those of the rock hyrax prey remains in this

study. Berger and Clarke (1995) rationalised that the presence of nyala (*Tragelaphus angasii*) in the Taung fossil assemblage implied a wetter, more tropical climate during deposition, which is unlike the modern habitat of Verreaux's eagles today (Visser, 1963; Gargett, 1971; Boshoff & Fabricius, 1986; Allan, 1988b; Gargett, 1990; Davies, 1994). Furthermore, based on the present low density of Verreaux's eagles along the Ghaap escarpment due to the insufficient crevices and fissures required for nesting (Anderson & Hohne, 2007), it is unlikely that there were large numbers of Verreaux's eagles nesting in the area in the Plio-Pleistocene.



Figure 45: A comparison of the talon damage to the hyrax orbits (above), Taung Child orbit floors (below left) and that of a cercopithecoid cranium (below right) collected by a Crowned eagle from the Ivory Coast's Tai Forest. (Lower two images taken from Berger, 2006).

CHAPTER 5

CONCLUSION

5.1 Questions

Some of the earlier questions asked were whether Verreaux's eagles preferentially sought out hyrax as a prey item? If not, what were the possible constraints that influenced prey selection? Lastly, were all prey species disarticulated in the same manner, and how is this disarticulation reflected on the skeletal remains, if at all? By approaching the results with these questions in mind, the interpretation of each was based on the environmental and thus immediate prey availability. How these elements were interpreted explained the prey selection, skeletal part representation and taphonomic markings on the prey skeletal remains.

Do Verreaux's eagles preferentially seek out hyrax as a prey item?

Overall the rock hyrax was a well-represented prey choice within the collections but there was no clear evidence to suggest that they were preferentially sought for by Verreaux's eagles. In order to find definitive evidence to the contrary, one would need to run a simultaneous census of the prey species in the Verreaux's eagles hunting range (P. Mundy- pers. comm., 2013). In nesting sites with natural surrounding vegetation such as Gladysvale, Klipriviersberg Artificial Nesting Platform, and all of the Karoo Nesting Sites (with the exception of De Aar Quarry), alternative prey items were abundant. Verreaux's eagles are capable of carrying prey items of up to approximately 20kg live adult weight, albeit in pieces (see Brain, 1981; Gargett, 1990). Due to their preference for nesting on cliff faces and rocky outcrops, the associated small mammal fauna will be species that occur in the same habitat with those same geological features, which would explain the absence of larger bodied grassland species in eagle's diet such as for those of the Rhodes Matopos National Park, Zimbabwe. It would appear that

Verreaux's eagles come across hyrax more often than any other small mammal items just by habitat preference alone. The high percentage of hyrax in their diet could merely be a reflection of the small mammal abundance in an area, rather than a preferential diet.

If not, what are the constraints that influence prey selection?

Certain nesting sites were in areas atypical for Verreaux's eagles, particularly those in the Karoo and the Gladysvale Nesting Site. The artificial nests in the Karoo were erected in order to help increase the range of large raptors and to reduce the occurrences of large raptors nesting on electrical pylons. Neither the Karoo areas nor the Gladysvale Nesting Site are dominated by large, steep rocky outcrops and cliff faces but rather rolling grasslands with the occasional small hill (Mucina & Rutherford, 2006). With such a landscape exists a more grassland inhabiting small faunal composition, as well as a large reptilian component (specifically for the Karoo as this is a semi-desert environment). Verreaux's eagles are then forced to seek alternative prey items- such as the larger contingent of lagomorphs and rodents.

Are all prey species disarticulated in the same manner, and how is this disarticulation reflected on the skeletal remains?

From the skeletal remains recovered in this study it was clear that different prey species were disarticulated in different ways due to their varying organ positions. Rock hyrax cranial material had consistent damage to the basicranium and orbits whereas there were essentially no hare, rabbit or helmeted guineafowl skulls. Access to the internal organs was either through the shoulder (scapula), pelvic girdles or keel in the case of birds. Damage was divided into 11 repeated and distinguishable markings that are unlike any made by mammalian carnivores (Buckland, 1822, 1823; Brain, 1981; Cruz-Urbe, 1991; Pickering, 1999; de Ruiter & Berger, 2000; Domínguez-Rodrigo & Piqueras, 2003; Walton & Joly, 2003; Pickering *et al.*, 2004; Skinner & Chimimba, 2005; Delaney-Rivera *et al.*, 2009; Kuhn *et al.*, 2010; Krajcarz & Krajcarz, 2012).

5.2 Hypotheses

A. Verreaux's eagles produce a characteristic taphonomic signature

This appears to be the case in comparison to the Crowned eagle characteristics that have been identified previously (Berger & Clarke, 1995; McGraw *et al.*, 2006; Gilbert *et al.*, 2009) as well as in comparison to those made by mammalian carnivores (Buckland, 1822, 1823; Brain, 1981; Cruz-Uribe, 1991; Pickering, 1999; de Ruiter & Berger, 2000; Domínguez-Rodrigo & Piqueras, 2003; Walton & Joly, 2003; Pickering *et al.*, 2004; Skinner & Chimimba, 2005; Delaney-Rivera *et al.*, 2009; Kuhn *et al.*, 2010; Krajcarz & Krajcarz, 2012). Also, in comparison to other large eagles, their taphonomic signature is unique. The prey selection compared to that of fish eagles is very different in both taxon and size. The Golden eagle, despite the difference in range, has a similar habitat preference and prey selection range. The Verreaux's eagle however appears to puncture the prey items far more frequently.

B. The taphonomic signature reflects this uniqueness with regards to prey choice selection, skeletal part-representation and taphonomic marking distribution across the skeletal elements

The results from this study indicate that when viewing an assemblage as a whole, with all of the damage types in conjunction with one another, one is able to identify the distinctive activity of Verreaux's eagle feeding. Of the collective criteria listed below in Table 13, a number have been amended in light of the characteristic Verreaux's eagle taphonomic signature. The presence of punctures (Berger & Clarke, 1995; Sanders *et al.*, 2003) has been amended to include three variants- coarse, circular and keyhole shaped punctures. Berger and Clarke noted that the skulls of primates were crushed- here that has been amended to rather refer to how the skulls of prey items (mostly rock hyrax) have had large areas of bone removal with crenulated and chewed fringes. The 'can-opener'

perforations of Sanders *et al.* (2003) were interpreted as keyhole punctures in this study. Finally, the presence of eggshells that Berger and Clarke found to be an indicator of the presence of a large raptor nesting were completely absent in this collection, despite collections having taken place after fledging had occurred at some sites (such as Upper Tonquani Nesting Site).

Table 13: Criteria presented in Table 1 (Section 1.2.2) and the characteristics for Verreaux's eagles as a result of this study.

Criterion	Author	Characteristically Verreaux's eagle
<i>Assemblage characteristics</i>		
Prey body size is below 20 Kilogrammes in adult live weight.	Berger & Clarke (1995)	Retained
Crania have occipitals removed and mandibular ramus damage, often the two are unhinged.	Berger & Clarke (1995) McGraw <i>et al.</i> (2006) Gilbert <i>et al.</i> (2009)	Retained
The presence of tortoise carapace with minimal to zero carnivore damage.	Berger & Clarke (1995)	Retained
The presence of large eggshell fragments.	Berger & Clarke (1995)	Rejected
The absence of adult hominins.	Berger & Clarke (1995) Gilbert <i>et al.</i> (2009)	Retained
<i>Damage characteristics</i>		
Depressed fractures	Berger & Clarke	Retained

	(1995)	
Punctures	Berger & Clarke (1995) Sanders <i>et al.</i> (2003) McGraw <i>et al.</i> (2006) Gilbert <i>et al.</i> (2009)	Amended
Crushed skulls	Berger & Clarke (1995)	Amended
V-shaped nicks	Berger & Clarke (1995) Sanders <i>et al.</i> (2003)	Retained
Can-opener perforations	Sanders <i>et al.</i> (2003)	Amended
Acid- etching	Schmitt (1995) Hockett (1996) Whitfield & Blaber (1978)	Retained

The seven characteristics of Verreaux's eagles as an amendment to those presented for large raptors by the authors listed above in Table 13 are as follows:

1. Rock hyraxes were always present in high numbers, but are not always necessarily the most dominant species.
2. Prey items are always below an average adult live weight of 20 kg.
3. There is always a NISP to MNI ratio of at least 3:1, regardless of the biome or prey species.

4. Assemblage comprised 10 different taphonomic markings, namely crenulated edges, removal occurrences, chewed edges, v-nicks, punctures (coarse, circular and keyhole), notching, scratches and acid etching, as well as a multitude of combinations thereof.
5. Natural nesting platforms on cliff faces or rock crevices are always above either seasonal or permanent water sources.
6. The presence of very few tortoise carapaces in the assemblage, always undamaged.

C. This taphonomic signature is a direct response to the environment

Environmental fluctuations have to date been studied extensively, especially in light of the Global Warming phenomenon currently taking place (see Thomas *et al.*, 2004). How biomes and their respective animals react to these natural and man-made shifts in the global temperatures have become increasingly important as conservationists aim to combat these shifts. Verreaux's eagles have been always pronounced as specialist hyrax hunters (Gargett, 1990). However with increasing temperatures and expansion of grassland biomes it appears that the Verreaux's eagle is adaptable. In areas such as the arid Nama- and Succulent Karoo where the availability of rock hyrax has dwindled, Verreaux's eagles have adapted to a more generalist feeding habit, by selecting higher quantities of lagomorph and ground-dwelling fowl. This implies that during the Plio-Pleistocene the Verreaux's eagle was possibly not as specialist a feeder as it appears to be now. Furthermore, the fact that the Highveld nesting sites are surrounded by many possible roosts and feeding perches could explain the absence of pellets found from below the nest sites as these would be expelled by adults at roosts more often (Ellis, 1979; Hockett, 1996). The Karoo nesting sites are in areas that do not have a large number of perches and thus the nesting platform becomes a regular perch where most of the feeding takes place – hence the high proportion of pellets and acid-etched skeletal remains.

5.3 Final thoughts

Verreaux's eagles were most likely not the large raptor to have accumulated the Taung hominin associated faunas as the criteria posed by Berger and Clarke (1995) overlap but do not perfectly match those unique to Verreaux's eagles. Interestingly though, one should perhaps consider that the collector may have been an extinct species of the genus *Aquila* since the pattern of tree nesting and feeding behaviour observed in both the Golden and Verreaux's eagles is very similar to that observed for the Taung primate fauna. It would be imprudent however to assume the exact species responsible for collecting a fossil assemblage as potential accumulators go extinct frequently, their feeding characteristics disappearing with them. Furthermore, even taxa that are extant have adapted their behaviour in response to changing climates and shifting landscapes and are not necessarily behaving as they would have millions of years ago.

Lastly, the largest problem with southern African cave sites is that these are time-averaged assemblages, and mixing of specimens from multiple accumulators and modifiers over thousands of years can lead to a composite of damage types and signatures, making identifying a single accumulator near impossible. The Gladysvale Nesting Site accumulations have indicated that there was a removal of skeletal remains from below the nest as there was not a continuous growth in the accumulation but rather a fluctuation (increased from 1992 to 1995 and then a decrease in remains from 1995 to 2000). Where these remains were deposited is unclear, but it is feasible that they could collect in a crevice or cavity which over time would result in a larger fossil assemblage. This is possibly as a result of fluctuations with rainfall levels, and as such the intensity of water flow down the ravine, removing more or less skeletal remains accordingly.

Actualistic taphonomic studies are irreplaceable in today's palaeontological community. Deciphering the events of the past is near impossible since climate, vegetation, biomes and taxa are never a stagnant system but rather are continually in flux with minute shifts in the ecosystem. However, by examining extant species in as natural a setting as possible one can begin to gain an insight into the complex scenarios active thousands of years ago.

5.4 Future research

This study has high-lighted the need for similar research projects on smaller mammalian carnivores as well as alternative large raptors such as the Martial eagle and Golden eagle. In particular the Golden eagle warrants additional research, chiefly in areas where its range overlaps with that of primates, such as the Golden snub-nose monkey (*Rhinopithecus roxellana*) in China. By expanding our understanding of larger raptor feeding behaviours and consequent taphonomic signatures, we can begin to develop our understanding of the large raptor ecology during the Plio-Pleistocene. Furthermore, understanding this time period will aid in extrapolating the environmental stressors and carnivore evasions that would have driven hominin evolution.

In addition, an expansion of the methodologies used here is necessary, not only for the interpretation of Verreaux's eagle taphonomy but of all large raptors. Species, age and sex profiles of the prey items collected by large raptors should be included to provide evidence towards the selection criteria of these birds. Also, collecting downstream from the nesting sites will provide clarity regarding the potential fluvial involvement in fossil deposition along escarpment plateaus.

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APPENDIX A:

Data Sheet

Verreaux's Eagle Project, Stephanie Edwards Baker

University of the Witwatersrand

Date:		Time:		
Location (including farm name):		GPS Co- ord's:		
Dominant vegetation type (e.g. Grassland, Savanna etc):		No. of nest sites for this breeding pair:		
Nest type (e.g. artificial, cliff etc)			Nest height (if possible):	
No. of prey remains below the nest:			No. of prey remains in the nest (if possible):	
Interesting observations (e.g. no breeding this season, heavy rains prior to collection etc):				

APPENDIX B

Highveld nesting sites

SITE ACCESSION	ELEMENT	ORIENTATION	SPECIES	NOTES ON TAPHONOMY
KNP1	FEMUR	LEFT	<i>Numida meleagris</i>	
KNP2	PELVIS	LEFT	<i>Pronolagus</i> spp.	Ilium/pubis bridge removed
KNP3	PELVIC GIRDLE	COMPLETE	<i>Procavia capensis</i>	
KNP4	6 LUMBAR VERTEBRAE AND DISCS	/	<i>Procavia capensis</i>	Articulated
KNP5	SKULL	/	<i>Procavia capensis</i>	Scratches on left orbital shelf
KNP6	SKULL	/	UNIDENTIFIABLE	
KNP7	SKULL CAP	/	UNIDENTIFIABLE	
KNP8	FEMUR	LEFT	<i>Procavia capensis</i>	
KNP9	SKULL + MANDIBLE	COMPLETE	UNIDENTIFIABLE	
KNP10	PELVIS	RIGHT	<i>Procavia capensis</i>	
KNP11	KEEL	/	<i>Numida meleagris</i>	

KNP12	FEMUR	LEFT	<i>Procavia capensis</i>	Juvenile
KNP13	SKULL CAP	/	UNIDENTIFIABLE	
KNP14	TIBIOTARSUS + FIBULA	LEFT	<i>Numida meleagris</i>	
KNP15	SCAPULA	RIGHT	<i>Procavia capensis</i>	Missing blade
KNP16	SKULL AND HEMI-MANDIBLE	/ AND RIGHT	<i>Procavia capensis</i>	Juvenile
KNP17	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	
KNP18	FEMUR	LEFT	<i>Pronolagus spp.</i>	2 pieces
KNP19	SCAPULA	RIGHT	<i>Procavia capensis</i>	Perfect puncture on spine and missing blade
KNP20	HUMERUS	LEFT	<i>Procavia capensis</i>	Juvenile
KNP21	SKULL	COMPLETE	<i>Procavia capensis</i>	Juvenile
KNP22	PELVIC GIRDLE	COMPLETE	<i>Numida meleagris</i>	
KNP23	SKULL FRAGMENTS	/	UNIDENTIFIABLE	
KNP24	VERTEBRAL COLUMN	/	UNIDENTIFIABLE	
KNP25	MANDIBLE	LEFT	<i>Procavia capensis</i>	Juvenile
KNP26	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Puncture on right heel
KNP27	MAXILLA	COMPLETE	<i>Procavia capensis</i>	

KNP28	PELVIC GIRDLE	RIGHT SECTION	<i>Numida meleagris</i>	Notching and puncture marks
KNP29	MAXILLA	COMPLETE	<i>Procavia capensis</i>	2 pieces
KNP30	SKULL CAP	/	UNIDENTIFIABLE	
KNP31	VERTEBRAL COLUMN AND RIBS	/	<i>Procavia capensis</i>	
KNP32	SKULL	COMPLETE	<i>Procavia capensis</i>	
KNP33	MANDIBLE	COMPLETE	UNIDENTIFIABLE	
KNP34	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Juvenile
KNP35	SKULL	/	<i>Procavia capensis</i>	
KNP36	SKULL	/	<i>Procavia capensis</i>	
KNP37	SKULL	/	<i>Procavia capensis</i>	
KNP38	SKULL	/	<i>Procavia capensis</i>	
KNP39	SKULL	/	<i>Procavia capensis</i>	
KNP40	SKULL	/	<i>Procavia capensis</i>	
KNP41	SKULL	/	<i>Procavia capensis</i>	
KNP42	SKULL	/	<i>Procavia capensis</i>	
KNP43	SKULL	/	<i>Procavia capensis</i>	

KNP44	SKULL	/	<i>Procavia capensis</i>	
KNP45	SKULL	/	<i>Procavia capensis</i>	
KNP46	SKULL	/	<i>Procavia capensis</i>	
KNP47	SKULL	/	<i>Procavia capensis</i>	
KNP48	SKULL	/	<i>Procavia capensis</i>	
KNP49	SKULL	/	<i>Procavia capensis</i>	
KNP50	SKULL	/	<i>Procavia capensis</i>	
KNP51	SKULL	/	<i>Procavia capensis</i>	
KNP52	SKULL	/	<i>Procavia capensis</i>	
KNP53	SKULL	/	<i>Procavia capensis</i>	
KNP54	SKULL	/	<i>Procavia capensis</i>	
KNP55	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	
KNP56	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	
KNP57	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	
KNP58	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	
KNP59	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	
KNP60	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	

KNP61	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	
KNP62	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	
KNP63	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	
KNP64	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	
KNP65	MANDIBLE	LEFT	<i>Procavia capensis</i>	
KNP66	MANDIBLE	LEFT	<i>Procavia capensis</i>	
KNP67	MANDIBLE	LEFT	<i>Procavia capensis</i>	
KNP68	MANDIBLE	LEFT	<i>Procavia capensis</i>	
KNP69	MANDIBLE	LEFT	<i>Procavia capensis</i>	
KNP70	MANDIBLE	LEFT	<i>Procavia capensis</i>	
KNP71	MANDIBLE	LEFT	<i>Procavia capensis</i>	
KNP72	MANDIBLE	LEFT	<i>Procavia capensis</i>	
KNP73	MANDIBLE	LEFT	<i>Procavia capensis</i>	
KNP74	MANDIBLE	LEFT	<i>Procavia capensis</i>	
KNP75	MANDIBLE	LEFT	<i>Procavia capensis</i>	
KNP76	MANDIBLE	LEFT	<i>Procavia capensis</i>	
KNP77	HUMERUS	LEFT	<i>Procavia capensis</i>	Juvenile

KNP78	MANDIBLE	RIGHT	<i>Procavia capensis</i>	
KNP79	MANDIBLE	RIGHT	<i>Procavia capensis</i>	
KNP80	MANDIBLE	RIGHT	<i>Procavia capensis</i>	
KNP81	MANDIBLE	RIGHT	<i>Procavia capensis</i>	
KNP82	MANDIBLE	RIGHT	<i>Procavia capensis</i>	
KNP83	MANDIBLE	RIGHT	<i>Procavia capensis</i>	
KNP84	MANDIBLE	RIGHT	<i>Procavia capensis</i>	
KNP85	MANDIBLE	RIGHT	<i>Procavia capensis</i>	
KNP86	MANDIBLE	RIGHT	<i>Procavia capensis</i>	
KNP87	MANDIBLE	RIGHT	<i>Procavia capensis</i>	
KNP88	CRANIAL FRAGMENTS	/	UNIDENTIFIABLE	
KNP89	CRANIAL FRAGMENTS	/	UNIDENTIFIABLE	
KNP90	CRANIAL FRAGMENTS	/	UNIDENTIFIABLE	
KNP91	CRANIAL FRAGMENTS	/	UNIDENTIFIABLE	
KNP92	CRANIAL FRAGMENTS	/	UNIDENTIFIABLE	
KNP93	CRANIAL FRAGMENTS	/	UNIDENTIFIABLE	
KNP94	CRANIAL FRAGMENTS	/	UNIDENTIFIABLE	

KNP95	CRANIAL FRAGMENTS	/	UNIDENTIFIABLE	
KNP96	CRANIAL FRAGMENTS	/	UNIDENTIFIABLE	
KNP97	CRANIAL FRAGMENTS	/	UNIDENTIFIABLE	
KNP98	CRANIAL FRAGMENTS	/	UNIDENTIFIABLE	
KNP99	4 THORACIC VERTEBRAE	/	<i>Procavia capensis</i>	In articulation
KNP100	VERTEBRAE- CERVICAL?	/	UNIDENTIFIABLE	Taken to tm
KNP101	VERTEBRAE	/	UNIDENTIFIABLE	
KNP102	SCAPULA AND CORACOID	LEFT	<i>Numida meleagris</i>	
KNP103	SCAPULA	LEFT	<i>Numida meleagris</i>	
KNP104	ULNA AND RADIUS	RIGHT	<i>Procavia capensis</i>	
KNP105	5 LUMBAR VERTEBRAE	/	UNIDENTIFIABLE	Taken to tm
KNP106	PELVIS	COMPLETE	<i>Procavia capensis</i>	
KNP107	PELVIS	LEFT	<i>Procavia capensis</i>	Notching and bone removal
KNP108	PELVIS	LEFT	<i>Procavia capensis</i>	Notching and bone removal
KNP109	PELVIS	RIGHT	<i>Procavia capensis</i>	
KNP110	SCAPULA	LEFT	<i>Procavia capensis</i>	Blade missing
KNP111	SCAPULA	LEFT	<i>Procavia capensis</i>	Blade missing

KNP112	PELVIC GIRDLE	RIGHT	<i>Numida meleagris</i>	
UTM1-1	SKULL	/	<i>Procavia capensis</i>	Broken basi-cranium and right zygomatic arch
UTM1-2	SKULL	/	<i>Procavia capensis</i>	Broken basi-cranium
UTM1-3	SKULL	/	<i>Procavia capensis</i>	Broken basi-cranium and right orbit roof damage with left orbit puncture
UTM1-4	SKULL	/	<i>Procavia capensis</i>	Back of skull removed and both orbits punctured
UTM1-5	SKULL	/	<i>Procavia capensis</i>	Back of skull removed and both orbits punctured
UTM1-6	SKULL AND LEFT MANDIBULAR HEEL	/	<i>Procavia capensis</i>	Broken basi-cranium and both orbits punctured
UTM1-7	SKULL AND MANDIBLE	/	<i>Procavia capensis</i>	In articulation
UTM1-8	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Knotched right ramus
UTM1-9	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Juvenile
UTM1-10	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Cracked right heel (natural)
UTM1-11	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Knotched right ramus

UTM1-12	MAXILLA FRAGMENT	LEFT	<i>Procavia capensis</i>	Juvenile, chewed
UTM1-13	MANDIBLE	LEFT	<i>Procavia capensis</i>	Keyholes and chewed
UTM1-14	MANDIBLE	LEFT	<i>Procavia capensis</i>	Associated with #15
UTM1-15	MANDIBLE	RIGHT	<i>Procavia capensis</i>	Associated with #14
UTM1-16	MANDIBLE	RIGHT	<i>Procavia capensis</i>	Knotched ramus
UTM1-17	MANDIBLE	RIGHT	<i>Procavia capensis</i>	Cracked on left side
UTM1-18	MANDIBLE	RIGHT	<i>Pronolagus</i> spp.	Knotched ramus
UTM1-19	FEMUR	LEFT	<i>Procavia capensis</i>	
UTM1-20	FEMUR	LEFT	<i>Procavia capensis</i>	Juvenile
UTM1-21	FEMUR	RIGHT	<i>Procavia capensis</i>	Juvenile, no distal epiphysis, chewed
UTM1-22	FEMUR	RIGHT	<i>Procavia capensis</i>	Juvenile, no distal epiphysis and shaft
UTM1-23	FEMUR	RIGHT	<i>Procavia capensis</i>	No distal or proximal epiphyses
UTM1-24	FEMUR	RIGHT	<i>Procavia capensis</i>	Distal epiphysis only and shaft
UTM1-25	TIBIA	LEFT	<i>Procavia capensis</i>	Proximal epiphysis only
UTM1-26	RADIUS	LEFT	<i>Oreotragus</i> <i>oreotragus</i>	Juvenile, associated with #28
UTM1-27	TIBIA	RIGHT	<i>Procavia capensis</i>	Lateral portion of distal epiphysis and

				partial shaft
UTM1-28	HUMERUS	LEFT	<i>Oreotragus oreotragus</i>	Juvenile, associated with #26, olecranon broken via weathering
UTM1-29	PELVIS	LEFT	<i>Procavia capensis</i>	Chewed illium and ischium-pubis bridge
UTM1-30	PELVIS	RIGHT	<i>Procavia capensis</i>	Puncture on illium
UTM1-31	HUMERUS, ULNA AND RADIUS	LEFT	<i>Pronolagus</i> spp.	In articulation
UTM2-1	FEMUR	LEFT	<i>Procavia capensis</i>	Greater tubercle damage
UTM2-2	PELVIC GIRDLE	RIGHT ISCHIUM	<i>Numida meleagris</i>	Chewing, knotching, punctures, crenulated edges
UTM2-3	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Chewed coronoids
UTM2-4	PELVIS	COMPLETE	<i>Procavia capensis</i>	Illium chewed and knotted
UTM2-5	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Keyhole on right heel
UTM2-6	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Left heel broken
UTM2-7	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Subadult, left coronoid/ heel removed
UTM2-8	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Subadult, left heel circular puncture
UTM2-9	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Subadult, both coronoids removed
UTM2-10	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Juvenile, both coronoids removed

UTM2-11	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	No damage
UTM2-12	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Both coronoids removed
UTM2-13	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Subadult, both coronoids removed, both heels knotted
UTM2-14	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Left coronoid removed
UTM2-15	MANDIBLE	LEFT	<i>Procavia capensis</i>	Coronoid removed
UTM2-16	MANDIBLE	RIGHT	<i>Procavia capensis</i>	Juvenile, coronoid removed
UTM2-17	MANDIBLE	RIGHT	<i>Procavia capensis</i>	Juvenile, coronoid removed
UTM2-18	MANDIBLE	RIGHT	<i>Procavia capensis</i>	Juvenile, coronoid removed
UTM2-19	MANDIBLE	RIGHT	<i>Procavia capensis</i>	Juvenile, coronoid removed, heel chewed, crenulated edges
UTM2-20	UNIDENTIFIABLE BONE FRAGMENT		UNIDENTIFIABLE	
UTM2-21	SKULL	COMPLETE	<i>Procavia capensis</i>	Occipital removed, orbit floors punctured
UTM2-22	SKULL	COMPLETE	<i>Procavia capensis</i>	Occipital removed, orbit floors punctured, right zygomatic removed
UTM2-23	SKULL	COMPLETE	<i>Procavia capensis</i>	Occipital damaged, orbit floors punctured, right zygomatic removed

UTM2-24	SKULL	FRONT ONLY	<i>Procavia capensis</i>	Crenulated edges
UTM2-25	SKULL	FRONT ONLY	<i>Procavia capensis</i>	Crenulated edges, orbits punctured
UTM2-26	SKULL	FRONT ONLY	<i>Procavia capensis</i>	Crenulated edges, orbits punctured
UTM2-27	SKULL	FRONT ONLY	<i>Procavia capensis</i>	Juvenile, crenulated edges
UTM2-28	TEMPORAL BONE	RIGHT	<i>Procavia capensis</i>	Crenulated edges
UTM2-29	MAXILLA	RIGHT	<i>Procavia capensis</i>	Crenulated edges
UTM2-30	MAXILLA	COMPLETE	<i>Procavia capensis</i>	Juvenile, crenulated edges
UTM2-31	MAXILLA	LEFT	<i>Procavia capensis</i>	Juvenile, crenulated edges
UTM2-32	MAXILLA	LEFT	<i>Procavia capensis</i>	Juvenile, crenulated edges
UTM2-33	MAXILLA	LEFT	<i>Procavia capensis</i>	Crenulated edges
UTM2-34	MAXILLA	LEFT	<i>Procavia capensis</i>	Juvenile, crenulated edges
UTM2-35	MAXILLA	RIGHT	<i>Procavia capensis</i>	Juvenile, crenulated edges
UTM2-36	PELVIS	COMPLETE	<i>Procavia capensis</i>	Ilium chewed and knotted, keyhole on right ischium
UTM2-37	PELVIS	LEFT	<i>Procavia capensis</i>	Ilium chewed and knotted
UTM2-38	PELVIS	LEFT	<i>Procavia capensis</i>	Ilium chewed and knotted, ischium-pubis bridge broken

UTM2-39	PELVIS	LEFT	<i>Procavia capensis</i>	Ilium keyhole, chewed and notched, ischium-pubis bridge broken
UTM2-40	PELVIS	LEFT	<i>Procavia capensis</i>	Ilium notched, ischium-pubis bridge broken
UTM2-41	PELVIS	LEFT	<i>Procavia capensis</i>	Ilium and ischium notched, ischium-pubis bridge broken
UTM2-42	PELVIS	LEFT	<i>Procavia capensis</i>	Juvenile, no damage
UTM2-43	PELVIS	LEFT	<i>Procavia capensis</i>	Juvenile, ilium crenulated
UTM2-44	PELVIS	LEFT	<i>Procavia capensis</i>	Juvenile, ilium crenulated, ischium keyholed
WSBG-1	SKULL WITH MANDIBLE	/	<i>Procavia capensis</i>	Missing basi-cranium
WSBG-2	SKULL CAP	RIGHT	<i>Procavia capensis</i>	Damage to orbital roof
WSBG-3	MANDIBLE	LEFT	<i>Procavia capensis</i>	Juvenile, damage to ramus and heel
WSBG-4	MAXILLA FRAGMENT WITH PARTIAL ZYGOMATIC	RIGHT	<i>Procavia capensis</i>	Damage to maxilla roof
WSBG-5	SCAPULA	LEFT	<i>Procavia capensis</i>	Blade removed
WSBG-6	HUMERUS	LEFT	<i>Procavia capensis</i>	Subadult

WSBG-7	HUMERUS	RIGHT	<i>Pronolagus</i> spp.	Proximal epiphysis removed
WSBG-8	ULNA AND RADIUS	LEFT	<i>Procavia capensis</i>	
WSBG-9	ULNA	LEFT	<i>Procavia capensis</i>	Juvenile, distal portion broken
WSBG-10	SKULL CAP	/	<i>Numida meleagris</i>	Weathered along crest
WSBG-11	ILLIUM	LEFT	<i>Procavia capensis</i>	Juvenile, weathering
WSBG-12	CALCANEUM	LEFT	<i>Pronolagus</i> spp.	
WSBG-13	CALCANEUM	LEFT	<i>Pronolagus</i> spp.	
WSBG-14	FEMUR	LEFT	<i>Procavia capensis</i>	Juvenile
WSBG-15	ASTRAGULAS	LEFT	<i>Raphicerus campestris</i>	Juvenile
WSBG-16	TIBIA	LEFT	<i>Raphicerus campestris</i>	Juvenile
WSBG-17	TIBIA	LEFT	<i>Pronolagus</i> spp.	Fibula broken midshaft
WSBG-18	TIBIA	LEFT	<i>Pronolagus</i> spp.	Fibula broken midshaft
WSBG-19	TIBIA	RIGHT	<i>Pronolagus</i> spp.	Calcanuem in articulation
WSBG-20	TIBIA	RIGHT	<i>Pronolagus</i> spp.	Distal portion broken off
WSBG-21	TIBIA	RIGHT	<i>Pronolagus</i> spp.	Proximal epiphysis removed

WSBG-22	TIBIA	RIGHT	<i>Pronolagus</i> spp.	
WSBG-23	METATARSAL	LEFT	<i>Raphicerus campestris</i>	Juvenile
WSBG-24	TIBIA	RIGHT	<i>Pronolagus</i> spp.	Subadult, weathered
WSBG-25	PELVIS	LEFT	<i>Procavia capensis</i>	Juvenile, puncture on dorsal ischium
WSBG-26	PELVIS	RIGHT	<i>Procavia capensis</i>	
WSBG-27	PELVIS	LEFT	<i>Procavia capensis</i>	Chewed illiac and pubis-ischium bridge
WSBG-28	PELVIS	LEFT	<i>Pronolagus</i> spp.	Chewed illiac and pubis-ischium bridge
WSBG-29	PELVIS	LEFT	<i>Lepus saxatilis</i>	Chewed ischium-pubis, puncture on medial illiac
WSBG-30	SACRUM	/	<i>Pronolagus</i> spp.	
WSBG-31	PELVIS	LEFT	UNIDENTIFIABLE	Baby illium
WSBG-32	PELVIS	RIGHT	UNIDENTIFIABLE	Baby illium
WSBG-33	PELVIS	LEFT	UNIDENTIFIABLE	Baby ischium
WSBG-34	PELVIS	RIGHT	UNIDENTIFIABLE	Baby ischium
WSBG-35	LUMBAR VERTEBRAE (3)	/	<i>Pronolagus</i> spp.	In articulation
WSBG-36	LUMBAR VERTEBRAE (3)	/	<i>Pronolagus</i> spp.	In articulation

WSBG-37	LUMBAR VERTEBRAE (2)	/	<i>Procavia capensis</i>	Juvenile, associated with #38
WSBG-38	SACRAL JOINT	/	<i>Procavia capensis</i>	Juvenile, associated with #37
WSBG-39	VERTEBRAE	/	cf. <i>Tyto alba</i>	
WSBG-40	FEMUR, TIBIOTARSUS, FIBULA AND METATARSUS	LEFT	<i>Numida meleagris</i>	In articulation
WSBG-41	VERTEBRAL FRAGMENTS		UNIDENTIFIABLE	Juvenile
WSBG-42	KEEL	/	<i>Numida meleagris</i>	Chewed edges
WSBG-43	KEEL	/	<i>Numida meleagris</i>	Chewed edges, notching and nicks
WSBG-44	KEEL	/	<i>Numida meleagris</i>	Chewed edges, notching and nicks
WSBG-45	KEEL	/	<i>Numida meleagris</i>	Weathered
WSBG-46	KEEL	/	<i>Numida meleagris</i>	Nicks and punctures
WSBG-47	KEEL	/	<i>Numida meleagris</i>	Chewed edges, notching and nicks
WSBG-48	KEEL	/	<i>Numida meleagris</i>	Chewed edges, notching and nicks
WSBG-49	KEEL	/	<i>Numida meleagris</i>	Chewed edges, notching and nicks
WSBG-50	KEEL	/	<i>Numida meleagris</i>	Chewed edges, notching and nicks
WSBG-51	KEEL	/	<i>Numida meleagris</i>	Chewed edges, notching and nicks
WSBG-52	KEEL	/	<i>Numida meleagris</i>	Chewed edges, notching and nicks

WSBG-53	KEEL	/	<i>Numida meleagris</i>	Chewed edges, notching and nicks
WSBG-54	KEEL	/	<i>Numida meleagris</i>	Chewed edges, notching and nicks
WSBG-55	HUMERUS	RIGHT	<i>Numida meleagris</i>	Puncture on proximal surface
WSBG-56	HUMERUS	LEFT	<i>Numida meleagris</i>	
WSBG-57	HUMERUS	RIGHT	<i>Numida meleagris</i>	
WSBG-58	HUMERUS	LEFT	<i>Numida meleagris</i>	
WSBG-59	HUMERUS	RIGHT	<i>Numida meleagris</i>	
WSBG-60	HUMERUS	RIGHT	<i>Numida meleagris</i>	Broken bridge on proximal surface
WSBG-61	HUMERUS	RIGHT	<i>Numida meleagris</i>	Missing proximal shaft
WSBG-62	HUMERUS	RIGHT	<i>Numida meleagris</i>	Missing proximal shaft
WSBG-63	HUMERUS	RIGHT	<i>Numida meleagris</i>	Missing shaft and distal end
WSBG-64	CORACOID AND SCAPULA*	LEFT	<i>Numida meleagris</i>	In articulation, *broken blade
WSBG-65	CORACOID AND SCAPULA*	LEFT	<i>Numida meleagris</i>	In articulation, *broken blade
WSBG-66	CORACOID AND SCAPULA*	LEFT	<i>Numida meleagris</i>	In articulation, *broken blade
WSBG-67	CORACOID	LEFT	<i>Numida meleagris</i>	
WSBG-68	CORACOID AND SCAPULA*	RIGHT	<i>Numida meleagris</i>	In articulation, *broken blade
WSBG-69	CORACOID AND SCAPULA*	RIGHT	<i>Numida meleagris</i>	In articulation, *broken blade

WSBG-70	CORACOID AND SCAPULA*	RIGHT	<i>Numida meleagris</i>	In articulation, *broken blade
WSBG-71	CORACOID AND SCAPULA*	RIGHT	<i>Numida meleagris</i>	In articulation, *broken blade
WSBG-72	CORACOID	RIGHT	<i>Numida meleagris</i>	
WSBG-73	SCAPULA	LEFT	<i>Numida meleagris</i>	Broken
WSBG-74	SCAPULA	LEFT	<i>Numida meleagris</i>	Broken
WSBG-75	METATARSAL	RIGHT	<i>Numida meleagris</i>	
WSBG-76	BONE FRAGMENT	/	UNIDENTIFIABLE	In same bag as #77
WSBG-77	BONE FRAGMENT	/	UNIDENTIFIABLE	In same bag as #76
WSBG-78	TIBIOTARSUS	RIGHT	<i>Numida meleagris</i>	
WSBG-79	TIBIOTARSUS	LEFT	<i>Numida meleagris</i>	
WSBG-80	TIBIOTARSUS	LEFT	<i>Numida meleagris</i>	Proximal epiphysis removed
WSBG-81	TIBIOTARSUS	LEFT	<i>Numida meleagris</i>	Distal portion broken off
WSBG-82	TIBIOTARSUS	LEFT	<i>Numida meleagris</i>	Proximal epiphysis removed
WSBG-83	TIBIOTARSUS	RIGHT	<i>Numida meleagris</i>	Partial fibula attached
WSBG-84	TIBIOTARSUS	RIGHT	<i>Numida meleagris</i>	Proximal epiphysis removed
WSBG-85	TIBIOTARSUS	LEFT	<i>Numida meleagris</i>	Proximal and distal epiphysis removed
WSBG-86	TIBIOTARSUS	RIGHT	<i>Numida meleagris</i>	Distal shaft preserved only

WSBG-87	TIBIOTARSUS	LEFT	<i>Numida meleagris</i>	Proximal epiphysis removed
WSBG-88	FEMUR AND PARTIAL PELVIS GIRDLE*	LEFT	<i>Numida meleagris</i>	In articulation, *chewed
WSBG-89	FEMUR† AND PARTIAL PELVIS GIRDLE*	RIGHT	<i>Numida meleagris</i>	In articulation, *chewed †distal epiphysis removed
WSBG-90	PELVIC GIRDLE FRAGMENT	LEFT	<i>Numida meleagris</i>	Chewed
WSBG-91	PELVIC GIRDLE FRAGMENT	/	<i>Numida meleagris</i>	Chewed and knotting
WSBG-92	PELVIC GIRDLE FRAGMENT	LEFT	<i>Numida meleagris</i>	Puncture
WSBG-93	PELVIC GIRDLE FRAGMENT	RIGHT	<i>Numida meleagris</i>	Chewed
WSBG-94	PELVIC SOCKET	RIGHT	<i>Numida meleagris</i>	Heavily chewed
WSBG-95	PELVIC GIRDLE FRAGMENT	RIGHT	<i>Numida meleagris</i>	Heavily chewed and notch underneath
WSBG-96	PELVIC GIRDLE FRAGMENT	LEFT	<i>Anas</i> sp.	Knotting, crenulated edges, key-holes, talon punctures etc.
WSBG-97	PELVIC GIRDLE FRAGMENT	RIGHT	<i>Numida meleagris</i>	Chewed
WSBG-98	PELVIC GIRDLE FRAGMENT	LEFT	<i>Numida meleagris</i>	Chewed and knotting
WSBG-99	PELVIC GIRDLE FRAGMENT	RIGHT	<i>Numida meleagris</i>	Chewed and knotting
WSBG-100	PELVIC GIRDLE FRAGMENT	LEFT	<i>Numida meleagris</i>	Chewed

WSBG-101	PELVIC GIRDLE FRAGMENT	RIGHT	<i>Numida meleagris</i>	Keyhole and chewing
WSBG-102	PELVIC GIRDLE FRAGMENT	LEFT	<i>Numida meleagris</i>	Chewed and knotting
WSBG-103	FUSED VERTEBRAE AND RIBS (2)	/	AVES sp.	Bi-punctures and chewed
WSBG-104	FUSED VERTEBRAE (PELVIC GIRDLE)	/	<i>Numida meleagris</i>	Heavily chewed
WSBG-105	SACRAL EPIPHYSIAL JOINT (DISTAL PORTION)	/	<i>Numida meleagris</i>	Heavily chewed
WSBG-106	TIBIOTARSUS	LEFT	<i>Numida meleagris</i>	Proximal epiphysis removed
GVE92-1	LEFT HUMERUS	LEFT	AVES sp.	
GVE92-2	RIGHT FEMUR	RIGHT	<i>Lepus</i> sp.	Puncture on medial distal trochanter
GVE92-3	BONE FRAGMENT*	N/A	AVES sp.	
GVE92-4	THORACIC VERTEBRAE	N/A	LAGOMORPH	
GVE92-5	MANDIBLE	N/A	<i>Procavia capensis</i>	Weathered
GVE92-6	LEFT PELVIS	LEFT	LAGOMORPH	
GVE92-7	RIGHT HUMERUS (DISTAL)	RIGHT	<i>Procavia capensis</i>	Shaft removed; damage to medial trochanter
GVE92-8	POSTERIOR CRANIUM	N/A	<i>Procavia capensis</i>	
GVE92-9	LEFT PELVIS	LEFT	LAGOMORPH	

GVE92-10	LUMBAR VERTEBRAE	N/A	<i>Lepus sp.</i>	
GVE92-11	RIGHT MANDIBLE FRAGMENT	RIGHT	<i>Procavia capensis</i>	
GVE92-12	LEFT FEMUR	LEFT	LAGOMORPH	
GVE92-13	MANDIBLE		<i>Procavia capensis</i>	Beak damage
GVE92-14	RIGHT PELVIS	RIGHT	LAGOMORPH	
GVE92-15	SACRUM	N/A	AVES sp.	
GVE92-16	RIGHT TIBIA (PROX) AND PATELLA	RIGHT	LAGOMORPH	Longitudinal fracture
GVE92-17	RIGHT HUMERUS*	RIGHT	AVES sp.	
GVE92-18	ARTICULATED TARSOMETATARSUS AND 4 DIGITS*	RIGHT	AVES sp.	
GVE92-19	4 DISTAL PHALANGES WITH KERATIN SHEATHES*	UNKNOWN	AVES sp.	
GVE92-20	KEEL	N/A	AVES sp.	3 punctures
GVE92-21	MAXILLA	N/A	<i>Procavia capensis</i>	
GVE92-22	RIGHT TIBIA	RIGHT	LAGOMORPH	Longitudinal fracture
GVE92-23	7 ARTICULATED LUMBAR VERTEBRAE AND SACRUM	N/A	LAGOMORPH	Acid damage ?

GVE92-24	SKULL	N/A	<i>Procavia capensis</i>	Inside left occipital- puncture
GVE92-25	MANDIBLE	N/A	<i>Procavia capensis</i>	
GVE92-26	LEFT HUMERUS (DISTAL)	LEFT	AVES sp.	
GVE92-27	KEEL	N/A	AVES sp.	
GVE92-28	SACRUM	N/A	<i>Numida meleagris</i>	
GVE92-29	RIGHT FEMUR	RIGHT	LAGOMORPH	
GVE92-30	LEFT FEMUR	LEFT	AVES sp.	
GVE92-31	LEFT PELVIS	LEFT	LAGOMORPH	
GVE92-32	RADIUS?	UNKNOWN	AVES sp.	
GVE92-33	RIGHT HUMERUS	RIGHT	AVES sp.	
GVE92-34	LEFT FEMUR	LEFT	AVES sp.	
GVE92-35	ARTICULATED TARSOMETATARSUS AND 4 DIGITS	UNKNOWN	AVES sp.	
GVE92-36	LUMBAR VERTEBRAE	N/A	<i>Procavia capensis</i>	
GVE92-37	RIGHT HUMERUS	RIGHT	AVES sp.	
GVE92-38	RIGHT PELVIS	RIGHT	<i>Procavia capensis</i>	
GVE92-39	RIGHT ARTICULATED ULNA AND	RIGHT	LAGOMORPH	

	RADIUS			
GVE92-40	LUMBAR VERTEBRAE	N/A	<i>Procavia capensis</i>	
GVE92-41	FURCULA	LEFT	AVES sp.	
GVE92-42	RIB FRAGMENT	N/A	UNIDENTIFIABLE	
GVE92-43	LEFT FEMUR (DISTAL)	LEFT	<i>Procavia capensis</i>	
GVE92-44	SKULL	N/A	<i>Procavia capensis</i>	Brain case removed; indentation on skull roof
GVE92-45	LEFT HUMERUS	LEFT	AVES sp.	
GVE92-46	STERNUM	N/A	AVES sp.	
GVE92-47	LEFT TIBIA	LEFT	LAGOMORPH	
GVE92-48	LEFT FEMUR (DISTAL)	LEFT	AVES sp.	
GVE92-49	SKULL	N/A	<i>Procavia capensis</i>	Brain case removed; ironization
GVE92-50	LEFT INCISOR	LEFT	<i>Procavia capensis</i>	
GVE92-51	LEFT MANDIBLE	LEFT	<i>Procavia capensis</i>	
GVE92-52	RIGHT PELVIS	RIGHT	<i>Procavia capensis</i>	
GVE92-53	BRAIN CASE	N/A	<i>Papio hamadryas ursinus</i>	Left parietal indented

GVE92-54	CRANIUM	N/A	<i>Lepus sp.</i>	
GVE92-55	CRANIUM FRAGMENTS	N/A	<i>Procavia capensis</i>	
GVE92-56	2 ARTICULATED LUMBAR VERTEBRAE	N/A	LAGOMORPH	
GVE92-57	RIGHT TIBIA, CALCANEUS, ASTRAGULUS	RIGHT	LAGOMORPH	
GVE92-58	CRANIUM	N/A	<i>Procavia capensis</i>	Brain case removed
GVE92-59	MANDIBLE	N/A	<i>Procavia capensis</i>	
GVE92-60	CRANIUM	N/A	<i>Procavia capensis</i>	Brain case removed
GVE95-1	LEFT PELVIS	LEFT	<i>Procavia capensis</i>	
GVE95-2	SACRUM	N/A	<i>Lepus sp.</i>	
GVE95-3	SKULL	N/A	<i>Procavia capensis</i>	
GVE95-4	LUMBAR VERTEBRAE	N/A	<i>Lepus sp.</i>	
GVE95-5	MAXILLA	N/A	<i>Procavia capensis</i>	Heavy damage; yellow colouration?
GVE95-6	ARTICULATED VERTEBRAL COLUMN WITH LOWER LIMBS	N/A	<i>Lepus sp.</i>	
GVE95-7	MANDIBLE	N/A	<i>Procavia capensis</i>	/
GVE95-8	LEFT PELVIS	LEFT	<i>Lepus sp.</i>	Damaged epiphysis

GVE95-9	RIGHT DISTAL TIBIA	RIGHT	<i>Lepus</i> sp.	
GVE95-10	LUMBAR VERTEBRAE	N/A	<i>Lepus</i> sp.	
GVE95-11	LEFT PELVIS	LEFT	<i>Lepus</i> sp.	
GVE95-12	PELVIS FRAGMENT	UNKNOWN	<i>Lepus</i> sp.	Ends removed
GVE95-13	ULNA	LEFT	AVES sp.	/
GVE95-14	LEFT METATARSAL	LEFT	BOVID SIZE CLASS 1	Juvenile; green colouration?
GVE95-15	LEFT PELVIS	LEFT	JUV. <i>Procavia</i> <i>capensis</i>	Ilium puncture
GVE95-16	RIGHT TIBIA (PROXIMAL)	RIGHT	<i>Lepus</i> sp.	Longitudinal fracture
GVE95-17	LEFT PELVIS	LEFT	<i>Lepus</i> sp.	
GVE95-18	RIGHT TIBIOTARSUS (DISTAL)	RIGHT	AVES sp.	
GVE95-19	LEFT TIBIA (DISTAL)	LEFT	<i>Lepus</i> sp.	
GVE95-20	RIGHT PROXIMAL TIBIA	RIGHT	<i>Lepus</i> sp.	
GVE95-21	RIGHT PELVIS	RIGHT	<i>Lepus</i> sp.	
GVE95-22	RIGHT HUMERUS	RIGHT	<i>Lepus</i> sp.	
GVE95-23	LUMBAR VERTEBRAE	N/A	<i>Lepus</i> sp.	

GVE95-24	LEFT TIBIA	LEFT	<i>Lepus sp.</i>	
GVE95-25	LEFT TIBIA	LEFT	<i>Lepus sp.</i>	
GVE95-26	RIGHT TIBIA (PROXIMAL)	RIGHT	<i>Lepus sp.</i>	Longitudinal fracture
GVE95-27	RIGHT TIBIA, CALCANEUS, ASTRAGULUS, CUBOID	RIGHT	<i>Lepus sp.</i>	
GVE95-28	RIGHT PELVIS	RIGHT	<i>Procavia capensis</i>	
GVE95-29	LEFT PELVIS	LEFT	<i>Procavia capensis</i>	Possible beak damage
GVE95-30	LEFT PELVIS	LEFT	<i>Procavia capensis</i>	Nicks
GVE95-31	LEFT PELVIS	LEFT	<i>Lepus sp.</i>	Nicks
GVE95-32	LEFT SCAPULA	LEFT	<i>Procavia capensis</i>	Shredded blade
GVE95-33	RIGHT PELVIS	RIGHT	<i>Lepus sp.</i>	
GVE95-34	KEEL	N/A	AVES sp.	Indented corners
GVE95-35	RADIUS	UNKNOWN	AVES sp.	/
GVE95-36	SKULL AND MANDIBLE	N/A	<i>Procavia capensis</i>	Puncture on left zygomatic base
GVE95-37	SKULL	N/A	<i>Procavia capensis</i>	Brain case removed; indentation on skull roof
GVE95-38	PARTIAL SKULL AND LEFT MANDIBLE	LEFT	<i>Procavia capensis</i>	Brain case removed; indentation on skull

				roof
GVE95-39	SKULL AND MANDIBLE	N/A	<i>Procavia capensis</i>	Brain case removed; indentation on skull roof
GVE95-40	MANDIBLE	N/A	<i>Chlorocebus pygerythrus</i>	Most teeth missing
GVE95-41	CARAPACE FRAGMENT	N/A	TESTUDINE	
GVE95-42	BRAIN CASE	N/A	<i>Canis mesomelas</i>	Beak damage
GVE95-43	SKULL	N/A	<i>Procavia capensis</i>	Right zygomatic missing
GVE95-44	CRANIAL VAULT	N/A	<i>Procavia capensis</i>	Puncture on occipital
GVE95-45	MAXILLA	N/A	<i>Procavia capensis</i>	
GVE95-46	LEFT HUMERUS (DISTAL)	LEFT	UNIDENTIFIABLE	
GVE95-47	LEFT FEMUR	LEFT	<i>Lepus sp.</i>	
GVE95-48	LEFT HIND FOOT	LEFT	<i>Lepus sp.</i>	
GVE95-49	RIGHT TIBIA	RIGHT	<i>Lepus sp.</i>	
GVE95-50	RIGHT FEMUR	RIGHT	<i>Lepus sp.</i>	
GVE95-51	RIGHT TIBIA (DISTAL)	RIGHT	<i>Lepus sp.</i>	
GVE95-52	TIBIA WITH UNFUSED EPIPHYSIS		BOVID SIZE CLASS	

			1	
GVE95-53	LEFT HUMERUS	LEFT	<i>Lepus</i> sp.	
GVE95-54	LEFT TIBIA (PROXIMAL)	LEFT	<i>Lepus</i> sp.	
GVE95-55	LEFT TIBIA	LEFT	<i>Lepus</i> sp.	
GVE95-56	LEFT HUMERUS	LEFT	AVES sp.	
GVE95-57	CRANIAL FRAGMENTS	N/A	UNIDENTIFIABLE	
GVE95-58	RIGHT HUMERUS	RIGHT	<i>Lepus</i> sp.	
GVE95-59	RIGHT HUMERUS	RIGHT	AVES sp.	
GVE95-60	FURCULA	LEFT	AVES sp.	
GVE95-61	CRANIAL FRAGMENTS	N/A	UNIDENTIFIABLE	
GVE95-62	LONG BONE SHAFT FRAGMENT	N/A	UNIDENTIFIABLE	
GVE95-63	LEFT ULNA SHAFT	LEFT	UNIDENTIFIABLE	
GVE95-64	HUMERUS SHAFT FRAGMENT	UNKNOWN	BOVID SIZE CLASS 1	Porcupine gnawing
GVE95-65	RADIUS	UNKNOWN	BOVID SIZE CLASS 2	
GVE95-66	LUMBAR VERTEBRAE	N/A	<i>Lepus</i> sp.	

GVE95-67	PARTIAL MANDIBLE	N/A	<i>Procavia capensis</i>	
GVE95-68	LUMBAR VERTEBRAE	N/A	<i>Lepus sp.</i>	
GVE95-69	LUMBAR VERTEBRAE	N/A	<i>Procavia capensis</i>	
GVE95-70	RIGHT TIBIA	RIGHT	<i>Lepus sp.</i>	
GVE95-71	RIGHT FEMUR (DISTAL)	RIGHT	<i>Procavia capensis</i>	
GVE95-72	LONG BONE SHAFT FRAGMENT	N/A	UNIDENTIFIABLE	
GVE95-73	CRANIAL FRAGMENTS	N/A	UNIDENTIFIABLE	
GVE95-74	LEFT PELVIS	LEFT	<i>Lepus sp.</i>	
GVE95-75	CARAPACE FRAGMENT	N/A	TESTUDINE	
GVE95-76	LEFT PELVIS	LEFT	<i>Lepus sp.</i>	
GVE95-77	PARIETAL FRAGMENTS	N/A	cf. <i>Canis mesomelas</i>	
GVE95-78	SACRUM	N/A	<i>Procavia capensis</i>	
GVE95-79	LEFT FEMUR	LEFT	<i>Lepus sp.</i>	
GVE95-80	MANDIBLE	N/A	<i>Procavia capensis</i>	Nicks
GVE95-81	0	LEFT	<i>Lepus sp.</i>	
GVE95-82	SKULL AND MANDIBLE	N/A	<i>Procavia capensis</i>	Left parietal indented

GVE95-83	LEFT FEMUR (DISTAL)	LEFT	<i>Lepus sp.</i>	
GVE95-84	FEMUR SHAFT	UNKNOWN	AVES sp.	
GVE00-1	MANDIBLE	N/A	<i>Procavia capensis</i>	
GVE00-2	MANDIBLE	N/A	<i>Procavia capensis</i>	
GVE00-3	LEFT MANDIBLE	LEFT	<i>Lepus sp.</i>	Indented ramus
GVE00-4	RIGHT FRONTAL CRANIAL VAULT FRAGMENT	RIGHT	<i>Cercopithecus aethiopicus</i>	
GVE00-5	LEFT PELVIS	LEFT	<i>Procavia capensis</i>	
GVE00-6	LEFT PELVIS	LEFT	<i>Lepus sp.</i>	
GVE00-7	LEFT PELVIS	LEFT	<i>Procavia capensis</i>	Nicks
GVE00-8	LEFT PELVIS	LEFT	<i>Lepus sp.</i>	Puncture on iliac
GVE00-9	LEFT PELVIS	LEFT	<i>Lepus sp.</i>	
GVE00-10	RIGHT PELVIS	RIGHT	<i>Lepus sp.</i>	Nicks
GVE00-11	LEFT TIBIA	LEFT	<i>Lepus sp.</i>	
GVE00-12	LEFT TIBIA (PROXIMAL)	LEFT	<i>Lepus sp.</i>	Scratches
GVE00-13	RIGHT TIBIA	RIGHT	<i>Lepus sp.</i>	Cracked
GVE00-14	RIGHT HUMERUS	RIGHT	<i>Lepus sp.</i>	

GVE00-15	LEFT FEMUR	LEFT	<i>Lepus sp.</i>	Bad weathering, longitudinal fracturing
GVE00-16	RIGHT RADIUS	RIGHT	<i>Lepus sp.</i>	Longitudinal fracture
GVE00-17	LEFT FEMUR (DISTAL)	LEFT	<i>Procavia capensis</i>	
GVE00-18	RIB FRAGMENT	N/A	UNIDENTIFIABLE	
GVE00-19	SHAFT FRAGMENT	N/A	UNIDENTIFIABLE	
GVE00-20	LUMBAR VERTEBRAE	N/A	<i>Lepus sp.</i>	
GVE00-21	LUMBAR VERTEBRAE	N/A	<i>Lepus sp.</i>	Damaged epiphysis
GVE00-22	3 LUMBAR VERTEBRAE	N/A	<i>Lepus sp.</i>	
GVE00-23	PORCUPINE FAECES	N/A	N/A	
GVE00-24	SACRUM	N/A	<i>Numida meleagris</i>	2 punctures
GVE00-25	SACRUM	N/A	<i>Numida meleagris</i>	Heavy damage
GVE00-26	SACRUM	N/A	<i>Numida meleagris</i>	Heavy damage and nicks
GVE00-27	SACRUM	N/A	AVES sp.	
GVE00-28	LEFT HUMERUS	LEFT	AVES sp.	
GVE00-29	RIGHT HUMERUS	RIGHT	AVES sp.	3 shaft puncture holes
GVE00-30	RIGHT HUMERUS	RIGHT	AVES sp.	
GVE00-31	LEFT RADIUS AND ULNA	LEFT	AVES sp.	

GVE00-32	LEFT ULNA	LEFT	AVES sp.	
GVE00-33	LEFT TIBIA	LEFT	<i>Numida meleagris</i>	
GVE00-34	FEATHER	N/A	AVES sp.	

Karoo nesting sites

SITE ACCESSION	ELEMENT	ORIENTATION	SPECIES	NOTES ON TAPHONOMY
PZ1-1	MANDIBLE	COMPLETE	HERPESTIDAE	Weathered
PZ1-2	MANDIBLE	RIGHT	<i>Pronolagus</i> spp.	Puncture from top and bottom beak
PZ1-3	MANDIBLE	LEFT	<i>Procavia capensis</i>	
PZ1-4	MANDIBLE	RIGHT	<i>Procavia capensis</i>	
PZ1-5	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Left heel chewed
PZ1-6	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Both coronoids removed
PZ1-7	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Both coronoids removed
PZ1-8	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Both coronoids removed
PZ1-9	SKULL	N/A	<i>Procavia capensis</i>	Orbits punctured
PZ1-10	SKULL	N/A	<i>Procavia capensis</i>	Orbits punctured; occipital removed right zygomatic broken
PZ1-11	MUZZLE	RIGHT	<i>Procavia capensis</i>	Heavily damaged along fringes
PZ1-12	MUZZLE	RIGHT	<i>Procavia capensis</i>	Heavily damaged along fringes
PZ1-13	MUZZLE	RIGHT	<i>Procavia capensis</i>	Heavily damaged along fringes

PZ1-14	SKULL AND MANDIBLE ATTACHED	N/A	<i>Procavia capensis</i>	Left and right heel, zygomatic, occipital removed, orbits punctured
PZ1-15	FEMUR	RIGHT	<i>Canis familiaris</i>	Juvenile
PZ1-16	PELVIS	COMPLETE	<i>Procavia capensis</i>	Juvenile
PZ1-17	ARTICULATED FEMUR AND PELVIS	RIGHT	<i>Procavia capensis</i>	Pubis broken
PZ1-18	FRONTAL	N/A	HERPESTIDAE	Chewed edges
PZ1-19	ARTICULATED PELVIS, SACRUM AND 4 LUMBAR VERT.	N/A	<i>Pronolagus sp.</i>	
PZ1-20	SACRUM	N/A	<i>Pronolagus sp.</i>	Broken distal portion
PZ1-21	LUMBAR VERTEBRAE (4)	N/A	<i>Pronolagus sp.</i>	
PZ1-22	ARTICULATED TARSAL+ PHALANGES	LEFT	<i>Pronolagus sp.</i>	Subadult- stored in one bag
PZ1-23	FEMUR	RIGHT		From one pellet
PZ1-24	ATLAS	N/A		
PZ1-25	PATELLA			
PZ1-26	SACRUM	N/A		
PZ1-27	TIBIOTARSUS	PROXIMAL	LARGE RAPTOR	
PZ1-28	TIBIOTARSUS	DISTAL	(VULTURE SIZED)	

PZ1-29	ULNA	PROXIMAL	LARGE RAPTOR (VULTURE SIZED)	
PZ1-30	TIBIA	LEFT	<i>Procavia capensis</i>	Acid etching along surface
PZ1-31	FEMUR	LEFT	AVES	Acid etching along surface
PZ1-32	CARAPACE	COMPLETE	TESTUDINE	No damage
PZ1-33	MANDIBLE	COMPLETE	HERPESTIDAE	
PZ1-34	MANDIBLE	LEFT	<i>Procavia capensis</i>	
PZ1-35	MANDIBLE	RIGHT	<i>Procavia capensis</i>	
PZ1-36	CRANIAL FRAGMENT	N/A	<i>Procavia capensis</i>	
PZ1-37	MUZZLE	N/A	<i>Procavia capensis</i>	Heavily damaged along fringes
PZ1-38	PELVIS	RIGHT	<i>Procavia capensis</i>	
PZ1-39	PELVIS	RIGHT	<i>Procavia capensis</i>	
PZ1-40	PELVIS	RIGHT	<i>Procavia capensis</i>	
PZ1-41	PELVIS	LEFT	<i>Procavia capensis</i>	
PZ1-42	FULLY ARTICULATED HIND QUARTERS (LUMBAR VERT DOWN TO PHALANGES, BOTH SIDES)	N/A	<i>Pronolagus sp.</i>	

PZ2-1	SKULL	N/A	<i>Procavia capensis</i>	Crushing on nasal only
PZ2-2	SKULL	N/A	<i>Procavia capensis</i>	Orbit punctures
PZ2-3	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Heels chewed, coronoids removed
PZ2-4	MUZZLE	N/A	<i>Procavia capensis</i>	Heavily damaged along fringes
PZ2-5	MAXILLA	RIGHT	<i>Procavia capensis</i>	Heavily damaged along fringes
PZ2-6	CRANIAL FRAGMENTS	N/A	<i>Procavia capensis</i>	Heavily damaged along fringes
PZ2-7	CRANIAL FRAGMENTS	N/A	<i>Procavia capensis</i>	Heavily damaged along fringes
PZ2-8	CRANIAL FRAGMENTS	N/A	<i>Procavia capensis</i>	Heavily damaged along fringes
PZ2-9	CRANIAL FRAGMENTS	N/A	<i>Procavia capensis</i>	Heavily damaged along fringes
PZ2-10	CRANIAL FRAGMENTS	N/A	<i>Procavia capensis</i>	Heavily damaged along fringes
PZ2-11	CRANIAL FRAGMENTS	N/A	<i>Procavia capensis</i>	Heavily damaged along fringes
PZ2-12	CRANIAL FRAGMENTS	N/A	<i>Procavia capensis</i>	Heavily damaged along fringes
PZ2-13	CRANIAL FRAGMENTS	N/A	<i>Procavia capensis</i>	Heavily damaged along fringes
PZ2-14	CRANIAL FRAGMENTS	N/A	<i>Procavia capensis</i>	Heavily damaged along fringes
PZ2-15	CRANIAL FRAGMENTS	N/A	<i>Procavia capensis</i>	Heavily damaged along fringes
PZ2-16	CRANIAL FRAGMENTS	N/A	<i>Procavia capensis</i>	Heavily damaged along fringes
PZ2-17	CRANIAL FRAGMENTS	N/A	<i>Procavia capensis</i>	Heavily damaged along fringes

PZ2-18	CRANIAL FRAGMENTS	N/A	<i>Procavia capensis</i>	Heavily damaged along fringes
PZ2-19	CRANIAL FRAGMENTS	N/A	<i>Procavia capensis</i>	Heavily damaged along fringes
PZ2-20	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Heel damaged
PZ2-21	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Coronoid removed, juvenile
PZ2-22	TIBIA	LEFT	<i>Procavia capensis</i>	Juvenile
PZ2-23	TIBIA	RIGHT		
PZ2-24	PELVIS	LEFT	<i>Procavia capensis</i>	Heavily damaged along fringes
PZ2-25	FEMUR	LEFT	<i>Procavia capensis</i>	
PZ2-26	FEMUR	RIGHT		
PZ2-27	CARAPACE	N/A	TESTUDINE	
PZ2-28	CARAPACE	N/A	TESTUDINE	
PZ2-29	HUMERUS	LEFT	<i>Procavia capensis</i>	Juvenile
PZ2-30	INCISOR 2	LEFT	<i>Procavia capensis</i>	
PZ2-31	INCISOR 2	LEFT	<i>Procavia capensis</i>	Upper
PZ2-32	ARTICULATED FEMUR AND TIBIA, 4 CLAWS	RIGHT	<i>Procavia capensis</i>	Acid etching
PZ2-33	VERTEBRAL BODY	N/A	UNIDENTIFIABLE	

PZ2-34	SCAPULA	LEFT	RODENTIA	Chewed edges, acid etched
PZ2-35	FEMUR		UNIDENTIFIABLE	Juvenile, acid etching
PZ2-36	LBF		UNIDENTIFIABLE	Acid etching
PZ2-37	PHALANGES, VERTEBRAE, CLAWS	N/A	<i>Procavia capensis</i>	Acid etching
PZ2-38	3 RIB FRAGMENTS		UNIDENTIFIABLE	
PZ2-39	FEATHER SPINES	N/A	<i>Numida meleagris</i>	
PZ2-40	RIB FRAGMENT			
PZ2-41	ATLAS	N/A	UNIDENTIFIABLE	Same pellet
PZ2-42	FEMUR		UNIDENTIFIABLE	
PZ2-43	ATLAS, LBF, DISTAL PHALANGES(5)	N/A	FELIDAE	
PZ2-44	LBF	N/A	UNIDENTIFIABLE	Acid etching
PZ2-45	VERTEBRAL BODY	N/A	<i>Procavia capensis</i>	
PZ2-46	LBF, SCAPULA	RIGHT (SCAPULA)	UNIDENTIFIABLE	Pellet included large stick
PZ2-47	VERTEBRAE (2)	N/A	LIZARD	
PZ2-48	SCAPULA	LEFT	LIZARD	
PZ2-49	ARTICULATED HIND FOOT	N/A	<i>Pronolagus sp.</i>	

PZ2-50	VERTEBRA AND LBF	N/A	LIZARD	
PZ2-51	TOOTH	N/A	<i>Procavia capensis</i>	
PZ2-52	TOOTH	N/A	<i>Procavia capensis</i>	
PZ2-53	TOOTH	N/A	<i>Procavia capensis</i>	
PZ2-54	TOOTH	N/A	<i>Procavia capensis</i>	
PZ2-55	TOOTH	N/A	<i>Procavia capensis</i>	
PZ2-56	AUDITORY BULLAE	N/A	<i>Procavia capensis</i>	
PZ2-57	AUDITORY BULLAE	N/A	<i>Pronolagus</i> sp.	
PZ2-58	VERTBRAE (2)	N/A	TESTUDINE	
PZ2-59	ARTICULATED PELVIS, FEMUR, TIBIA	RIGHT	<i>Procavia capensis</i>	Massive v-knotch on illiac
PZ2-60	VERT FRAGMENTS	N/A	UNIDENTIFIABLE	
PZ2-61	LBFS			
PZ2-62	PELVIC GIRDLE	N/A	SMALL AVES	
PZ2-63	VERTEBRAE (2)	N/A	UNIDENTIFIABLE	
PZ2-64	TOOTH	N/A	<i>Procavia capensis</i>	
DAQ-1	TIBIA	RIGHT	BOVID SIZE CLASS 1	Newborn, weathered
DAQ-2	FEMUR	RIGHT	<i>Pronolagus</i> sp.	Greater trocanter chewed

DAQ-3	TIBIA	LEFT	<i>Pronolagus</i> sp.	2 pieces, splintered parallel to shaft
DAQ-4	FEMUR	LEFT	<i>Pronolagus</i> sp.	2 pieces, splintered parallel to shaft
DAQ-5	SKULL	COMPLETE	<i>Procavia capensis</i>	Left basicranium/ zygomatic broken, right orbit punctured
DAQ-6	SKULL	COMPLETE	<i>Procavia capensis</i>	Bot orbits punctured, orbit arch snapped
DAQ-7	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Both heels chewed, left coronoid missing
DAQ-8	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Both heels chewed, right coronoid missing
DAQ-9	NINE VERTBRAE (4 ARTICULATED)	N/A	<i>Procavia capensis</i>	Spines broken on some
DAQ-10	SKULL	N/A	<i>Suricata suricatta</i>	Rt orbit punctured, scratches above parietal, zyg+orbit arch and occipital removed
DAQ-11	SKULL	N/A	<i>Suricata suricatta</i>	Lt orbit punctured twice, auditory bullae removed, puncture left temporal, occipital removed
DAQ-12	TIBIA	RIGHT	<i>Pronolagus</i> sp.	Three shaft splinters
DAQ-13	FEMUR	RIGHT	<i>Canis familiaris</i>	Talon puncture, crushing, surface

				scratches, foeva damage
DAQ-14	FEMUR	LEFT	<i>Canis familiaris</i>	Proximal trochanter damaged
DAQ-15	ILLIAC BLADE	LEFT	<i>Aepyceros melampus</i>	Unfused, blade chewed
DAQ-16	ARTICULATED TIBIA, METATARSAL, TARSALS	RIGHT	BOVID SIZE CLASS 1	Juvenile;puncture below caudal lateral trochanter, distal metatarsal chewed
DAQ-17	ARTICULATED FEMUR, TIBIA, TARSALS, METATARSALS, PHALANGES+ HOOV SHEATHES	RIGHT	BOVID SIZE CLASS 1	Fur attached from ankle down, femur shaft chewed
DAQ-18	MAXILLA FRAGMENT	N/A	<i>Lepus sp.</i>	
TK-1	SKULL	COMPLETE	<i>Procavia capensis</i>	Both orbits punctured, left orbit arch broken
TK-2	SKULL	COMPLETE	<i>Procavia capensis</i>	Right orbit punctured, scratches across skull
TK-3	SKULL	COMPLETE	<i>Procavia capensis</i>	Both zygomatics broken
TK-4	SKULL	COMPLETE	<i>Procavia capensis</i>	Right orbit punctured
TK-5	SKULL	COMPLETE	<i>Procavia capensis</i>	Left orbit- nasal- zygomatic removed,

				both auditory bullae and occipital removed
TK-6	MUZZLE	N/A	<i>Procavia capensis</i>	Heavily chewed along fringes
TK-7	SKULL	COMPLETE	HERPESTIDAE	2 pieces- break divides behind orbits, orbits punctured, left temporal punctured
TK-8	CARAPACE	N/A	TESTUDINE	
TK-9	SKULL	N/A	AVES- RAPTOR, SIZE OF FALCON	Heavily chewed along fringes
TK-10	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Right heel damaged, both coronoid missing
TK-11	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Both heel damaged, both coronoid missing
TK-12	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Left coronoid broken
TK-13	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	
TK-14	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Left heel damage, right heel removed completely

TK-15	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Juvenile, both coronoids missing
TK-16	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	Juvenile, both heels missing
TK-17	MANDIBLE	COMPLETE	<i>Procavia capensis</i>	
TK-18	MANDIBLE	LEFT	<i>Procavia capensis</i>	Heel and coronoid missing
TK-19	MANDIBLE	LEFT	<i>Procavia capensis</i>	
TK-20	FEMUR	RIGHT	<i>Pronolagus sp.</i>	
TK-21	FEMUR	RIGHT	<i>Procavia capensis</i>	
TK-22	ARTICULATED LUMBAR VERT (3) AND SACRUM	N/A	<i>Pronolagus sp.</i>	
TK-23	PELVIS	LEFT	<i>Procavia capensis</i>	Iliac punctured
TK-24	PELVIS	LEFT	<i>Procavia capensis</i>	
TK-25	PELVIS	LEFT	<i>Procavia capensis</i>	Juvenile, illiac v-knotched
TK-26	PELVIS	RIGHT	<i>Procavia capensis</i>	Iliac knotted, ischium-pubis bridge removed
TK-27	ARTICULATED LUMBAR VERT (3)	N/A	<i>Procavia capensis</i>	
TK-28	VERTEBRA	N/A	<i>Procavia capensis</i>	
TK-29	SACRUM	N/A	<i>Procavia capensis</i>	Caudal facet removed

TK-30	SACRAL FRAGMENT	N/A	UNIDENTIFIABLE	Acid etched
TK-31	HUMERUS	UNIDENTIFIABLE	cf. RODENT	Shaft only
TK-32	BF	UNIDENTIFIABLE	UNIDENTIFIABLE	
TK-33	HUMERUS	RIGHT	<i>Pronolagus</i> sp.	Both epiphyses acid etched
TK-34	TIBIA	RIGHT	<i>Procavia capensis</i>	Proximal epiphysis etched
TK-35	MAXILLA FRAGMENT	N/A	<i>Lepus</i> sp.	Heavily chewed along fringes
TK-36	MAXILLA FRAGMENT	LEFT	<i>Lepus</i> sp.	Heavily chewed along fringes
TK-37	SKULL CAP	N/A	<i>Procavia capensis</i>	Heavily chewed along fringes
TK-38	TIBIA	RIGHT	<i>Lepus</i> sp.	Puncture on mid lateral shaft
TK-39	TIBIA	RIGHT	<i>Lepus</i> sp.	Proximal epiphysis only
TK-40	ATLAS AND AXIS	N/A	<i>Procavia capensis</i>	Axis blade notched
TK-41	SKULL CAP	N/A	AVES- RAPTOR, SIZE OF VULTURE	Heavily chewed along fringes
TK-42	ASSORTED LOOSE TEETH	N/A	<i>Procavia capensis</i>	
LV-1	DECIDUOUS UPPER MOLAR	LEFT	OVIS sp.	
LV-2	FEMUR	RIGHT	<i>Procavia capensis</i>	Subadult, heavily acid etched
LV-3	TIBIA	LEFT DISTAL		

LV-4	ULNA	LEFT PROXIMAL		
LV-5	RADIUS	LEFT PROXIMAL		
LV-6	6 VERT FRAGS	N/A		
LV-7	1 VERT DISC	N/A		
LV-8	ASTRAGULUS	RIGHT		
LV-9	METATARSAL+PROXIMAL PHALANX	N/A		
LV-10	BF			
LV-11	KERATIN HOOF	N/A	BOVID SIZE CLASS 2	Juvenile
LV-12	LOWER MOLAR	N/A		
LV-13	LOWER INCISOR	N/A		
LV-14	BF	N/A	UNIDENTIFIABLE	
LV-15	CRANIAL FRAGMENTS	N/A	LAGOMORPH	Juvenile
LV-16	LBF (15)	N/A	UNIDENTIFIABLE	
LV-17	ARTICULATED LUMBAR VERTEBRAE (3)	N/A	UNIDENTIFIABLE	
LV-18	TOOTH FRAGMENTS	N/A	BOVID SIZE CLASS 1	Juvenile
GK-1	ARTICULATED FRONT PAW	RIGHT	<i>Procavia capensis</i>	

GK-2	VERTEBRAE+LBF	N/A	UNIDENTIFIABLE	Single pellet
GK-3	ARTICULATED SCAPULA TO PHALANGES	LEFT	RODENTIA	
GH-1	SCAPULA, 3 VERTEBRAE, RIB FRAG	N/A	UNIDENTIFIABLE	1 pellet
GH-2	BONE FRAGS (9)	N/A	UNIDENTIFIABLE	1 pellet
GH-3	WOOD			
GH-4	RIB FRAGMENTS	N/A	UNIDENTIFIABLE	1 pellet
KP-1	SKULL	N/A	<i>Procavia capensis</i>	Heavily damaged
KP-2	ARTICULATED VERTEBRAE	N/A	UNIDENTIFIABLE	1 pellet
KP-3	HUMERUS	DISTAL	UNIDENTIFIABLE	
KP-4	LBF	N/A	UNIDENTIFIABLE	
KP-5	10 VERTEBRAE, 5 RIBS		UNIDENTIFIABLE	
KP-6	ARTICULATED FORELIMB		<i>Procavia capensis</i>	
KP-7	ARTICULATED FOOT		<i>Lepus sp.</i>	