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Cohen, Brigette Fiona

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ACTUALISTIC INVESTIGATION OF BONE MODIFICATION ON LEPORIDS BY CARACAL (*Caracal caracal*) AND HONEY BAGDER (*Mellivora capensis*); AN INSIGHT TO THE TAPHONOMY OF COOPER'S CAVE, SOUTH AFRICA

Brigette Cohen

A dissertation submitted to the faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Masters of Science (Palaeontology)

May, 2013

Declaration

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

_____

(Signature of candidate)

30 May 2013

ABSTRACT

Small carnivores and middle-sized mammals (mesomammals) are ubiquitous in fossil sites in South Africa, but their taphonomy is poorly understood. This study presents an actualistic investigation of bone modification by two captive small carnivores; the caracal (*Caracal caracal*) and honey badger (*Mellivora capensis*), housed at the Johannesburg Zoo. The carnivores were fed domestic rabbit (*Oryctolagus cuniculus*) carcasses as proxies for mesomammals and the bone modification of the resulting refuse and scatological assemblages were assessed in terms of their skeletal part representation, breakage patterns, digestive modifications and tooth marks. The investigation revealed that skeletal part representation and breakage patterns in the caracal and honey badger assemblages resembled those reported from other small carnivores. The caracal and honey badger assemblages were distinct from other carnivores in having overall light digestive modifications and a high frequency of tooth marks. Digestion was greater and tooth marks less frequent in the caracal than in the honey badger. Results were applied to the fossil assemblage of Cooper's D which has a large assemblage of mesomammals and small carnivores. While a taphonomic analysis of Cooper's D has not been published, initial results suggest that small carnivores had a great potential as contributors in the formation of the assemblage. The findings of this study emphasise the need for employing a variety of bone modifications in the identification of a small carnivore as an accumulator since there is rarely a single characteristic that is diagnostic for a particular carnivore.

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CHAPTER ONE

BACKGROUND AND INTRODUCTION

1.1. Introduction

Taphonomists and zooarchaeologists spend a great deal of time reconstructing the history of faunal assemblages. Insights into the processes responsible for faunal assemblage accumulation are often inferred through diagnostic bone surface modification and skeletal element patterning. In African palaeontological sites, carnivores have been implicated as the major accumulators of vertebrate fossil assemblages, with limited contribution from rodents and birds of prey. The challenge has however been in determining the specific species of carnivore, rodent and/or raptor responsible for bone accumulation. To address this, researchers (e.g., Binford, 1981; Haynes, 1980; 1982; 1983; Brain, 1981) have conducted field, laboratory and actualistic studies aimed at documenting bone modification attributes specific to each biotic agent. Such attributes form a template with which bone modifications in fossil assemblages are compared.

1.2. Previous Studies of Carnivore Induced Modifications

1.2.1. Carnivore modification on micromammal remains

The majority of carnivore taphonomic research has centred on how large mammalian carnivores modify large bodied prey carcasses (Sutcliffe, 1970; Skinner *et al.* 1980; Pickering *et al*. 2004; Domínguez-Rodrigo, 1999; Cavallo and Blumenschine, 1989; Pickering and Carlson, 2004). Similarly much research on small carnivores has investigated their modifications on microfauna. For example, Andrews and Evans (1983) and Andrews (1990) investigated the taphonomic signatures of remains of microfauna from the scats of a number of small carnivores in both wild and captive settings. Their study included investigation of felids (feral cat and margay) canids (bat-eared fox; red fox; arctic fox and coyote), herpestids (white-tailed mongoose), viverrids (genet) and small mustelids (pine martin, otter and mink). The researchers found that the canids produced more intense modifications on microfauna than the herpestids, viverrids and mustelids, but that the small felids produced extreme levels of modification. Bone

remains from felid scats were reduced to very small fragments with rounded edges and severe digestive corrosion. Matthews (2002) investigated the taphonomic signature of caracal (*Caracal caracal*), serval (*Leptailurus serval*) and black-backed jackal (*Canis mesomelas*) from scatological samples of wild taxa in South Africa. The investigation revealed similar bone modifications within the caracal sample to Andrews and Evans's feral cat and margay assemblages. The serval scats, on the other hand, were more similar to those produced by canids or herpestids. Breakage patterns in the back-backed jackal resembled those of Andrews and Evans' canids (Matthews, 2002).

Thus it is apparent that bone remains of microfauna are abundant in scatological samples of small carnivores. Mongooses display relatively little destruction on microfaunal carcasses, while canids and felids produce high levels of modification. Studies such as Andrews (1990) and Fernández-Jalvo (1995) have shown that small carnivores are important potential accumulators of microfaunal remains in fossil assemblages. Many of these carnivores are opportunistic predators that also feed on larger prey. There is a paucity of research on small carnivore modifications in Africa, especially South Africa. The modification patterns of African small carnivores on larger prey remains like leporids (rabbits and hares) is poorly understood.

1.2.2. Carnivore modification on mesomammal remains

Mesomammals are those larger bodied taxa, too big to be considered microfauna, but too small for macrofauna. They include mammals within the size ranges of hares (genus *Lepus*), hyraxes (family Procaviidae) and springhares (*Pedetes capensis*). These and other taxa with a size range of about 1 Kg to 15 Kg are often overlooked in fossil assemblages and their taphonomy is not well understood. Mesomammals are an important resource for medium and small sized carnivores, for example hyraxes and similar sized prey can make up as much as 40% of leopard (*Panthera pardus*) diet (Skinner and Chimimba, 2005). In 1981, Brain discovered hyrax remains in leopard lairs with characteristic damage to the cranium and mandible (posterior parts completely removed) and a profound absence of postcranial elements. Feeding of hyrax carcasses to captive leopard and cheetah (*Acinonyx jubatus*) produced similar bone modifications as observed from the lair. The remains of mesomammal prey in scats from the

puma (*Puma concolor*) found a greater degree of completeness than microfaunal remains and moderate levels of digestion (Montalvo *et al.* 2007).

Schmitt and Juell (1994) described leporid bones from coyote (*Canis latrans*) scats from wild individuals as being extensively corroded and highly mechanically damaged. Refuse in coyote kill sites varied between seasons but in the summer months was observed to contain discarded elements like leporid feet. Refuse and scats from captive and wild foxes (*Vulpes vulpes*) were investigated by Lloveras *et al*. (2012) in an experimental study using domestic rabbit carcasses. Rabbit remains from fox scats were heavily digestively corroded and highly fragmented. Remains from the captive fox carcass refuse, on the other hand, were frequently complete and rarely tooth marked. On the other hand, refuse remains from wild fox dens in Poland also have a high frequency of complete remains but were intensively tooth marked and gnawed (Krajcarz and Krajcarz, 2012). Lynx (*Lynx pardinus*) scats from wild individuals were found to contain leporid remains with extensive breakage, heavy corrosion and a near absence of tooth marks (Lloveras *et al*. 2008b). Modification in leporid remains from the lynx was not as intensive as on microfaunal remains in other small felids. Álvarez *et al*. (2012) investigated refuse remains from Geoffroy's cat (*Leopardus geoffroyi*), a small felid similar in size to a domestic cat, which was experimentally fed domestic rabbit. Refuse remains had low survival and fewer complete remains than observed in the fox refuse. Thus much work on mesomammal taphonomy has focussed on how small carnivores modify leporid remains. Such research has investigated bone modification in both refuse and scat assemblages and been undertaken with both wild and captive taxa. Some investigations have shown captive individuals display similar modification patterns to wild ones while in other studies captive and wild carnivores differed. Currently no research has been conducted on small carnivore modifications of mesomammals in South Africa.

Leporidae are the primary food source for many small carnivores in Europe and the Americas including the lynx, fox and coyote (Schmitt and Juell, 1994; Lloveras *et al.* 2008a; 2012). Fossil mesomammal assemblages, particularly Leporidae are abundant in many Upper Paleolithic deposits across Europe (Hockett and Haws, 2002; Castel, 1999; Lloveras *et al.* 2012). Leporidae may have presented an important resource for early human populations, and

understanding the potential accumulators or taphonomic biases of these leporid assemblages, particularly whether they were accumulated by carnivores or humans, is essential in interpreting human subsistence strategies in the Paleolithic (Hockett and Haws, 2002). Mesomammals and small carnivores are commonly recovered in fossil and archaeological deposits in South Africa (Klein *et al.* 2007), but the taphonomy of these assemblages and how they relate to human evolution is poorly understood.

This investigation sought to fill some of the gaps in our understanding of small carnivore and mesomammal taphonomy in South Africa by conducting actualistic experimentation; feeding mesomammal remains to captive small carnivores, namely the caracal (*Caracal caracal*) and honey badger (*Mellivora capensis*). The African caracal, at an average of 12 Kg, is the largest of the small cats and has been described as the African version of a lynx (Estes, 1991). The caracal is found in arid regions and dry savannas of Africa and North Africa, spreading through to Asia (Skinner and Chimimba, 2005). It feeds on a wide variety of prey, but hyraxes and similar sized prey appear to be the mainstay of its diet in many parts (Skinner and Chimimba, 2005; Moolman, 1984). In the Mountain Zebra National Park, South Africa, 53% of caracal diet was hyrax (Grobler, 1981). Caracal remains are found in many fossil deposits in South Africa. The caracal has been identified in the Miocene from Langebaanweg (Hendey, 1974), in the Plio-Pleistocene from Swartkrans, Sterkfontein and Drimolen (Watson, 1993; Reynolds and Kibii, 2011; O'Regan and Mentor, 2009) and in archaeological (Middle and Late Stone Age) deposits from Diepkloof Rock Shelter, Sehonghong Shelter, Equus, Eland's Bay, Boomplaas, Nelson's Bay and Melkhoutboom Caves (Steele and Klein, 2013; Klein *et al*. 1991; Klein, 1972; Klein, 1978; Plug and Badenhorst, 2001). Matthews (2002) is currently the only taphonomic investigation of the caracal, focusing on microfaunal remains. The honey badger is a large mustelid similar in size to the caracal (12 Kg; Skinner and Chimimba, 2005). Honey badgers are practically ubiquitous south of the Sahara, and tolerate a wide variety of conditions (Estes, 1991). The social organisation of honey badgers is not well understood and they have been observed foraging in pairs, small groups or singularly.

The honey badger is an opportunistic insectivore and carnivore, and microfauna and

insects (scorpions and spiders) have been noted as the primary prey in several regions (Skinner and Chimimba, 2005; Kruuk and Mills, 1983). However they are known to predate on small carnivores and mesomammals (for example; aardwolf, bat-eared fox, springhare) opportunistically, even pirating prey from other carnivores (Skinner and Chimimba, 2005). The honey badger is an extremely proficient excavator and when resting they will withdraw to burrows or caves. The honey badger has an origin in South Africa going back into the Miocene (Langebaanweg; Hendey 1974) and is known from Plover's Lake (De Ruiter *et al*. 2008) and several archaeological deposits including Diepkloof Rock Shelter, Blombos, Redcliffe, Equus, Eland's Bay and Nelson's Bay Caves (Steele and Klein, 2013; Henshilwood *et al.* 2001; Klein *et al*. 1991; 1972; Plug and Badenhorst, 2001). The genus (*Mellivora*) is also known from Swartkrans (De Ruiter, 2003). Both the caracal and honey badger are also known from numerous Holocene deposits (Plug and Badenhorst, 2001). No previous taphonomic research has been conducted on the honey badger. The honey badger and caracal are thus commonly occurring small carnivores (Skinner and Chimimba, 2005). Both have been recorded to feed on leporids and are known to frequent rocky areas or caves (Kingdom, 1977). Thus they were utilised in this investigation both for their availability and their potential as contributors.

1.3. Cooper's Cave Fossil Assemblage

Cooper's Cave is a Plio-Pleistocene deposit of the *Cradle of Humankind* World Heritage Site, approximately 45 Km from Johannesburg. The cave occurs in a karstic landscape of dolomites from the Monte Christo Formation (Malmani Subgroup, Transvaal Supergroup), close to the world renowned Sterkfontein Cave (De Ruiter *et al.* 2009). The Cooper's D deposit of the cave was first opened in 1999 and has since produced an extensive bone assemblage of over 8488 identified specimens. Hominin remains from Cooper's include *Paranthropus robustus* and early *Homo* (Berger *et al*. 2003; Steininger *et al*. 2008). This faunal assemblage is extremely diverse and abundant with numerous small carnivores and mesomammals (Table 1.1). Cooper's D has the best constrained ages of any *P. robustus* deposit in South Africa and uranium-lead dating places the Cooper's D deposit between 1.4 and 1.5 Million years ago (De Ruiter *et al.* 200; Steininger, 2011). The abundance of small carnivores and mesomammals at Cooper's

makes this deposit ideal for investigating taphonomy in these taxa.

1.4. Aims and Hypotheses

This investigation sought to expand knowledge of mesomammal taphonomy by generating actualistic taphonomic data of mesomammal carcass modification by modern day predators, utilising rabbits as a proxy. Such information was used to create a template of bone modification for each carnivore. Lloveras *et al*. (2012) and Álvarez *et al*. (2012) have shown the importance of investigating both carcass remains and scatological bones. These factors provide testable hypotheses; 1) Bone modification will vary depending on predator responsible and that each predator taxon will leave a distinct taphonomic signature on mesomammal remains, 2) Both carcass remains and scatological data provide essential bone modification information and using both data sets can provide a better taphonomic signature for these predators. Such experimental analyses may prove to be useful tools in analysing the preservation potential of remains in a palaeontological context (Montalvo *et al.* 2007) and will provide implications that may be relevant from multiple viewpoints including palaeontological, archaeological and ecological perspectives (Mondini and Muñoz, 2008).

Table 1.1. Small carnivores and mesomammals from Cooper's D

Specific name	Common name	MNI
Family Felidae		
Caracal caracal	Caracal	2
Felis silvestris	African wild cat	3
Family Canidae		
Canis mesomelas	Black-backed jackal	5
Canis sp.	Dog	2
Family Herpestidae		
Herpestes ichneumon	Egyptian mongoose	2
Suricata sp.	Meerkat	3
Cynictis penicillata	Yellow mongoose	2
Family Mustelidae		
Poecilogale albinucha	African stripped weasel	1
Family Hystricidae		
Hystrix africaeaustralis	Porcupine	4
Family Pedetidea		
Pedetes sp.	Springhare	2
Family Procaviidae		
Procavia antiqua	Extinct hyrax	5
Procavia transvaalensis	Extinct hyrax	1
Family Leporidae		
cf. *Lepus* sp.	Cape or scrub hare	12

Adapted from De Ruiter *et al.* (2009)

CHAPTER 2

MATERIALS AND METHODS

2.1. Materials

Domestic rabbit carcasses were fed to two caracals and two honey badgers (a male and female in both cases) housed at the Johannesburg Zoo, South Africa. Both sets of carnivores were housed in enclosures that included both an open-air area and a small close-able night room. Both parts of the enclosures are equipped with observation windows. The honey badger's enclosure was twice the size of the caracal's and included two night rooms. However the honey badgers spent much of the day together in a small plastic shelter in one of these night rooms.

Domestic rabbit (*Oryctolagus cuniculus*) was used in the feeding experiments for its availability. Two sizes of rabbits were utilised during these experiments; a medium-sized rabbit of approximately 1.7 Kg and a large rabbit, approximately 3 Kg. Osteologically both sizes of rabbits were sub-adult with some epiphyseal areas still undergoing ossification at the time of death. Rabbits were sourced by the zoo nutritionist (Lorna Fuller) from known sources of animal feed, following Johannesburg Zoo protocol. The rabbits were acquired freshly killed and kept frozen until needed. The carcasses were defrosted overnight before being presented to the carnivores.

2.2. Methods

2.2.1. Feeding

Before any experimental feedings were undertaken, animal ethics clearance for the use of domestic rabbit carcasses to be fed to captive carnivores of the Johannesburg Zoo was obtained from the University of the Witwatersrand Animal Ethics Screening Committee (Clearance certificate number: 2011/15/01; Date 2011/03/29). Feedings were undertaken during the winter months of June and July 2011. One carcass per individual carnivore was presented once a week, on a normal feeding day in lieu of the usual feed, which typically consisted of small chunks of cut beef (with bone) and occasionally juvenile chicken or mice

carcasses. Thus, the rabbits were not fed as extras outside of the normal feeding schedule reducing the likelihood that satiation could have affected the carnivores. While whole rabbit carcasses were a novel food for the carnivores the feeding of whole carcasses of smaller animals was not unusual, and the carnivores had been fed rabbit meat on previous occasions. Feedings were undertaken in the mornings between 9 and 11 am as close to the normal feeding time as possible. The caracals were fed five times, and the honey badgers three times. The animal keeper and I presented the carcasses to the carnivores following the normal feeding procedures. During feeding, the caracals were always separated, the male in the night room and the female in the open area, except for on one occasion. The honey badgers were fed together in the night room. During the feedings, fellow students from the Palaeosciences Centre, University of the Witwatersrand, Johannesburg assisted with observing and digitally and manually recording feeding behaviours of the carnivores.

2.2.2. Carcass remains and scat collection

Prior to the feedings all old carcass and scat remains were removed from the carnivore enclosures. The morning after the feedings, with the assistance of the animal keepers, carcass remains and scats were collected. Individual carcasses were placed in separate plastic bags, sealed and labelled (carnivore species and date). Multiple carcass parts were bagged together where they occurred in close proximity, separate from the other carcass. Carcasses that were found in separate parts of the enclosure were likewise bagged separately. Where it was not possible to separate parts between the two carcasses then all remains were bagged together. All scats were bagged together as it was not possible to identify which individual carnivore the scats had come from. While it is not known how long it would take for the carnivores to digest rabbit prey it was considered that 24 hours would be sufficient for carnivores of this size. All scat and carcass samples collected were kept frozen until analysis.

2.2.3. Cleaning of the carcass refuse

Each carcass was analysed separately. Carcass remains were removed from the freezer and defrosted overnight. The remains were photographed and skin and viscera removed with

forceps, scalpel and scissors, taking precaution not to induce marks on the bones. Breaks and missing elements were noted. The carcasses were then presented to newly established dermestid beetle colonies at the University of the Witwatersrand. The beetles consisted of two colonies kept in large glass tanks in an environmentally controlled insectarium. Carcasses were presented to the beetle colonies one at a time. Where the carcasses consisted of only a few isolated legs or fragments, two carcasses were placed in a single tank but every precaution was taken to avoid cross contamination. After all flesh was removed from the carcasses the bones were retrieved. These bones were then cleaned and degreased by soaking for three days in a 50% ammonia-water solution. The bones were then ready to be analysed for modifications.

2.2.4. Scat disintegration and bone retrieval

Similar to carcass remains, each scat was analysed separately. Scats from each feeding of each carnivore species were removed from the freezer and allowed to defrost for several hours. Each individual scat was removed from the bag, weighed and measured. The scat was then gently teased apart with forceps and any bone remains were removed and rinsed in a dilute ammonia solution to remove all clinging faecal material. After rinsing, bone remains were laid out to dry thoroughly. Once dry, bones from each scat were bagged and the carnivore, feeding date and bag and scat number noted. Standard precautions were taken in handling the scats including wearing a mask and latex gloves and working with the scats in a secluded and well-ventilated area. All faecal material, gloves, masks, and paper towels that came into contact with the faecal material were disposed of safely. All other tools were cleaned with ammonia.

2.2.5. Bone modification analysis

Anatomical representation

Taphonomic assessment of bone remains was carried out with the aid of a light microscope (Olympus S2X16; X40) in the Taphonomy Laboratory at the Palaeosciences Centre, University of the Witwatersrand, Johannesburg, courtesy of Dr. Lucinda Backwell. The maximum lengths of all bone specimens were measured using digital callipers to one decimal place, and articulation with other bones was noted. Bone remains were identified to skeletal

part using rabbit skeletons from the comparative collections of the Palaeosciences Centre as well as cleaned skeletal remains from non-ingested carcasses. Skeletal part representations of a typical rabbit skeleton are given in Table 2.2. Every effort was made to reliably identify remains. The majority of unidentifiable remains were less than 4 mm in length and as a result refitting of long bone shaft fragments was not possible.

Once the bones had been identified, skeletal part frequencies were then calculated. These frequencies are essential in analysing key data of an assemblage's taphonomic history. The fundamental quantitative measures employed were: the number of identifiable specimens (NISP) and minimum number of elements (MNE). NISP is the number of identified specimens (Grayson 1989; Klein & Cruz-Uribe 1984). It is a count of the number of specimens identifiable to skeletal element. MNI is the minimum number of individuals necessary to account for a specified set of skeletal elements. It is a measure of the number of individuals that contributed to an assemblage. MNE is the minimum number of skeletal elements necessary to account for the number of remains (NISP) of that skeletal element observed in the assemblage. It is the highest probable estimate of the original number of that skeletal element that contributed to the assemblage (Bunn 1982, 1986; Bunn & Kroll 1986). The MNE is essential for estimating the survival or frequency of portions of skeletal elements in the assemblage.

The use of NISP and MNI are not without their faults and some researchers argue against the continued use of these measures (Plug and Plug, 1990). Some of the biggest problems with using NISP is that it cannot account for the interdependence of elements from a skeleton and it has a strong potential for overrepresentation of some species or elements within the sample (Lyman, 2008). The use of MNI solves the problem of interdependence (with NISP) but presents difficulties in that as a minimum value it cannot be used for calculations and that different aggregates from within an assemblage will produce different MNI values. The problems with NISP and MNI outlined here will not greatly bias the results of this investigation as the number of source skeletons is known and which allowed for the calculation of relative survival of elements as shown below. These issues are of importance however when comparing the results of different taphonomic studies and caution must always be used.

Derived and actual MNE values (dMNE, aMNE respectively) were utilised to calculate

the percentage survivorship of skeletal parts following the methodology outlined by Lyman (1994). In this experimental investigation the actual number of rabbits fed to each carnivore was known, thus the actual MNE could be calculated. The derived MNE was determined from the elements recovered in the refuse and scatological assemblages. Thus survivorship was calculated from the proportional relationship between the derived MNE and the actual MNE:

%survivorship = (dMNE/aMNE) X 100.

Survivorship in skeletal elements was compared to the structural density assays for those parts in the domestic rabbit (*Oryctolagus cuniculus*) as outlined by Pavao and Stahl (1999), in order to test the relationship between bone density and survival of that element.

Breakage patterns

A series of breakage classes was created for each element. For the long bones, metapodials, pelvis, scapula, mandible and cranium the same classification system as Lloveras *et al*. (2008a), was used and is shown in Figure 2.1. To this classification an additional class was added for the scapula acromion. Cranial remains in the caracal and honey badger scat assemblages followed this classification system well; however these cranial categories were not adequate for describing remains from the refuse assemblages. This classification system did not allow for description of varying degrees of semi-completeness, which was observed in the caracal and honey badger refuse. Thus cranial survival in the refuse assemblages was based on the relative completeness and survival of individual cranial bones. For the other elements, compact bones such as carpals, tarsals and patella were classed as complete (C) or fragmented (F); ribs were classified as isolated proximal part (head and/or tubercle; HT), isolated shaft (S) and both (HTS); vertebrae were classed as complete (C), vertebral body (VB), vertebral epiphysis (VE), spinous process (SP), transverse process (TP), and zygopophyses (including cranial and caudal articular facets; ZYG).

Digestion related modification

Initially I intended to classify the digestive damage according to the criteria outlined by Andrews (1990) and Fernández-Jalvo and Andrews (1992) for micromammals. This

methodology has five classes of digestive damage (light to severe) on bones that was based on levels of pitting, rounding of edges, and etching or alteration on the bone surface. However, preliminary analysis of bones in this study indicated that this methodology would prove difficult to utilise. Many of the bone remains displayed multiple digestive characteristics at different levels of damage, for example a single bone might have light etching but at the same time heavy rounding and pitting. Such bones would not fit well into traditional classification strategies. As a result of this disparity I separated different digestion related modifications and investigated each one separately. Included in this analysis were traditional modification patterns such as surface etching, pitting and rounded edges together with the digestion related modifications (foramen excavation, corrosive holes, slimming, undulations, cupules and desquamation) described by Esteban-Nadal *et al.* (2010) in their investigation of scatological bone remains from wild wolves.

Digestion related modification analysed include:

Surface etching (Plate 2.1) was where the bone surface displayed a corroded appearance as a result of passing through the digestive tract of a carnivore and being exposed to digestive enzymes (Lyman, 1994). Etching intensity was classed as 0 - no damage; 1 - light; 2 - moderate; 3 - heavy; or 4 - severe.

Corrosive pitting (Plate 2.2) was the appearance of patches of densely distributed fine holes in the bone surface. The severity of damage was classed as either 0 - no damage; 1 - light; 2 - moderate; 3 - heavy; or 4 - severe.

Rounding of edges (Plate 2.3) was where sharp broken edges and fractures have been smoothed and rounded. Rounding was assessed in terms of the intensity of the rounding and was classed as either 0 - no damage; 1 - light; 2 - moderate; 3 - heavy; or 4 - severe.

Staining (Plate 2.4) was a characteristic noted by Schmitt and Juell (1994) in leporid remains from coyote scats. They described colour changes observed on bones but did not quantify the degree of staining. Staining was classified into four arbitrarily chosen classes, beige or no staining; light brown (light staining); dark brown (heavy staining); and black (severe staining). I considered the darker the colour the more intense the degree of staining.

Transparency (Plate 2.5) was a digestive modification not previously recorded by other

taphonomic studies. The bone surface developed an almost “glassy” finish and both the cortical bone and the cortex became translucent so that the bone was see-through. This can be both localised and affect the entire bone. Transparency was likely the result of mineral leaching during exposure to acid digestive juices, but there was no destruction of the bone beyond slight slimming (see below).

Foramen enlargement or excavation (Plate 2.6A, B and C) was where digestive acids entered an existing foramen and corrode the foramen. On some occasions this corrosion was limited to the foramen opening, resulting in an enlarged foramen opening. On other occasions the acid corroded the foramen along its length so that a channel was formed with enlarged openings at both ends.

Corrosive holes (Plate 2.6D) or perforations were the appearance of randomly distributed little holes in the bone surface (Esteban-Nadal *et al*. 2010). These openings were the result of chemical effects from the digestive juices. Typically the digestive juices would enter through the holes (once made) into the bone and destruction of underlying bone material would take place such that the corrosive holes would appear to have no bottom, unlike tooth pits or punctures. Corrosive holes unlike pitting were not densely distributed.

Slimming (Plate 2.6E and F) was a decrease or disappearance in the cortical bone (Esteban-Nadal *et al*. 2010). There was no destruction of the bone and the bone retained its anatomical structure and shape; however cortical thickness was reduced compared to undigested bones. This was observed in remains from both the large and small carcasses and was not an aspect of size.

Undulations (Plate 2.6G) was where the surface of the bone had continuous elevated and depressed areas (Esteban-Nadal *et al*. 2010).

Desquamation (Plate 2.6H and I) was where the surface was exfoliated but with no observable cracks (Esteban-Nadal *et al*. 2010). The surface displayed localised and often very thin areas of flaking.

Cupules (Plate 2.6J) were small circular depressions with concave bottoms found on the bone surface (Esteban-Nadal *et al*. 2010). They can be isolated or concentrated and bear no relation to tooth marks.

Tissue retention (Plate 2.6K) was where a bone or bones retained small pieces of soft tissue. This is usually in the form of connective tissue.

Tooth marks

Several different carnivore tooth marks were observed on the rabbit bones and teeth. The number of tooth marks and type of mark on each bone was recorded. Analysis Five Digital Imaging Software (Olympus soft imaging solutions) was used to measure the size of circular tooth marks and the width of elongated tooth marks.

Pits (Plate 2.7A, B and C) were depressions in which compact or cortical bone could be seen in the bottom (Campmas and Beauval, 2008). *Punctures* (Plate 2.7D) on the other hand, were holes in which spongy bone could be seen in the bottom (Campmas and Beauval, 2008). *Scours* (Plate 2.7E and F) were grooves in the bone in which compact bone could be seen at the bottom (Campmas and Beauval, 2008). This differed from furrows (Haynes, 1980) which punctured through the cortical bone. *Notches* (Plate 2.7G and H) were areas where bone material had been removed or chipped back from the bone edge, often associated with a tooth mark. These likely relate to Binford's (1981) chipping back modification. A c*renulated edge* (Plate 2.7I) was where the carnivore had punctured through thin bone and created an edge with a profile similar to the dentition of the carnivore (Binford, 1981). *Crush* mark (Plate 2.7J, K and L) was a carnivore tooth mark type that is not previously described by taphonomic researchers. In a crush, a localised area of the bone had been depressed and fractured into the medullar cavity, from pressure being applied by carnivore teeth. This differed from a puncture or similar tooth mark in that the crush did not conform to the shape of carnivore dentition but had a shape more like a snapped stick. Other tooth marks such as pits may be associated with the crush.

Table 2.1. Skeletal part representation of a rabbit skeleton

Skeletal element	n
Cranium	1
Mandible	2
Upper Postcanine	12
Lower Postcanine	10
Incisor	6
Cervical	5
Atlas	1
Axis	1
Thorasic	13
Lumbar	7
Sacrum	1
Caudal	16
Rib	24
Scapula	2
Humerus	2
Radius	2
Ulna	2
Pelvis	2
Femur	2
Tibia	2
Carpal	14
Tarsal	10
Patella	2
Metacarpal	10
Metatarsal	8
Phalange	50
Total	**207**

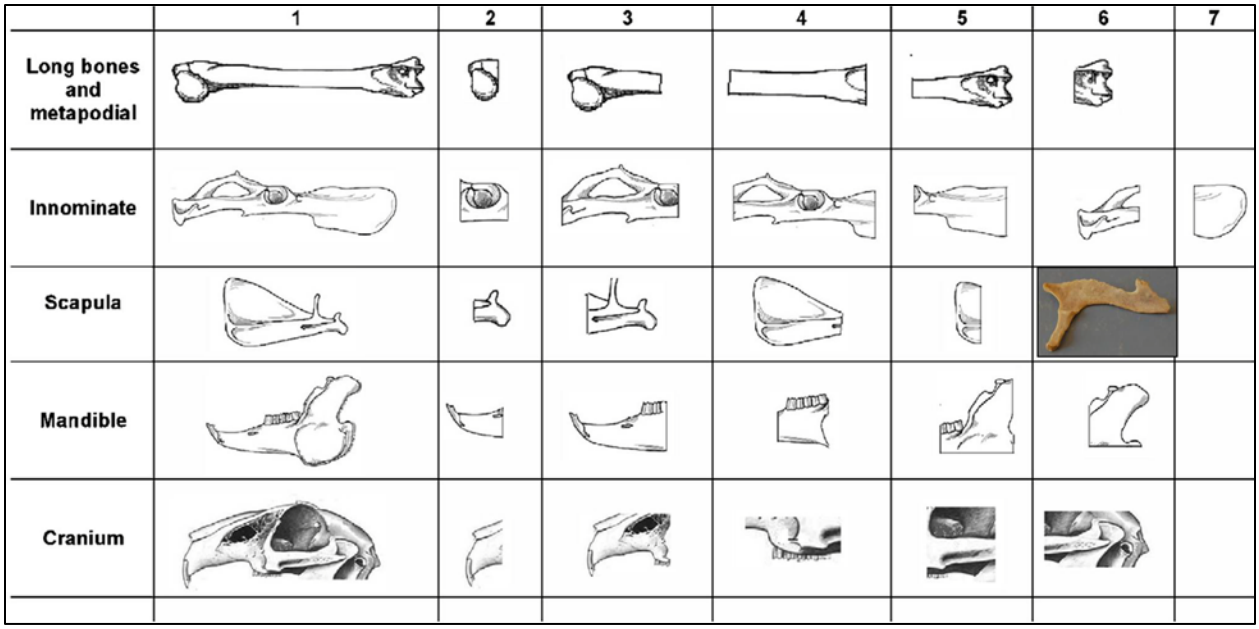


Figure 2.1. Breakage classes in rabbit remains from small carnivore feedings. *Long bones and metapodial* were classified as: 1, complete (C); 2, proximal epiphysis (PE); 3, proximal epiphysis + shaft (PES); 4, shaft (S); 5, shaft + distal epiphysis (SDE); 6, distal epiphysis (DE). *Pelvis* as: 1, complete (C); 2, acetabulum (A); 3, acetabulum + ischium (AIS); 4, acetabulum + ischium + ilium (AISIL); 5, acetabulum + ilium (AIL); 6, ischium (IS); 7, ilium (IL). *Scapula* as: 1, complete (C); 2, glenoid cavity (GC); 3, glenoid cavity + neck (GCN); 4, neck + fossa (NF); 5, fossa or blade (F), 6, acromion (ACR). *Mandible* as: 1, complete (C); 2, incisive part (IP); 3, mandible body + incisive part (MBI); 4, mandible body (MB); 5, mandible body + branch (MBB); 6, condylar process (CP). *Cranium* as: 1, complete (C); 2, incisive bone (IB); 3, incisive bone + maxilla (IBM); 4, maxilla (M); 5, zygomatic arch (ZA); 6, neurocranium (or braincase) (NC). *Adapted from Lloveras* et al*. (2008b).*

Table 2.2. Skeletal element, breakage classes and other abbreviations used in the text

Skeletal Elements	**Abbreviation**
Atlas	atl
Axis	axs
Cranium	cra
Carpal and tarsal	c/t
Caudal vertebra	caud
Dentition	dent
Femur	fem
Humerus	hum
Incisor	I
Lower postcanine	LPC
Lumbar vertebra	lumb
Mandible	man
Metapodial	mps
Metacarpal	mcs
Metatarsal	mts
Patella	pat
Pelvis	pel
Phalange	phl
Radius	rad
Scapula	sca
Thoracic vertebra	thor
Tibia	tib
Ulna	uln
Upper postcanine	UPC
Vertebra	vert
Breakage Patters	
Skeletal Parts	
Complete	C
Proximal epiphysis	PE
Proximal epiphysis with shaft	PES
Shaft	S
Distal epiphysis with shaft	SDE
Distal epiphysis	DE
Acetabulum	A
Acetabulum with ischium	AIS
Acetabulum with ischium and ilium	AISIL
Acetabulum with ilium	AIL
Ischium	IS
Ilium	IL

Glenoid cavity	GC
Glenoid cavity and neck	GCN
Scapula neck and fossa	NF
Scapula blade (or fossa)	F
Acromion	ACR
Incisive part of mandible	IP
Mandibular body and incisive part	MBI
Mandibular body	MB
Mandibular body and branch	MBB
Condylar process	CP
Incisive part of cranium	IB
Incisive bone and maxilla	IBM
Maxilla	M
Zygomatic arch	ZA
Neurocranium	NC
General Abbreviations	
Average	Avg
Indeterminate	Indet.
Minimum number of Individuals	MNI
Number of Identified Specimens	NISP

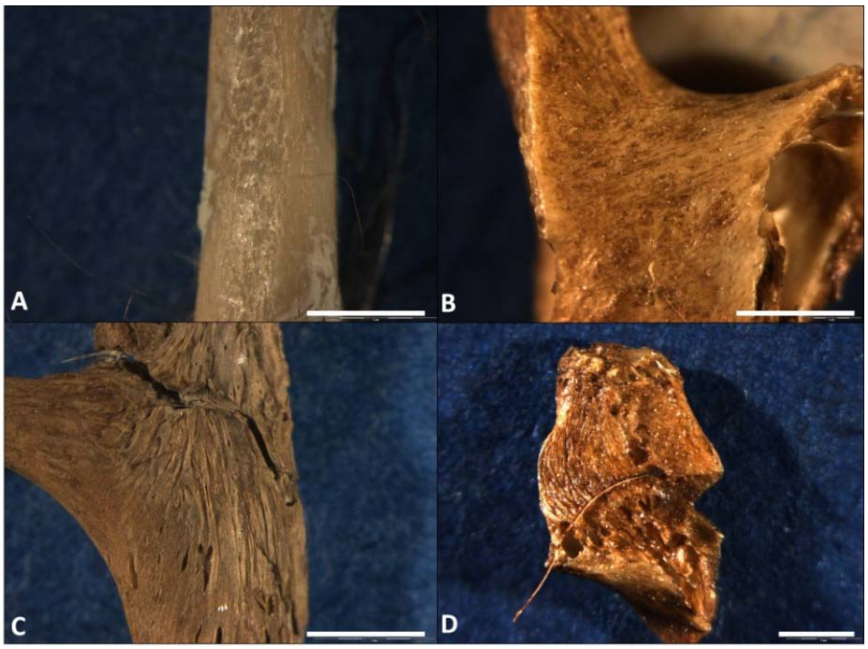


Plate 2.1. Categories of surface etching in digested bones A) metapodial showing light etching; B) moderate etching on a pelvic fragment; C) rib with heavy etching; D) zygopophysis of a lumbar vertebra with severe etching. *Scale bar* is 2 mm

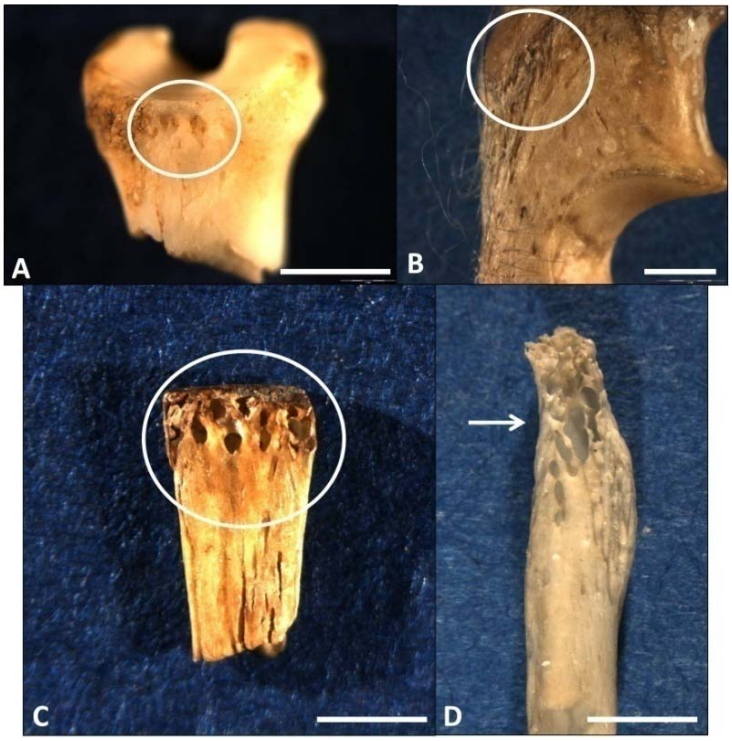


Plate 2.2. Categories of corrosive pitting in digested bones A) light pitting on a proximal phalange; B) ulna with moderate pitting; C) rib with heavy pitting and D); rib with severe pitting. *Scale bar* is 2 mm

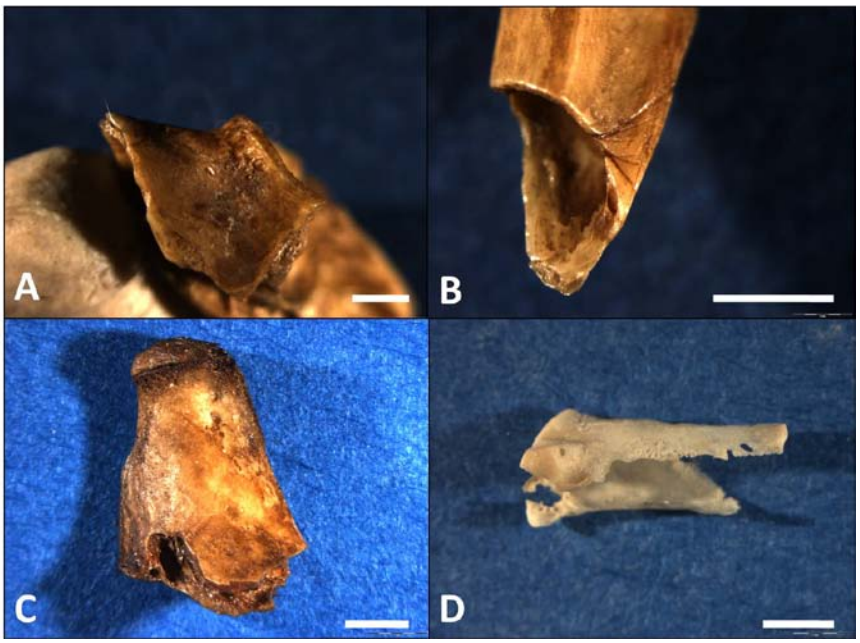


Plate 2.3. Categories of rounding of edges in digested bones A) pelvic fragment with light rounding; B) moderate rounding on a rib; C) zygopophysis of a lumbar vertebra with heavy rounding; D) metapodial showing severe rounding resulting in a thin, feathered edge. *Scale bar* is 2 mm

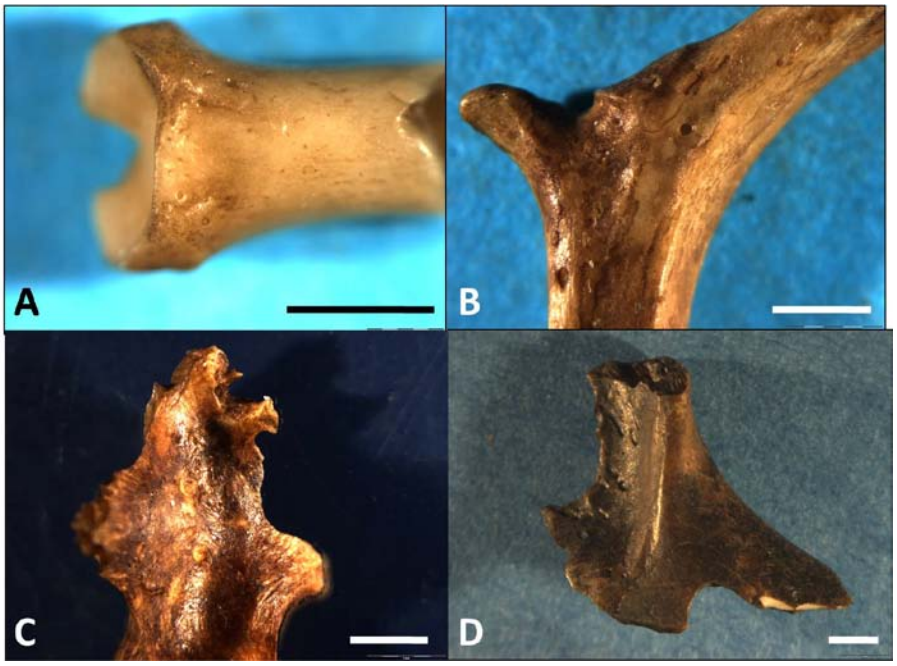


Plate 2.4. Categories of staining in digested bones A) unstained proximal phalange (beige colour); B) rib with light brown (light) staining; C) lumbar vertebra with dark brown (heavy staining) staining; D) pelvic fragment with black (severe) staining. *Scale bar* is 2 mm

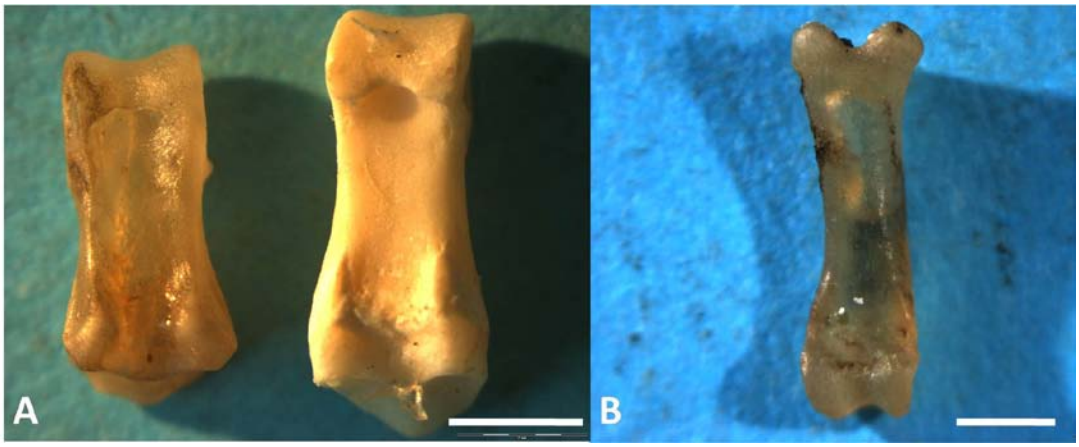


Plate 2.5. Transparency in digested bones A) second phalange from a carnivore scat (left) showing glassy, slightly slimmed surface and light transparency compared to a non-ingested phalange (right); B) proximal phalange with heavy transparency where background shows clearly through the bone. *Scale bar* is 2 mm

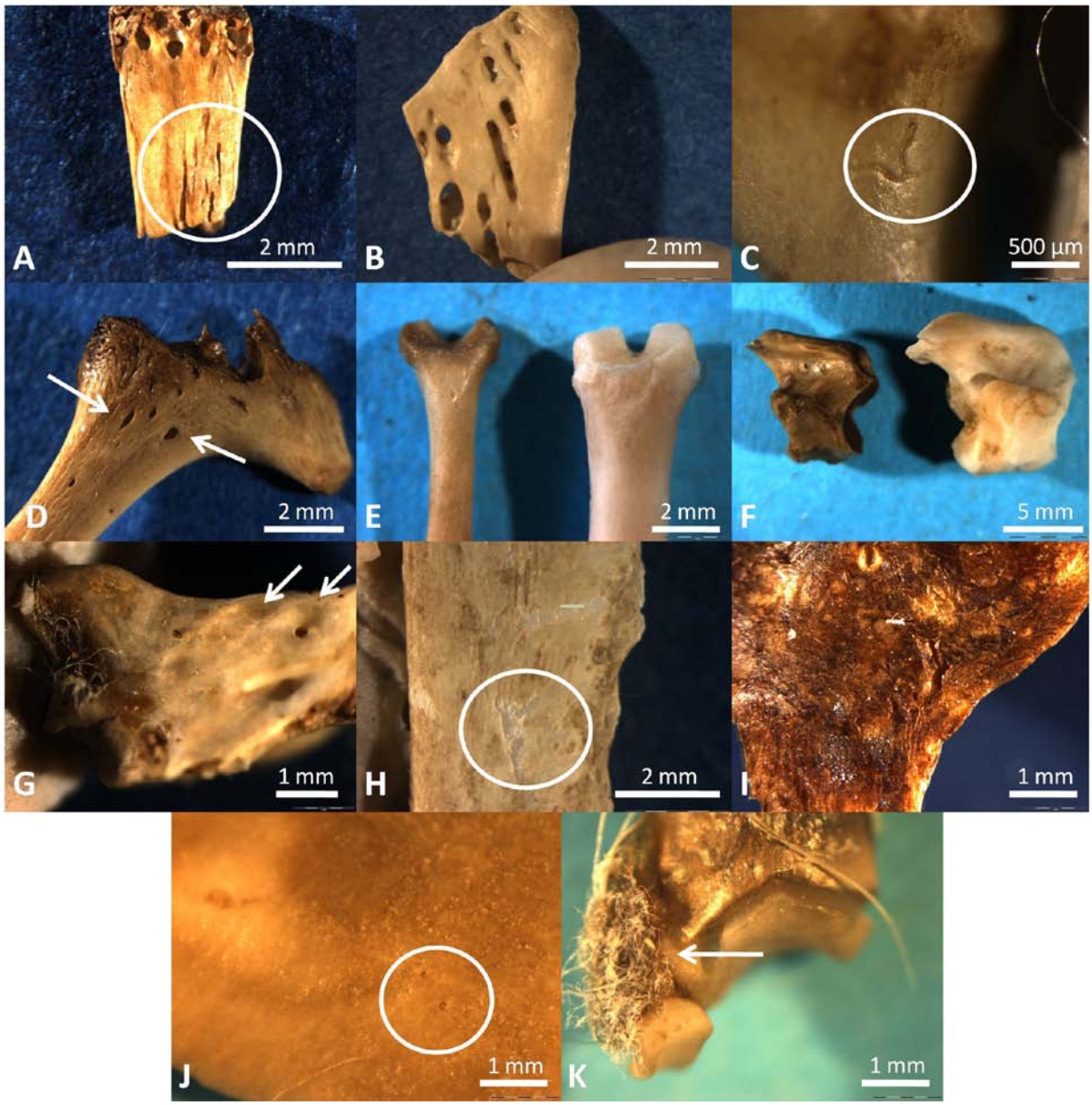


Plate 2.6. Typology of digestive modifications on bone remains A) rib showing foramen excavation (circled) and corrosive pitting; B) atlas with extreme foramen excavation; C) close-up of localised foramen excavation on a proximal phalange; D) scapula with corrosive holes; E) a slimmed proximal phalange shown on left compared to a non-digested phalange on the right; F) a slimed carpal (left) shown against a non-ingested carpal (right); G) corrosive holes and undulations (arrows) on a caudal vertebra; H) lumbar vertebra with bone surface exfoliation or desquamation; I) lumbar vertebra with etching, showing localised exfoliation; J) rib with cupules; K) articulated sesamoids and distal phalange with retained flesh (arrow)

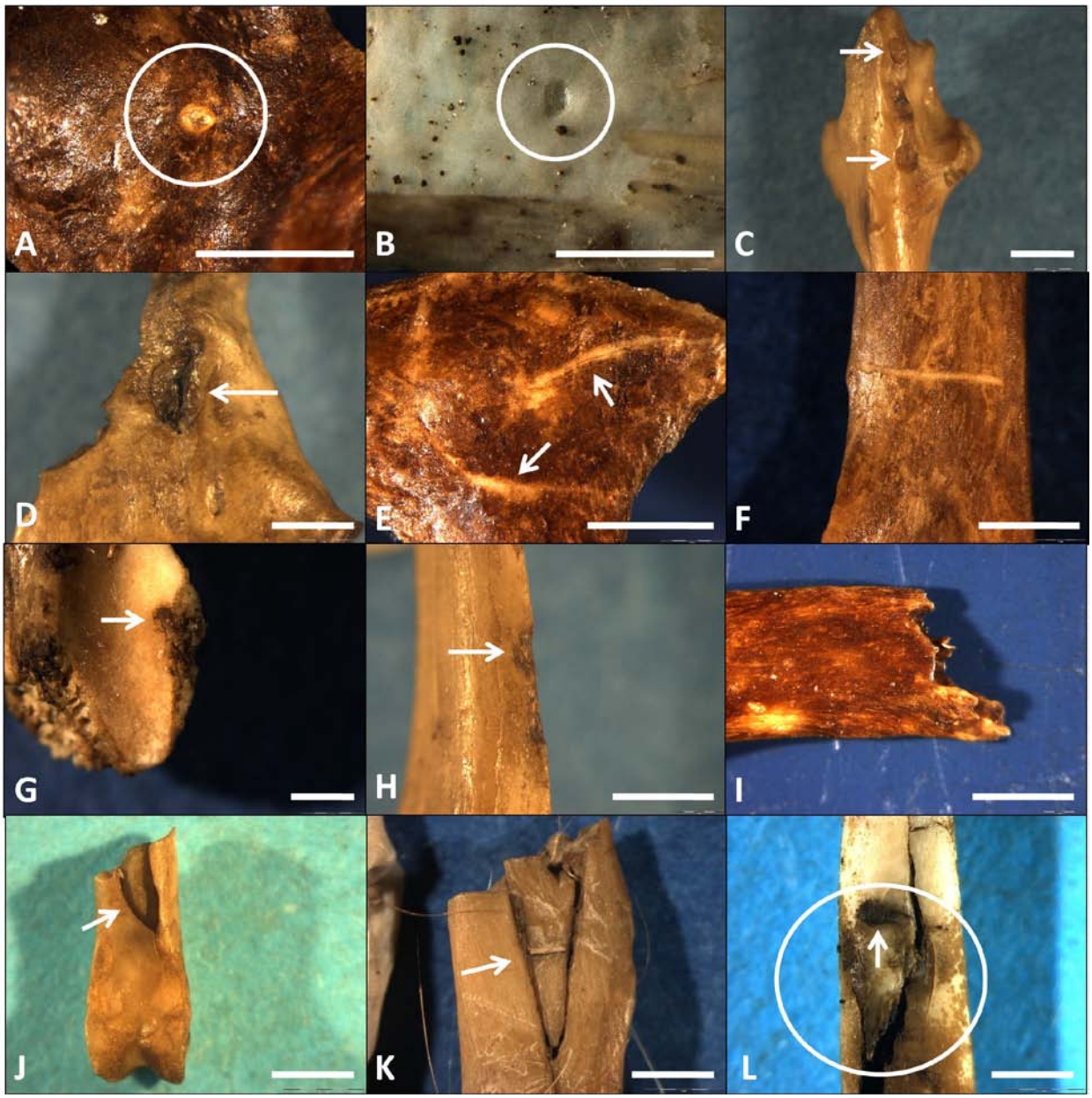


Plate 2.7. Typology of small carnivore tooth mark types on bone remains A) tooth pit on a lumbar vertebra; B) scapula with tooth pit; C) calcaneus with multiple tooth pits; D) tooth puncture on the atlas, note depression of cortical bone inward; E) scour marks on a lumbar vertebra; F) lumbar vertebra with multiple scour marks; G) notching on a femur fragment; H) notching on a lumbar vertebra; I) lumbar vertebra fragment with a crenulated edge; J) proximal phalange with crushing; K) crushing on a lumbar vertebra; L) rib with crush mark showing how flakes of bone are depressed into the bone cavity and with an associated tooth pit (arrow). *Scale bar* is 2 mm

CHAPTER 3

CARACAL FEEDING

Results

Two adult caracals, a male and female, were fed varied-sized freshly thawed rabbit carcasses on five occasions (Table 3.1). During feeding, the individuals were separated and each presented with a rabbit carcass. Apart from covering the carcass remains with straw or grass, no transportation of carcass remains after feeding cessation was observed. This chapter presents the results of the five feedings and Table 3.1 provides a summary of the feedings and carcass remains and scats collected as well as bone skeletal remains retrieved from the scats.

3.1. Refuse Assemblage

Remains from a total of nine carcasses were recovered (Table 3.1). One carcass from feeding 1 consisted of the partially consumed cranium and mandible, while the remaining carcass consisted of several articulated distal appendages (Plate 3.1). Remains from feeding 2 consisted of articulated distal appendages (feet) and a few skeletal elements from a single carcass. A partial cranium, pelvis and foot were recovered from one carcass in feeding 3, as well as various maxillary fragments from the second carcass. A single carcass from feeding 4 consisted of two feet and the other carcass was reduced to a few unidentifiable fragments. The remaining carcasses from feeding 5 consisted of the feet and a selection of skeletal elements. A schematic presentation of relative frequency of skeletal parts of both carcasses from each feeding is depicted in Figure 3.1. Survival in the crania is outlined in Table 3.2 while in Table 3.3 the number of identified specimens (NISP) per element, as well as resulting minimum number of elements (MNE) and a calculation of the percentage survival in the refuse assemblage is depicted. Skeletal element survival rate from the refuse assemblage is further depicted as a line graph in Figure 3.2

3.1.1. Anatomical part representation of the refuse assemblage

Cranium and mandible

As shown in Table 3.2 cranial remains were not recovered from several feedings. Two semi-complete crania were recovered from feedings 1 and 3. These crania were missing the occipitals and basicranium (sphenoid and petrous). The remaining cranial remains were represented by fragments of the maxilla (8.3%). Thus cranial survival in the caracal refuse assemblage was 30.5% (Table 3.3). Mandibular fragments were recovered from feedings 1 and 2 (Figure 3.1), for an overall survival of 10%. In feeding 1 four mandibular fragments were recovered associated with the partial cranium, representing a single mandible. The most common dental remains were the upper postcanine dentition with a survival rate of 26.7%, much higher than the lower postcanine and incisor dentition with survival rates of 8% and 8.3% respectively. Many dental remains were *ex-situ*. No cranial, mandibular or dental remains were recovered from feeding 4 indicating that consumption of the rabbit head by the caracals was complete on this occasion. It is not clear why the rabbit crania were completely consumed on this occasion.

Forelimb and shoulder

Humeral and scapula remains were absent in the refuse assemblage (Table 3.3). The radius and ulna were recovered in feedings 1, 2 and 5 for a survival of 20%, each.

Hindlimb

The tibia was absent in the refuse assemblage (Table 3.3). A single pelvic remain was recovered from feeding 3, while a single femur was recovered in feeding 5. Thus survival in the pelvis and femur was 5%.

Extremities

The extremities were the most abundant elements in the refuse assemblage (Figure 3.2). Phalange elements were recovered in all feedings, while the carpal, tarsal, metacarpal and metatarsal elements were recovered in all feedings except feeding 3 (Table 3.3). Feeding 5 had the highest representation of the extremities (Figure 3.1). Survival in the carpal and metacarpal elements was slightly lower (30%) than in the phalange (39.8%) and the tarsal and metatarsal elemetns (40%).

Vertebral column and ribcage

No vertebral remains or ribs were recovered in the refuse assemblage (Table 3.3).

3.1.2. Completeness and breakage patterns in the refuse assemblage

Elements from the refuse assemblage were compared to a series of breakage classes, devised for each element (Chapter Two) in order to identify patterns, possibly linked to carnivore feeding behaviour. Figure 3.3 shows the relative frequency of complete elements in the assemblage, while Table 3.4 shows frequency (n) and relative frequency of breakage patterns in the refuse assemblage. The number of complete remains was high (95.9%) in the refuse assemblage.

Cranium and mandible

A cranium from feeding 1 and another from feeding 3 were 75% complete, missing only the occipitals, sphenoid and petrous bones (Table 3.2). The remaining four crania were each represented by fragments of the maxilla and were only 8.3% complete. Mandibular remains were mostly (40%) represented by the incisive part and the condylar process, as well as the robust mandibular body with incisive part (Table 3.4). All dental remains were complete.

Forelimb and shoulder

The only forelimb elements in the refuse assemblage were the radius and ulna which were complete (Figure 3.3).

Hindlimb

Only one pelvic remain was recovered in the refuse assemblage. This fragment included the acetabulum with part of the ilium and ischium (Table 3.4). A femoral shaft was recovered.

Extremities

All carpal and tarsal, metapodial and phalange elements were complete and unbroken (Table 3.4).

3.2. Scat Assemblage

The caracals together produced an average of 8.4 scats per feeding. The scats averaged 24.2 mm wide and had a wet mass of 19.3 g. Scats' lengths varied widely between individual scats, hence this criterion was considered uninformative for this study. The scatological assemblage collected after the five feedings consisted of 42 individual scats, of which 13 (31%) did not contain any bone remains (Table 3.1). The average density of bone remains per scat was 18.6, with a maximum of 67 recovered from a single scat. The total number of remains from the scats was high (>100) from feeding one, three and four and very high (>200) from feeding five, however no remains were recovered from the scats of feeding two (Figure 3.4). Thus a total of 534 bone and teeth remains were extracted from 29 scats. The maximum length of recovered bones was only recorded for identifiable bones and is depicted, as a histogram, in Figure 3.5. The length averaged 10.7mm, but a maximum of 22.2mm was recorded (Figure 3.5).

3.2.1. Anatomical part representation of the scat assemblage

As discussed, a total of 534 bone and teeth remains, of which 223 (41.4%) were identifiable to skeletal element, were recovered from the scats (Table 3.1). Table 3.5 portrays the number of identified specimens (NISP) per element, the resulting minimum number of elements (MNE), expected survival after feeding (ES) and a calculation of the percentage survival of remains from the scat assemblage. The minimum number of individuals (MNI), or rabbit carcasses, calculated from bone remains recovered from the scats was four, however for the calculation of survival in Table 3.5 the actual MNI (10) was utilised in order to obtain an accurate estimate. The expected survival (ES) shows the percentage of elements that were missing from the refuse assemblage and should have been recovered in the scats in the absence of loss from digestion. Skeletal element survival rate as determined from the scat assemblage is further depicted as a line graph in Figure 3.6. Figure 3.4 shows a schematic presentation of relative frequency of skeletal parts of both carcasses from each feeding. Figure 3.7 depicts the skeletal element survival rate from the scat assemblage compared to the expected survival after the feedings.

Cranium and mandible

The survival of cranial remains in the refuse assemblage was 30.5%, thus the expected survival for crania in the scat assemblage was 69.5% (Table 3.5). The survival of cranial remains in the scat assemblage was 30%, indicating a loss of 39%. The cranium had the greatest survival rate in the scat assemblage (Figure 3.6). Survival in the mandible was 20%, much less than the expected (90%) from the refuse (Figure 3.7). The lower postcanines had the greatest (15%) survival of the dental remains, followed by the incisors (10%) and the upper postcanines (6.7%).

Forelimb and shoulder

The expected survival for the scapula and humerus was high (100%), as no remains from these elements were recovered in the refuse assemblage (Table 3.5). The scapula had the greatest survival of the forelimb elements of 10%. The remaining forelimb remains, the humerus, radius and ulna had 5% survival. This indicates a loss of 75% for the radius and ulna.

Hindlimb

Expected survival in the hindlimb was very high, 100% for the tibia and 95% each for the pelvis and femur (Table 3.5). The pelvis had the greatest (25%) survival of the hindlimb elements, followed by the femur (20%) and the tibia (10%). Thus, hindlimb elements experienced a loss of between 70% and 90%.

Extremities

The extremities had an expected survival of between 60.2% and 65.8% (Table 3.5). Survival in the extremities was low. The carpal and tarsal elements were absent in the scat assemblage. Survival in the metapodial elements was 1.7%, while the phalange had the lowest survival in the scat assemblage of 1% (Figure 3.6).

Vertebral column and ribcage

No vertebral remains were recovered from the refuse assemblage, thus all vertebra had an expected survival of 100% (Table 3.5). The scat assemblage was dominated (NISP, %NISP) by vertebra and rib elements. This is, however, a factor of fragmentation and the high number of ribs and vertebrae in a typical skeleton as the survival rate of these elements was very low, >7.5%. The atlas and axis had the greatest survival of the vertebral remains of 20% each. Other vertebra had varying degrees of survival; other cervical vertebra (4%), thoracic (2.3%), lumbar

(7.1%), and caudal (1.9%). The rib, despite having an expected survival of 100% had an actual survival of 5.8%.

3.2.2. Completeness and breakage patterns in the scat assemblage

The relative frequency of complete elements in the scat assemblage is displayed in Figure 3.8. The frequency (n) and relative frequency of breakage patterns in the scat assemblage are depicted in Table 3.6. Of the 223 identifiable bones in the scat assemblage only 44 (11.3%) were complete and unbroken. Complete bones were limited to the small, dense elements such as phalanges, metapodials, patella, caudal vertebra and dentition. Figure 3.9 displays the relative frequency of articulated remains in the scat assemblage. Articulated remains occurred in only 13 (6.7%) of the total assemblage and were noted in vertebral, rib and distal phalange remains.

Cranium and mandible

Cranial remains in the refuse assemblage were predominantly fragments of the neurocranium (81.8%) and the zygomatic arch (Table 3.6). Mandibular remains were represented by the mandibular body (42.9%), mandibular body with incisive part (28.6%) and the condylar process (28.6%). Most of the dentition was complete (Figure 3.8) with only one incisor, upper postcanine and lower postcanine each being fragmented.

Forelimb and shoulder

Only two scapula fragments were recovered in the scat assemblage, one was from the glenoid cavity and the other was from the scapula blade (Table 3.6). The single humeral fragment came from the distal epiphysis. The radial fragment included the distal epiphysis with a portion of the shaft. The ulna was represented by the proximal epiphysis with shaft (50%) and a portion of the isolated shaft.

Hindlimb

The pelvis was represented mostly by the ischium (50%), as well as by the isolated acetabulum (16.7%), acetabulum with ilium (16.7%) and by the ilium (16.7%; Table 3.6). Femoral remains were limited to the proximal epiphysis (66.7%) and the proximal epiphysis

with shaft (33.3%), while the tibia was represented equally by the distal epiphysis with shaft (50%) and the isolated shaft (50%). Patella remains were complete (Figure 3.8).

Extremities

Carpal and tarsal elements were absent in the scat assemblage. All phalange specimens and a single metapodial were complete (Figure 3.8). The remaining metapodial elements were represented by the proximal epiphysis with shaft, the distal epiphysis and the distal epiphysis with shaft (Table 3.6). Articulation in the phalange elements was known, either as third phalange articulated to one or more proximal phalange or as third phalange articulated to sesamoids (Plate 3.2).

Vertebral column and ribcage

The most common breakage classes in the vertebra were the zygopophyses and the vertebral bodies (Table 3.6). The atlas was represented entirely by the zygopophyses and the axis entirely by the vertebral body. Cervical vertebra were represented by zygopophyses (42.9%) and transverse processes (42.9%) and also by the vertebral arch (14.3%). Thoracic vertebra were represented equally by the vertebral arch and spinous processes. Lumbar vertebra were most commonly represented by zygopophyses (46.7%), followed by transverse processes (26.7%), vertebral body (16.7%), isolates epiphyses (6.7%) and spinous processes. Caudal vertebra were represented predominantly by vertebral bodies (60%) and by isolated epiphyses (20%). Additionally, complete caudal vertebra were also known (Figure 3.8). The majority of articulated remains in the scat assemblage were vertebra (Figure 3.9). In the vertebra, articulation normally occurred as complete vertebra articulated in anatomical position (Plate 3.2), or as epiphyses detached from their vertebral bodies but still articulated together in anatomical position.

3.2.3. Digestion related modifications in the scat assemblage

Remains from the caracal scats display a variety of digestion related modifications such as surface etching, corrosive pitting and rounding of edges (Figures 3.10, 3.11 and 3.12; Tables 3.7, 3.8 and 3.9). Also identified was staining (Figure 3.13, Table 3.10). Other modifications include foramen excavation, corrosive holes, slimming, undulations, desquamation and remaining tissue (Figure 3.14, Table 3.11). Digestion in the dentition is outlined in Figure 3.15 and Table 3.12.

Etching

Etching (Plate 3.3E, G and H) was noted on 95.5% of remains in the scat assemblage (Figure 3.10). Most etching was of a light (43.8%) to moderate (35.4) intensity, and severe etching was rare (4.7%). Etching was observed on all elements except a single cranial remain (Table 3.7). Light etching was recorded on every element except the scapula. Heavy and severe etching were absent from the appendicular skeleton, and postcranial axial remains were prone to greater levels of etching.

Corrosive pitting

The majority (56.7%) of remains did not have corrosive pitting modification (Figure 3.11). Pitting was mostly moderate (13.9%) to heavy (12.9%) in intensity. The atlas, axis metapodials and humerus lacked pitting (Table 3.8). Moderate pitting was observed in the cranium, mandible, cervical, thoracic, lumbar vertebra, ribs, radius, ulna, pelvis and femur. Heavy pitting was observed in the cranium, mandible, cervical, lumbar, caudal vertebrae, rib, scapula, tibia and patella (Plate 3.3I and J). Severe pitting was limited to the axial skeleton and the femur.

Rounding of edges

Rounding of edges was observed in 86.6% of remains. The majority (53.6%) of rounding was of a heavy intensity (Figure 3.12), and severe rounding was very rare (2.1%). Severe rounding (Plate 3.3D) was observed on the rib, metapodial and phalange (Table 3.9). The autopodium did not display any other rounding. Heavy rounding was recorded on all elements except the autopodium and patella.

Staining

A 65.5% of remains in the scat assemblage were unstained (Figure 3.13). Staining was predominantly of a light (29.9%) intensity, with little heavy (4.6%) staining. Severe (black) staining was absent in the scat assemblage. The axis, scapula, humerus, radius, tibia, metapodial and phalange were unstained (Table 3.10). Dark staining was limited to the postcranial axial skeleton including the cervical, thoracic, lumbar and caudal vertebra and rib (Plate 3.3E and F).

Transparency

Transparency was observed on only two (1%) remains, a phalange and a lumbar vertebra.

Excavated foramina

Excavated foramina (Plate 3.3B and L) were observed on 45.4% of remains (Figure 3.14). This modification was absent from the atlas, humerus, radius, tibia and patella (Table 3.11). Excavated foramina were abundant on the ulna, 100% of which had excavated foramina and on the mandible 71.4% of which were modified.

Corrosive holes

Corrosive holes (Plate 3.3L) were a highly common digestive modification that occurred on 70.6% of remains (Figure 3.14). Corrosive holes were found on all elements except the patella (Table 3.11). They were highly abundant on the atlas, thoracic vertebra and forelimb (scapula, humerus, radius, and ulna) 100% of which had corrosive holes.

Slimming

A 24.7% of remains were slimmed (Figure 3.14). Slimming (Plate 3.3B and G) was absent from the atlas, cervical, thoracic, caudal vertebrae, humerus and patella (Table 3.11). Slimming was particularly abundant on the appendicular skeleton, occurring on 100% of radii, 75% of metapodials and 50% of scapulae and ulnae each.

Undulations

Undulations were observed on a single (0.5%) remain in the scat assemblage, a rib (Figure 3.14).

Cupules

Cupules were not observed in the caracal scat assemblage.

Desquamation

A 16.5% of remain in the scat assemblage had desquamation modification (Figure 3.14). Desquamation (Plate 3.3K) was limited to the axial skeleton and was observed in the cranium, axis, cervical, lumbar vertebra and rib (Table 3.11). Desquamation was most common on the axis (33.3%) and the rib elements (29.4%).

Tissue retention

Typically the retention of tissue would indicate that digestion was not occurring, but all bones with remaining tissue bore other evidence of digestive modifications. Perhaps indicating that some tissue is resistant to digestion or that some elements, or parts thereof, were protected, by skin and fur, from being digested. Tissue retention was observed in 4.1% of remains in the scats (Figure 3.14), occurring on the axis, lumbar vertebra, ulna and phalange (Table 3.11), it was most common on the axis (66.7%) and the ulna (50%).

Digestion in the dentition

Digestion was observed in all but 2 (6.9%) dental remains in the scat assemblage. Most digestion in the dentition was of a heavy (48.3%) intensity, followed by light (27.6%) and moderate (24.1%) digestion (Figure 3.15). Incisor elements show predominantly light (83.3%) digestion and heavy digestion was absent in the incisor (Table 3.12). The postcanine dentition were predominantly heavily digested (Plate 3.4).

3.2.4. Tooth marks in the scat assemblage

As depicted in Table 3.13 a total of 64 tooth marks were found on 45 (23.2%) of the scat assemblage. Tooth marks were absent from the atlas, caudal vertebra, scapula, humerus, radius, femur and phalange. Figure 3.16 shows the relative frequency of tooth mark types in the assemblage. The most common tooth marks in the assemblage were pits and crenulated edges (21.9%), followed by scours and crush marks (20.3%), notches were rare (3.1%). The average width of tooth marks and the standard deviation are shown in Table 3.14. Pits and scours had the smallest average width of 0.3 mm. Punctures had a larger average width of 0.8 mm. Of

note, tooth marks on dental remains had a smaller average width (0.2 mm) than tooth marks on the bone remains. Plate 3.5 shows a selection of tooth marked bones from the caracal scat assemblage.

Tooth pits

Fourteen tooth pits (Plate 3.5A, B and C) were observed on six elements (Table 3.13). Tooth pits were observed on lumbar vertebra, rib elements and the tibia. They were most common on the tibia where they occurred on 50% of specimens.

Punctures

A total of eight punctures (Plate 3.5C, D, E and F) were noted on eight elements (Table 3.13). Punctures were noted on the lumbar vertebra and rib, and were more common on the latter element (11.8%).

Notches

Notches (Plate 3.5J) were the least common tooth marks in the caracal scat assemblage (Figure 3.16). A single notch was observed on a lumbar vertebra (3.3%) and another (25%) on a metapodial (Table 3.13).

Scours

Thirteen scour marks were observed on 12 remains (Table 3.13). Scours were recorded on the cranium, mandible, lumbar vertebra, rib, pelvis and patella (Plate 3.5G, H and I). Scours were most abundant on the patella (50%).

Crush marks

A total of 13 crush marks were recorded in the caracal scat assemblage (Table 3.13). Crush marks were limited to the axial skeleton and were recorded the cranium, cervical, thoracic, lumbar vertebrae and rib (Plate 3.5L). They were most common on the thoracic (25%) and lumbar vertebra (23.3%).

Crenulated edges

Crenulated edges were highly common in the scat assemblage, with 14 recorded modifications (Table 3.13). Crenulated edges were observed on the axial skeleton including the cranium, axis, thoracic, lumbar vertebra and ribs, as well as the ulna. Crenulated edges (Plate

3.5K) were most common on the ulna (50%) and axis (33.3%).

3.3. Caracal Discussion and Conclusions

3.3.1. Skeletal part representation of the refuse assemblage

Distinct patterns appear from feeding of rabbit carcasses to caracals on the five occasions. Most notable are the absence, in the refuse assemblage, of the scapula, humerus, tibia, rib cage and vertebral column, and a near absence of femur and pelvis in all the five feedings. Their absence suggests preferential consumption of parts of the skeleton with the most flesh (humerus, hindlimb and vertebral column) and a need to gain access to internal organs (rib cage). The high survival of crania and the autopodium (carpal, tarsal, metapodial and phalange elements) in the caracal refuse assemblage suggests that these skeletal parts are not preferentially consumed due to their low possession of flesh. Comparison of the survival of skeletal elements in the refuse assemblage to the structural density assays of those parts in domestic rabbit (Pavao and Stahl, 1999) indicate that there was no correlation between element density and survival in the refuse assemblage (Figure 3.17).

The frequency of complete elements in the refuse assemblage is much greater than in the scat assemblage (Table 3.15). Almost all remains in the refuse assemblage including all recovered long bones, dentition and autopodial remains were complete and unbroken. The incomplete elements were represented by high density portions. For instance, the mandible was represented by the mandibular body and incisive part and the pelvis was represented by the areas around and including the acetabulum. Cranial remains were either fragmentary or near complete. Complete crania were missing their posterior parts, presumably destroyed by the carnivore in order to provide access to the brain. The carcasses from which these skulls derived had originally been presented to the female caracal and the remains were recovered where the female had rested. However, the possibility that the male also fed on these carcasses before they were collected cannot be ruled out. Other cranial remains consisted of robust maxilla fragments.

3.3.2. Comparison with other carnivore refuse assemblages

The caracal refuse assemblage most closely resembled refuse from captive foxes (Lloveras *et al*. 2012) and the coyote (Schmitt and Juell, 1994). The caracal, fox, coyote and Geoffroy's cat (Álvarez *et al.* 2012) were characterised by high representation of the autopodium and an absence or near absence of rib and vertebra (Table 3.16). In addition the caracal, fox and coyote had an absence or near absence of the mandible, dentition, pelvis, femur, scapula, humerus, vertebra and rib. The only elements to survive in the coyote refuse were, in fact, the distal feet. The poor survival of these elements indicates a preferential consumption of high yield parts of the skeleton and the high survival of the autopodium indicates disregard of low yield parts such as the feet. The percentage of complete remains in small carnivore refuse assemblages was high; especially in the autopodium. There was a much greater frequency of complete long bones in the caracal than the fox or Geoffroy's cat. Mesomammal cranial remains like those observed in the caracal refuse, with the posterior parts removed, were also observed in refuse from caracal in the Eastern Cape (Grobler, 1981) and from medium sized felids like the leopard and cheetah (Brain, 1981).

The fox assemblage differed from that of the caracal in that entire crania were consumed and the tibia was one of the most frequent (72.7%) elements recovered in the fox refuse. The survival of the tibia in the fox refuse sample is unlikely to be a factor of density as other robust elements such as the femur did not survive. The modifications on the refuse assemblage from Geoffroy's cat were different to the modifications observed in the caracal assemblage. Geoffroy's cat differs from the caracal in that the elements with the highest survival were the pelvis, femur and tibia, indicating a possible preferential discard of hindlimb elements. Complete crania were noted in Geoffroy's cat, however no damage to the posterior parts was recorded.

Coyote kill/feeding loci were characterised during summer months by the presence of hanks of *Lepus* fur, small clumps of viscera and articulated distal appendages, all in association with fresh scats (Schmitt and Juell, 1994). The articulated distal appendages consisted of the tibiae and ulnae/radii, which were snapped at mid shaft and their associated muscle mass reduced to tendons but with the distal elements still complete within the skin. This is strikingly

similar to the abandoned feet recovered in the caracal assemblage (Plate 3.6). Kill sites from the winter months were noted to contain only hair and fresh droppings. Schmitt and Juell argued that when larger sized prey are predictably abundant, low utility elements such as the articulated feet will not be consumed by coyotes. A similar pattern was identified in captive coyotes of the Utah State University (Schmitt and Juell, 1994). When feeding schedules were consistent, coyotes would commonly abandon low meat-yielding crania and distal appendages. The similarities in refuse assemblages of caracals (this study), captive foxes (Lloveras *et al*. 2012) and captive and wild coyotes (Schmitt and Juell 1994) suggests a natural behaviour or feeding pattern in small carnivores when resources are abundant. Resulting skeletal part representations, if found in an archaeological or palaeontological situation for these or similar small carnivores can then be used to interpret the possible resource availability or environmental conditions at the time of deposition.

3.3.3. Skeletal part representation of the scat assemblage

Survival of remains in the caracal scat assemblage was low; except for the cranium, all elements recorded below 25% survival rate, though the expected survival was above 60% (Table 3.5). Notable was the absence of carpal and tarsal elements, and very low representation of metapodial, phalange, and caudal vertebra (Table 3.15). Elements with high survival were the cranium and mandible, atlas and axis, pelvis and femur. Compared to the structural density assays of skeletal elements in domestic rabbit (Pavao and Stahl, 1999), it is evident that there was no correlation between element density and survival in the scat assemblage (Figure 3.18). From Figure 3.19, it is apparent that elements with high survival in the refuse assemblage (autopodia) had poor survival in the scat assemblage, and *vice versa*, elements with low survival in the refuse had high survival in the scat assemblage. The skeletal part representation in the refuse and scat assemblages complement each other with little overlap. This may be a useful consideration when trying to identify the origin of palaeontological assemblages.

The degree of fragmentation in the caracal scat assemblage was very high (Table 3.15) and elements exhibited an average fragment size of 10.7 mm. Completeness of remains in the scat assemblage was rare and most complete elements were limited to small compact bones

like the patella, dentition, phalanges and caudal vertebra. All long bones were broken and most elements were represented by the most robust parts of the bones. Cranial remains were represented by fragments of the neurocranium and zygomatic arch, however the robust maxilla was absent. The survival of the more fragile neurocranium and zygomatic fragments may reflect efforts by the carnivore to dislocate the mandible during feeding, resulting in intense fragmentation. Dental remains, all of which were isolated, were mostly complete.

Digestive corrosion in the caracal assemblage was extensive. However modification was overall of a light intensity with only localised examples of heavy or severe digestive modifications. The most common modification was etching, which was light and heavy rounding of edges. Pitting and staining were uncommon and staining was never darker than a heavy intensity (dark brown colouration). Other commonly recorded digestive modifications were corrosive holes, foramen excavation and slimming. Autopodial remains were least affected by digestive modification. Rounding of edges, in particular was rare in autopodial remains, but where found was severe. This could be the result of skin and tissue encasing the autopodial remains and protecting them from modification. The severity of rounding on some autopodial elements suggests sensitivity to rounding in these elements when exposed. The cranium and mandible and elements of the forelimb show light digestive modifications. The hindlimb and ribs were more intensively modified while the vertebra show the greatest sensitivity to digestion. All dental remains show digestive modifications, with incisor teeth predominantly lightly digested and the postcanine dentition (upper and lower) predominantly heavily digested.

Tooth marks were noted 28.4% of remains in the caracal scat assemblage. In general tooth marks were most common on the axial skeleton, especially the lumbar vertebra and rib elements but were rare in the appendicular skeleton (long bones) and autopodium. A number of elements lacked tooth marks including the atlas, caudal vertebra, scapula, humerus, radius, femur and phalange. The concentration of tooth marks on the axial skeleton may stem from extensive chewing on these areas by the carnivore in order to extract muscle mass from the back. Tooth marks in the long bones and most of the ribs were situated only on the shaft (Table 3.17), most likely due to flesh removal. Most tooth marks on the vertebra were situated on the

zygopophyses followed by the vertebral body. These were some of the most common vertebral parts recovered and the large number of tooth marks on these parts may be the result of the carnivore trying to disarticulate the spine. In the mandible tooth marks were situated on the condylar process, perhaps coming from efforts by the carnivore to disarticulate the jaw. The most common tooth mark types were pits, crenulated edges, scours and crush marks.

The average width of tooth pits in the caracal was extremely small (0.3 mm), much smaller than tooth marks found in any other carnivores. Delaney-Rivera *et al*. (2009) in their investigation with size-class 2 bovids noted that a range of small carnivores and medium-sized felids produce tooth pits less than 2 mm in length. The caracal was observed to leave tooth pits from 2.9 to 1.7 mm in length (Delaney-Rivera *et al.* 2009), much greater than the tooth pit sizes found in this caracal sample. The smallest tooth pits found by Delaney-Rivera *(ibid.)* were 0.7 mm from the red fox (*Vulpes vulpes*). Thus tooth pits in this caracal sample were much smaller than previous studies of the caracal or any other carnivore investigated. The small tooth pits size may be a result of the much smaller size of prey fed to our caracals. The effort required to extract flesh is much less for a caracal or small carnivore when feeding on small sized prey like leporids than when feeding on larger prey like bovids. Thus for a given carnivore, smaller prey would be expected to display smaller, less intense tooth marks than would be seen in larger prey. Further studies that investigate the size and characteristics of tooth marks of carnivores in small prey would be beneficial.

3.3.4. Comparison to other carnivore scat assemblages

Caracal scatological remains most closely resembled those from fox (Lloveras *et al.* 2012) scats than any other small carnivore. The caracal, fox and lynx (Lloveras *et al.* 2008a) scatological assemblages were characterised by high survival of the cranium, mandible, femur and pelvis and an absence or near absence of carpal and tarsal elements (Table 3.18). The fox and lynx additionally display high survival in all appendicular (excluding the autopodium) elements. In the caracal and fox the autopodium and dental remains had the lowest survival. Survival in the caracal scat assemblage was poor compared to other small carnivores. The percentage of complete remains was low in the caracal, fox and Geoffroy's cat (Álvarez *et al*. 2012), very low in the coyote (Schmitt and Juell, 1994) but high in the lynx. Complete long

bones were absent in the caracal, fox and coyote. Most complete remains in the lynx, fox and caracal were elements of the autopodium. Fragment size and breakage patterns were similar in the lynx, fox and caracal with most elements represented by their most robust parts. Cranial remains in the lynx and fox were mostly represented by the neurocranium and zygomatic arch, however unlike the caracal other cranial remains were also represented.

Digestion in the caracal, fox and lynx was extensive, observed on almost 100% of remains. The caracal was distinct from other small carnivores in that bone remains were lightly digested. However dental remains in all carnivores had heavy digestion. The coyote is the only other small carnivore in which staining was identified in the assemblage. Staining in the coyote remains appears to resemble the light brown and dark brown staining observed in the caracal, but the relative intensity of staining was not quantified in the coyote assemblage. Severe rounding, resulting in thin, feathered edges was observed in both the caracal and the coyote (Plate 3.7). Articulated remains were observed in low frequencies in the caracal, lynx and puma (Plate 3.8). There were a greater number of tooth marks in the caracal than other small carnivores, and placement of tooth marks on remains in small carnivores was irregular. The most common tooth marks in the caracal and fox assemblages were pits, crenulated edges and scours.

The fox differed from the caracal in the greater survival of remains and digestive modifications, and the low frequency of tooth marks. The fox lacked articulated remains. Only preliminary results that do not address digestion, tooth marks or breakage were available from scats of Geoffroy's cat (Álvarez *et al*. 2012). These preliminary results support the earlier conclusion (refuse assemblage) that the taphonomic pattern of Geoffroy's cat is very different to the caracal. The elements that were best represented in Geoffroy's cat were the phalange, while the mandible, pelvis and tibia were minimal (Table 3.18). Thus, bone modification in Geoffroy's cat is different to the caracal, but until further data is published very little interpretation can be made of this information.

The lynx had the greatest survival of remains in the scat assemblage with high representation in the dentition and a near absence of vertebra and rib elements. Digestion in bone and dental remains in the lynx was heavy, but less intense than in the fox. The lynx had

the smallest average length of remains in the small carnivores but a greater degree of completeness. Tooth marks in the lynx remains were extremely rare, with only four (0.26%) of remains displaying puncture marks. Lloveras *(ibid.)* attributes the near absence of tooth marks in the lynx to a feeding behaviour that differs from carnivores that produce higher numbers of tooth marked bones or to digestive damage in the lynx gut masking evidence of tooth marks.

No estimates of the survival of remains in the coyote scatological assemblage were available, but it was observed that there were high numbers of dentition and that hindlimb elements were scarce. Breakage in the coyote differed from other small carnivores as survival of less robust parts of the skeleton was common. Cranial remains in the coyote were highly fragmented and many parts were represented, such as the neurocrania and premaxillas. Schmitt and Juell (1994) describe extensive digestive corrosion on the coyote remains including pitting, polishing and rounding of edges. Many remains in the coyote were heavily digested. The researchers do not record the presence or absence of tooth marks in the coyote scat assemblage.

Survival of mesomammal remains in puma (Montalvo *et al.* 2007) scats was low, as observed in the caracal, however unlike the caracal the elements with the greatest representation were the metapodial, vertebra, tibia, humerus and ulna. Mandibular and dental remains had poor survival. The researchers noted that breakage in mesomammal prey in the puma scats was less than in the large prey but greater than in the microfauna remains. This they attributed to the carnivore consuming small prey the size of rodents whole. This is an important point to note as it has implications for archaeological or palaeontological contexts. A very high level of breakage in a microfaunal or mesofaunal assemblage does not necessarily denote a large sized predator, but may in fact point to a smaller predator as the more likely accumulating agent. Corrosion in armadillo scutes from the puma scats varied from a weak polishing to intense deterioration that exposed the inner spongy bone, which does not resemble digestion damage seen in the caracal. Corrosion in the dentition was light and often limited to degraded parts of dentine.

Modification patterns of small felids such as feral cat (*Felis catus*) and margays (*Leopardus wiedii*) on microfauna was more intense than the modification patterns observed

from similar sized felids on mesomammals (Andrews, 1990; Andrews and Evans, 1983). Small felids were found to be extreme modifiers of microfaunal bone remains as scat assemblages consisted of small and unidentifiable fragments with severe corrosion. A single caracal scat from South Africa, concurred (Matthews, 2002). Thus small felids inflict a much greater degree of destruction on microfauna than observed on larger mesomammal prey.

To conclude the caracal presents a distinct pattern of preferential feeding on high yield parts such as the pelvic and shoulder girdles, stylopodium and ribcage and the discarding of low yield parts, for instance the distal appendages. This feeding behaviour, shown in captivity, reflects consumption behaviour by wild small carnivores in periods of high food availability. Caracal refuse most closely resembled remains from fox and coyote refuse. The caracal scat assemblage was overall most similar to the fox's. The caracal differs from other small mammals in a number of characteristics, but the most distinct is the generally light levels of digestion, especially in bone remains and the large number of tooth marks. Small carnivores show many similarities when feeding on mesomammal prey, however small carnivore modifications of smaller prey animals were more intense, indicating that mesomammal remains were more resistant to carnivore modifications than microfauna.

Table 3.1. Outline of feedings, carcass refuse and scats collected in the caracal

Feeding	Quantity fed	Size	Carcass remains collected (n)	Scats collected (n)	Scats without bones (n)	Identifiable remains (n)	Unidentifiable remains (n)	Remains in scats (n)
1	2	L	2	3	-	44	56	100
2	2	M	1	5	5	-	-	-
3	2	M	2	8	1	59	48	107
4	2	M	2	13	5	31	75	106
5	2	L	2	13	2	89	132	221
Totals	**10**		**9**	**42**	**13**	**223**	**311**	**534**

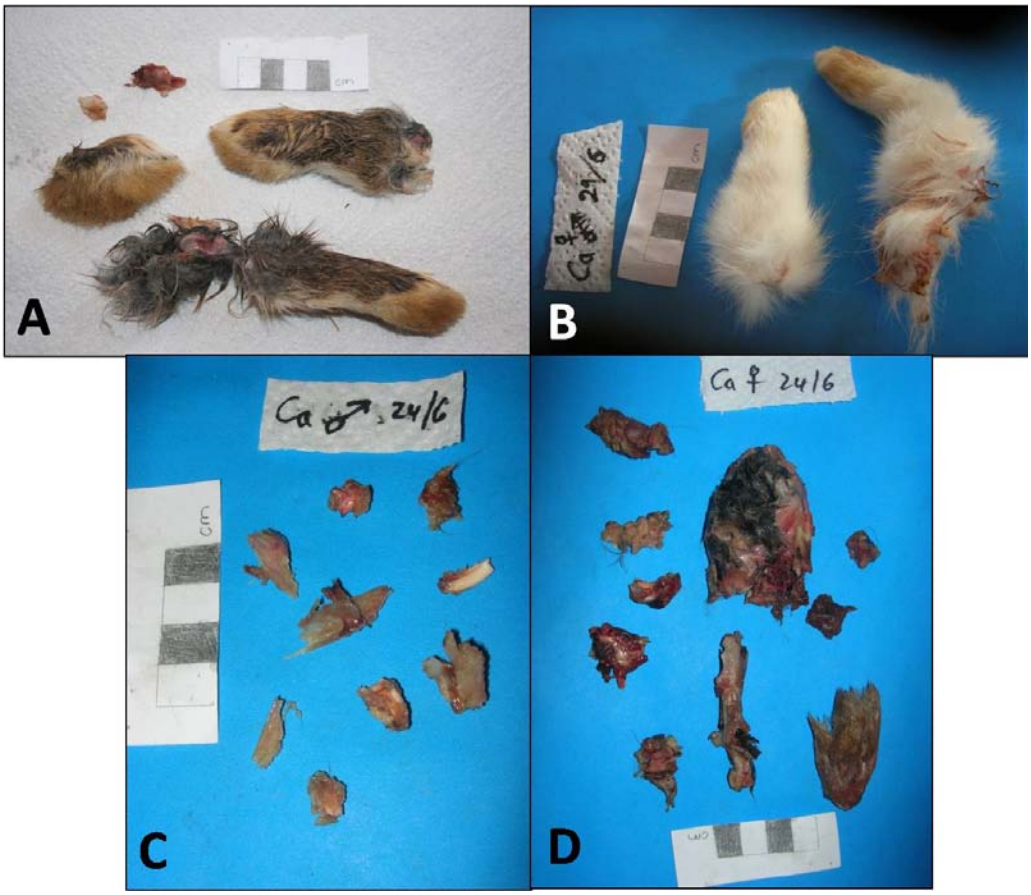
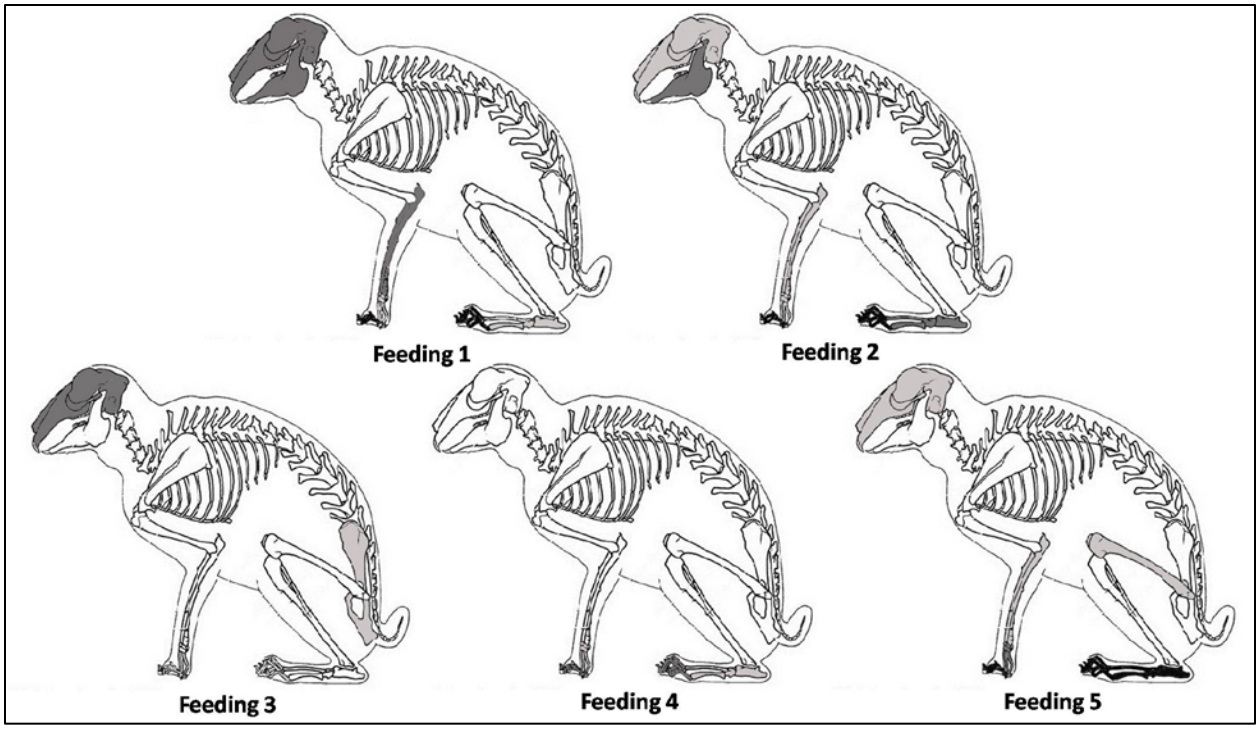


Plate 3.1. Some examples of carcass refuse collected from caracal feedings A) and B) articulated distal appendages (feet) from feedings 1 and 4, respectively; C) maxillary fragments from feeding 3; D) partial cranium, distal foot, pelvis, and unidentifiable fragments from feeding 3



Survival (%)	
	Absent
	1 - 33% Poor representation
	34 - 66% Moderate representation
	67 - 100% Good representation

Figure 3.1. A schematic representation of the relative frequency of parts in each caracal feeding event from the carcass refuse

Table 3.2. Cranial survival from the caracal refuse

	Feeding 1		Feeding 2		Feeding 3		Feeding 4		Feeding 5	
Skull bones	Cranium 1	Cranium 2	Cranium 1	Cranium 2	Cranium 1	Cranium 2	Cranium 1	Cranium 2	Cranium 1	Cranium 2
Maxilla	X	-	X	-	X	X	-	-	X	X
Premaxilla	X	-	-	-	X	-	-	-	-	-
Nasals	X	-	-	-	X	-	-	-	-	-
Frontals	X	-	-	-	X	-	-	-	-	-
Lacrimal	X	-	-	-	X	-	-	-	-	-
Zygomatic	X	-	-	-	X	-	-	-	-	-
Temporal	X	-	-	-	X	-	-	-	-	-
Parietal	X	-	-	-	X	-	-	-	-	-
Occipital	-	-	-	-	-	-	-	-	-	-
Sphenoid	-	-	-	-	-	-	-	-	-	-
Palantine	X	-	-	-	X	-	-	-	-	-
Petrous	-	-	-	-	-	-	-	-	-	-
Survival (%)	**75**	**0**	**8.3**	**0**	**75**	**8.3**	**0**	**0**	**8.3**	**8.3**

Table 3.3. Anatomical composition of the caracal refuse assemblage

	Feeding 1 NISP	Feeding 2 NISP	Feeding 3 NISP	Feeding 4 NISP	Feeding 5 NISP	Total MNE	Survival (%)
Cranium	1	1	8	-	18	6	30.5
Mandible	4	1	-	-	-	2	10
Upper Postcanine	12	6	12	-	2	32	26.7
Lower Postcanine	-	5	-	-	3	8	8
Incisor	2	1	2	-	-	5	8.3
Vertebra indet.	-	-	-	-	-	-	-
Cervical	-	-	-	-	-	-	-
Atlas	-	-	-	-	-	-	-
Axis	-	-	-	-	-	-	-
Thoracic	-	-	-	-	-	-	-
Lumbar	-	-	-	-	-	-	-
Caudal	-	-	-	-	-	-	-
Rib	-	-	-	-	-	-	-
Scapula	-	-	-	-	-	-	-
Humerus	-	-	-	-	-	-	-
Radius	2	1	-	-	1	4	20
Ulna	2	1	-	-	1	4	20
Pelvis	-	-	1	-	-	1	5
Femur	-	-	-	-	1	1	5
Tibia	-	-	-	-	-	-	-
Carpal	7	7	-	7	21	42	30
Tarsal	5	10	-	5	20	40	40
Metacarpal	5	5	-	5	15	30	30
Metatarsal	4	8	-	4	16	32	40
Phalange	37	37	13	25	87	199	39.8
Number carcasses	**2**	**1**	**2**	**2**	**2**	**9**	

For abbreviations see Table 2.2, page 18

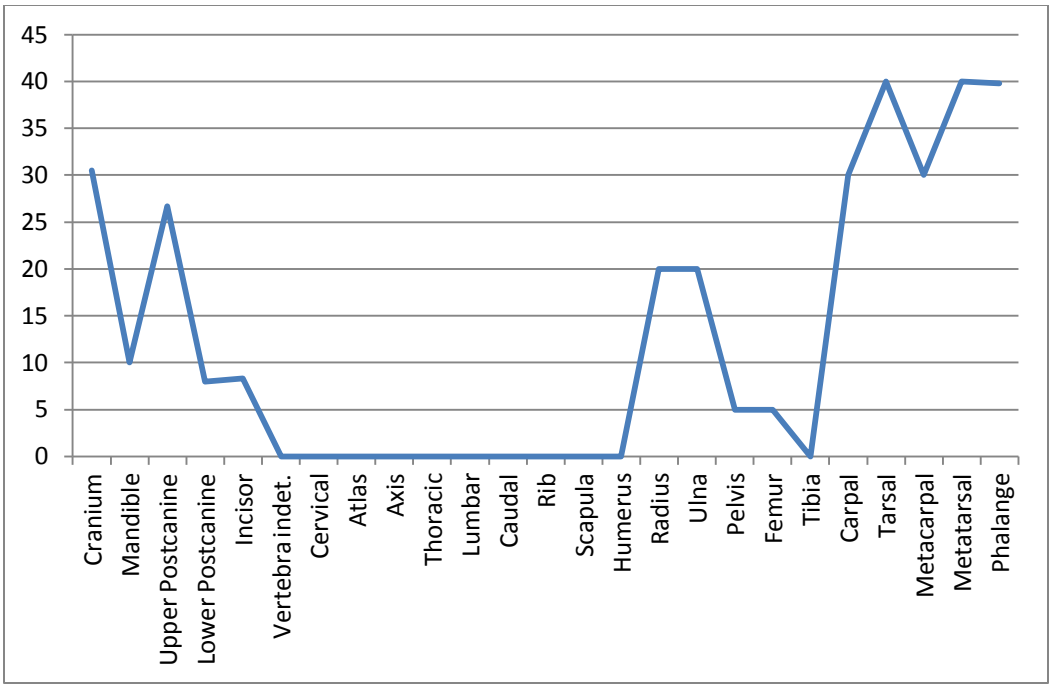


Figure 3.2. Survival (%) of remains in the caracal refuse assemblage

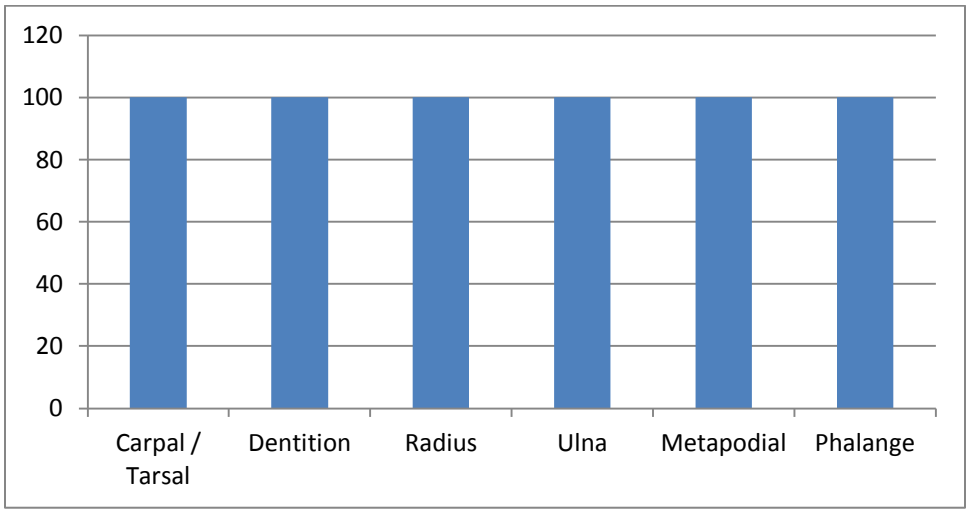
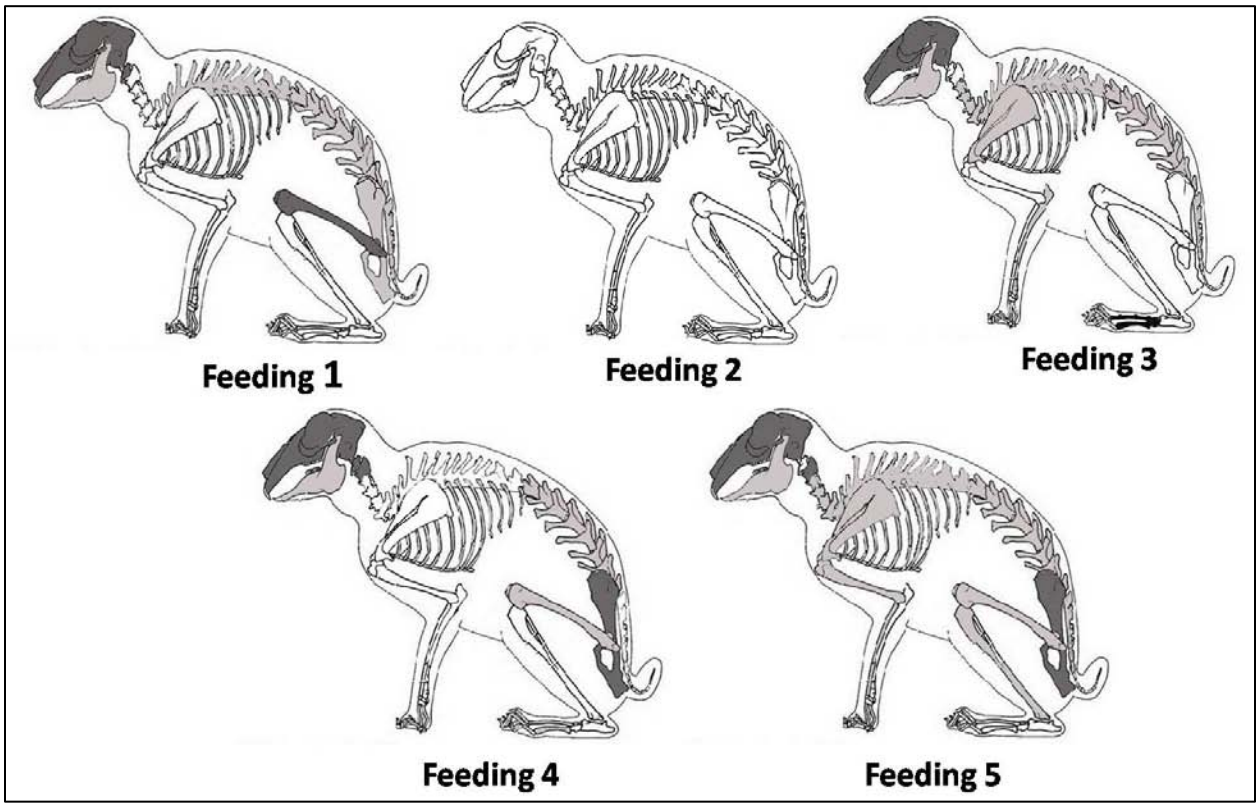


Figure 3.3. Relative frequency (%) of completeness in elements from the caracal refuse assemblage

Table 3.4. Distribution of elements in the caracal refuse according to breakage categories

	IP		MBI		CP	
Mandible	**N**	**%**	**N**	**%**	**N**	**%**
	2	40	1	20	2	40
	C		**S**			
Long bones, metapodial and phalange	**N**	**%**	**N**	**%**		
Radius	4	100	-	-		
Ulna	4	100	-	-		
Femur	-	-	1	100		
Metapodial	62	100	-	-		
Phalange	199	100	-	-		
	AISIL					
Pelvis	**N**	**%**				
	1	100				
	C					
Carpal / Tarsal	**N**	**%**				
	82	100				
	C					
Dentition	**N**	**%**				
Incisor	5	100				
Upper Postcanine	32	100				
Lower Postcanine	8	100				

For abbreviations and explanations see Table 2.2, page 18



Survival (%)	
	Absent
	1 - 33% Poor representation
	34 - 66% Moderate representation
	67 - 100% Good representation

Figure 3.4. A schematic representation of the relative frequency of parts in each feeding event from the caracal scat assemblage

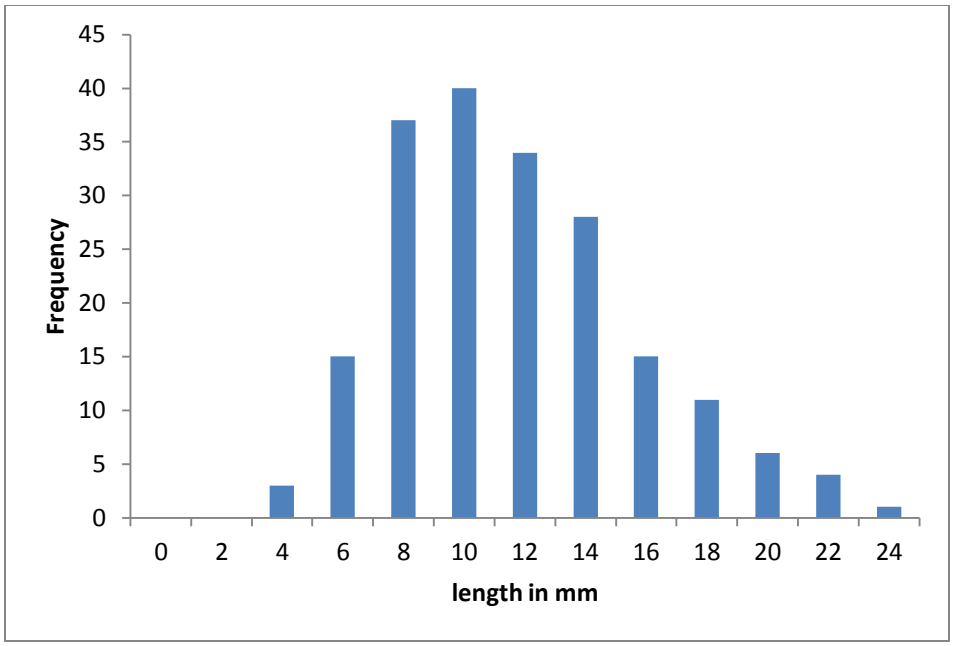


Figure 3.5. Histogram showing the maximum lengths of identifiable remains in the caracal scat assemblage

Table 3.5 Anatomical composition of the caracal scat assemblage

Skeletal Element	NISP	% NISP	MNE	ES from Feeding (%)	Survival (%)
Cranium	22	9.9	3	69.5	30
Mandible	7	3.1	4	90	20
Upper Postcanine	8	3.6	8	73.3	6.7
Lower Postcanine	15	6.7	15	92	15
Incisor	6	2.7	6	91.7	10
Vertebra indet.	32	14.3	7	100	1.7
Cervical	7	3.1	2	100	4
Atlas	2	0.9	2	100	20
Axis	3	1.3	2	100	20
Thoracic	4	1.8	3	100	2.3
Lumbar	30	13.5	5	100	7.1
Caudal	5	2.2	3	100	1.9
Rib	51	22.9	15	100	5.8
Scapula	2	0.9	2	100	10
Humerus	1	0.4	1	100	5
Radius	1	0.4	1	80	5
Ulna	2	0.9	1	80	5
Pelvis	6	2.7	5	95	25
Femur	6	2.7	4	95	20
Tibia	2	0.9	2	100	10
Carpal / Tarsals	-	-	-	65.8	-
Patella	2	0.9	2	100	10
Metapodial	4	1.8	3	65.6	1.7
Phalange	5	2.2	5	60.2	1
Total	**223**		**101**		

Abbreviations: NISP, Number of Identified Elements; %NISP, Number of Identified Elements expressed as a percentage of the whole assemblage; MNE, Minimum Number of Elements; ES, Expected survival after feeding

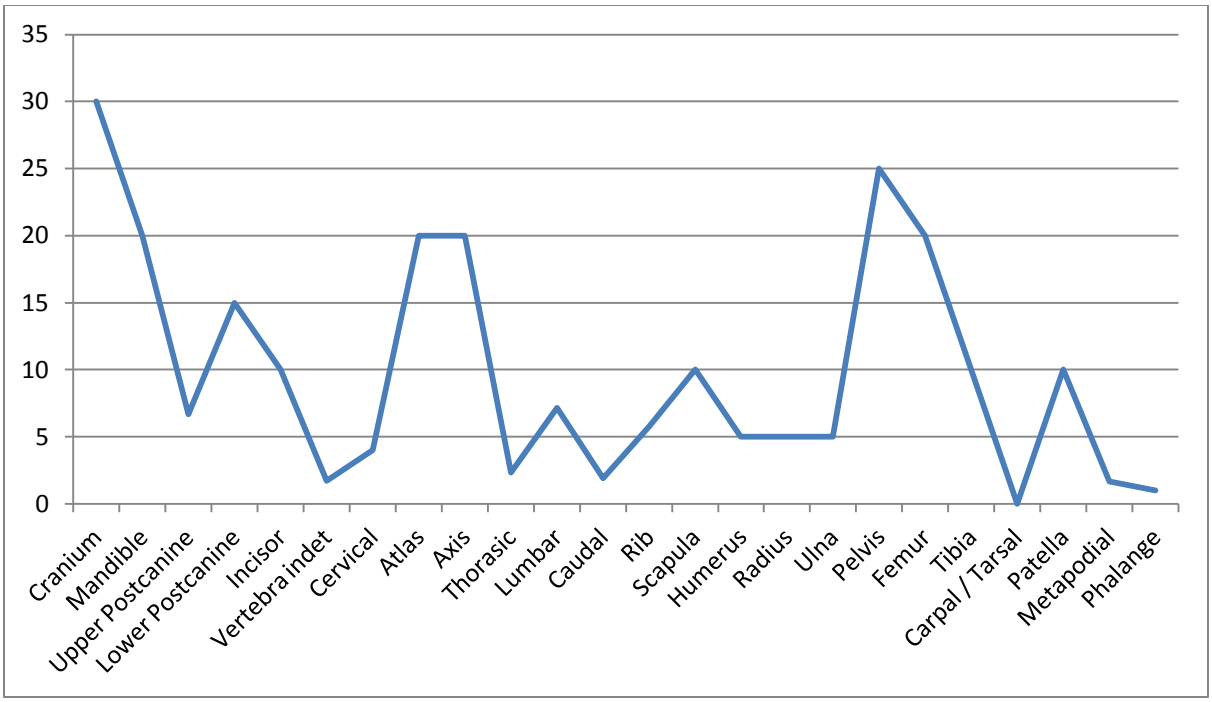


Figure 3.6. Survival (%) of remains in the caracal scat assemblage

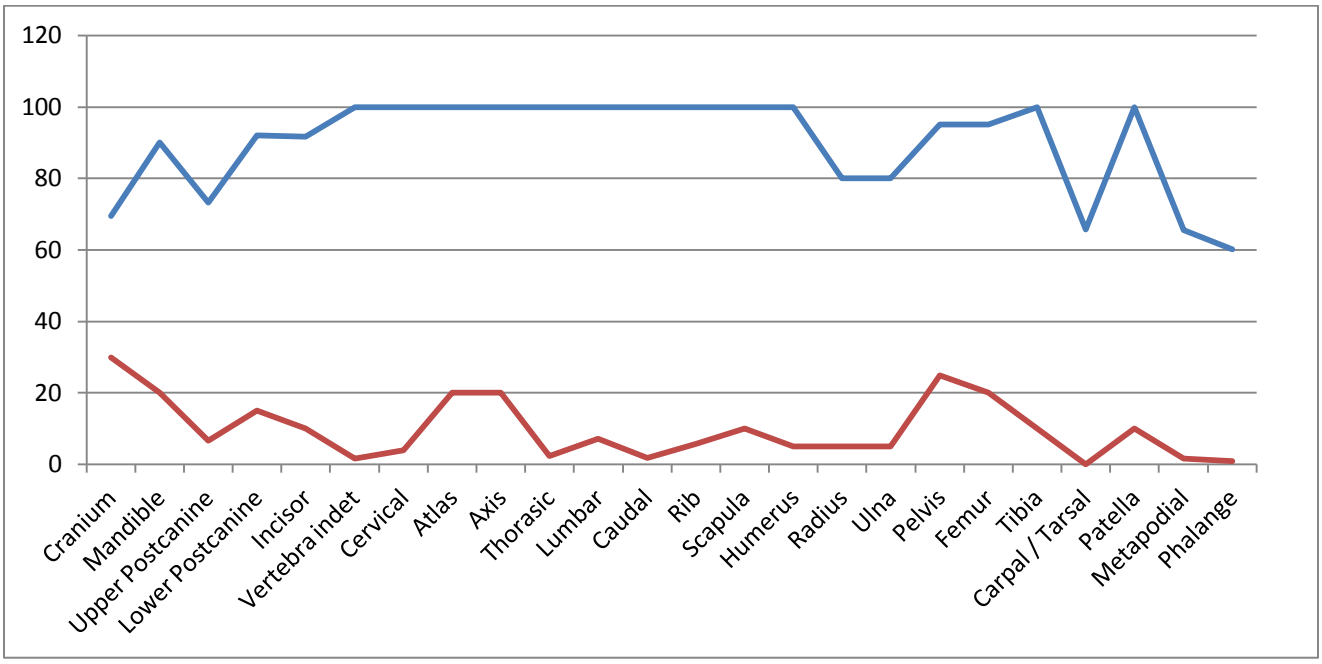


Figure 3.7. Expected survival (ES) of elements after feeding against survival of elements from the caracal scat assemblage

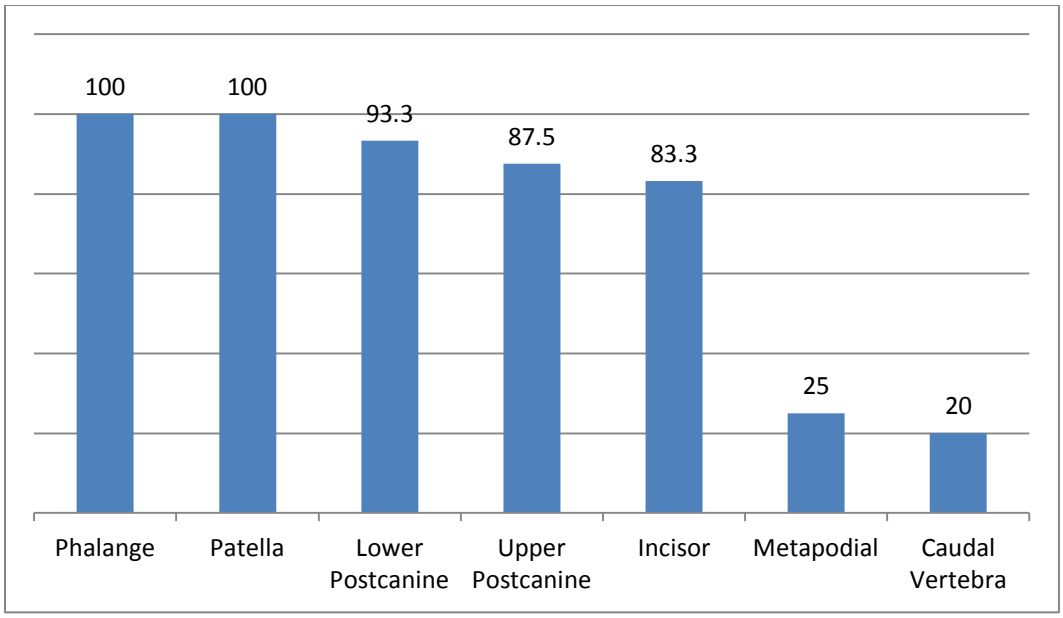


Figure 3.8. Relative frequency (%) of completeness in elements from the caracal scat assemblage

Table 3.6. Distribution of elements in the caracal scat assemblage according to breakage categories

	A		AIL		IS		IL	
Pelvis	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**
	1	16.7	1	16.7	3	50	1	16.7
	MBI		**MB**		**CP**			
Mandible	**n**	**%**	**n**	**%**	**n**	**%**		
	2	28.6	3	42.9	2	28.6		
	ZA		**NC**					
Cranium	**n**	**%**	**n**	**%**				
	4	18.2	18	81.8				
	GC		**F**					
Scapula	**n**	**%**	**n**	**%**				
	1	50	1	50				
	HT		**S**		**HTS**			
Rib	**n**	**%**	**n**	**%**	**n**	**%**		
	6	11.8	36	70.6	9	17.6		
	C							
Patella	**n**	**%**						
	2	100						
	C		**F**					
Dentition	**n**	**%**	**n**	**%**				
Incisor	5	83.3	1	16.7				
Upper postcanine	7	87.5	1	12.5				
Lower postcanine	14	93.3	1	6.7				

Table 3.6 (continued). Distribution of elements in the caracal scat assemblage according to breakage categories

	C		VB		VE		VA		SP		TP		ZYG	
Vertebrae	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**
Vertebra indet.	-	-	13	40.6	8	25	3	9.4	1	3.1	-	-	7	21.9
Atlas	-	-	-	-	-	-	-	-	-	-	-	-	2	100
Axis	-	-	3	100	-	-	-	-	-	-	-	-	-	-
Cervical	-	-	-	-	-	-	1	14.3	-	-	3	42.9	3	42.9
Thoracic	-	-	-	-	-	-	2	50	2	50	-	-	-	-
Lumbar	-	-	5	16.7	2	6.7	-	-	1	3.3	8	26.7	14	46.7
Caudal vertebra	1	20	3	60	1	20	-	-	-	-	-	-	-	-
Totals	**1**		**24**		**11**		**6**		**4**		**11**		**26**	

Long bones, metapodial and phalange	C		PE		PES		S		SDE		DE	
	n	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**
Humerus	-	-	-	-	-	-	-	-	-	-	1	100
Radius	-	-	-	-	-	-	-	-	1	100	-	-
Ulna	-	-	-	-	1	50	1	50	-	-	-	-
Femur	-	-	4	66.7	2	33.3	-	-	-	-	-	-
Tibia	-	-	-	-	-	-	1	50	1	50	-	-
Metapodial	1	25	-	-	1	25	-	-	1	25	1	25
Phalange	5	100	-	-	-	-	-	-	-	-	-	-
Totals	**6**		**4**		**4**		**2**		**3**		**2**	

For abbreviations see Table 2.2, page 18

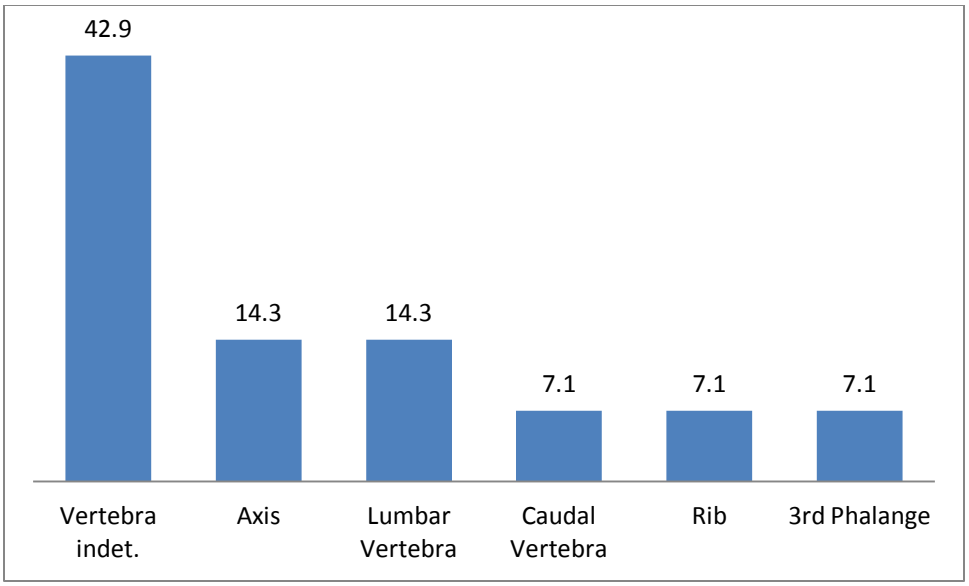


Figure 3.9. Relative frequency (%) of articulated remains in elements from the caracal scat assemblage

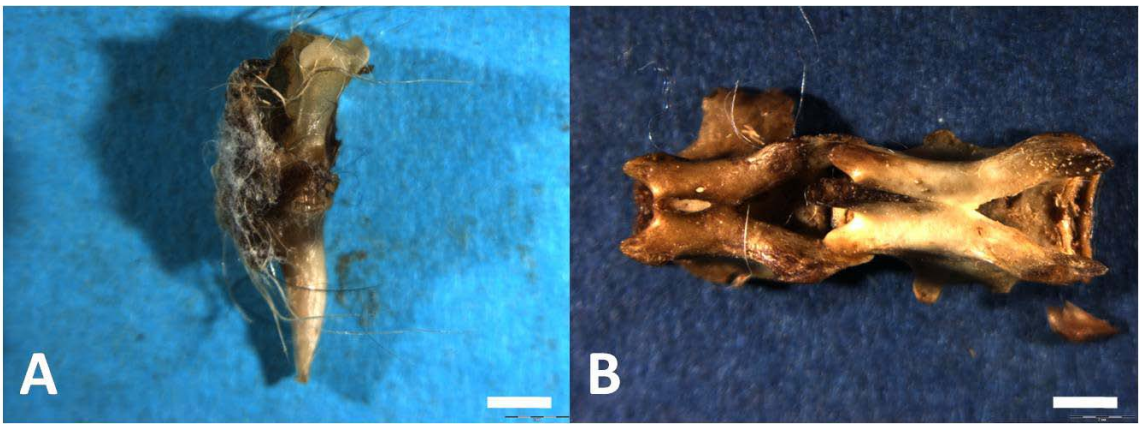


Plate 3.2. Articulation in remains from the caracal scats. A) articulation between distal and second phalanges; B) articulation between caudal vertebrae (dorsal view). *Scale bar* 2 mm

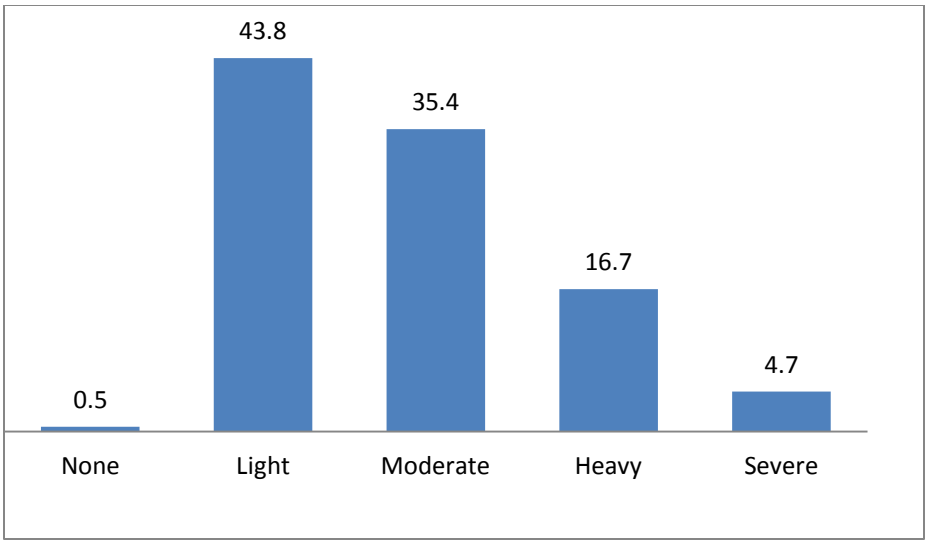


Figure 3.10. Relative frequency (%) of surface etching in the caracal scat assemblage

Table 3.7. Intensity of surface etching on elements in the caracal scat assemblage

	0 - None		1 - Light		2 - Moderate		3 - Heavy		4 - Severe	
	n	%	n	%	n	%	n	%	n	%
Cranium	1	4.5	15	68.2	4	18.2	2	9.1	-	-
Mandible	-	-	4	57.1	2	28.6	1	14.3	-	-
Vertebra indet.	-	-	14	43.8	8	25	6	18.8	4	12.5
Cervical	-	-	2	28.6	3	42.9	1	14.3	1	14.3
Atlas	-	-	1	50	1	50	-	-	-	-
Axis	-	-	2	66.7	1	33.3	-	-	-	-
Thoracic	-	-	4	100	-	-	-	-	-	-
Lumbar	-	-	12	40	9	30	7	23.3	2	6.7
Caudal	-	-	1	20	2	40	1	20	1	20
Rib	-	-	12	23.5	26	51	13	25.5	-	-
Scapula	-	-	-	-	1	50	1	50	-	-
Humerus	-	-	1	100	-	-	-	-	-	-
Radius	-	-	1	100	-	-	-	-	-	-
Ulna	-	-	1	50	1	50	-	-	-	-
Pelvis	-	-	2	33.3	4	66.7	-	-	-	-
Femur	-	-	3	50	3	50	-	-	-	-
Tibia	-	-	2	100	-	-	-	-	-	-
Patella	-	-	2	100	-	-	-	-	-	-
Metapodial	-	-	1	25	3	75	-	-	-	-
Phalanges	-	-	4	80	-	-	-	-	1	25

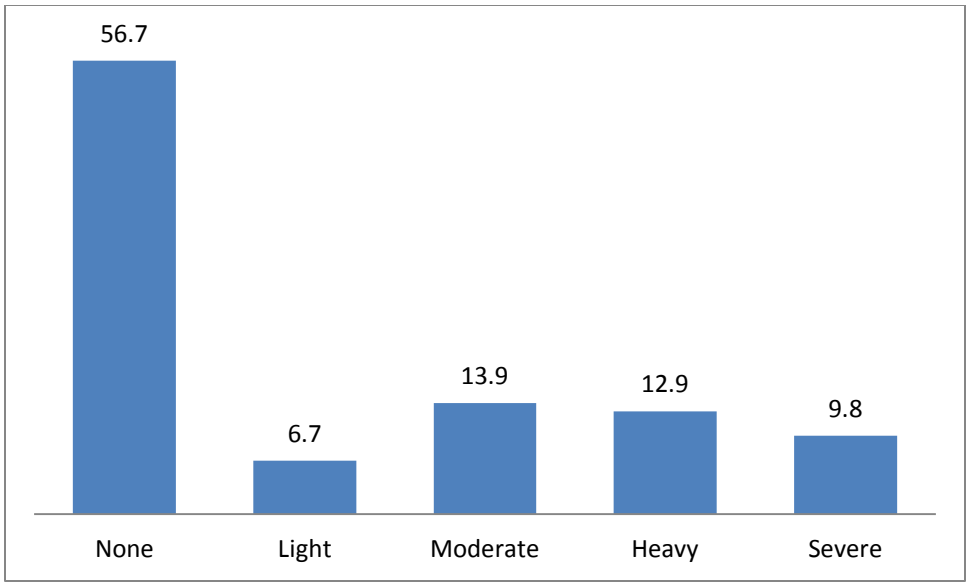


Figure 3.11. Relative frequency (%) of corrosive pitting in the caracal scat assemblage

Table 3.8. Intensity of corrosive pitting on elements in the caracal scat assemblage

	0 - None		1 - Light		2 - Moderate		3 - Heavy		4 - Severe	
	n	%	n	%	n	%	n	%	n	%
Cranium	15	68.2	2	9.1	2	9.1	2	9.1	1	4.5
Mandible	4	57.1	1	14.3	1	14.3	1	14.3	-	-
Vertebra indet.	14	43.8	1	3.1	6	18.8	6	18.8	5	15.6
Cervical	3	42.9	-	-	1	14.3	2	28.6	1	14.3
Atlas	2	100	-	-	-	-	-	-	-	-
Axis	3	100	-	-	-	-	-	-	-	-
Thoracic	3	75	-	-	1	25	-	-	-	-
Lumbar	15	50	4	13.3	6	20	3	10.0	2	6.7
Caudal	1	20	-	-	-	-	1	20	3	60
Rib	33	64.7	1	2	5	9.8	6	11.8	6	11.8
Scapula	1	50	-	-	-	-	1	50	-	-
Humerus	1	100	-	-	-	-	-	-	-	-
Radius	-	-	-	-	1	100	-	-	-	-
Ulna	-	-	1	50	1	50	-	-	-	-
Pelvis	3	50	1	16.7	2	33.3	-	-	-	-
Femur	3	50	1	16.7	1	16.7	-	-	1	16.7
Tibia	1	50	-	-	-	-	1	50	-	-
Patella	-	-	-	-	-	-	2	100	-	-
Metapodial	4	100	-	-	-	-	-	-	-	-
Phalange	4	80	1	20	-	-	-	-	-	-

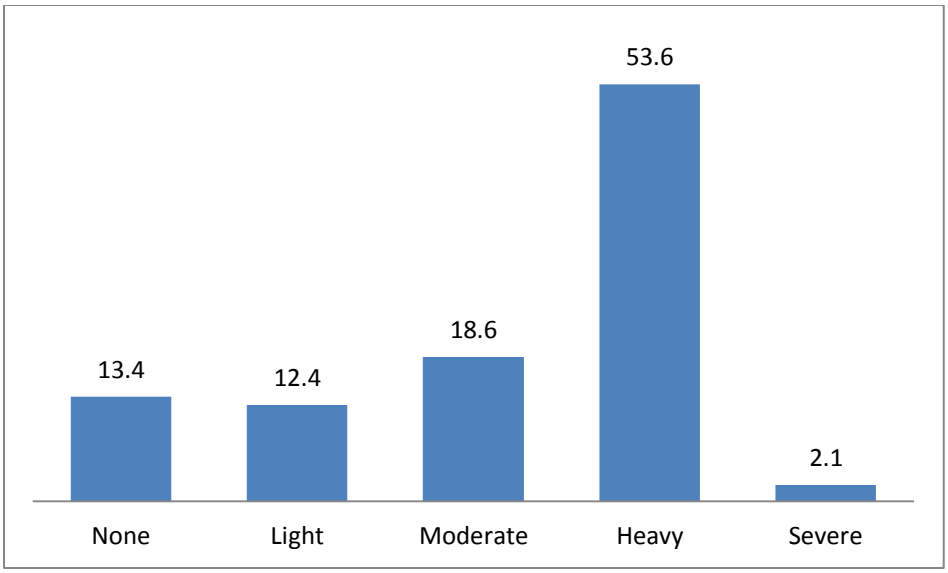


Figure 3.12. Relative frequency (%) of rounding of edges in the caracal scat assemblage

Table 3.9. Intensity of rounding of edges on elements in the caracal scat assemblage

	0 - None		1 - Light		2 - Moderate		3 - Heavy		4 - Severe	
	n	%	n	%	n	%	n	%	n	%
Cranium	-	-	6	27.3	9	40.9	7	31.8	-	-
Mandible	2	28.6	1	14.3	1	14.3	3	42.9	-	-
Vertebra indet.	8	25	8	25.0	3	9.4	13	40.6	-	-
Cervical	1	14.3	2	29	-	-	4	57.1	-	-
Atlas	-	-	1	50	-	-	1	50	-	-
Axis	-	-	-	-	1	33.3	2	66.7	-	-
Thoracic	-	-	-	-	2	50	2	50	-	-
Lumbar	3	10	3	10	6	20	18	60	-	-
Caudal	1	20	1	20	1	20	2	40	-	-
Rib	-	-	1	2	9	17.6	39	76.5	2	3.9
Scapula	-	-	-	-	-	-	2	100	-	-
Humerus	-	-	-	-	-	-	1	100	-	-
Radius	-	-	-	-	-	-	1	100	-	-
Ulna	1	50	-	-	-	-	1	50	-	-
Pelvis	-	-	-	-	2	33.3	4	66.7	-	-
Femur	1	16.7	1	16.7	1	16.7	3	50	-	-
Tibia	-	-	-	-	1	50	1	50	-	-
Patella	2	100	-	-	-	-	-	-	-	-
Metapodial	3	75	-	-	-	-	-	-	1	25
Phalange	4	80	-	-	-	-	-	-	1	25

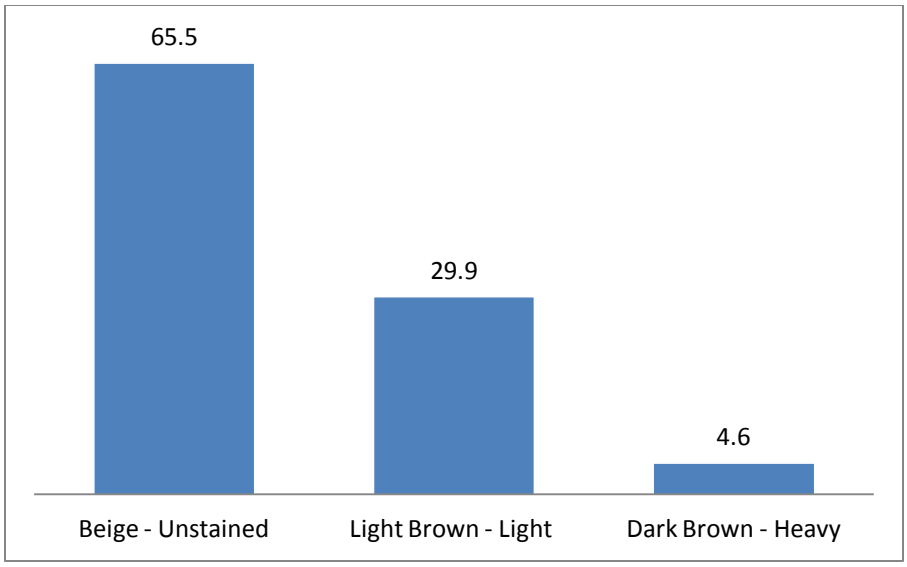


Figure 3.13. Relative frequency (%) of staining in the caracal scat assemblage

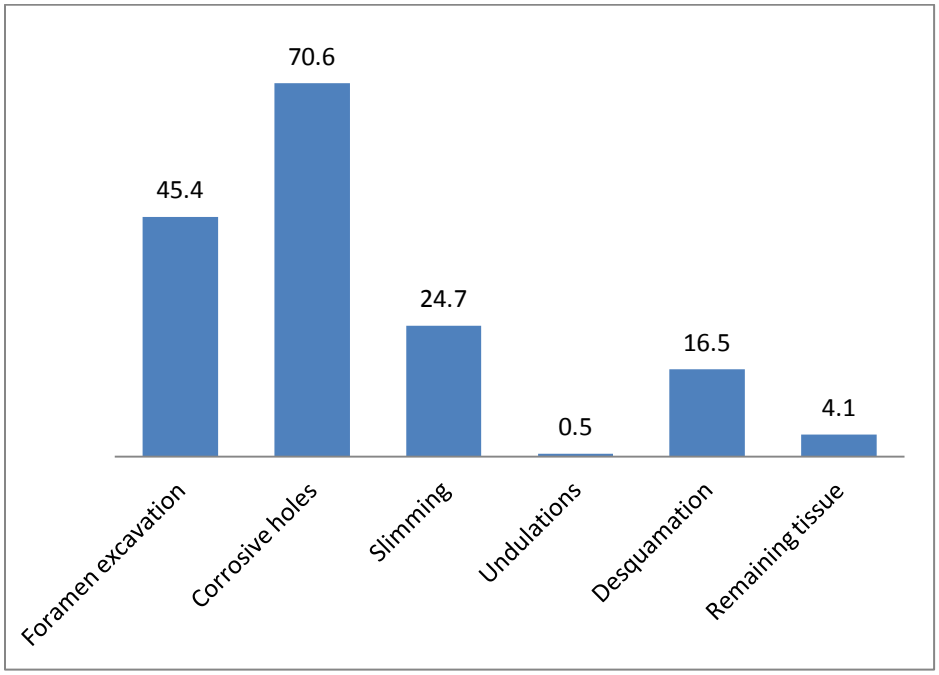


Figure 3.14. Relative frequency (%) of digestive modifications in the caracal scat assemblage

Table 3.10. Intensity of staining on elements in the caracal scat assemblage

	Beige Unstained		Light Brown Light staining		Dark Brown Heavy staining	
	n	**%**	**n**	**%**	**N**	**%**
Cranium	15	68.2	7	31.8	-	-
Mandible	4	57.1	3	42.9	-	-
Vertebra indet	20	62.5	11	34.4	1	3.1
Cervical	2	28.6	4	57.1	1	14.3
Atlas	1	50	1	50	-	-
Axis	3	100	-	-	-	-
Thoracic	1	25	2	50	1	25
Lumbar	18	60	9	30	3	10
Caudal	3	60	-	-	2	40
Rib	37	72.5	13	25.5	1	2.0
Scapula	2	100	-	-	-	-
Humerus	1	100	-	-	-	-
Radius	1	100	-	-	-	-
Ulna	1	50	1	50	-	-
Pelvis	4	66.7	2	33.3	-	-
Femur	3	50	3	50	-	-
Tibia	2	100	-	-	-	-
Patella	-	-	2	100	-	-
Metapodial	4	100	-	-	-	-
Phalange	5	100	-	-	-	-
Totals	**127**		**58**		**9**	

Table 3.11. Digestive modifications on elements in the caracal scat assemblage

	Foramen Excavation		Corrosive holes		Slimming		Desquamation		Tissue retained	
	n	%	n	%	n	%	n	%	n	%
Cranium	10	45.5	12	54.5	5	22.7	3	13.6	-	-
Mandible	5	71.4	1	14.3	3	42.9	-	-	-	-
Vertebra indet	15	46.9	28	87.5	13	40.6	3	9.4	2	6.3
Cervical	3	42.9	6	85.7	-	-	1	14.3	-	-
Atlas	-	-	2	100	-	-	-	-	-	-
Axis	2	66.7	1	33.3	1	33.3	1	33.3	2	66.7
Thoracic	2	50	4	100	-	-	-	-	-	-
Lumbar	10	33.3	24	80	5	16.7	9	30	2	6.7
Caudal	3	60	4	80	-	-	-	-	-	-
Rib	27	52.9	33	64.7	9	17.6	15	29.4	-	-
Scapula	1	50	2	100	1	50	-	-	-	-
Humerus	-	-	1	100	-	-	-	-	-	-
Radius	-	-	1	100	1	100	-	-	-	-
Ulna	2	100	2	100	1	50	-	-	1	50
Pelvis	3	50	5	83.3	2	33.3	-	-	-	-
Femur	1	16.7	4	66.7	2	33.3	-	-	-	-
Tibia	-	-	1	50	1	50	-	-	-	-
Patella	-	-	-	-	-	-	-	-	-	-
Metapodial	2	50	3	75	3	75	-	-	-	-
Phalange	2	40	3	60	1	20	-	-	1	20
Totals	**88**		**137**		**48**		**32**		**8**	

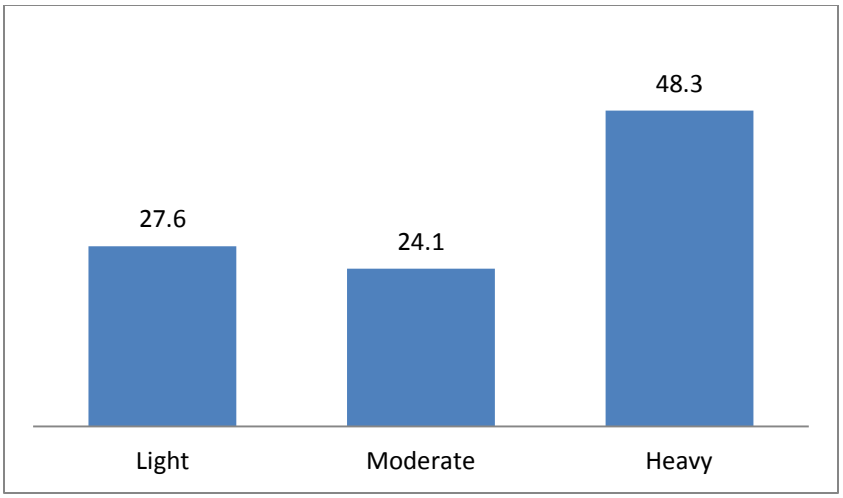


Figure 3.15. Relative frequency (%) of digestion in dental remains in the caracal scat assemblage

Table 3.12. Intensity of digestion in dental remains in the caracal scat assemblage

	Light		Moderate		Heavy	
	n	%	n	%	n	%
Incisor	5	83.3	1	16.7	-	-
Upper postcanine	2	25	2	25	4	50
Lower postcanine	1	6.7	4	26.7	10	66.7

Table 3.13. Frequency of tooth marks on elements in the caracal scat assemblage

	Pits			Punctures			Notches			Scours			Crush		Crenulated edges		Total		
	n	%	FM	n	%	FM	n	%	FM	n	%	FM	n	%	n	%	n	%	FM
Cranium	-	-	-	-	-	-	-	-	-	1	4.5	1	2	9.1	1	4.5	4	18.2	4
Mandible	-	-	-	-	-	-	-	-	-	1	14.3	1	-	-	-	-	1	14.3	1
Vertebra indet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	9.4	3	9.4	3
Cervical	-	-	-	-	-	-	-	-	-	-	-	-	1	14.3	-	-	1	14.3	1
Axis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	33.3	1	33.3	1
Thoracic	-	-	-	-	-	-	-	-	-	-	-	-	1	25	1	25	1	25	2
Lumbar	1	3.3	8	2	7	2	1	3.3	1	4	13.3	5	7	23.3	3	10	13	43.3	26
Rib	4	7.8	5	6	11.8	6	-	-	-	4	7.8	4	2	3.9	4	7.8	16	31.4	21
Ulna	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	50	1	50	1
Pelvis	-	-	-	-	-	-	-	-	-	1	16.7	1	-	-	-	-	1	16.7	1
Tibia	1	50.0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	50	1
Patella	-	-	-	-	-	-	-	-	-	1	50	1	-	-	-	-	1	50	1
Metapodial	-	-	-	-	-	-	1	25	1	-	-	-	-	-	-	-	1	25	1
Totals	**6**		**14**	**8**		**8**	**2**		**2**	**12**		**13**	**13**		**14**		**45**		**64**

Abbreviations: n, the frequency of elements with tooth marks; % n, relative to the total number of that element as a percentage; FM, frequency of individual tooth marks. Total n indicates the number of elements with tooth marks; Total % indicates the percentage of the total elements that are tooth marked and Total FM indicates the number of individual tooth marks from each element

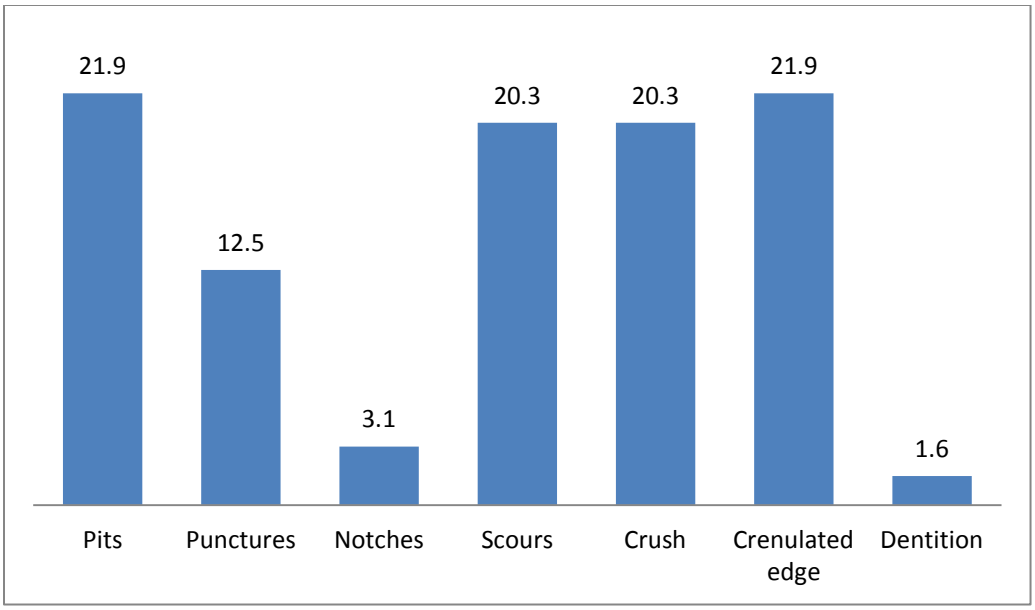


Figure 3.16. Relative frequency (%) of tooth marks in the caracal scat assemblage

Table 3.14. Average width of tooth marks in the caracal scat assemblage

	Average	Standard Deviation
Pits	0.3	0.1
Punctures	0.8	0.3
Scours	0.3	0.1
Notches	-	-
Dentition	0.2	-

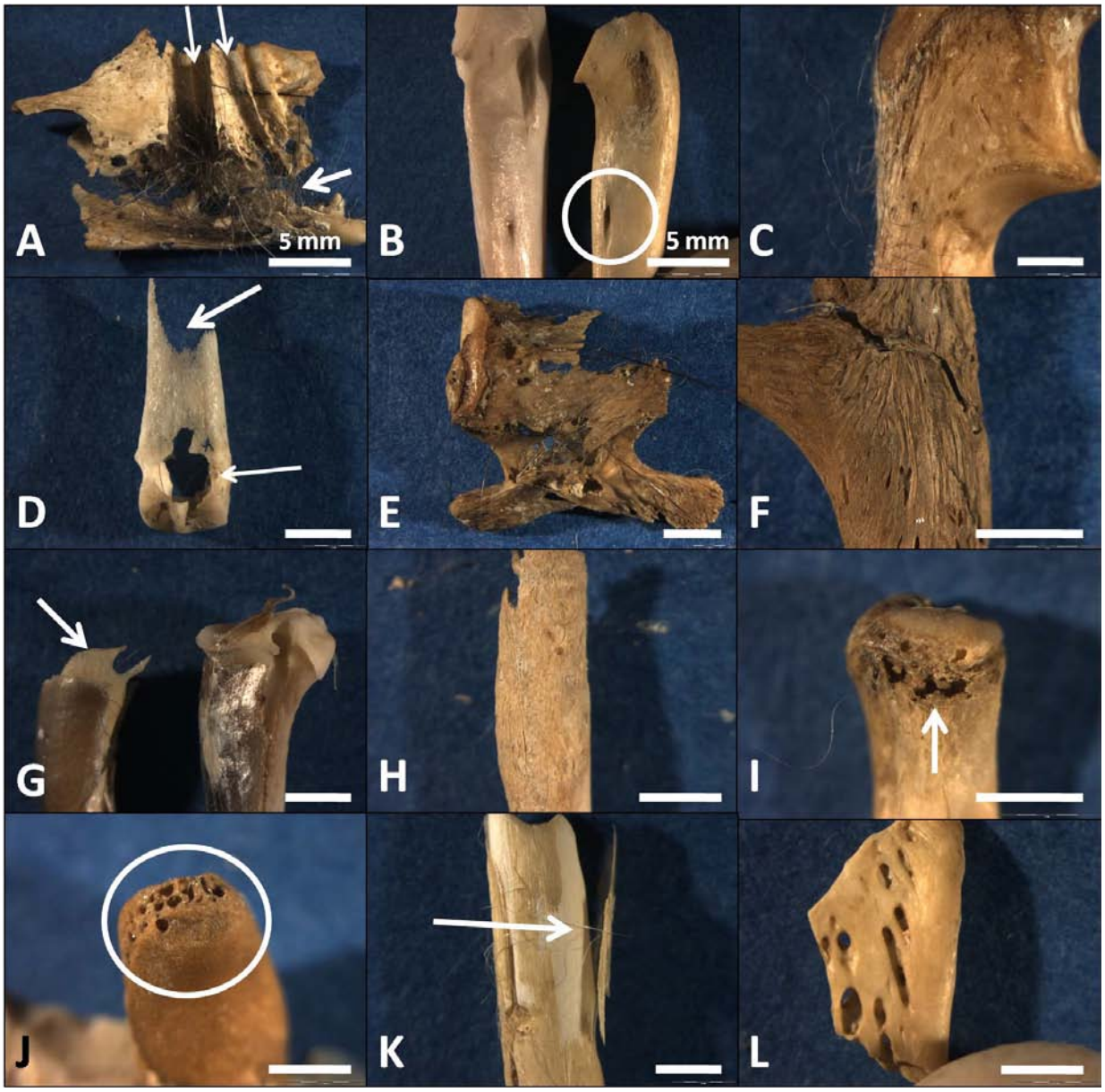
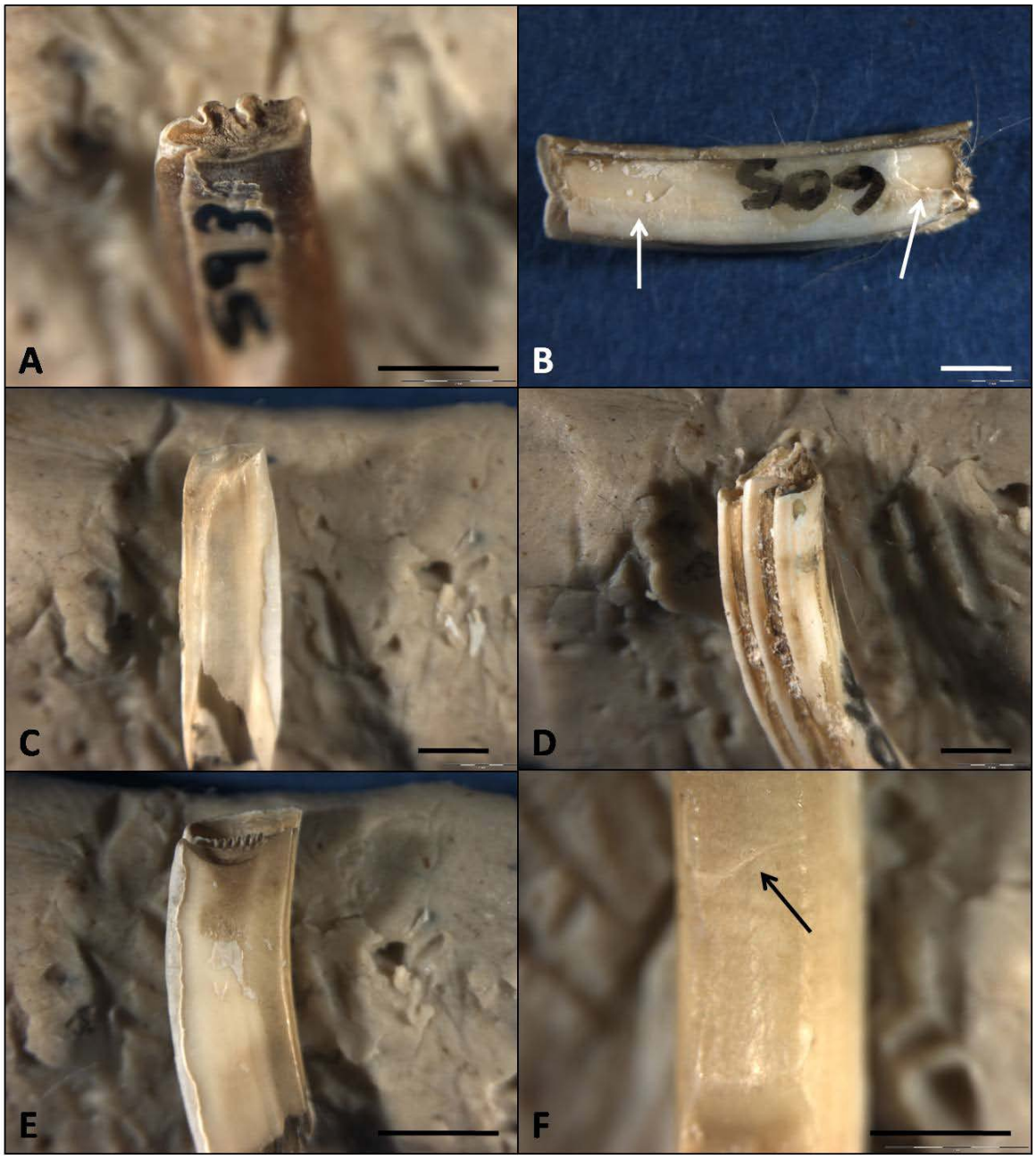


Plate 3.3. Alterations on remains from the caracal scat assemblage produced by digestion A) heavy digestion in a mandibular fragment, note the empty alveoli (small arrows) and how remaining pieces of hair and faecal matter are holding the broken fragments together (big arrow); B) ulna fragment from caracal scats (right) compared to a non-ingested ulna (left) from a rabbit carcass, note slimming and enlargement of the foramen (circle) in the ingested bone; C) ulna fragment showing light brown staining, moderate pitting and corrosive holes; D) distal metapodial with sever rounding, resulting in thin feathered edges (big arrow) and a large heavily corroded hole (small arrow); E) heavily corroded vertebra showing severe etching, corrosive holes and foramen excavation with dark brown staining; F) rib fragment with heavy etching, corrosive holes and foramen excavation as well as dark brown staining; G) distal phalange from caracal scats (left) compared to non-ingested phalange (right), the ingested

phalange is severely slimmed and etched, especially where bone is exposed and not protected by the claw sheath; H) heavily etched rib fragment; I) rib fragment with severe corrosive pitting; J) patella with heavy corrosive pitting; K) rib fragment with heavy desquamation resulting in exfoliation of the bone surface; L) fragment from the atlas with severe corrosive holes. *Scale bar* 2 mm, except where otherwise stated



<u>Plate 3.4. Digestion and tooth marks in dental remains from the caracal scat assemblage</u> A) upper postcanine showing heavy digestion, note the rounded corners of the salient edges and removal of enamel near the alveolar margin; B) lower postcanine with moderate digestion, note removal of localised areas of enamel along the length; C) incisor showing heavy digestion, with removal of enamel along entire length and strong rounding; D) lower postcanine with heavy digestion, digestion has penetrated below the alveolar level and there has been extensive removal of the dentine and enamel; E) upper postcanine with heavy digestion and removal of dentine and enamel; F) lower incisor with light digestion and carnivore scour mark. *Scale bar* is 2 mm

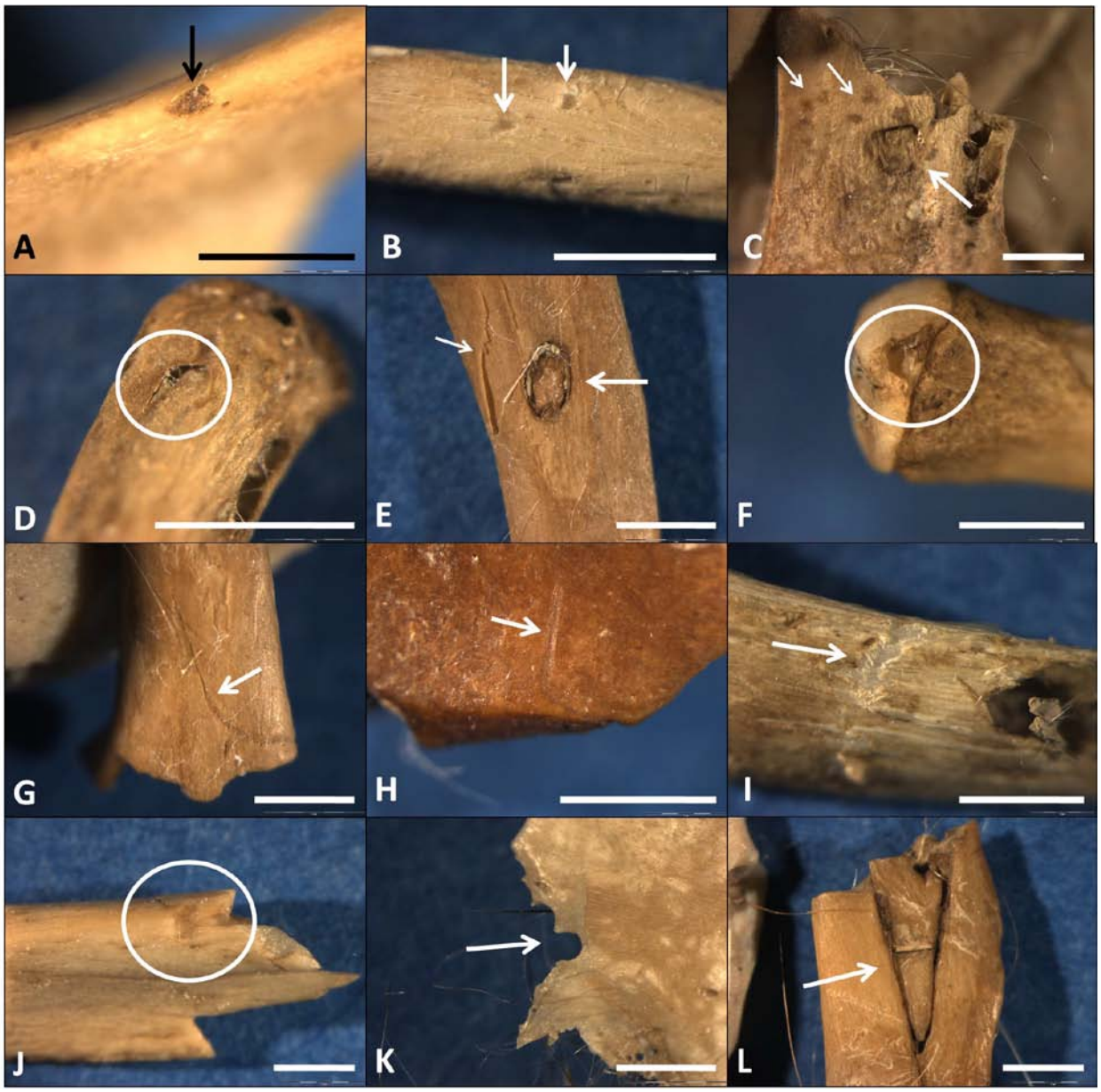


Plate 3.5. Tooth marks on bone remains from the caracal scat assemblage A) tibial fragment with tooth pit; B) rib showing multiple tooth pits; C) lumbar vertebrae with multiple tooth marks, including tooth pits (small arrows) and a tooth puncture (large arrow); D) tooth puncture on a rib; E) rib showing a tooth puncture (large arrow) and desquamation (small arrow); F) rib head with tooth puncture; G) scour mark on rib; H) scour mark on the pelvis; I) rib showing a scour mark; J) notch in a lumbar vertebra; K) crenulated edges on a mandibular fragment; L) crushing of a thoracic vertebra. *Scale bar* is 2 mm

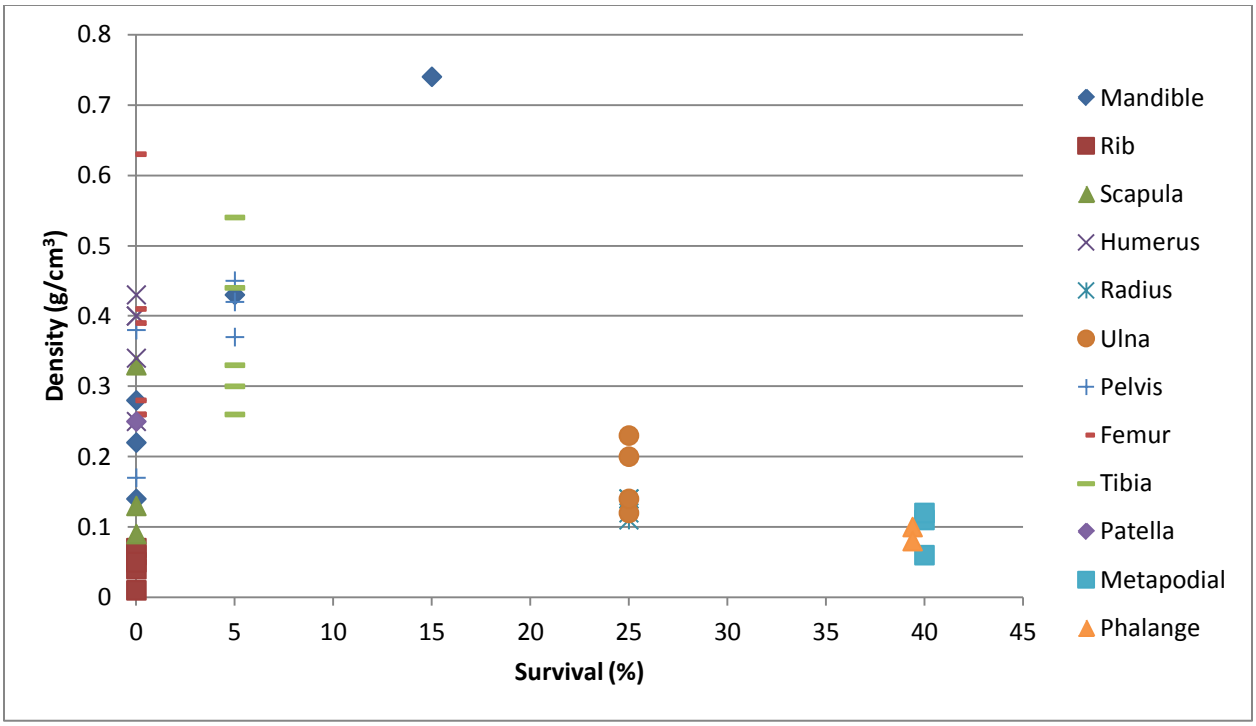


Figure 3.17. Structural density assays of domestic rabbit compared to survival (%) of elements in the caracal refuse assemblage

Table 3.15. Anatomical composition and breakage in the caracal refuse and scatological assemblages

	Refuse assemblage	Scat assemblage
Number of remains (n)	406	223
Average survival (%)	12.5	9.9
Maximum survival (%)	40	30
Survival > 20%	cra, UPC, rad, uln, c/t, mps, phl	cra, man, pel, fem, atl, axs
Survival< 10%	man, LPC, I, pel, fem	UPC, I, vert, sca, hum, rad, uln, tib, pat, phl
Survival = 0%	sca, hum, rib, vert, tib	c/t
Avg. max fragment size (mm)	-	10.7
Complete remains (%)	95.9	15.7
Complete long bones (%)	100	-

For abbreviations and explanations see Table 2.2, page 18

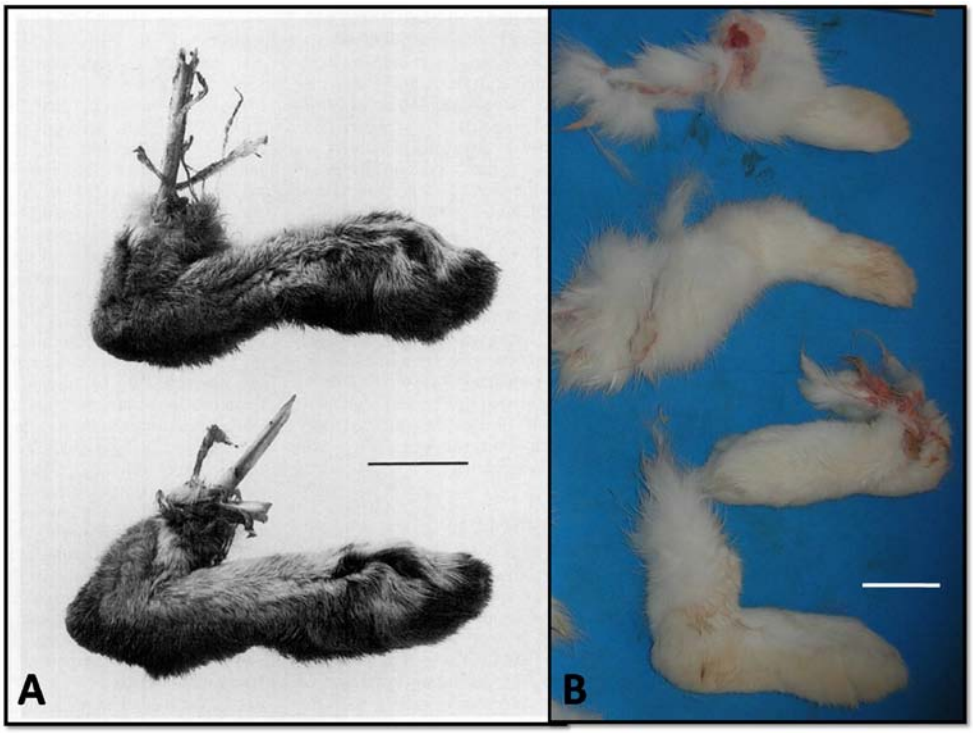


Plate 3.6. Discarded distal appendages in the coyote and caracal A) distal appendages from coyote refuse, adapted from Schmitt and Juell (1994); B) distal appendages from caracal refuse. *Scale bar* is 3 cm in both cases

Table 3.16. Comparison of the anatomical composition and breakage of leporid remains between the caracal and small carnivore refuse assemblages

Leporid predator comparisons	**Caracal** *Caracal caracal*	**Fox** *Vulpes vulpes*	**Geoffroy's Cat** *Leopardus geoffroyi*	**Coyote** *Canis latrans*	**Caracal** *Caracal caracal*
Reference	Present study	Lloveras *et al.*(2012)	Álvarez *et al.* (2012)	Schmitt and Juell (1994)	Grobler (1981)
Number of remains (n)	406	639	439	-	-
Average survival (%)	12.5	25.6	40.2	-	-
Maximum survival (%)	40	89.8	87.5	-	-
Survival > 30%	autopodium	tib, autopodium	cra, man, hum, rad, uln, pel, fem, tib, c/t, mts	distal appendages	cranium, viscera, tail and feet
Survival < 10%	man, dent, pel, fem	man, LPC, hum, vert	vert, mcs	-	-
Survival = 0%	sca, hum, rib, vert, tib	cra, sca,rib, pel, dent, fem, pat	rib	-	-
Avg max fragment size (mm)	-	19.3	-	-	-
Complete remains (%)	95.9	89.4	88.8	-	-
Complete long bones (%)	100	5.4	15	-	-
Teeth marks (%)	-	9.5	19.8	-	-

For abbreviations and explanations see Table 2.2, page 18

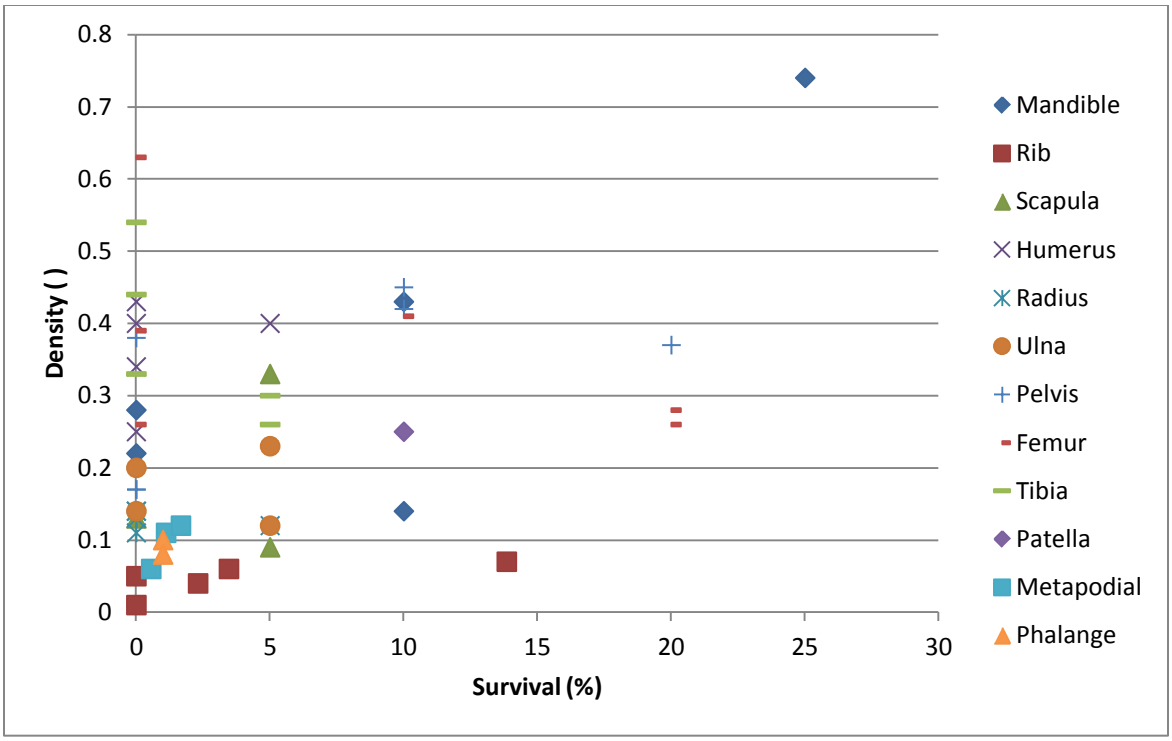


Figure 3.18. Structural density assays of domestic rabbit compared to survival (%) of elements in the caracal scat assemblage

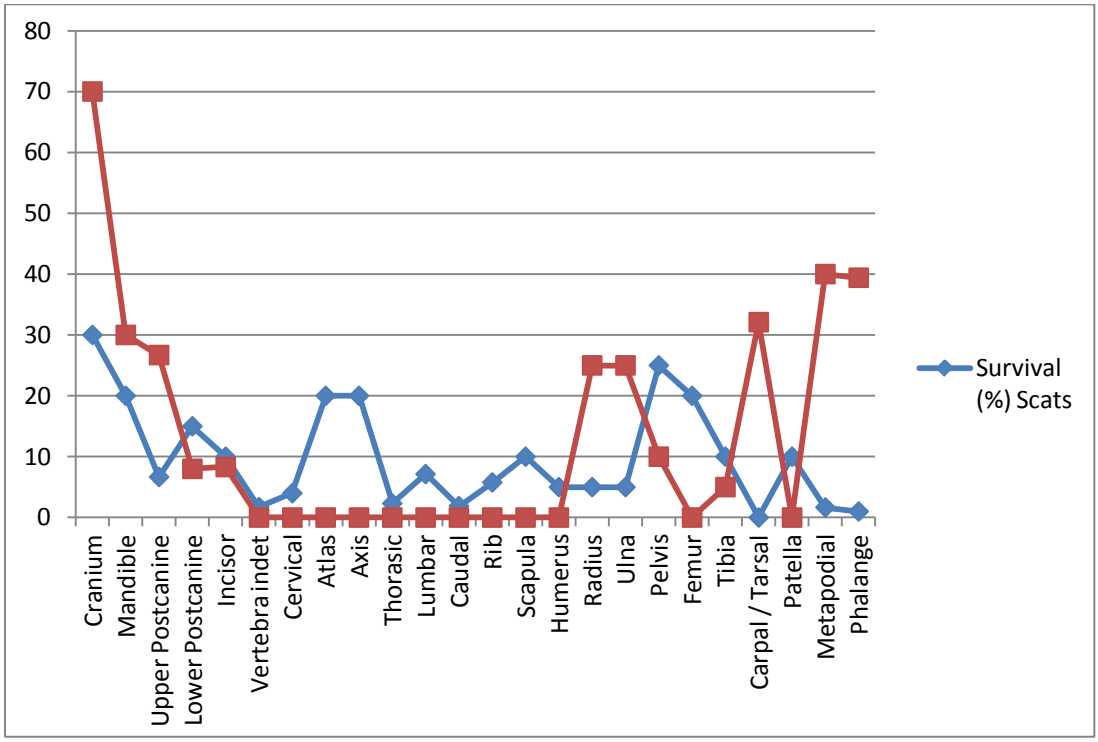


Figure 3.19. Survival (%) of elements in the caracal scat and refuse assemblages

Table 3.17. Distribution of tooth marks on elements relative to breakage classes in the caracal scat assemblage

	IS							
Pelvis	**n**	**%**						
	1	100						
	VB		**SP**		**TP**		**ZYG**	
Vertebra	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**
Vertebra indet.	1	33.3	0	0	0	0	2	66.7
Axis	1	100	0	0	0	0	0	0
Cervical	0	0	0	0	0	0	1	100
Thoracic	0	0	1	100	0	0	0	0
Lumbar	2	15.4	0	0	5	38.5	6	46.2
Long bones, metapodial and phalange	**S**							
	n	**%**						
Ulna	1	100						
Tibia	1	100						
Metapodial	1	100						
	CP							
Mandible	**n**	**%**						
	1	100						
	ZA		**NC**					
Cranium	**n**	**%**	**n**	**%**				
	2	50.0	2	50.0				
	HT		**S**					
Rib	**n**	**%**	**n**	**%**				
	6	12.5	10	62.5				

For abbreviations and explanations see Table 2.2, page 18

Table 3.18. Comparison of the anatomical composition, breakage, digestion and tooth marks on leporid remains between the caracal and small carnivore scat assemblages

Leporid predator comparisons	**Caracal** *Caracal caracal*	**Coyote** *Canis latrans*	**Fox** *Vulpes vulpes*	**Lynx** *Lynx pardinus*	**Geoffroy's Cat** *Leopardus geoffroyi*
Reference	Present study	Schmitt and Juell (1994)	Lloveras *et al.*(2012)	Lloveras *et al*. (2008a)	Álvarez *et al.* (2012)
Number of remains (n)	223	840	265	1522	294
Average survival (%)	9.9	.	25.6	42.9	34
Maximum survival (%)	30	.	83.3	86.9	.
Identifiable remains (%)	41.4	.	.	36.1	.
Survival > 20%	cra, man, atl, axs, pel, fem	Dent ¢	man, cra, appendicular	man, cra, mps, phl, appendicular	cra, phl, c/t ¢
Survival < 10%	dent, vert, rib, scap, hum, rad, uln, tib, mp, phl	hindlimb ¢	c/t	-	man, pel, tib¢
Survival = 0%	c/t	-	mcs	-	.
Avg max fragment size (mm)	10.7	27.5*	9.1	7.1	.
Complete remains (%)	15.7	7.1	12	43	15
Complete long bones (%)	-	-	-	2.5	.
Articulated remains (%)	6.7	.	-	9.7	.
Digested remains (%)	99.9	.	99.5	97.2	.
Intensity digestion bones	Light	Heavy	Heavy	Heavy	.
Intensity digestion dental	Heavy	Heavy	Heavy	Heavy	.
Teeth marks (%)	28.4	.	3	0.26	1.6

For abbreviations see Table 2.2, page 18. (*)In the coyote no average value of fragment size was available so we present the maximum fragments size recorded. (¢) Percentage survival is not given. (-) presents a zero value. (.) comparable data not available

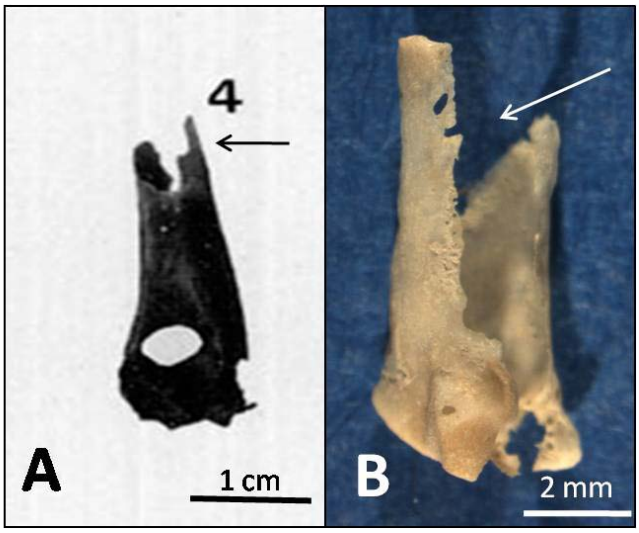


Plate 3.7. Severe corrosion with feathering of edges in the caracal and coyote scat assemblages A) distal humeri from the coyote showing severe rounding and feathering on the broken edge, adapted from Schmitt and Juell (1994); B) proximal metapodial from the caracal with severe rounding and feathering

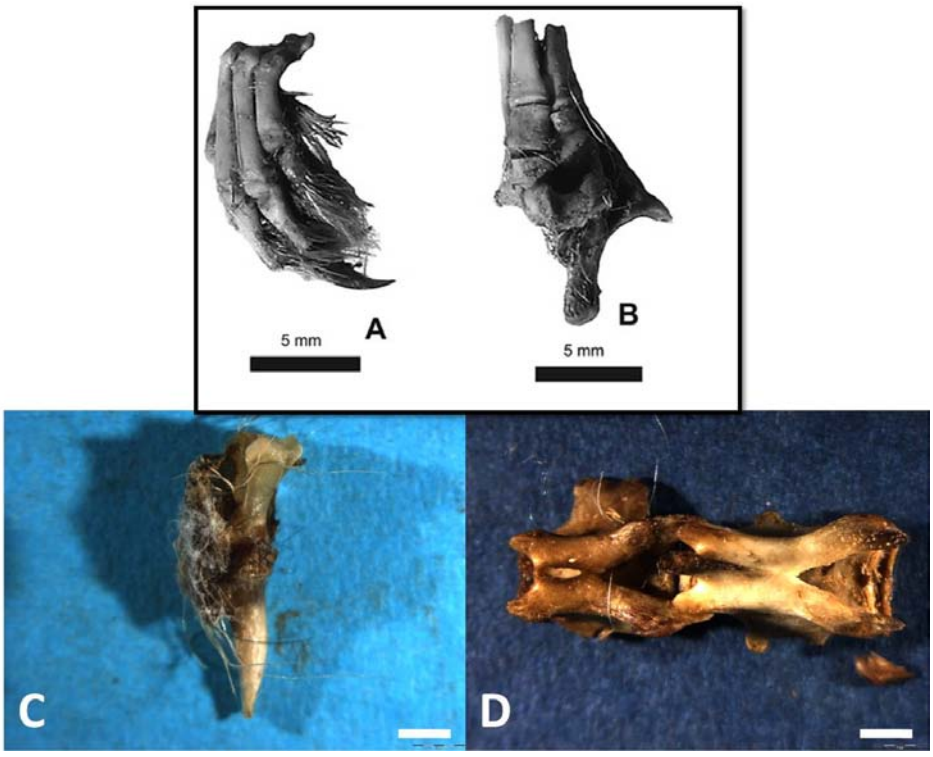


Plate 3.8. Articulated remains from the puma and caracal scat assemblages A and B) articulated distal appendages from the puma scats, adapted from Montalvo *et al.* 2007); C) phalanges from the caracal scats and D) caudal vertebrae from the caracal scats. *Scale bar* is 2 mm except where otherwise stated

CHAPTER 4
HONEY BADGER FEEDING

Results

Two adult honey badgers, a male and a female, were fed varied sized freshly thawed rabbit carcasses on three occasions (Table 4.1). The badgers were observed to move the carcasses around during feeding but after cessation of feeding carcasses were not moved. No attempt at caching was observed and the remains of carcasses were recovered in the same night room where the carnivores were fed together. Table 4.1 provides a summary of the feedings and carcass remains and scats collected as well as bone skeletal remains retrieved from the scats.

4.1. Refuse Assemblage

Remains from a total of six carcasses were recovered (Table 4.1). Two partial skins were recovered from feeding 1, as well as bone fragments from a single carcass. The second carcass from feeding 1 was represented by a maxillary fragment (Plate 4.1). In feeding 2 a few skeletal elements from both carcasses were recovered while feeding 3 had abundant refuse remains including two partial skins with attached skeletal elements, some of which were still in anatomical position. A schematic presentation of relative frequency of skeletal parts of both carcasses from each feeding is depicted in Figure 4.1. Survival in the crania is displayed in Table 4.2. Table 4.3 depicts the number of identified specimens (NISP) per element, as well as resulting minimum number of elements (MNE) and a calculation of the percentage survival. Skeletal element survival rate from the refuse assemblage is further depicted as a line graph in Figure 4.2.

4.1.1. Anatomical part representation of the refuse assemblage

Cranium and mandible

As shown in Table 4.2 remains from both crania were recovered in all feedings. In feeding 3 cranial remains had the best survival; one of the crania was complete with no visible

feeding damage (Plate 4.1, C), while the other cranium was missing the basicranium and occipitals. A cranium from feeding 1 was missing the basicranium and occipitals, while the other was only represented by a maxillary fragment (8.3%). Both crania from feeding 2 displayed an extreme degree of feeding damage where the basicranium and occipitals were missing as well as the anterior parts (nasal, pre/maxilla and zygomatic arch). Thus survival of the cranium in the honey badger refuse assemblage was 47.1% (Table 4.3).

In feeding 3 both mandibles were recovered (Table 4.3). Four mandibular fragments were recovered from feeding 1, representing a single mandible, while in feeding 2, five fragments from a single mandible were recovered for a survival in the mandible of 33%. Dental remains were common in the honey badger refuse assemblage, with the upper postcanine dentition recording the greatest survival rate of 59.7% (Figure 4.2), the lower postcanine at 45% and inciso at 44.4%.

Forelimb and shoulder

The humerus and ulna were absent in feedings 1 and 2, while the scapula and radius were missing in feeding 2 (Table 4.3). In feeding 3 all forelimb elements were recovered with a higher representation of the radius and ulna. Forelimb and shoulder remains had generally low survival, with the humerus recording the poorest survival (8.3%) in the refuse assemblage (Figure 4.2). The radius had the best survival of 33.3%, the ulna 25%, and the scapula 16.7%.

Hindlimb

More hindlimb (pelvis, femur, tibia) elements were recovered in feeding 3 than in feedings 1 and 2 (Table 4.3). Single pelvic remains were recovered in feedings 1 and 2, however the pelvis had 100% representation in feeding 3 (Figure 4.1). Femoral remains were found in all feedings, and the tibia was absent in feeding 2. The lowest overall survival in the hindlimb was the tibia 25%, while the pelvis and femur had 50% each.

Extremities

With the exception of singular elements of metatarsal, intermediate and distal phalanges from feeding 1, the rest of the autopodial remains were recovered from feeding 3 (Table 4.3). This resulted in a survival rate of 33.3% to 35.4% in the autopodium.

Vertebral column and ribcage

Five lumbar and two sacral vertebrae recovered from feeding 3 were the only vertebral remains in the refuse assemblage. Survival of the sacrum was at 33.3% and 11.9% for the lumbar vertebra (Table 4.3). Rib elements were absent in the refuse assemblage.

4.1.2. Completeness and breakage patterns in the refuse assemblage

The elements from the refuse assemblage were compared to a series of breakage classes, devised for each element (Chapter Two) in order to identify patterns, possibly linked to carnivore feeding behaviour. Figure 4.3 shows the relative frequency of complete elements in the assemblage, while Table 4.4 shows frequency (n) and relative frequency of breakage patterns in the refuse assemblage.

Cranium and mandible

Only a single cranium (from feeding 3) was complete (Figure 4.3). The remaining cranium from feeding 3 was missing the occipital, sphenoid and petrous bones (Table 4.2). A single cranium from feeding 1 displayed the anterior parts of the skulls from the premaxilla to the zygomatic, while the posterior parts were absent. The second cranium from feeding 1 consisted of a maxilla fragment. Both crania from feeding 2 show extensive feeding damage and consist of the frontal, temporal and parietal bones. Mandibular remains were most commonly represented by the robust mandibular body with incisive part (50%) and by complete (25%) mandibles (Table 4.4). The latter were all recovered in feeding 3, these complete mandibles had only limited damage to the ramus and condylar process. All dental remains were complete (Figure 4.3).

Forelimb and shoulder

A complete scapula was recovered from feeding 3. Also recovered from the feedings was a fragment of the scapula neck, and a portion of the neck and blade (Table 4.4). Of the remaining forelimb elements, a complete radius and ulna were recovered while, 75% of the radii and 66.7% of the ulnae consisted of the distal epiphysis with portion of the shaft. The humerus was represented by the distal epiphysis with portion of the shaft.

Hindlimb

Complete pelvis, albeit with minor feeding damage to the iliac crest and ischial tuberosity, were recovered in feeding 3 (Table 4.4). Other pelvic fragments consisted of the most robust areas of the bone, the acetabulum and surrounding parts. Half of all femoral remains recovered were shafts. A third of femurs consisted of the distal epiphysis with a portion of the shaft and a single complete femur (from feeding 3) was recovered. Two thirds of tibial remains were complete, and the remaining fragment was a proximal epiphysis.

Extremities

All carpal, tarsal, metacarpal and phalange elements were found complete (Figure 4.3) except for a metatarsal (Table 4.4). This fragment consisted of the distal epiphysis with shaft and originated from the isolated toe recovered from feeding 1.

Vertebral column and ribcage

Lumbar vertebra were complete, albeit with some feeding damage to the boundary of the transverse processes (Table 4.4). Sacrum were unmodified. Rib were absent in the assemblage.

4.2. Scat Assemblage

The honey badgers together produced an average of 7.7 scats per feeding. The scats had an average width of 27.3 mm with a wet mass of 26.2 g. The honey badger scatological sample after the three feedings consisted of 23 individual scats of which 6 (26.1%) contained no bone remains (Table 4.1). The average density of bone remains per scat was 159.3, with a maximum of 615 remains recovered from a single scat. The honey badger scats produced more than 200 remains in feeding 1, more than 800 in feeding 2 and 1536 in feeding 3. In total, the honey badger sample consisted of 2708 bone remains of which 384 were identifiable to skeletal element. The maximum length of recovered bones was only recorded for identifiable bones and is depicted, as a histogram, in Figure 4.4. The average length of the identifiable skeletal remains is 10.9 mm and the largest recorded length was 28.1 mm.

4.2.1. Anatomical representation of the scat assemblage

As discussed a total of 2708 bone remains were collected from the scats, of which 384

(14.2%) were identifiable to skeletal element. Table 4.5 portrays the number of identified specimens (NISP) per element, the resulting minimum number of elements (MNE), expected survival after feeding (ES) and a calculation of the percentage survival of scat remains. The minimum number of individuals (MNI), or rabbit carcasses, calculated from bone remains recovered from the scats was six, the same as the actual number of rabbits fed to the honey badgers. The expected survival (ES) shows the percentage of elements that were missing from the refuse assemblage and should have been recovered in the scats in the absence of loss from digestion. Figure 4.5 shows a schematic presentation of relative frequency of skeletal parts of both carcasses from each feeding. Skeletal element survival rate as determined from the scat assemblage is further depicted as a line graph in Figure 4.6. Figure 4.7 depicts the skeletal element survival rate from the scat assemblage compared to the expected survival after the feedings.

Cranium and mandible

Survival of crania in the refuse assemblage was 47.1%, thus the expected survival for crania in the scat assemblage was 52.9% (Table 4.5). The survival of cranial remains in the scat assemblage was 50% indicating a minor loss of only 2.9% of cranial remains. Mandibular remains were recovered in feedings 2 and 3, and were absent in feeding 1 (Figure 4.5). Mandibular remains recovered in the scats had a survival of 16.7%, much lower than the expected 66.7% from the refuse (Figure 4.7). Dental remains were scarce in the scats. Upper postcanine were absent and there were only 5 (8.3%) lower postcanines and 2 (5.6%) incisors in the scat sample, which was not only the lowest survival in the scat sample (Figure 4.6) but also much lower than expected from the refuse assemblage (40 – 55.6%).

Forelimb and shoulder

The expected survival for the humerus was high, 91.7% (Table 4.5). However, only 50% of humeral elements were recovered from the scat assemblage, indicating a loss of 41.7% (Figure 4.7). Humeral remains were especially abundant in feeding 3 (Figure 4.5). Expected survival in the scapula was 83.3% and survival in the scapula was only 33.3%, indicating a loss of 50%. In the radius the expected survival was 66.7%, however the survival in the radius was low

at 16.7%. Radial remains had a loss of 50% and were only recovered in feeding 2. The ulna had an expected survival of 75%, but was absent in the scat assemblage.

Hindlimb

Both the pelvis and femur had a moderate expected survival of 50% (Table 4.5). Survival in the femur was 50%, the same as expected (Figure 4.7), suggesting that femoral remains did not undergo loss from digestion. The pelvis had only a moderate survival of 33.3%, indicating a loss of 16.7%. The tibia had the greatest expected survival of the hindlimb elements of 75%. Tibial remains were found in feedings 1 and 2, but were absent in feeding 3. The tibia had only a moderate survival in the scats of 41.7%.

Extremities

As the extremities were only recovered from a single feeding in the refuse assemblage the expected survival of these elements was high (65.7 – 66.7). However survival in all the extremities was extremely low (Table 4.5). As none of the distal appendages were consumed in feeding 3, no elements from the extremities were recovered in feeding 3 (Figure 4.5). Carpal, tarsal and metapodial remains were poorly represented in all feedings and had a survival of only 6.9% and 8.3%, respectively. The phalange were the only element of the extremities found in abundance, in feeding 2. Thus, survival in the phalange was slightly higher at 10%.

Vertebral column and ribcage

Except for the lumbar and the sacral vertebra remains, other vertebra had an expected survival of 100% (Table 4.5). The expected survival in the lumbar vertebra was 88.1%, while that of the sacrum was 66.7%. Only 31% of the lumbar vertebra were recovered from the scat assemblage indicating a loss of 57.1% through digestion. No sacral remains were recovered from the scat assemblage. The atlas and axis had the greatest survival (33.3%) of all vertebra remains. Other vertebra had varying degrees of survival; other cervical vertebra (26.7%), caudal vertebra (13.5%) and the thoracic at 9%. The ribs, despite having an expected survival of 100% had an actual survival of only 8.3%.

4.2.2. Completeness and breakage patterns in the scat assemblage

The relative frequency of complete elements in the scat assemblage is displayed in Figure 4.8. The frequency (n) and relative frequency of breakage patterns in the scat assemblage are depicted in Table 4.6. Of the 384 identifiable bones in the scat assemblage only 45 (11.7%) were complete and unbroken. Complete bones were limited to the small compact bones such as phalange, patella, carpal and tarsal, caudal vertebra and dentition. Figure 4.9 displays the relative frequency of articulated remains in the scat assemblage. Articulated remains occurred in only 33 (8.6%) of the total scat assemblage and was found in vertebra, carpal and tarsal, metapodial and phalange elements.

Cranium and mandible

Numerous cranial remains were recovered in the scats, all of which were fragments of the neurocranium (Table 4.6). The mandible was represented by both the robust mandibular body with incisive part (50%) and by the condylar process. Completeness was high (71.4%) in the dentition (Figure 4.8). All incisor remains were complete, as well as 60% of all lower postcanine dentition.

Forelimb and shoulder

Scapula remains were abundant in the scat assemblage and all breakage classes were identified, save complete elements (Table 4.6). Most scapula remains were isolated fragments of the scapula blade (59.3%) and the blade with the scapula neck (11.1%). In 22.2% of cases the very fragile acromion process was recovered (Plate 4.2). Recovery of the glenoid region was minimal, with single recoveries of the glenoid and the glenoid with a portion of the neck. The humerus was mostly represented by the proximal epiphysis (83.3%) and to a lesser extent the distal epiphysis with a portion of the shaft (16.7%). Radial remains consisted of the distal epiphysis (50%) and shaft (50%).

Hindlimb

Many breakage classes were recognised in the pelvis (Table 4.6). The acetabulum, acetabulum with ilium and ischium, acetabulum with ilium, and the ilium were each represented by a single fragment (14.3%). The most common breakage was the ischium which

was represented by three (42.9%) fragments. Femoral remains were most commonly represented by proximal epiphyses (58.8%). Other femora include the proximal epiphysis with a portion of the shaft (11.8%) and the distal epiphysis (29.4%). Tibial remains consisted of shaft (37.5%), proximal epiphysis (50%) and proximal epiphysis with shaft (12.5%).

Extremities

Completeness was high in the extremities (Figure 4.8). A 72.7% of carpal and tarsal elements were complete as well as the patella, and 63.9% of the phalange. Of the remaining phalange, 22.2% were represented by the proximal epiphysis, 5.6% by the proximal epiphysis with shaft and 8.3% by the distal epiphysis with shaft (Table 4.6). There were no complete metapodial. Metapodials remains were represented by the distal epiphysis with shaft (60%), proximal epiphysis (30%) and the proximal epiphysis with shaft.

Vertebral column and ribcage

The atlas was represented by zygopophyses (66.7%) and transverse processes (33.3), while the axis was represented by the vertebral body (66.7%) and vertebral arches (33.3%; Table 4.6).The other cervical vertebra were represented by isolated zygopophyses (71.4%), vertebral arches (14.3%) and transverse processes (14.3%). The majority of the thoracic vertebra were represented by spinous process (87.5%) and by vertebral arches (12.5%). All breakage classes were noted in the lumbar vertebra. These classes include; zygopophyses (49.4%), transverse processes (29.6%), vertebral body (8.6%) and vertebral arch (3.6%). The lumbar vertebra are represented by a single (1.2%) vertebral epiphysis. Completeness in the caudal vertebra was recorded at 53.3% (Figure 4.8). Of the remaining caudal vertebra, a third were represented by the vertebral body, 6.7% by vertebral arch and spinous process. The majority of rib elements consisted of the shaft (76.8%). The head and tubercle were recovered in 10.7% of the ribs and the head with a portion of the shaft was noted in 12.5% of the ribs.

4.2.3. Digestion related modifications in the scat assemblage

Remains from the honey badger scats display a variety of digestion related modifications such as surface etching, corrosive pitting and rounding of edges (Figures 4.10, 4.11 and 4.12; Tables 4.7, 4.8 and 4.9). Also identified was staining (Figure 4.13, Table 4.10) and

transparency (Figure 4.14, Table 4.11). Other modifications include foramen excavation, corrosive holes, slimming, undulations, cupules, desquamation and remaining tissue (Figure 4.15, Table 4.12). Digestion in the dentition is outlined in Figure 4.16 and Table 4.13.

Etching

Etching (Plate 4.3A, C and E) was frequent in the honey badger assemblage occurring on 91.9% of skeletal elements (Figure 4.10). Most etching was of a light (46.4%) to moderate (29.7%) intensity while severe etching (0.8%) was rare (Table 4.7). Light etching was noted in all elements in the caracal scat assemblage except the radius and patella. The elements that tended towards a greater degree of etching were the rib (46.4%), tibia (50%) and patella (100%) which were predominantly moderately etched and the radius (100%) which was predominantly heavily etched. This would suggest that these elements were more prone to etching. Moderate etching was absent in the mandible, atlas, thoracic vertebra, humerus and radius. Heavy etching was absent in the cranium, atlas, axis, humerus and carpal/tarsal, while severe etching was only observed in the lumbar vertebra, tibia and carpal/tarsal.

Corrosive pitting

Corrosive pitting (Plate 4.3I and J) was observed in over a third (38.3%) of remains (Figure 4.11). Light pitting was noted in 13.8% including the cranium, cervical, lumbar, caudal vertebra, ribs, humerus, pelvis, femur and autopodium (Table 4.8). A 7.6% of remains had moderate pitting which occurred on the mandible, cervical, thoracic, lumbar vertebra, rib, humerus, femur, tibia, carpal/tarsal and phalange. Heavy pitting was noted in 7.8% of remains, including the cervical, lumbar, and caudal vertebra, rib, scapula, pelvis, and femur. Severe pitting was more common (9.6%) than moderate or heavy pitting and was observed in many low density remains like the cervical, axis, thoracic, lumbar and caudal vertebra as well as the rib, scapula, radius, femur and patella.

Rounding of edges

Rounding of edges (Plate 4.3H and L) was observed in 83.9% of remains (Figure 4.12). Light (13%) and moderate (22.4%) rounding were extensive in the assemblage occurring in all elements except the mandible, atlas, axis, patella and the radius, carpal/tarsal, patella

respectively (Table 4.9). Most rounding (48.2%) was of a heavy intensity and was noted in all elements except the humerus and patella. Severe rounding was observed in a single metapodial. The autopodial remains show a trend towards an absence of rounding, where the majority (carpal/tarsal, 45.5%; phalange 52.8%) of remains were not rounded.

Staining

A 29.2% of remains were unstained (Figure 4.13). Elements without staining include the cranium, cervical, axis, thoracic, lumbar, caudal vertebra, rib, scapula, humerus, pelvis, femur, tibia, carpal/tarsal, metapodial and phalange. Light staining was noted in 43.2% of the assemblage and was apparent in all elements (Table 4.10). The radius, pelvis, patella and phalange all lacked heavy staining, which was observed in 26% of remains. Severe staining was rare (1.6%), but occurred in the cranium, cervical vertebra, scapula and pelvis. Autopodial remains show the greatest resistance to staining as most of the specimens were unstained (carpals/tarsal, 54.4%; metapodial 50%; and phalange, 80.6%). The atlas (66.7%) and thoracic vertebra (62.5%) have a tendency towards heavy staining (Plate 4.3B, E and K).

Transparency

Transparency (Plate 4.3G) was noted in only 4.9% of remains (Figure 4.14). Transparency was mostly limited to the postcranial axial skeleton including the cervical, thoracic, lumbar, caudal vertebra and rib as well as the scapula and phalange (Table 4.11). All transparency was of a light intensity except in the rib (100%) and phalange (36%).

Excavated foramina

Excavated foramina (Plate 4.3J) were observed in 28.4% of remains in the scats (Figure 4.15). Excavated foramina were absent in the radius, tibia, carpal/tarsal and patella (Table 4.12). Excavated foramina were highly abundant on the mandible, 100% of which had excavated foramina and the atlas where two-thirds of remains were modified.

Corrosive holes

Corrosive holes (Plate 4.3D and F) were the most common digestive modification in the assemblage and were recorded on 47.9% of remains (Figure 4.15). Corrosive holes were noted in all elements (Table 4.12). They were particularly common in the caudal vertebra, 86.7% of which had corrosive holes.

Slimming

A 27.3% of remains were slimmed (Figure 4.15). Slimming (Plate 4.3A) was absent in the thoracic vertebra, pelvis and patella (Table 4.12). Slimming was highly common in the atlas (66.7%) and axis (100%), as well as the carpal/tarsal (63.6%).

Undulations

Only 2.6% of remains had undulations (Figure 4.15). These include the lumbar, caudal vertebra, rib, scapula and phalange (Table 4.12). Undulations were not seen in any of the high density remains. Where undulations (Plate 4.3 D) do occur, they are never found on more than 10% of specimens and were most common on the caudal vertebra (6.7%) and the rib (5.7%).

Cupules

Cupules occurred in 3.6% of remains (Figure 4.15). Cupules were observed in the cervical, lumbar vertebra, rib, carpal/tarsal and phalange (Table 4.12). Cupules were most commonly noted in the cervical vertebra (14.3%), carpal/tarsal (9.1%) and the rib (8.9%).

Desquamation

Desquamation (Plate 4.3E) was the rarest digestive modification in the scat assemblage, occurring on 1.3% of remains (Figure 4.15). There include the lumbar vertebra, rib and metapodial (Table 4.12). Desquamation was most common in the metapodial remains, 20% of which were modified.

Tissue retention

Typically the retention of tissue (Plate 4.3B) would indicate that digestion was not occurring, but all bones with remaining tissue bore other evidence of digestive modifications. Perhaps indicating that some tissue is resistant to digestion or that some elements, or parts thereof, were protected, by skin and fur, from being digested. A 4.2% of remains retained some tissue (Figure 4.15). These remains included vertebral fragments, lumbar, tibia and phalange elements (Table 4.12). Tissue was most commonly retained in the tibia (25%).

Digestion in the dentition

All dental (Plate 4.4) remains in the assemblage display digestion damage (Figure 4.16). This was mostly of a light (71.4%) intensity, and moderately digested remains were also observed (Table 4.13). Heavy and severe modifications were absent on the dentition. Light

digestion was noted on all incisor and 60% of lower postcanine dentition.

4.2.4. Tooth marks in the scat assemblage

As depicted in Table 4.14 a total of335 tooth marks were observed on 167 (43.5%) of remains from the honey badger scat assemblage. Figure 4.17 displays the relative frequency of tooth mark types in the assemblage. The most common tooth mark types were crush marks (28.4%) and scours (27.8%) followed by pits (21.5%), punctures were rare (2.4%). Average width of tooth marks and the standard deviation are shown in Table 4.15. Scours had the smallest average width of 0.2 mm. The average width of pits was 0.4 mm and punctures and notches had the greatest average width of 0.5 mm and 07 mm, respectively.

Tooth pits

A total of 72 tooth pits (Plate 4.5A, B and C) were observed on 34 elements (Table 4.14). Tooth pits were recorded on all elements except some axial specimens including the cranium, mandible, axis, thoracic and caudal vertebra. The radius also lacked tooth pits. Pits were most common in the tibia where they occurred on 37.5% of specimens. Of note is the appearance of carnivore tooth pits on dental remains from the scats (Plate 4.4). Tooth pits were noted on a lower postcanine and an incisor.

Punctures

Punctures (Plate 4.5D) were noted in eight remains for a total of 8 tooth marks (Table 4.14). Punctures were mostly identified on small low density elements such as the atlas, axis, caudal vertebra, rib, carpal/tarsal and metapodial. Puncture marks were also observed on some femur remains. Punctures were most common on the atlas and axis, where they occurred on a third of each.

Notches

A total of 27 notches (Plate 4.5E) were observed on 16 remains in the scat assemblage (Table 4.14). Notches were most common on the hindlimb remains occurring on the pelvis (14.3%), femur (17.6%) and tibia (25%). Other elements with notching were the lumbar vertebra, rib and scapula.

Scours

Scour marks (Plate 4.5G, H and I) were abundant in the scat assemblage with 93 marks occurring on 46 elements (Table 4.14). Scour marks appear in the appendicular skeleton, with the exception of the radius and carpal/tarsal. Several postcranial axial remains lacked scours including the atlas, axis, thoracic and caudal vertebra. Scours were most common in the mandible (50%) and in the hindlimb; pelvis (28.6%), femur (29.4%) and tibia (25%). Scour marks also appear in 11.8% of cranial remains.

Crush marks

Crush marks (Plate 4.5J, K and L) were the most common tooth marks in the assemblage, occurring 95 times (Table 4.14). They are found on all elements except the mandible, patella and metapodial. Crush marks were most commonly observed on the atlas (66.7%) and axis (66.7%). Crush marks were noted on the thoracic vertebra and the radius. In addition, a lower postcanine presented a crush mark.

Crenulated edges

A total of 40 remains with crenulated edges (Plate 4.5F) were recorded (Table 4.14). Crenulated edges occurred in the postcranial axial skeleton including the cervical, axis, lumbar vertebra and ribs. Crenulated edges also occur in the scapula and the hindlimb (pelvis and femur). Crenulated edges were most common in the axis (33.3%) and pelvis (28.6%).

4.3. Discussion and Conclusions

4.3.1. Skeletal part representation of the refuse assemblage

The honey badger refuse assemblage was characterised by high survival of the pelvis, femur and upper postcanine dentition (Table 4.16). Poor survival was observed in the scapula, humerus and lumbar vertebra, and there was an absence of all remaining vertebra and of the rib. The poor representation of these elements suggests preferential consumption of parts of the skeleton with high flesh yield. High survival of upper postcanine denbtition is linked to the high survival of maxilla remains, as there were few isolated dental remains in the refuse assemblage. Compared to the structural density assays of skeletal elements in domestic rabbit (Pavao and Stahl, 1999), it is evident that there was no correlation between element density

and survival in the refuse assemblage (Figure 4.18).

The frequency of complete elements was much higher in the refuse assemblage than in the scat assemblage (Table 4.16). Most complete remains were small compact bones like metapodial, phalange, carpal and tarsal, dentition and some vertebra. Complete remains were also observed in the pelvis, mandible, cranium and scapula. The greatest frequency of complete remains originated from feeding 3. A little less than a third of long bones were complete, and the incomplete elements in the assemblage were represented by high density portions. While some crania were extensively consumed, those from feeding 3 were left virtually intact. The occipitals and basicranium were the parts of the cranium commonly destroyed where crania were consumed, while the maxilla, frontal and parietal bones had the greatest survival. This is probably an attempt at accessing the brain more easily.

There were much greater numbers of bone remains from the refuse of feeding 3 than feedings 1 or 2. Plate 4.6 displays both carcasses from feeding 3, as recovered before cleaning. Visible in Plate 4.6A and B are two complete skins, turned inside-out with associated bone remains and all flesh stripped from the carcasses. In these carcasses the autopodia are undamaged, still in articulation and covered with skin. In carcass A, the ulna, radius and humerus of one leg extend from the autopodium in articulation. The flesh has been stripped from the remains and the skin peeled back over the distal parts of the arm. In carcass B, the tibia, femur and pelvis of one leg extend from the autopodium in articulation. These elements are separated from the skin and the flesh has been removed. Other isolated bone remains have been stripped of flesh and many of them are unmodified. The condition of these carcasses suggests an interesting feeding behaviour in that the skins were only opened at the belly. All flesh from the abdomen and thorax was stripped to the skin. The process of pulling meat and bones away from the skin and through the opening in the belly is likely what turned the skin inside-out. The legs were consumed from within the body starting at the proximal parts and the low yield autopodia were discarded. This process was followed up the neck so that the inferior part of the cranium was exposed first. In carcass B, the superior cranium remains attached to the body skin. Carnivores may preferentially open a carcass at the belly where the skin is soft and the nutritional yield high. Feeding from within the carcass allows the carnivore access to all

internal organs without having to make any further openings in the skin. Additionally in feeding 1, two partial skins were recovered along with several bone remains. These skins were opened at the anterior and posterior but otherwise undamaged, suggesting that these carcasses were fed on in the same manner as those from feeding 3.

4.3.2. Comparison with other carnivore refuse assemblages

Refuse remains in the honey badger were similar in many respects to refuse from Geoffroy's cat. The refuse assemblages were characterised by high survival in the femur and pelvis (Table 4.17). All carnivore refuse assemblages had an absence or near absence of the scapula, humerus, rib and vertebra; in the case of the coyote all elements except the distal feet were absent. Refuse assemblages in the small carnivores had a high percentage of complete remains, although the honey badger differs from the fox and Geoffroy's cat in having a much greater number of complete long bones. Most complete elements in small carnivore refuse assemblages were the small compact bones like the metapodial, phalange, carpal and tarsal, dentition and some vertebra. Most fragmented elements in the small carnivores were represented by their most robust parts. The level of fragmentation was greater in the fox and Geoffroy's cat than in the honey badger, this may be a factor of the smaller body size of the fox and Geoffroy's cat {body size in the fox is approximately 9 Kg (Walker *et al*. 1964), while male Geoffroy's cat reach about 4.9Kg (Álvarez *et al*. 2012)} compared to the honey badger (12 Kg; Estes, 1991).

Refuse remains in the fox differed from the honey badger (Lloveras *et al*. 2012). The tibia and autopodial elements had high representation in the fox, while the cranium and pelvis had poor representation. The refuse remains in the honey badger differed greatly from refuse remains described by Schmitt and Juell (1994) for the coyote. Coyote kill or feeding loci found in the summer months were noted to contain clumps of fur, viscera and articulated distal appendages. Winter feeding loci in the coyote contained only fur and scats, no bone remains. Honey badger refuse was not observed to contain fur or viscera. The honey badgers did not pluck fur from the rabbit carcasses but were more likely to discard the entire or partial skin. In feeding 3 articulated distal appendages were discarded by the honey badgers, however many

other skeletal elements were also recovered from the same feeding. Where honey badgers do discard low yield parts like the distal appendages they also discard many bone elements after stripping the flesh off. The reason for the high number of discarded remains in feeding 3 is unclear. Geoffroy's cat assemblage differs from that of the honey badger in that the cranium, mandible and tibia had good survival, and poor survival was noted in the dentition (Álvarez *et al*. 2012). Most dental remains in Geoffroy's cat were isolated. A few complete crania were noted, but most cranial remains consisted of fragments of the maxilla and zygomatic arch.

4.3.3. Skeletal part representation of the scat assemblage

The honey badger scatological assemblage was characterised by an absence of the ulna and upper postcanine dentition and a near absence of the remaining dentition, thoracic vertebra, rib, patella and autopodium (Table 4.16). The femur, cranium and humerus had high survival. The low survival of dental remains in the honey badger scats is a result of the low numbers of these remains that were consumed. Compared to the structural density assays of skeletal elements in domestic rabbit (Pavao and Stahl, 1999), it is evident that there was no correlation between element density and survival in the scat assemblage (Figure 4.19). From Figure 4.20, it is apparent that elements with high survival in the refuse assemblage (upper postcanine dentition, sacrum and metapodial) had poor survival in the scat assemblage, while elements with high survival in the scat assemblage (vertebra, humerus) had poor survival in the refuse assemblage. The skeletal part representation in the refuse and scat assemblages complement each other with little overlap. This may be a useful consideration when trying to identify the origin of palaeontological assemblages.

The honey badger had an extremely large assemblage of bones (2708) from the scats. However, only a fraction (14.2%) of these remains was identifiable. Majority of the unidentifiable remains from the scats were less than 3 mm in length. The retrieval of such a large number of very small remains likely indicates that breakage was very high and digestive corrosion very low, allowing preservation of small remains. The degree of fragmentation in the honey badger scat assemblage was high with fragments having an average maximum length of 10.9 mm. Complete remains were rare (11.7%) and most complete elements were small

compact bones like the carpal and tarsal, patella, dentition, phalange and caudal vertebra. There were no complete long bones and most elements were represented by the most resistant parts. One exception is the scapula, which was mostly represented by parts of the blade. These parts were typically remains from the natural edges of the bone, superior or inferior where bone density is greater. The most robust portion of the scapula, the glenoid was absent in scapula remains in the badger scats, possibly due to mastication on the joint in order to disarticulate the forelimb. On the other hand the delicate acromion was found in honey badger scats. It is possible that this portion of the scapula was sheared off and ingested whole along with the flesh, attached to the scapula. All cranial remains were represented by the neurocranium.

Digestive corrosion was extensive in remains from the honey badger scats, occurring on 91.9% of remains. Overall, digestive corrosion was of a light intensity with only localised areas of heavy or intense modification. The most common digestive modifications were light etching, heavy rounding and light staining. Transparency was observed in less than 5% of remains but both light and moderate transparency was observed. Corrosive pitting was uncommon and predominantly light; and severe rounding was not observed. The majority (70.8%) of remains were stained. Mostly staining was light but severe (black) staining was observed in several remains. Other commonly found digestive modifications were foramen excavation, corrosive holes and slimming. Undulations, cupules and desquamation were rare. Articulated remains and tissue retention were observed infrequently (<10%). Most dental remains were lightly digested and heavy and severe digestion were absent on these remains. Postcranial axial remains were most sensitive to digestive modification. In the rib elements, rounding and staining were heavy and a greater intensity of etching was observed, while transparency was commonly found on vertebral remains.

There was a very high frequency (43.5%) of tooth marked remains in the honey badger scat assemblage. In general tooth marks were rare on the autopodium and cranium, but were most common on the appendicular skeleton as well as the mandible, atlas and axis and rib. Tooth marks were also recorded in low frequency on dental remains. The placement of tooth marks on the remains appears to be irregular. Tooth marks were most commonly noted on the

scapular blade, rib shaft, ischium, mandibular body and neurocranium (Table 4.18). In the long bones tooth marks were frequently noted on the proximal epiphysis. The vertebral body, transverse process and zygopophyses were the most prevalent locations for tooth marks in the vertebra. The most common tooth mark types were crushes, scours and tooth pits. Punctures were rare. Punctures and notches had the largest average width of 0.5 mm, while less intrusive tooth marks like pits and scours were smaller.

Tooth marks in the honey badger were extremely small, ranging from 0.2 mm – 0.5 mm in width. Delaney-Rivera *et al*. (2009) noted that a range of small carnivores and medium-sized felids inflicted tooth pits less than 2 mm in length on size-class 2 bovid bones. The smallest tooth pits (0.7 mm) were produced by the red fox (*Vulpes vulpes*) while the small mustelid the skunk (*Mephitis mephitis*) inflicted tooth marks ranging from 0.95 mm to 3.6 mm in width. Refuse from fox dens were found to be extensively gnawed and tooth marked (Krajcarz and Krajcarz, 2012). The fox tooth marks varied from over 4 mm to less than 0.5 mm in width across a spectrum of different size prey. The very small tooth marks (<0.5mm) were presumed to be the result of action by the deciduous teeth of juvenile foxes (Plate 4.7). Thus tooth pits in the honey badger are at the lowest size range observed in small carnivores. The small tooth pit size may be a result of the small size of prey fed to honey badgers. The effort required to extract flesh is much less for a honey badger or small carnivore when feeding on small sized prey like leporids than when feeding on larger prey like bovids. Thus for a given carnivore, smaller prey would be expected to display smaller, less pronounced tooth marks than would be seen in larger prey. Caution must be utilised in a nesting or denning site where tooth marks from juvenile individuals may affect interpretations. Further studies that investigate the size and characteristics of tooth marks of carnivores in small prey would be beneficial.

4.3.4. Comparison to other carnivore scat assemblages

No taphonomic research has been previously conducted on the honey badger, and little is known of modification patterns in other members of the family. Andrews and Evans (1983) investigated microfaunal remains from collected scats from a number of small carnivores of the families Mustelidae, Herpestidae (white-tailed mongoose, *Ichneumia albicauda*) and Viverridae (*Genetta genetta*). The Mustelines included scats from the weasel (*Mustela nivalis*), polecat

(*Mustela putorius*) and stoat (*M. ermine*), as well as the pine martin (*Martes martes*). The honey badger, genet, pine martin and white-tailed mongoose were characterised by high survival of the cranium and humerus and low survival of the rib (Table 4.19). Autopodial remains were scarce in the honey badger, genet and white-tailed mongoose. Fragmentation was high in all small carnivores; particularly the *Mustela* sp. and complete remains were infrequent. Digestion in the pine martin, genet, white-tailed mongoose and *Mustela* sp. was greater than in bone and dental remains in the honey badger. Andrews and Evans identified several digestive modifications namely; rounding, polishing and corrosion. They described corrosion as a modification where the surface of the bone had been cut into and the subcortical bone exposed (this can be considered similar to corrosive pitting in the honey badger). Digestion was most intense in the *Mustela* species with deeply corroded and rounded bones and heavy digestion on the dentition. Digestion was lighter in the genet, followed by the pine martin and the white-tailed mongoose had the least intense digestion with little rounding, slight polishing and no digestion on the dentition. Articulated remains were recovered from the *Mustela* and pine martin scats, as well as the honey badger. Unlike the honey badger no tooth marks were observed in the genet, pine martin, *Mustela* or white-tailed mongoose. Thus, Andrews and Evans concluded that the skeletal part representation tended to reflect natural resistance to destruction of the bones as the most abundant elements were generally the mandible, incisors, femur and humerus. Digestive modifications, they concluded, are more important factors in distinguishing between bone assemblages of mammalian carnivores. Thus, when feeding on microfauna these very small carnivores produce bone assemblages similar in many regards to the larger honey badger modifications on mesomammals.

There were many similarities between the honey badger assemblage and leporid remains from scats of the red fox (Lloveras *et al.* 2012) and the lynx (Lloveras *et al.* 2008b). The honey badger, fox and lynx assemblages were characterised by high representation of the femur, cranium and humerus (Table 4.20). While the honey badger and fox were characterised by low representation in the dentition and autopodium. Average survival in the fox and honey badger was similar; however the maximum survival was lower in the honey badger than the fox and lynx. Fragmentation was great in scat remains from small carnivores and average fragment

size for the honey badger, fox and lynx was less than 10 mm. Complete remains were rare in the honey badger, coyote and fox but common in the lynx. Similarly, there were no complete long bones in the honey badger and fox and only a small number in the lynx. Complete remains in the honey badger, coyote, fox and lynx were limited to the small compact bones like the carpal and tarsal, patella, phalange and dentition. Most elements were represented by their most robust parts. Articulation was observed in the lynx and honey badger as well as the puma, but was absent from the fox and coyote. Nearly 100% of remains in the honey badger, fox and lynx display digestive modifications; however digestion in the fox and lynx was heavier than in the honey badger. The coyote is the only other small carnivore in which staining of digested remains was observed. Staining in the coyote was similar to the light and heavy (dark brown) staining observed in the honey badger, but did not reach the same high intensities (black staining). The frequency of tooth marked bones was far greater in the honey badger than observed in other carnivores. However the placement of tooth marks is irregular in all species.

Survival in the fox was greater than in the honey badger and the fox scapula and tibia had high representation (Table 4.20). Breakage patterns in the fox were highly similar to the honey badger, although cranial remains were represented by both the neurocranium and the zygomatic arch. Digestion in the fox remains was much greater than in the honey badger with most digestion of a heavy to severe intensity in the bone remains and of a moderate to heavy intensity in the dental remains. Tooth marks in the fox assemblage were rare occurring on only 1.7% (experimental scats) to 5.3% (collected scats) of remains. Lloveras *(ibid.)* attribute the low numbers of tooth marks in the fox scat assemblage to the high degree of breakage and digestion suffered by these remains. As breakage patterns in the fox and honey badger scat assemblages are very similar, digestion is likely an important factor masking tooth marks. This is supported by the high number of tooth marks (9.5%) in the fox refuse assemblage. This study did not investigate the presence of tooth marks in the refuse assemblage of the honey badger. Such research would be beneficial in the future as refuse remains may prove to be more intensively tooth marked and modifications on the refuse remains would be not be overlain by digestive corrosion. This is shown by Krajcarz's and Krajcarz's (2012) investigation of wild fox

refuse which found remains from fox dens to be extensively (over 40%) gnawed and tooth marked. The most common tooth marks in the fox were fractured (crenulated) edges and tooth pits, followed by punctures and scouring (Lloveras *et al*. 2012).

The lynx differed from the honey badger in the high survival of remains from the scats with high representation of the mandible, pelvis and dentition. Rib, vertebra and the carpal and tarsa had low representation. The number of complete remains was much higher in the lynx than the honey badger, however average fragment size was similar. This suggests that breakage was not high in the lynx as many elements were unbroken but where breakage did occur remains were reduced to a smaller size than seen in other carnivores. The most common cranial remain was the maxilla; however the neurocranium and zygomatic arch were also frequent. Articulated elements were more common in the lynx than the honey badger. Remains in the lynx scats were predominantly heavily digested. Tooth marks in the lynx assemblage were near absent, with only four (0.26%) remains marked with tooth punctures.

Leporid remains from wild coyote scats collected in North America were recorded to contain high numbers of dentition and a scarcity of hindlimb elements, however these are NISP values; no estimates of survival of skeletal elements was given (Schmitt and Juell, 1994). The researchers described extensive digestive corrosion on the coyote remains including pitting, polishing and rounding of edges that was more intense than digestion in the honey badger. They also described a lighter degree of staining. Staining in the coyote was characterised into four colour classes, which varied within the yellow or olive brown spectrum, which probably resembled our light brown staining; going up to a strong brown, similar to our dark brown staining. No intense (black) staining was described in the coyote. Fragmentation in the coyote was great but with survival of less robust parts of the skeleton. Cranial remains in the coyote, for example, were represented by an array of portions including the parietal, occipital and maxilla. Schmitt and Juell (1994) do not record the presence or absence of tooth marks in the coyote scat assemblage.

Álvarez *et al*. (2012) published only preliminary results from analysis of scats from Geoffroy's cat. Leporid remains in the scats from their experimental feedings show no resemblance to the honey badger scat remains. The elements that were best represented in

Geoffroy's cat were the phalange, while the mandible, tibia and pelvis were minimal. The researchers did not address digestive modifications or tooth marks. Analysis of mesomammals remains from scats of the large felid the puma (*Puma concolor*) differed greatly from honey badger remains (Montalvo *et al.* 2007). Breakage in the mesomammals was found to be less than in large prey remains but greater than in microfauna. The researchers attribute this to the carnivore consuming microfauna whole. A similar feeding pattern was also observed in the pine martin (Andrews, 1990). This has important implications for archaeological or palaeontological assemblages. A very high level of breakage in a microfaunal or mesofaunal assemblage does not necessarily denote a large sized predator, but may in fact point to a smaller predator as the more likely accumulating agent. There was a high representation of the ulna, metapodial and femur in the puma and a low representation of the scapula and dentition. Digestive corrosion in armadillo scutes was greater than digestion in the honey badger and displayed polishing and intense corrosion. However like the honey badger dental remains in the puma scats were only lightly digested.

To conclude, honey badgers feed on high yield parts, by opening the carcass at the belly and feeding from this opening alone leaving defleshed skins and some isolated or articulated bone remains. Remains from the honey badger scats include very many unidentifiable remains of a very small size. The honey badger assemblage was distinct from other small carnivores in having light digestion of bone and dental remains and a high frequency of tooth marks. Honey badger refuse resembled remains from Geoffroy's cat, however scatological remains from this felid differed greatly from those of the honey badger. Honey badger scatological remains most closely resembled the fox's. Puma destruction of mesomammal remains was greater than observed in small carnivores. Microfaunal remains from the scats of small mustelids, genet and the white-tailed mongoose have similar bone modifications to larger small carnivores on mesomammals. Thus general modification patterns or the degree of destruction on a known size prey animal can give an indication of the size range of the carnivore agent.

Table 4.1. Outline of feedings, carcass refuse and scats collected in the honey badger

Feeding	Quantity	Size	Carcass remains collected (n)	Scats collected (n)	Scats without bones (n)	Identifiable Remains (n)	Unidentifiable remains (n)	Total Remains in scats (n)
1	2	M	1	7	-	77	214	291
2	2	M	2	9	3	191	683	881
3	2	L, M	2	7	3	116	1420	1536
Totals	**6**		**5**	**23**	**6**	**384**	**2317**	**2708**

Table 4.2. Cranial survival from the honey badger refuse

	Feeding 1		Feeding 2		Feeding 3	
Skull bones	Cranium 1	Cranium 2	Cranium 1	Cranium 2	Cranium 1	Cranium 2
Maxilla	X	X	-	-	X	X
Premaxilla	X	-	-	-	X	X
Nasal	X	-	-	-	X	X
Frontal	X	-	X	X	X	X
Lacrimal	X	-	-	-	X	X
Zygomatic	X	-	-	-	X	X
Temporal	-	-	X	X	X	X
Parietal	-	-	X	X	X	X
Occipital	-	-	-	-	-	X
Sphenoid	-	-	-	-	-	X
Palantine	-	-	-	-	X	X
Petrous	-	-	-	-	-	X
Survival (%)	**49.8**	**8.3**	**24.9**	**24.9**	**74.7**	**100**

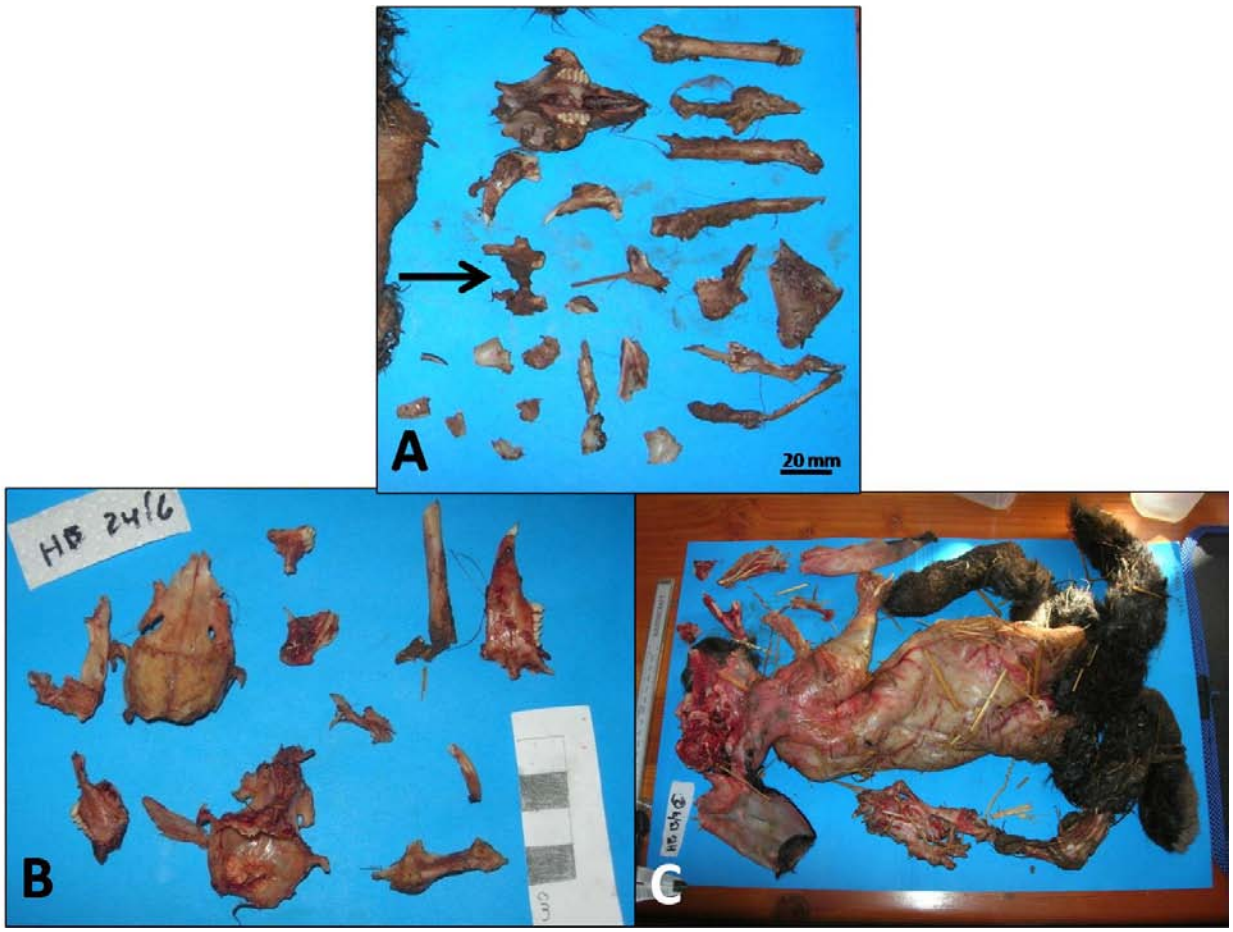
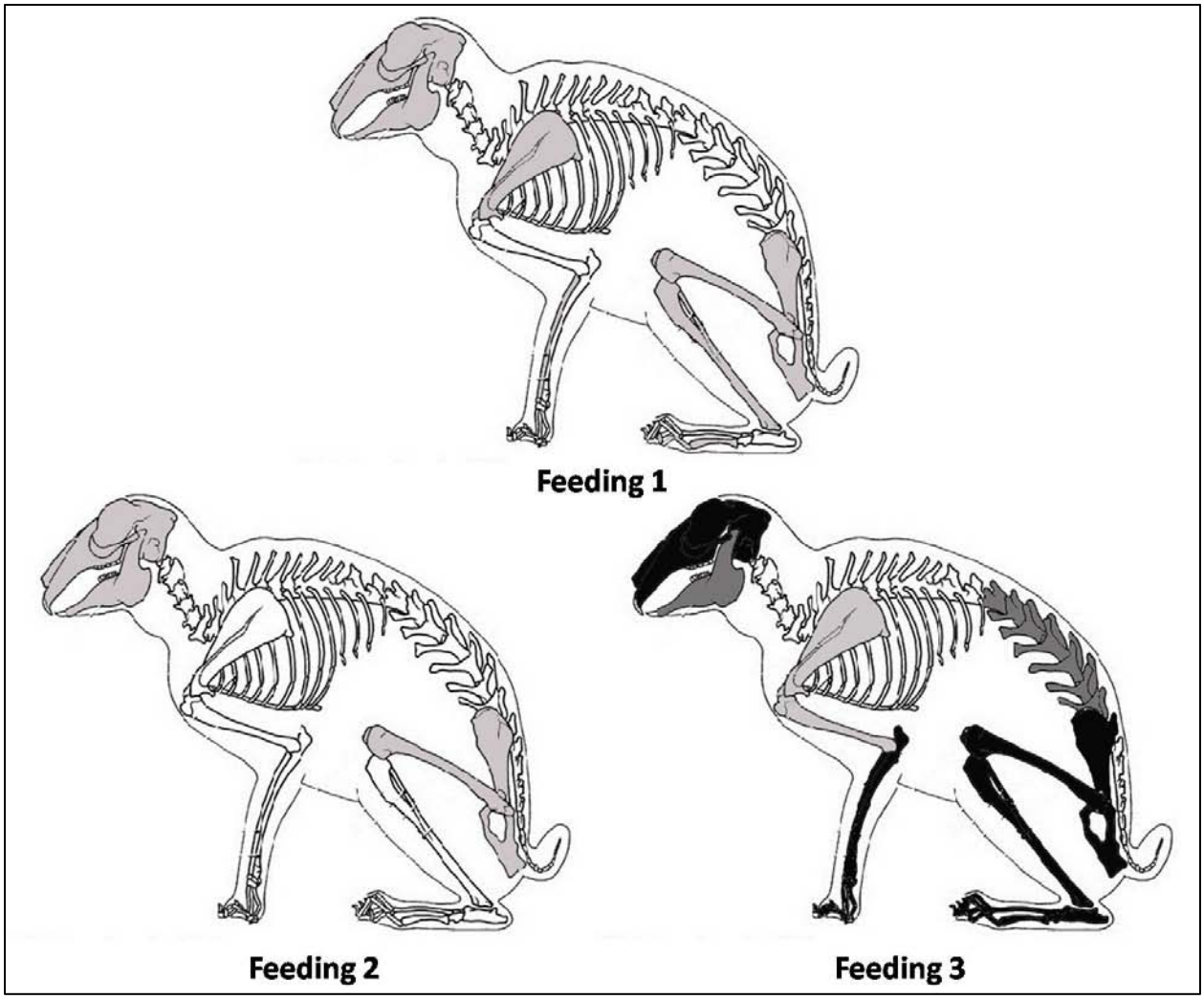


Plate 4.1. Some examples of carcass refuse collected from honey badger feedings A) feeding 1, bone fragments, second carcass represented by maxilla (arrow); B) bone remains from feeding 2; C) feeding 3 complete skin, turned inside out with various associated bone remains



Survival (%)	
	Absent
	1 - 33% Poor representation
	34 - 66% Moderate representation
	67 - 100% Good representation

Figure 4.1. A schematic representation of the relative frequency of parts in each honey badger feeding event from the refuse assemblage

Table 4.3. Anatomical composition of the honey badger refuse assemblage

	Feeding 1 NISP	Feeding 2 NISP	Feeding 3 NISP	Total MNE	Survival (%)
Cranium	2	3	2	6	47.1
Mandible	4	5	2	4	33.3
Upper Postcanine	16	3	24	43	59.7
Lower Postcanine	6	9	12	27	45
Incisor	2	2	12	16	44.4
Vertebra indet.	-	-	-	-	-
Cervical	-	-	-	-	-
Atlas	-	-	-	-	-
Axis	-	-	-	-	-
Thoracic	-	-	-	-	-
Lumbar	-	-	5	5	11.9
Sacrum	-	-	2	2	33.3
Caudal	-	-	-	-	-
Rib	-	-	-	-	-
Scapula	2	-	1	2	16.7
Humerus	-	-	1	1	8.3
Radius	1	-	3	4	33.3
Ulna	-	-	3	3	25
Pelvis	1	1	4	6	50
Femur	2	1	3	6	50
Tibia	1	-	3	3	25
Carpal	-	-	28	28	33.3
Tarsal	-	-	20	20	33.3
Patella	-	-	2	2	16.7
Metacarpal	-	-	20	20	33.3
Metatarsal	1	-	16	17	35.4
Phalange	3	-	100	103	34.3
Number of carcasses	**2**	**2**	**2**		

For abbreviations see Table 2.2, page 18

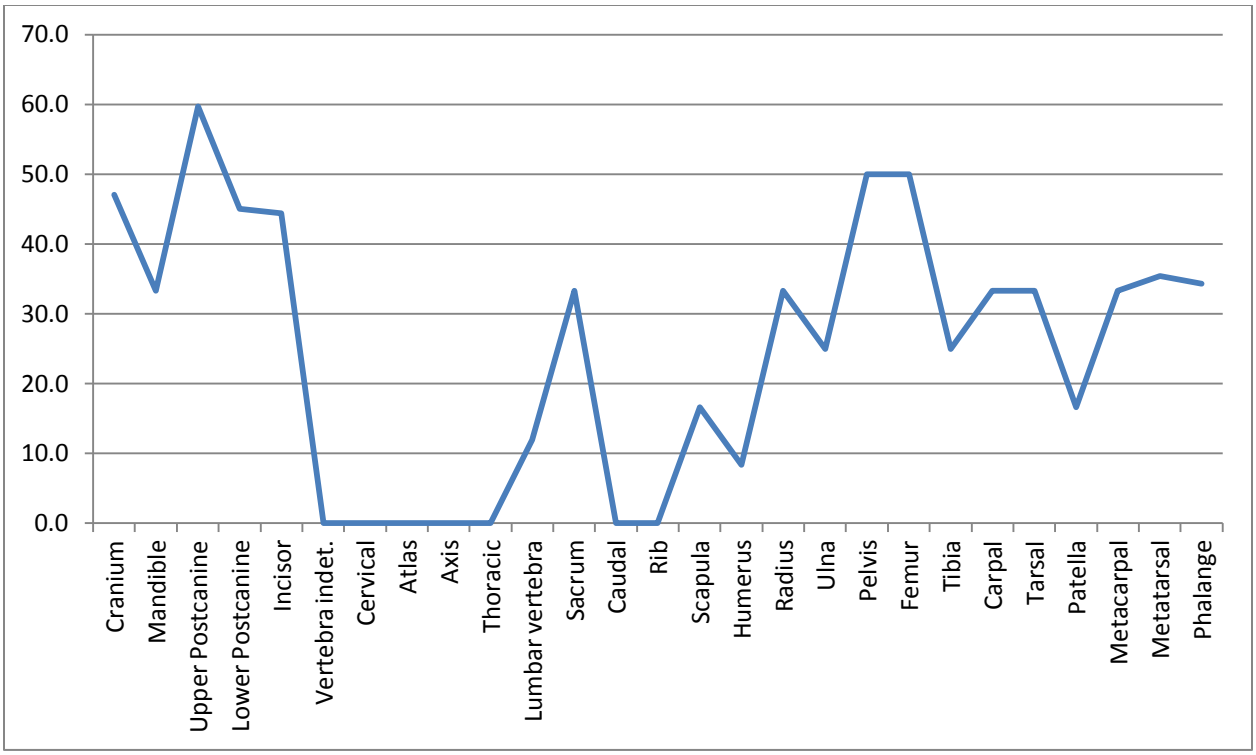


Figure 4.2. Survival (%) of elements in the honey badger refuse assemblage

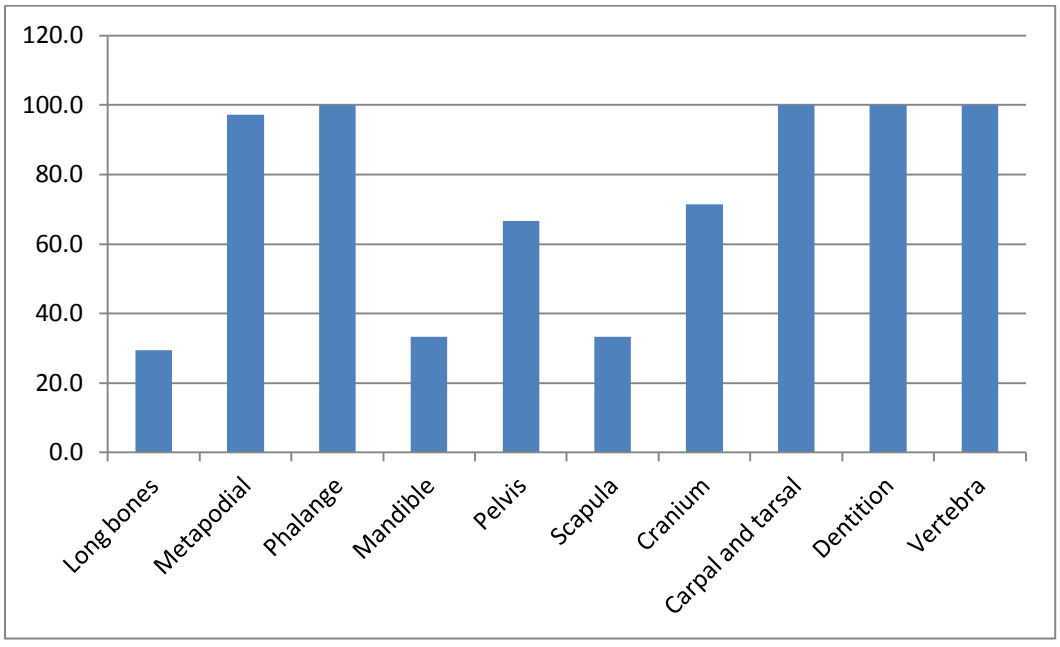


Figure 4.3. Relative frequency (%) of completeness in elements from the honey badger refuse assemblage

Table 4.4. Distribution of elements in the honey badger refuse assemblage according to breakage categories

Long bones and Metapodial	C		PE		S		SDE	
	n	%	n	%	n	%	n	%
Humerus	-	-	-	-	-	-	1	100
Radius	1	25	-	-	-	-	3	75
Ulna	1	33.3	-	-	-	-	2	66.7
Femur	1	16.7	-	-	3	50	2	33.3
Tibia	2	66.7	1	33.3	-	-	-	-
Metacarpal	20	100	-	-	-	-	-	-
Metatarsal	16	94.1	-	-	-	-	1	5.9
Phalange	103	100	-	-	-	-	-	-

	C		MBI		MBB		CP	
Mandible	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**
	3	25	6	50	1	8.3	2	16.7

	C		AIS		AISIL	
Pelvis	**n**	**%**	**n**	**%**	**n**	**%**
	4	66.7	1	16.7	1	16.7

	C		GCN		NF	
Scapula	**n**	**%**	**n**	**%**	**n**	**%**
	1	33.3	1	33.3	1	33.3

	C	
Carpal and tarsal	**n**	**%**
	48	100

	C	
Dentition	**n**	**%**
Upper postcanine	45	100
Lower postcanine	27	100
Incisor	16	100

	C	
Vertebrae	**n**	**%**
Lumbar vertebra	5	100
Sacrum	2	100

For abbreviations and explanations see Table 2.2, page 18

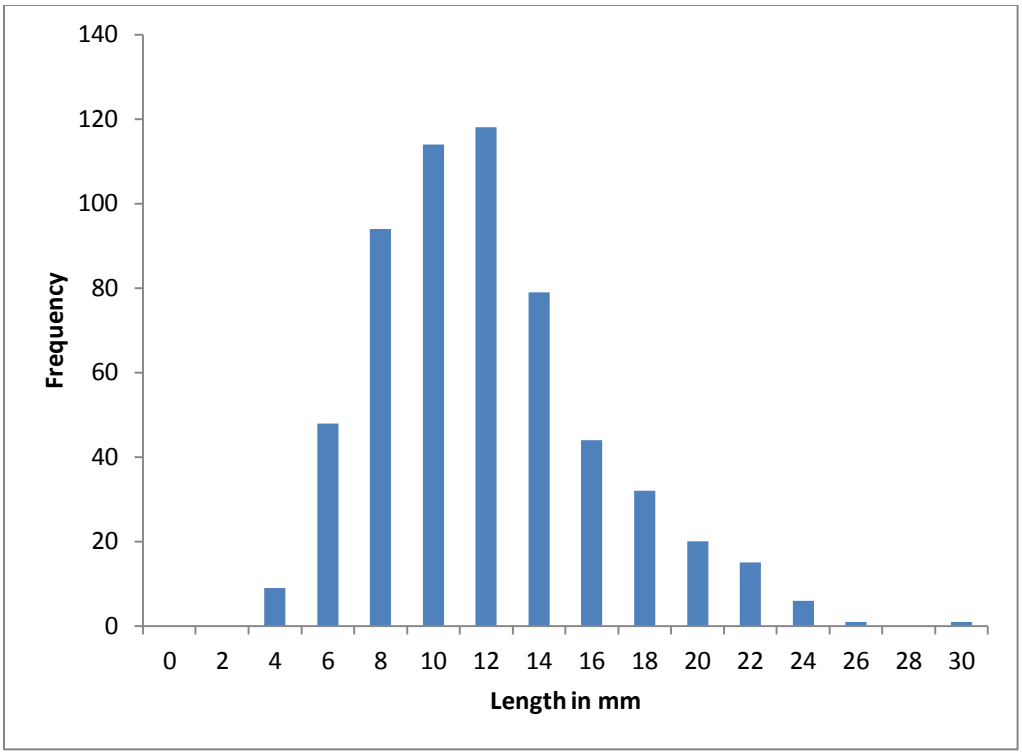
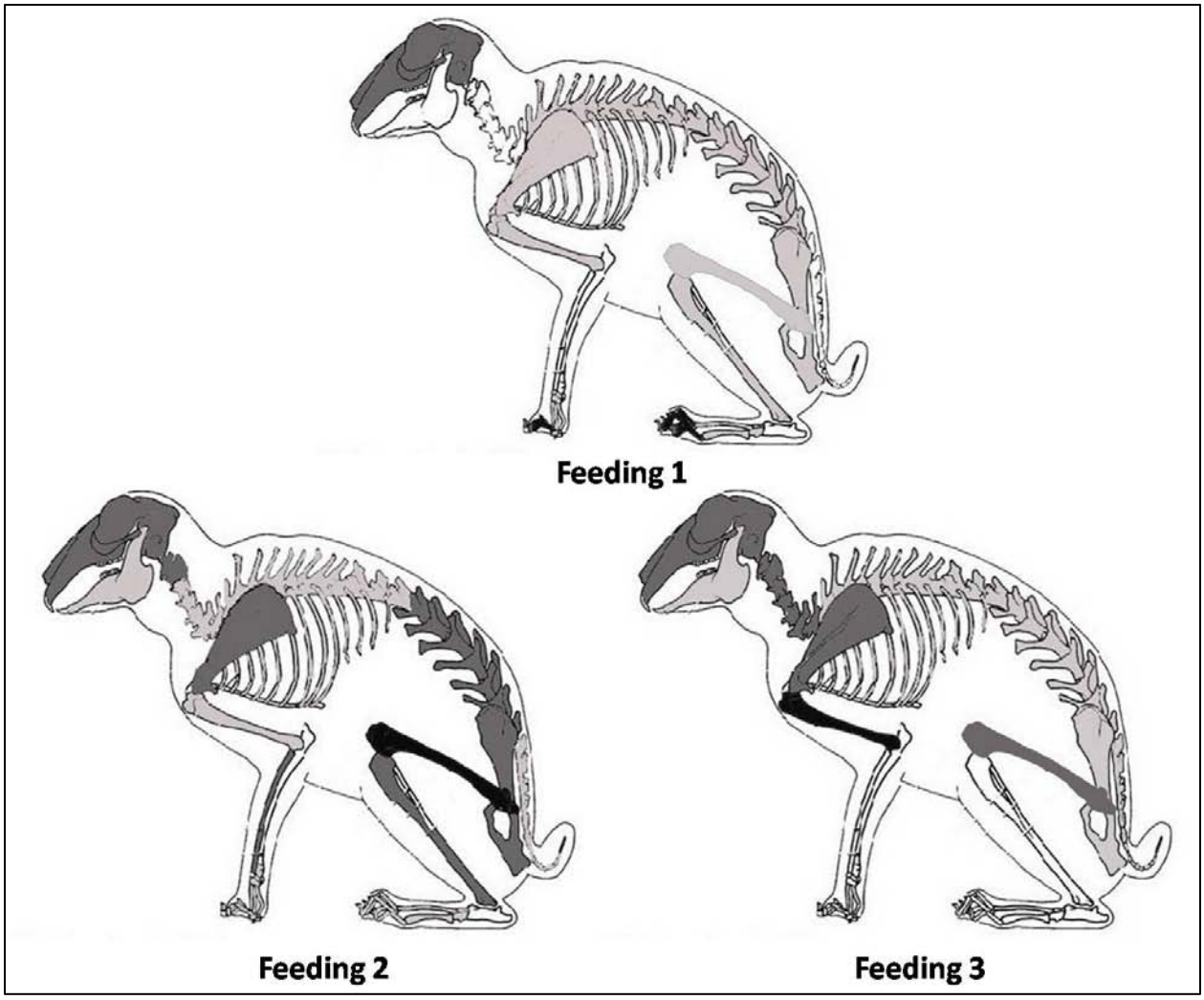


Figure 4.4. Histogram showing the maximum lengths of identifiable remains in the honey badger scat assemblage



Survival (%)	
	Absent
	1 - 33% Poor representation
	34 - 66% Moderate representation
	67 - 100% Good representation

Figure 4.5. A schematic representation of the relative frequency of parts in each honey badger feeding event from the scat assemblage

Table 4.5. Anatomical composition of the honey badger scat assemblage

Skeletal Element	NISP	% NISP	MNE	ES from feeding (%)	Survival (%)
Cranium	17	4.3	3	52.9	50
Mandible	2	0.5	2	66.7	16.7
Upper Postcanine	-	-	-	40.3	-
Lower Postcanine	5	1.3	5	55	8.3
Incisor	2	0.5	2	55.6	5.6
Vertebra indet.	60	15.3	11	100	4.5
Cervical	14	3.6	8	100	26.7
Atlas	3	0.8	2	100	33.3
Axis	3	0.8	2	100	33.3
Thoracic	8	2.0	7	100	9.0
Lumbar	81	20.7	13	88.1	31
Sacrum	-	-	-	66.7	-
Caudal	15	3.8	13	100	13.5
Rib	56	14.3	13	100	8.3
Scapula	27	6.9	4	83.3	33.3
Humerus	6	1.5	6	91.7	50
Radius	2	0.5	2	66.7	16.7
Ulna	-	-	-	75	-
Pelvis	7	1.8	4	50	33.3
Femur	17	4.3	10	50	50
Tibia	8	2.0	5	75	41.7
Carpal / Tarsal	11	2.8	10	66.7	6.9
Patella	1	0.3	1	83.3	8.3
Metapodial	10	2.6	9	65.7	8.3
Phalange	36	9.2	30	65.7	10
Total	**391**		**162**		

Abbreviations: NISP, Number of Identified Elements; %NISP, Number of Identified Elements expressed as a percentage of the whole assemblage; MNE, Minimum Number of Elements; ES, Expected survival after feeding

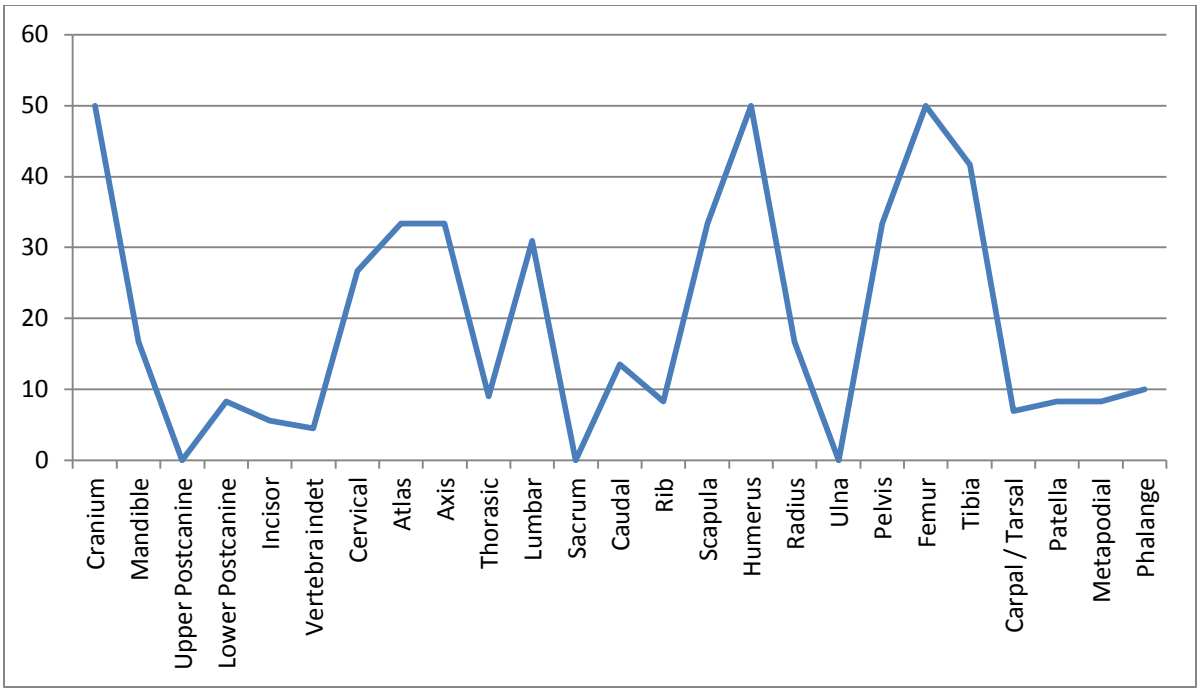


Figure 4.6. Survival (%) of elements in the honey badger scat assemblage

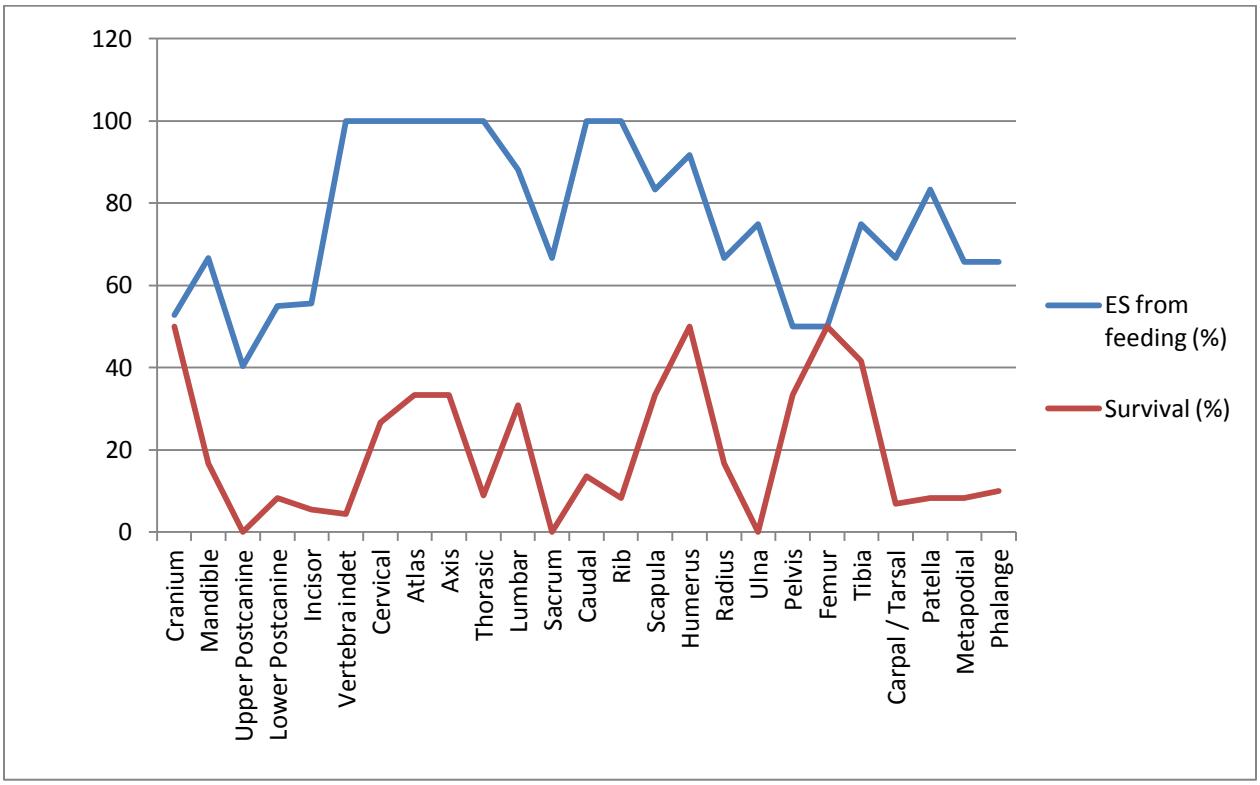


Figure 4.7. Expected survival (ES) of elements after feeding against survival of elements from the honey badger scat assemblage

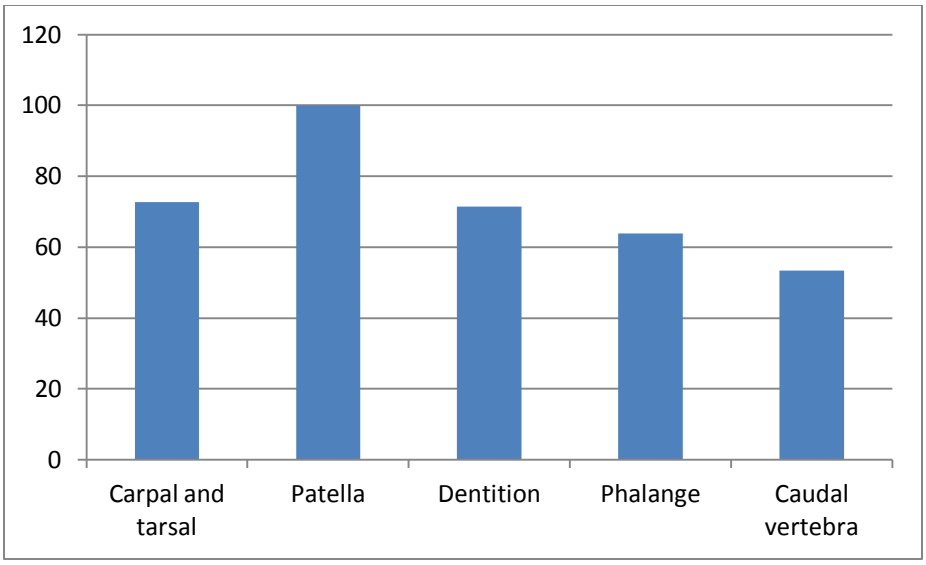


Figure 4.8. Relative frequency (%) of completeness in elements from the honey badger scat assemblage

Table 4.6. Distribution of elements in the honey badger scat assemblage according to breakage categories

	A		AISIL		AIL		IS		IL	
Pelvis	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**N**	**%**
	1	14.3	1	14.3	1	14.3	3	42.9	1	14.3
	GC		**GCN**		**NF**		**F**		**ACR**	
Scapula	**N**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**
	1	3.7	1	3.7	3	11.1	16	59.3	6	22.2
	HT		**S**		**HTS**					
Rib	**n**	**%**	**n**	**%**	**N**	**%**				
	6	10.7	43	76.8	7	12.5				
	MBI		**CP**							
Mandible	**N**	**%**	**n**	**%**						
	1	50	1	50						
	C		**F**							
Carpal and Tarsal	**n**	**%**	**N**	**%**						
	8	72.7	3	27.3						
	C		**F**							
Dentition	**N**	**%**	**n**	**%**						
Incisor	2	100	-	-						
Lower Postcanine	3	60	2	30						
	NC									
Cranium	**N**	**%**								
	17	100								
	C									
Patella	**n**	**%**								
	1	100								

Table 4.6 (continued). Distribution of elements in the honey badger scat assemblage according to breakage categories

	C		VB		VE		VA		SP		TP		ZYG	
Vertebra	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**
Vertebra indet.	-	-	29	48.3	13	21.7	11	18.3	3	5	2	3.3	2	3.3
Atlas	-	-	-	-	-	-	-	-	-	-	1	33.3	2	66.7
Axis	-	-	2	66.7	-	-	1	33.3	-	-	-	-	-	-
Cervical	-	-	-	-	-	-	2	14.3	-	-	2	14.3	10	71.4
Thoracic	-	-	-	-	-	-	1	12.5	7	87.5	-	-	-	-
Lumbar	-	-	7	8.6	1	1.2	3	3.7	6	7.4	24	29.6	40	49.4
Caudal	8	53.3	5	33.3	-	-	1	6.7	1	6.7	-	-	-	-
			43		**14**		**19**		**17**		**29**		**54**	

Long bones, metapodial and phalange	C		PE		PES		S		SDE		DE	
	n	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**
Humerus	-	-	5	83.3	-	-	-	-	1	16.7	-	-
Radius	-	-	-	-	-	-	1	50	-	-	1	50
Femur	-	-	10	58.8	2	11.8	-	-	-	-	5	29.4
Tibia	-	-	4	50	1	12.5	3	37.5	-	-	-	-
Metapodial	-	-	3	30	1	10	-	-	6	60	-	-
Phalange	23	63.9	8	22.2	2	5.6	-	-	3	8.3	-	-
	23		**30**		**6**		**4**		**10**		**6**	

For abbreviations and explanations see Table 2.2, page 18

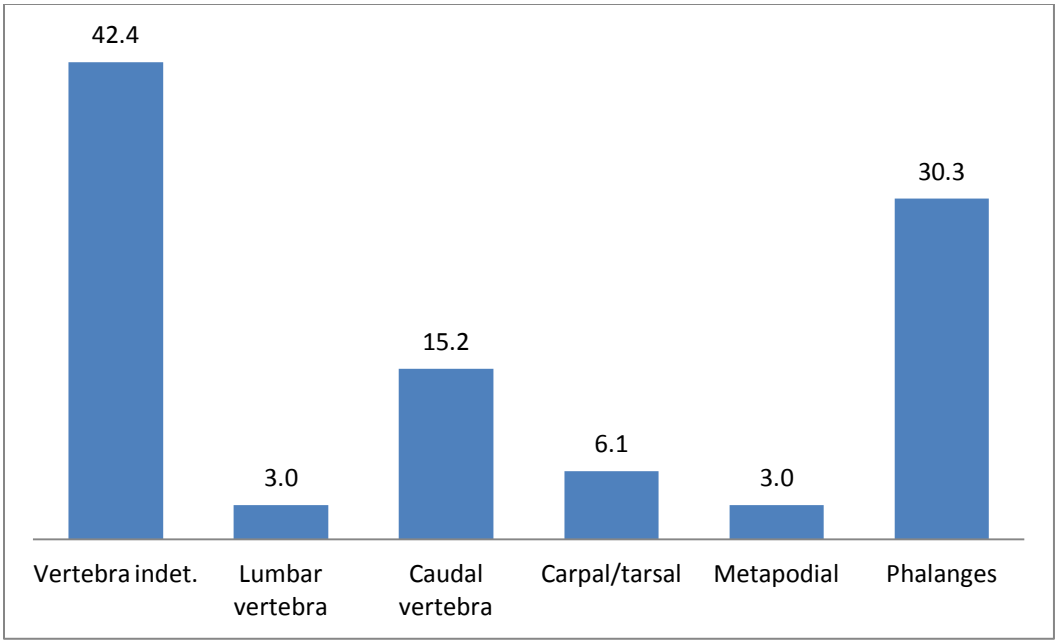


Figure 4.9. Relative frequency (%) of articulated remains in the honey badger scat assemblage

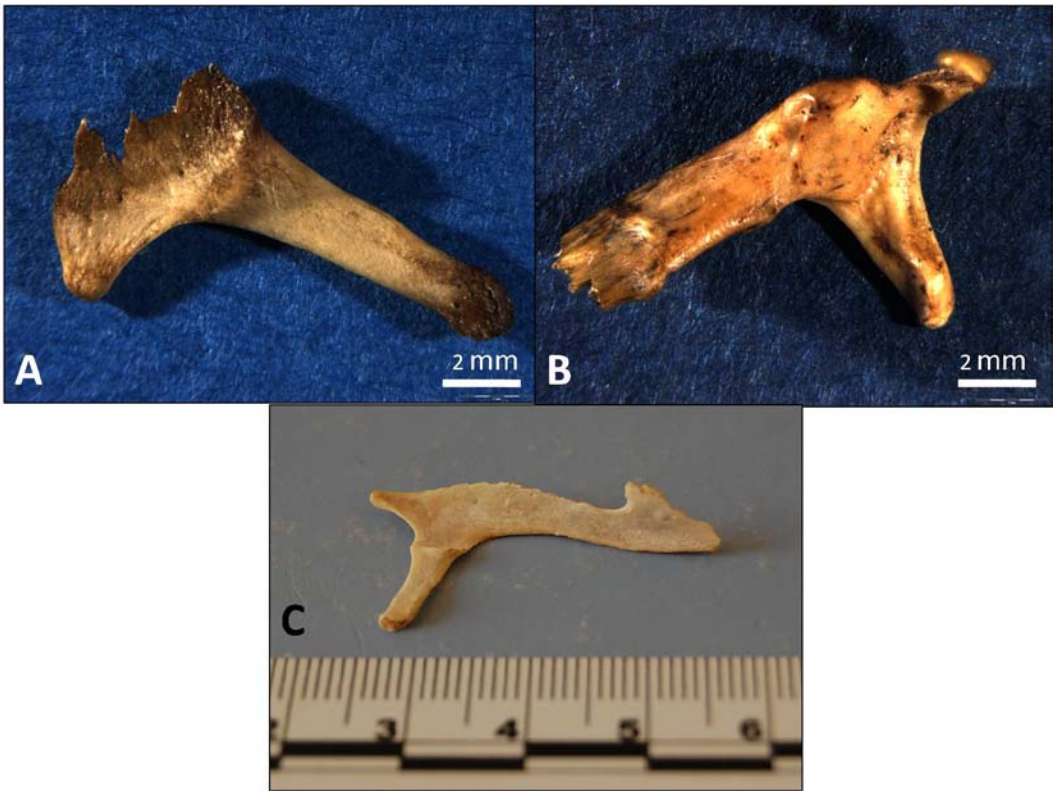


Plate 4.2. Comparison of acromia from the honey badger scats and a non-ingested carcass A) and B) acromia from the honey badger scats assemblage; C) acromion from a non-ingested rabbit carcass

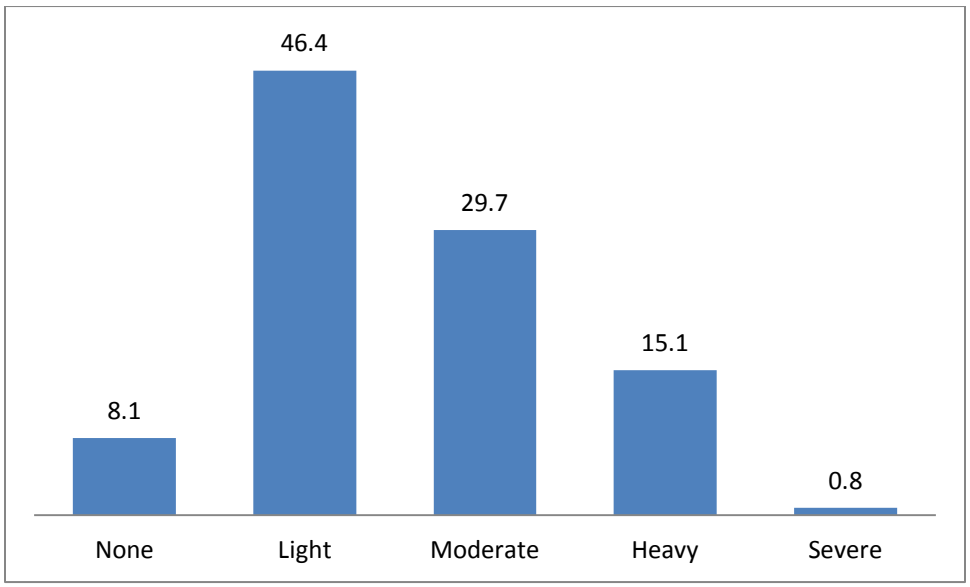


Figure 4.10. Relative frequency (%) of surface etching in the honey badger scat assemblage

Table 4.7. Intensity of surface etching on elements in the honey badger scat assemblage

	0 - None		1 - Light		2 - Moderate		3 - Heavy		4 - Severe	
	n	%	n	%	n	%	n	%	n	%
Cranium	5	29.4	9	52.9	3	17.6	-	-	-	-
Mandible	-	-	1	50	-	-	1	50	-	-
Vertebra indet.	9	15	23	38.3	17	28.3	11	18.3	-	-
Cervical	1	7.1	8	57.1	3	21.4	2	14.3	-	-
Atlas	-	-	3	100	-	-	-	-	-	-
Axis	-	-	2	66.7	1	33.3	-	-	-	-
Thoracic	-	-	5	62.5	-	-	3	37.5	-	-
Lumbar	1	1.2	34	42	31	38.3	14	17.3	1	1.2
Caudal	1	6.7	8	53.3	3	20	2	13.3	-	-
Rib	2	3.6	16	28.6	26	46.4	12	21.4	-	-
Scapula	-	-	14	51.9	11	40.7	2	7.4	-	-
Humerus	1	16.7	5	83.3	-	-	-	-	-	-
Radius	-	-	-	-	-	-	2	100	-	-
Pelvis	-	-	3	42.9	3	42.9	1	14.3	-	-
Femur	1	5.9	9	52.9	3	17.6	4	23.5	-	-
Tibia	-	-	1	12.5	4	50	2	25	1	12.5
Carpal/tarsal	1	9.1	8	72.7	1	9.1	-	-	1	9.1
Patella	-	-	-	-	1	100	-	-	-	-
Metapodial	-	-	8	80	1	10	1	10	-	-
Phalange	6	16.7	23	63.9	5	13.9	2	5.6	-	-

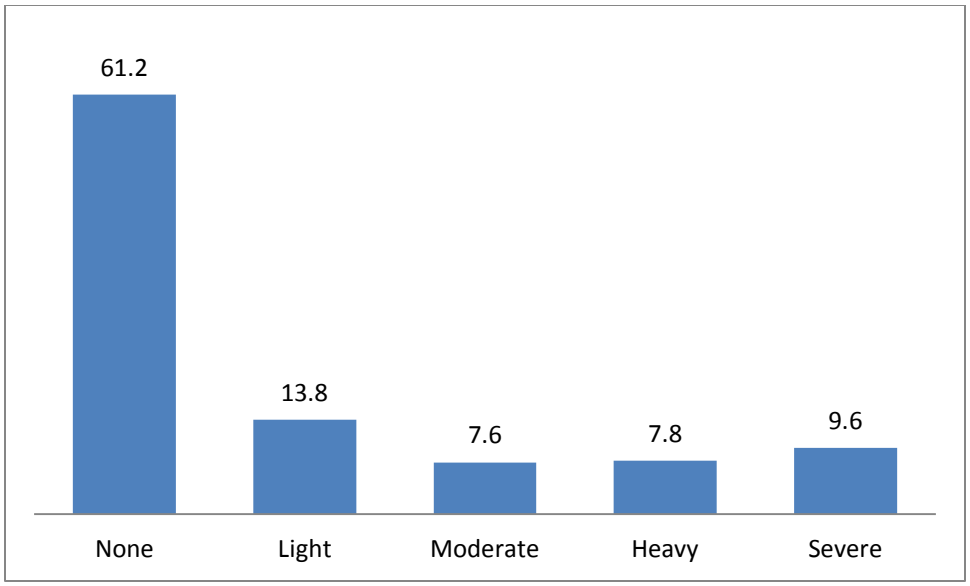


Figure 4.11. Relative frequency (%) of corrosive pitting in the honey badger scat assemblage

Table 4.8. Intensity of corrosive pitting on elements in the honey badger scat assemblage

	0 - None		1 - Light		2 - Moderate		3 - Heavy		4 - Severe	
	n	%	n	%	n	%	n	%	n	%
Cranium	16	94.1	1	5.9	-	-	-	-	-	-
Mandible	1	50	-	-	1	50	-	-	-	-
Vertebra indet.	34	56.7	9	15	4	6.7	9	15	4	6.7
Cervical	7	50	1	7.1	3	21.4	2	14.3	1	7.1
Atlas	3	100	-	-	-	-	-	-	-	-
Axis	2	66.7	-	-	-	-	-	-	1	33.3
Thoracic	4	50	-	-	1	12.5	-	-	3	37.5
Lumbar	39	48.1	16	19.8	6	7.4	7	8.6	13	16
Caudal	5	33.3	4	26.7	-	-	3	20	3	20
Rib	31	55.4	7	12.5	6	10.7	6	10.7	6	10.7
Scapula	23	85.2	-	-	-	-	1	3.7	3	11.1
Humerus	4	66.7	1	17	1	17	-	-	-	-
Radius	1	50	-	-	-	-	-	-	1	50
Pelvis	5	71.4	1	14.3	-	-	1	14.3	-	-
Femur	11	64.7	3	17.6	1	5.9	1	5.9	1	5.9
Tibia	5	62.5	-	-	3	37.5	-	-	-	-
Carpal/tarsal	5	45.5	5	45.5	1	9.1	-	-	-	-
Patella	-	-	-	-	-	-	-	-	1	100
Metapodial	8	80	2	20	-	-	-	-	-	-
Phalange	31	86.1	3	8.3	2	5.6	-	-	-	-

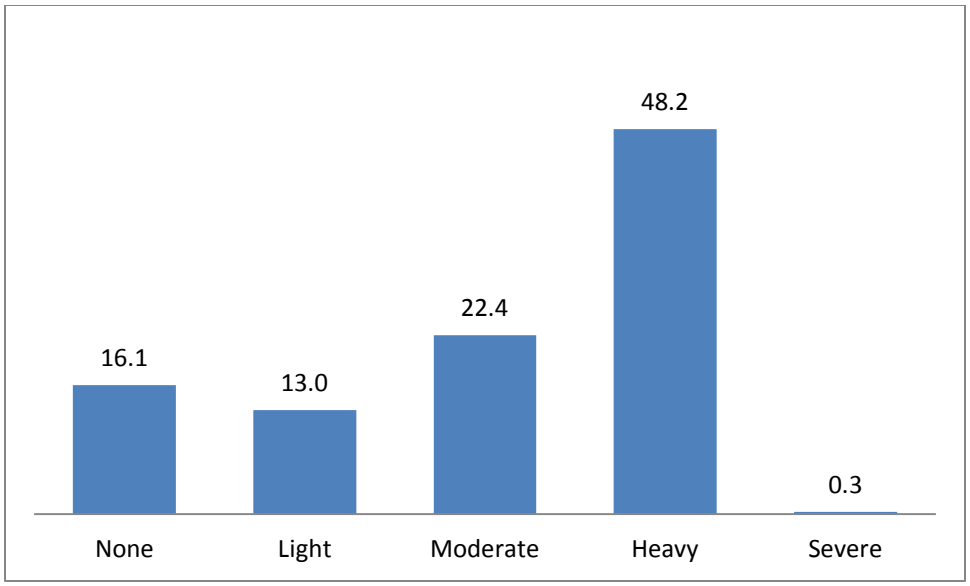


Figure 4.12. Relative frequency (%) of rounding of edges in the honey badger scat assemblage

Table 4.9. Intensity of rounding of edges on elements in the honey badger scat assemblage

	0 - None		1 - Light		2 - Moderate		3 - Heavy		4 - Severe	
	n	%	n	%	n	%	n	%	n	%
Cranium	2	11.8	1	5.9	2	11.8	12	70.6	-	-
Mandible	-	-	-	-	1	50	1	50	-	-
Vertebra indet.	11	18.3	4	6.7	21	35	24	40	-	-
Cervical	-	-	2	14.3	4	28.6	8	57.1	-	-
Atlas	-	-	-	-	2	66.7	1	33.3	-	-
Axis	1	33.3	-	-	1	33.3	1	33.3	-	-
Thoracic	-	-	1	12.5	3	37.5	4	50	-	-
Lumbar	4	4.9	11	13.6	22	27.2	44	54.3	-	-
Caudal	5	33.3	1	6.7	3	20	6	40	-	-
Rib	1	1.8	9	16.1	8	14.3	38	67.9	-	-
Scapula	9	33.3	3	11	3	11	12	44.4	-	-
Humerus	2	33.3	2	33.3	2	33.3	-	-	-	-
Radius	-	-	1	50	-	-	1	50	-	-
Pelvis	1	14.3	1	14.3	1	14.3	4	57.1	-	-
Femur	-	-	6	35.3	2	11.8	9	52.9	-	-
Tibia	1	12.5	2	25	1	12.5	4	50	-	-
Carpal/tarsal	5	45.5	2	18.2	-	-	4	36.4	-	-
Patella	1	100	-	-	-	-	-	-	-	-
Metapodial	-	-	1	10	5	50	3	30	1	10
Phalange	19	52.8	3	8.3	5	13.9	9	25	-	-

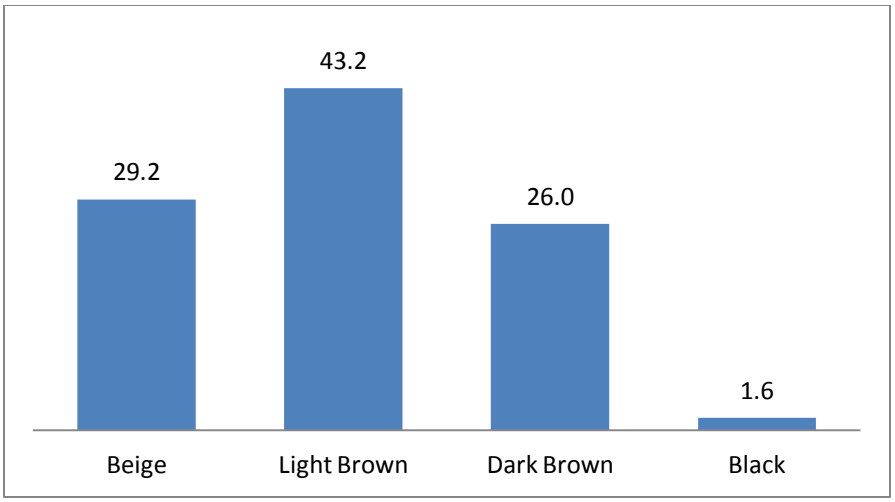


Figure 4.13. Relative frequency (%) of staining in the honey badger scat assemblage

Table 4.10. Intensity of staining on elements in the honey badger scat assemblage

	Beige Unstained		Light Brown Light staining		Dark Brown Heavy staining		Black Severe staining	
	n	%	n	%	n	%	n	%
Cranium	4	23.5	5	29.4	6	35.3	2	11.8
Mandible	-	-	1	50	1	50	-	-
Vertebra indet.	8	13.3	29	48.3	22	36.7	1	1.7
Cervical	3	21.4	5	35.7	5	35.7	1	7.1
Atlas	-	-	1	33.3	2	66.7	-	-
Axis	1	33.3	1	33.3	1	33.3	-	-
Thoracic	2	25	1	12.5	5	62.5	-	-
Lumbar	16	19.8	46	56.8	19	23.5	-	-
Caudal	3	20	7	46.7	5	33.3	-	-
Rib	17	30.4	22	39.3	17	30.4	-	-
Scapula	7	25.9	13	48.1	6	22.2	1	3.7
Humerus	2	33.3	3	50	1	16.7	-	-
Radius	-	-	2	100	-	-	-	-
Pelvis	2	28.6	4	57.1	-	-	1	14.3
Femur	3	17.6	8	47.1	6	35.3	-	-
Tibia	2	25	5	62.5	1	12.5	-	-
Carpal/tarsal	6	54.5	3	27.3	2	18.2	-	-
Patella	-	-	1	100	-	-	-	-
Metapodial	5	50	4	40	1	10	-	-
Phalange	29	80.6	5	13.9	-	-	-	-
Totals	**110**		**166**		**100**		**6**	

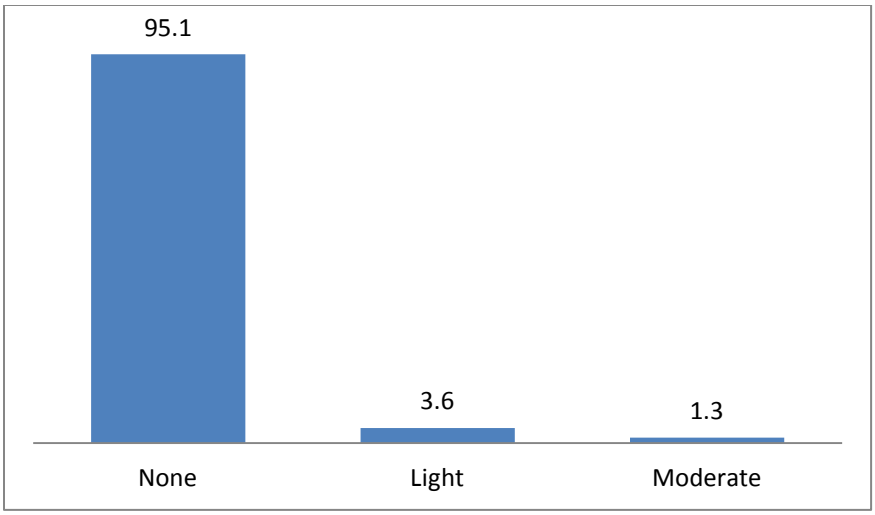


Figure 4.14. Relative frequency (%) of transparency in the honey badger scat assemblage

Table 4.11. Intensity of transparency on elements in the honey badger scat assemblage

	1 - Light		2 - Moderate	
	n	%	n	%
Cervical	2	100	-	-
Thoracic	1	100	-	-
Lumbar	2	100	-	-
Caudal	1	100	-	-
Rib	-	-	1	100
Scapula	1	100	-	-
Phalange	7	64	4	36

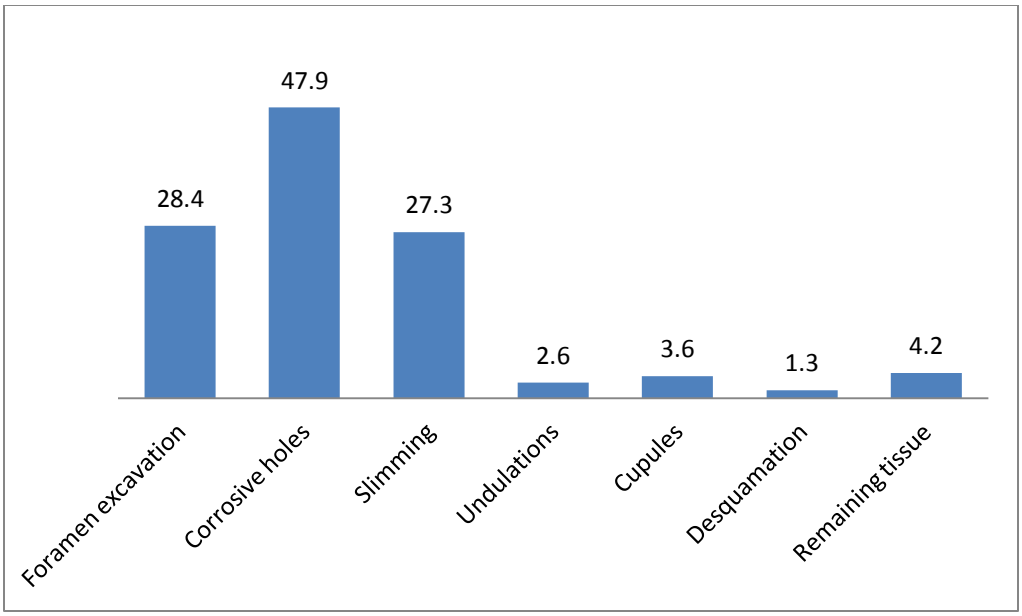


Figure 4.15. Relative frequency (%) of digestive modifications in the honey badger scat assemblage

Table 4.12. Digestive modifications on elements in the honey badger scat assemblage

	Foramen Excavation		Corrosive holes		Slimming		Undulations		Cupules		Desquamation		Tissue retained	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Cranium	8	47.1	6	35.3	1	5.9	-	-	-	-	-	-	-	-
Mandible	2	100	1	50	1	50	-	-	-	-	-	-	-	-
Vertebra indet.	11	18.3	31	51.7	22	36.7	2	3.3	1	1.7	-	-	9	15
Cervical	4	28.6	8	57.1	4	28.6	-	-	2	14.3	-	-	-	-
Atlas	2	66.7	2	66.7	2	66.7	-	-	-	-	-	-	-	-
Axis	1	33.3	2	66.7	3	100	-	-	-	-	-	-	-	-
Thoracic	2	25	3	37.5	-	-	-	-	-	-	-	-	-	-
Lumbar	27	33.3	46	56.8	16	19.8	2	2.5	3	3.7	1	1.2	1	1.2
Caudal	4	26.7	13	86.7	4	26.7	1	6.7	-	-	-	-	-	-
Rib	27	48.2	24	42.9	9	16.1	3	5.4	5	8.9	2	3.6	-	-
Scapula	11	40.7	11	40.7	3	11.1	1	3.7	-	-	-	-	-	-
Humerus	1	16.7	2	33.3	2	33.3	-	-	-	-	-	-	-	-
Radius	-	-	1	50	1	50	-	-	-	-	-	-	-	-
Pelvis	2	28.6	2	28.6	-	-	-	-	-	-	-	-	-	-
Femur	1	5.9	11	64.7	4	23.5	-	-	-	-	-	-	-	-
Tibia	-	-	1	12.5	4	50	-	-	-	-	-	-	2	25
Carpal/tarsal	-	-	6	54.5	7	63.6	-	-	1	9.1	-	-	-	-
Patella	-	-	1	100	-	-	-	-	-	-	-	-	-	-
Metapodial	1	10	5	50	6	60	-	-	-	-	2	20	-	-
Phalange	5	13.9	8	22.2	16	44.4	1	2.8	2	5.6	-	-	4	11.1
Totals	**109**		**184**		**105**		**10**		**14**		**5**		**16**	

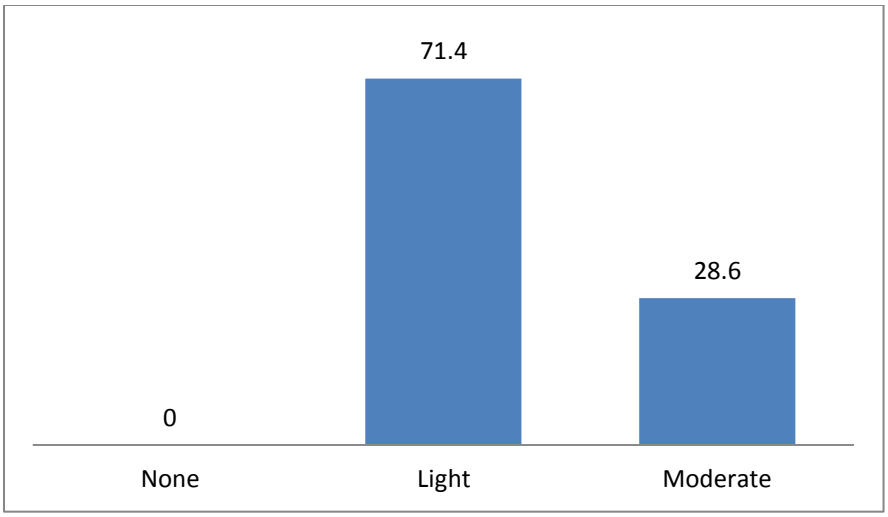


Figure 4.16. Relative frequency (%) of digestion in dental remains in the honey badger scat assemblage

Table 4.13. Intensity of digestion in dental remains in the honey badger scat assemblage

	Light		Moderate	
	n	%	n	%
Lower Postcanine	3	60	2	40
Incisor	2	100	-	-

Table 4.14. Frequency of tooth marks on elements in the honey badger scat assemblage

	Pits			Punctures			Notches			Scours			Crush		Crenulated edges		Total		
	n	%	FM	n	%	FM	n	%	FM	n	%	FM	n	%	n	%	n	%	FM
Cranium	-	-	-	-	-	-	-	-	-	2	11.8	11	2	11.8	-	-	4	23.5	13
Mandible	-	-	-	-	-	-	-	-	-	1	50	2	-	-	-	-	1	50	2
Vertebra indet.	2	3.3	2	-	-	-	2	3.3	3	2	3.3	4	13	21.7	4	6.7	22	36.7	26
Cervical	1	7.1	1	-	-	-	-	-	-	1	7.1	2	5	35.7	1	7.1	6	42.9	9
Atlas	1	33.3	5	1	33.3	1	-	-	-	-	-	-	2	66.7	-	-	3	100	8
Axis	-	-	-	1	33.3	1	-	-	-	-	-	-	2	66.7	1	33.3	3	100	4
Thoracic	-	-	-	-	-	-	-	-	-	-	-	-	3	37.5	-	-	3	37.5	3
Lumbar	5	6.2	9	-	-	-	4	4.9	8	14	17.3	31	23	28.4	14	17.3	39	48.1	85
Caudal	-	-	-	1	6.7	1	-	-	-	-	-	-	2	13.3	-	-	3	20	3
Rib	7	12.5	16	1	1.8	1	1	1.8	1	6	10.7	10	20	35.7	7	12.5	30	53.6	55
Scapula	6	22.2	14	-	-	-	3	11.1	5	6	22.2	9	9	33.3	10	37	18	66.7	47
Humerus	2	33.3	3	-	-	-	-	-	-	1	16.7	1	2	33.3	-	-	4	66.7	6
Radius	-	-	-	-	-	-	-	-	-	-	-	-	1	50	-	-	1	50	1
Pelvis	1	14.3	3	-	-	-	1	14.3	2	2	28.6	8	1	14.3	2	28.6	4	57.1	16
Femur	2	11.8	3	2	11.8	2	3	17.6	4	5	29.4	9	4	23.5	1	11.8	10	58.8	23
Tibia	3	37.5	7	-	-	-	2	25	4	2	25	2	4	23.5	-	-	5	62.5	17
Carpal/tarsal	1	9.1	5	1	9.1	1	-	-	-	-	-	-	1	9.1	-	-	3	27.3	7
Patella	1	100	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	100	1
Metapodial	1	10	2	1	10	1	-	-	-	2	20	2	-	-	-	-	3	30	5
Phalange	1	2.8	1	-	-	-	-	-	-	2	5.6	2	1	2.8	-	-	4	11.1	4
Totals	**34**		**72**	**8**		**8**	**16**		**27**	**46**		**93**	**95**		**40**		**167**		**335**

Abbreviations: n, the frequency of elements with tooth marks; % n, relative to the total number of that element as a percentage; FM, frequency of individual tooth marks. Total n indicates the number of elements with tooth marks; Total % indicates the percentage of the total elements that are tooth marked and Total FM indicates the number of individual tooth marks from each element.

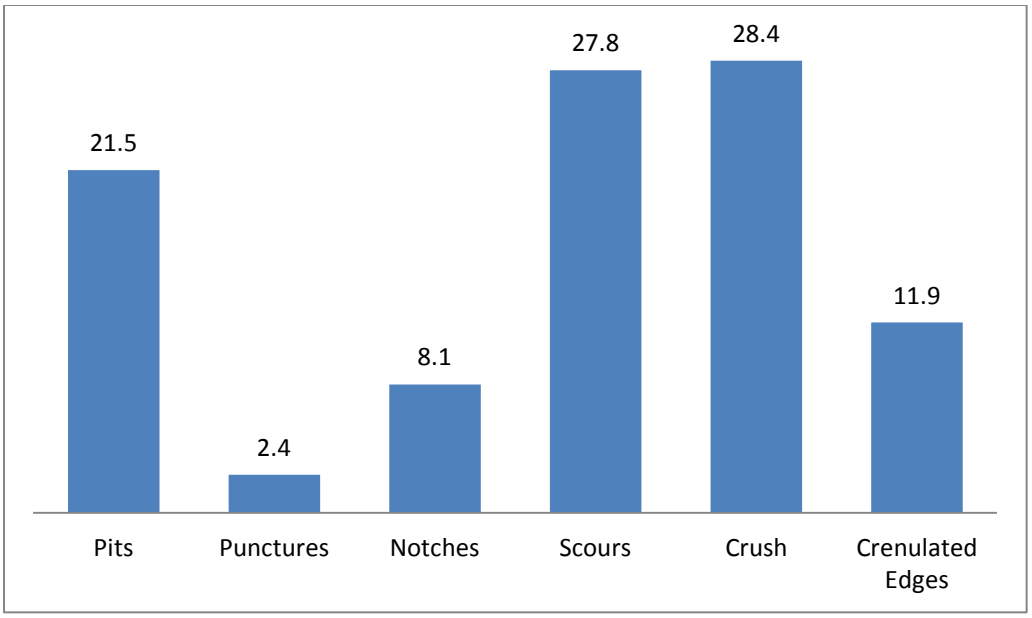


Figure 4.17. Relative frequency (%) of tooth marks in the honey badger scat assemblage

Table 4.15. Average width of tooth marks in the honey badger scat assemblage

	Average	Standard Deviation
Pits	0.4	0.2
Punctures	0.5	0.3
Scours	0.2	0.1
Notches	0.7	0.3
Dentition	0.5	-

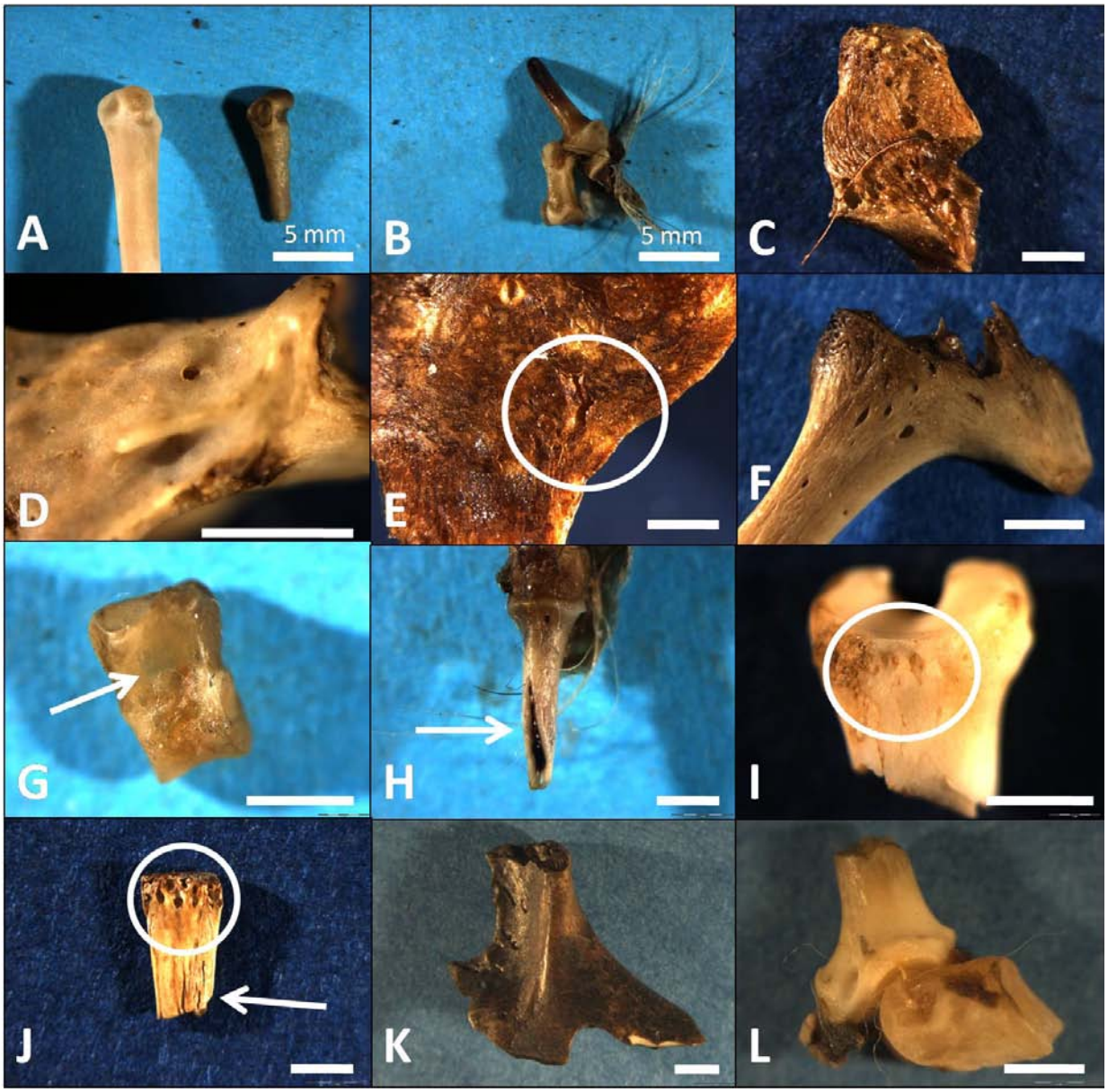


Plate 4.3. Alterations on remains from the honey badger scat assemblage produced by digestion A) metapodial from scats (right) showing moderate etching and intensive slimming compared to a non-ingested metapodial (left); B) articulated distal and middle phalanges with sesamoids, bones are lightly stained (light brown) and connective tissue with a few hairs is also present; C) a zygopophysis of a lumbar vertebra with severe etching; D) caudal vertebra with undulations and corrosive holes; E) moderately etched lumbar vertebra showing surface exfoliation or desquamation; F) acromion process from the scapula with corrosive holes; G) middle phalange with light transparency; H) distal phalange with heavy rounding of the broken edge; I) light pitting on a proximal phalange; J) rib with heavy corrosive pitting (circle) and excavated foramina (arrow); K) pelvic fragment with severe (black) staining; L) articulated proximal and middle phalanges

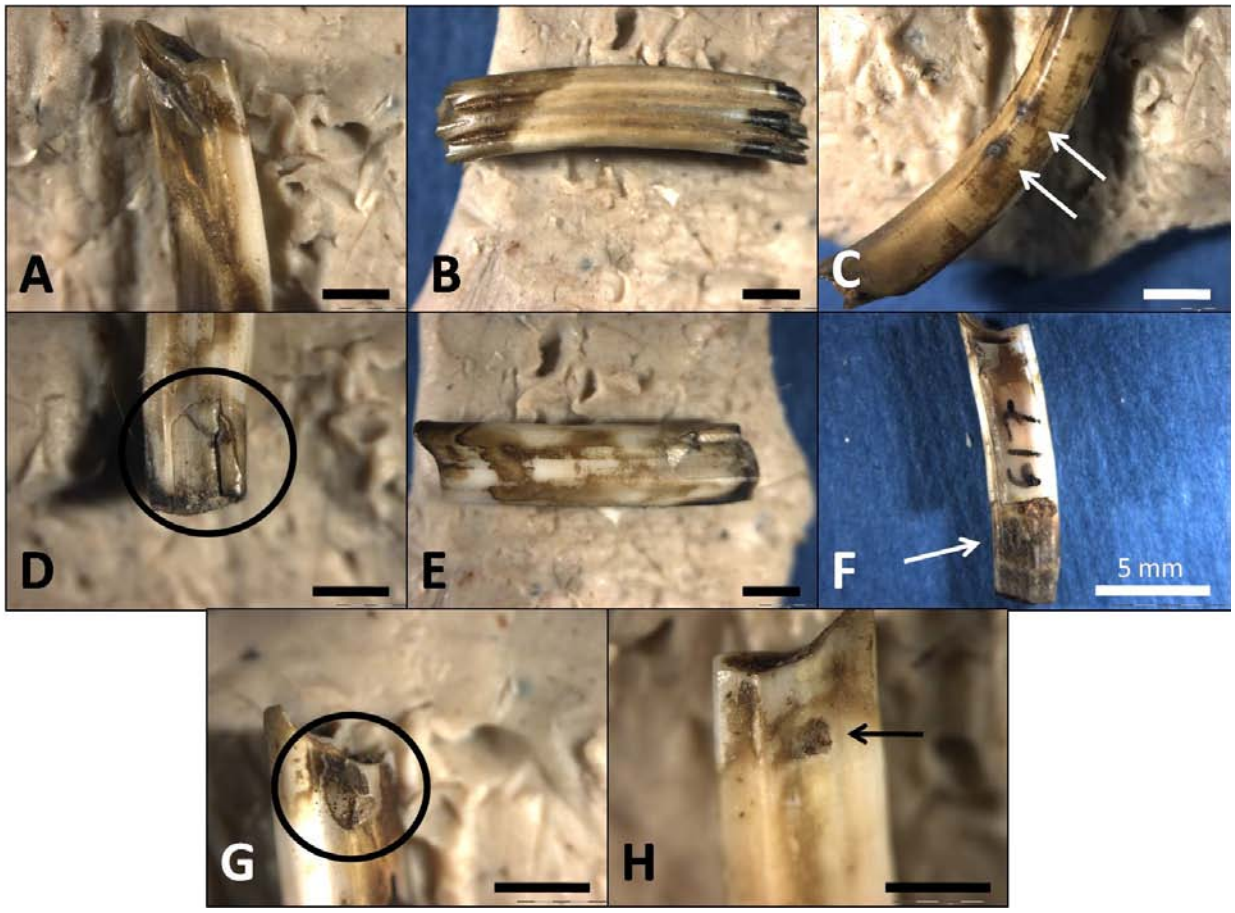


Plate 4.4. Digestion and tooth marks in dental remains from the honey badger scat assemblage A) lower postcanine, broken along length with light digestion; B) moderate digestion on a lower postcanine; C) lower incisor with light digestion and tooth pits (arrows); D) lightly digested lower postcanine with crush mark (circle); E) lower postcanine with light digestion; F) View of lower postcanine showing moderate digestion, note loss of enamel in lower part of tooth (arrow); G) close-up of tooth in F, showing crush mark (circle); H) close-up of tooth in F, showing a single tooth pit

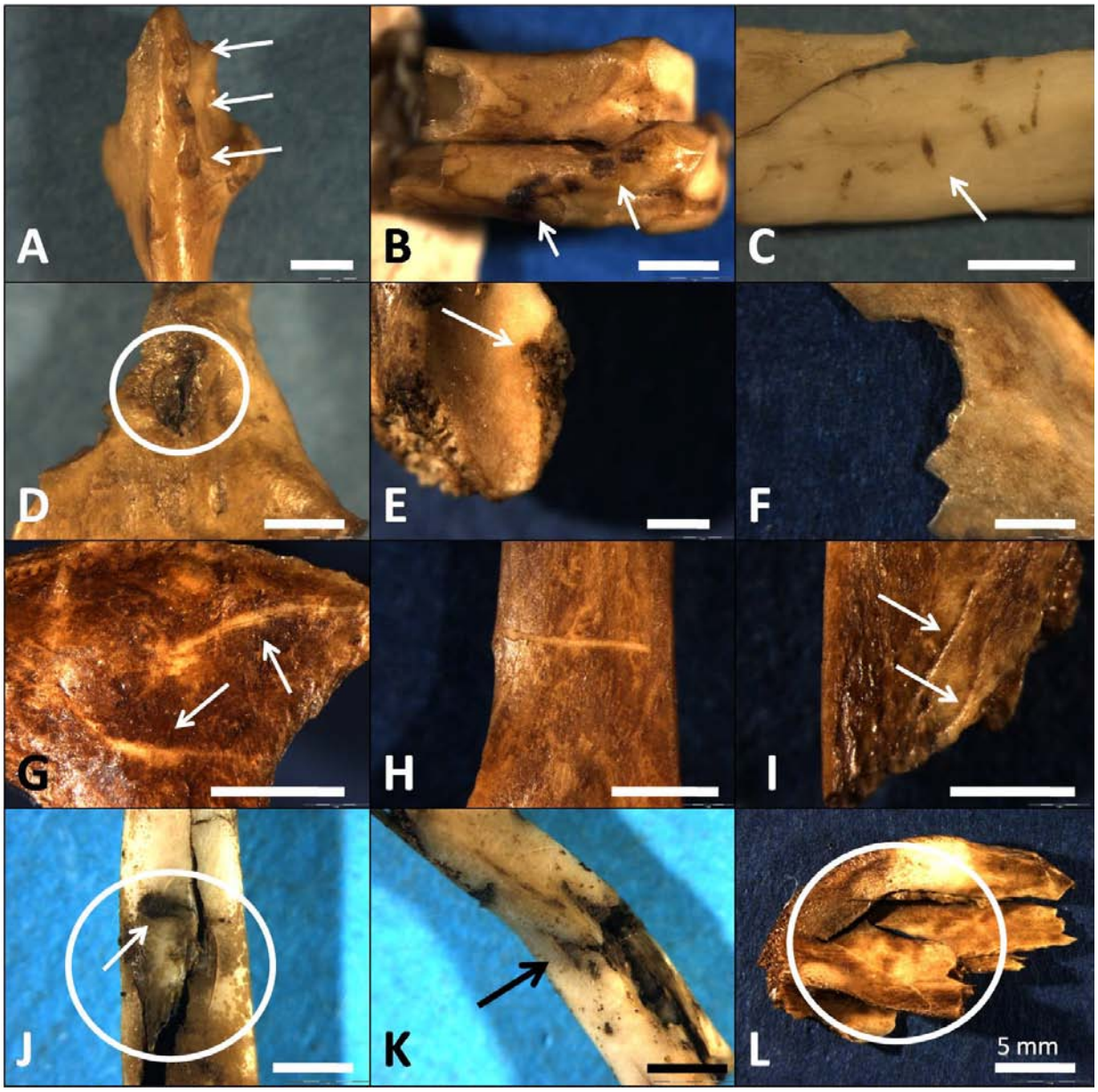


Plate 4.5. Tooth marks on bone remains from the honey badger scat assemblage A) multiple tooth pits on a calcaneum; B) articulated metapodials with tooth pits; C) lumbar vertebra with tooth pitting; D) puncture on atlas; E) notch mark on femur; F) crenulated edge on scapular blade; G) multiple scour marks on lumbar vertebra; H) lumbar vertebra with scour; I) scour marks on a lumbar vertebra; J) rib with crush mark (circle) and an associated tooth pit (arrow); K) crush mark on rib; L) scapular blade fragment with heavy crushing

Table 4.16. Anatomical composition and breakage in the honey badger refuse and scatological assemblages

	Refuse assemblage	Scat assemblage
Number of remains (n)	318	384
Average survival (%)	24.8	20
Maximum survival (%)	59.7	50
Survival > 50%	pel, fem, UPC	fem, cran, hum
Survival< 20%	lumb, sca, hum, pat	man, dent, thor, caud, rib, rad, pat, autopodium
Survival = 0%	vert (except lumbar), ribs	UPC, uln
Avg max fragment size (mm)	-	10.9
Complete remains (%)	78.4	11.7
Complete long bones (%)	29.4	-

For abbreviations see Table 2.2, page 18

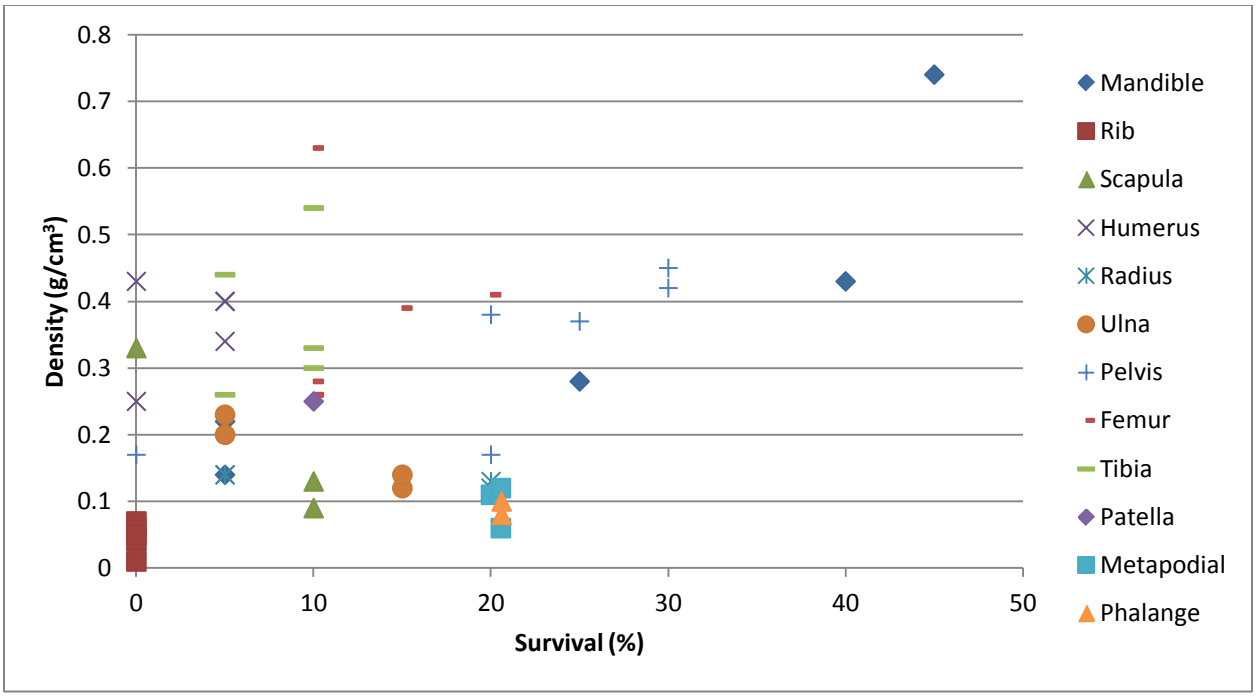


Figure 4.18. Structural density assays of domestic rabbit compared to survival (%) of skeletal elements in the honey badger refuse assemblage

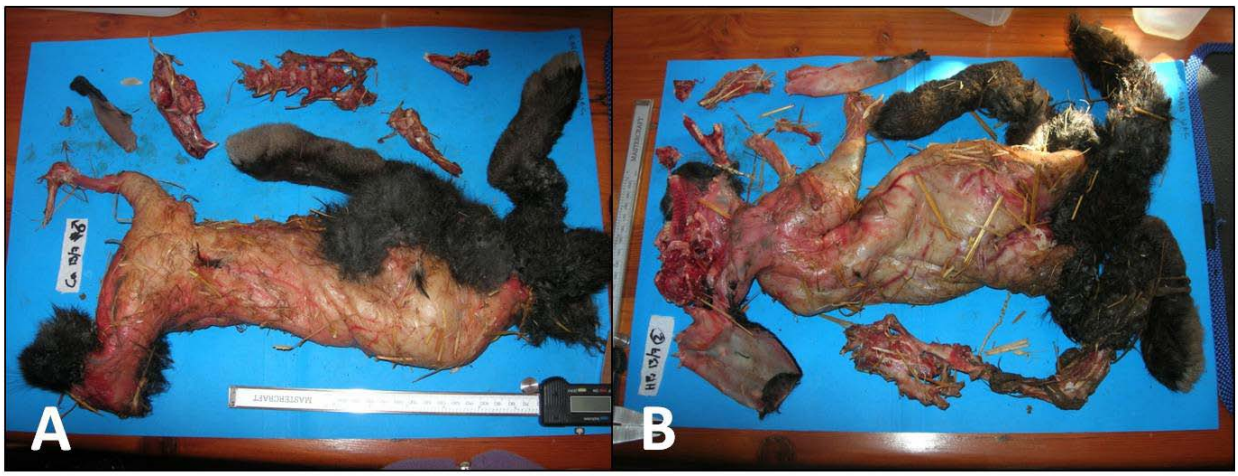


Plate 4.6. Carcass remains from feeding 3 in the honey badger

Table 4.17. Comparison of the anatomical composition, and breakage on leporid remains between the honey badger and small carnivore refuse assemblages

Leporid predator comparisons	**Honey Badger** *Mellivora capensis*	**Fox** *Vulpes vulpes*	**Geoffroy's Cat** *Leopardus geoffroyi*	**Coyote** *Canis latrans*
Reference	Present study	Lloveras *et al.*(2012)	Álvarez *et al.* (2012)	Schmitt and Juell (1994)
Number of remains (n)	318	639	439	-
Average survival (%)	24.8	25.6	40.2	-
Maximum survival (%)	59.7	89.8	87.5	-
Survival > 50%	pel, fem, UPC	tib, mts, phl	cra, fem, pel, tib, man, mts	distal appendages
Survival <10%	hum, lumb, sca, uln, tib, pat	man, LPC, hum, vert, mcs	mcs, UPC, sca, pat, phl	-
Survival = 0%	vert (except lumbar), ribs	cra, sca,rib, pel	rib	-
Avg max fragment size (mm)	-	19.3	-	-
Complete remains (%)	78.4	89.4	88.8	-
Complete long bones (%)	29.4	5.4	15	-
Teeth marks (%)	-	9.5	19.8	-

For abbreviations see Table 2.2, page 18

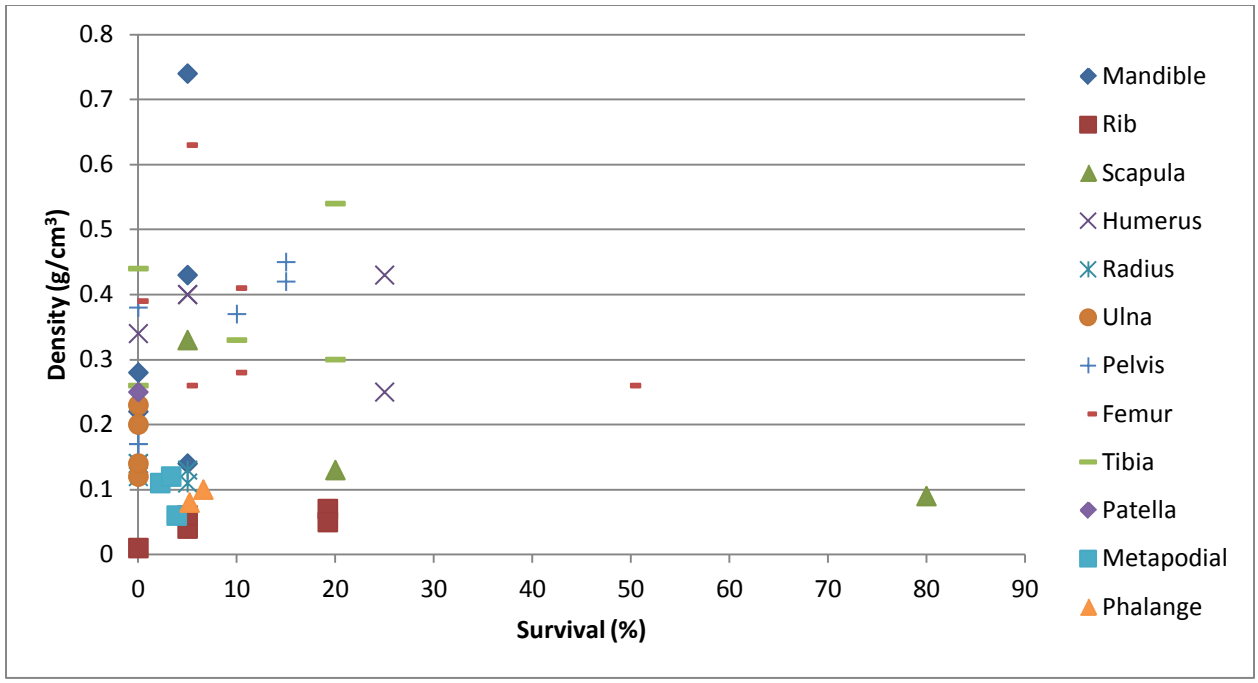


Figure 4.19. Structural density assays of domestic rabbit compared to survival (%) of elements in the honey badger scat assemblage

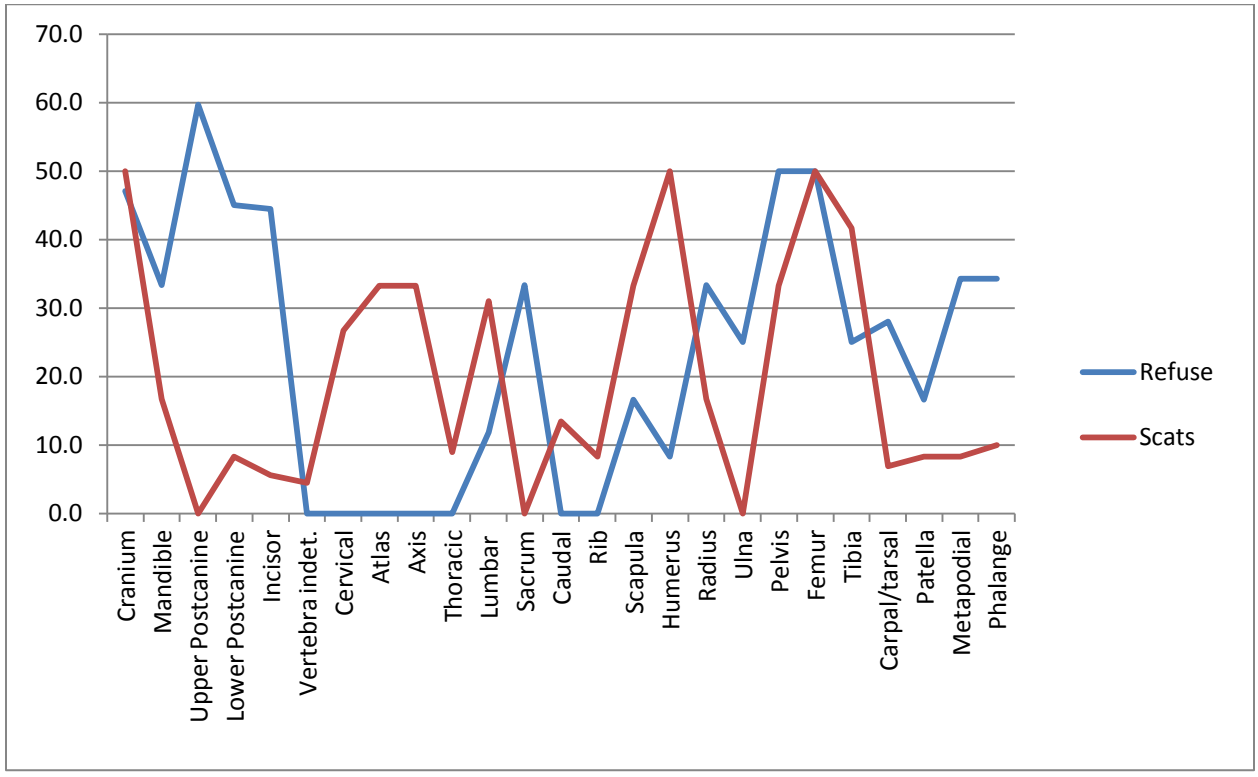


Figure 4.20. Survival (%) of elements in the honey badger scat and refuse assemblages

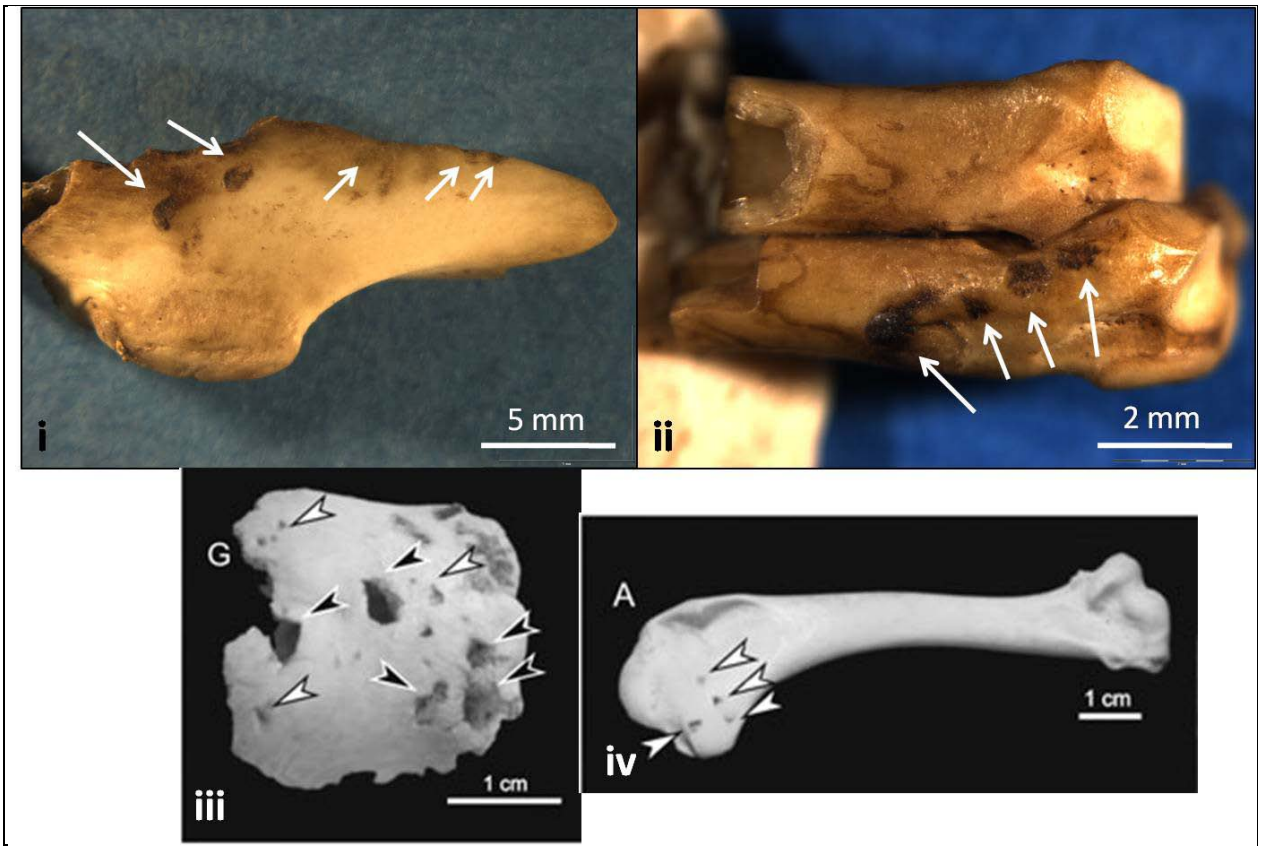


Plate 4.7. Comparison of tooth marks in the honey badger and fox i) Femoral fragment from honey badger scats with multiple tooth pits; ii) Articulated metapodials from honey badger scats with tooth pits; iii) *G. Gallus f. Domestica* cranium from fox refuse with punctures (black arrows) and very small tooth pits (white arrows); iv) *G. Gallus f. Domestica* humerus from fox refuse with small tooth pits. *Fox images adapted from Krajcarz and Krajcarz (2012)*

Table 4.18. Distribution of tooth marks on elements relative to breakage classes in the honey badger scat assemblage

	NF		F		ACR	
Scapula	**n**	**%**	**n**	**%**	**n**	**%**
	3	16.7	12	66.7	3	16.7
	HT		**S**		**HTS**	
Rib	**n**	**%**	**n**	**%**	**n**	**%**
	3	10	23	76.7	4	13.3
	IS		**IL**			
Pelvis	**n**	**%**	**n**	**%**		
	3	75	1	25		
	C		**F**			
Dentition	**n**	**%**	**n**	**%**		
Incisor	1	100	-	-		
Lower Postcanine	1	50	1	50		
	MBI					
Mandible	**n**	**%**				
	1	100				
	NC					
Cranium	**n**	**%**				
	4	100				
	F					
Carpal/tarsal	**n**	**%**				
	3	100				
	C					
Patella	**n**	**%**				
	1	100				

Table 4.18 (continued). Distribution of tooth marks on elements relative to breakage classes in the honey badger scat assemblage

	C		VB		VE		VA		SP		TP		ZYG	
Vertebra	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**
Vertebra indet.	-	-	13	59.1	1	4.5	5	22.7	1	4.5	1	4.5	1	4.5
Atlas	-	-	-	-	-	-	-	-	-	-	1	33.3	2	66.7
Axis	-	-	2	66.7	-	-	1	33.3	-	-	-	-	-	-
Cervical	-	-	-	-	-	-	-	-	-	-	1	20	4	80
Thoracic	-	-	-	-	-	-	-	-	3	100	-	-	-	-
Lumbar	-	-	5	12.8	1	2.6	1	2.6	2	5.1	16	41	14	35.9
Caudal	2	66.7	1	33.3	-	-	-	-	-	-	-	-	-	-

Long bones, metapodial and phalange	C		PE		PES		S		SDE		DE	
	n	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**
Humerus	-	-	3	75	-	-	-	-	1	25	-	-
Radius	-	-	-	-	-	-	-	-	-	-	1	100
Femur	-	-	5	50	1	10	-	-	-	-	4	40
Tibia	-	-	2	40	1	20	2	40	-	-	-	-
Metapodial	-	-	1	33.3	1	33.3	-	-	1	33.3	-	-
Phalange	1	25	1	25	1	25	-	-	1	25	-	-

For abbreviations and explanations see Table 2.2, page 18

Table 4.19. Comparison of the anatomical composition, breakage, digestion and teeth marks on remains between the honey badger, small mustelid, herpestid and viverrid scat assemblages

Predator comparisons	**Honey Badger** *Mellivora capensis*	**Pine Martin** *Martes martes*	**White-tailed Mongoose** *Ichneumia albicauda*	**Genet** *Genetta genetta*	***Mustela* sp.** *M. nivalis; M. putorius; M. erminea*
Reference	Present study	Andrews and Evans (1983)	Andrews and Evans (1983)	Andrews and Evans (1983)	Andrews and Evans (1983)
Number of remains (n)	2708	301	2135	5205	-
Average survival (%)	20	34.6	49.3	25.7	-
Maximum survival (%)	50	100	100	99.4	-
Survival > 50%	fem, cran, hum	hum, l, man, uln, cra	hum, dent, fem, man, cra, uln, vert	man, fem, l	-
Survival < 10%	uln, dent, rib, pat, mps, thor, phl	c/t, rib	-	rib, phl, mps, sca, c/t	-
Fragmentation	Great	Moderate	Great	Moderate	Great
Number unidentifiable bones	Great	Great	Great	Great	Great
Articulated remains	Occasional	Many	None	None	Many
Fragmentation dental remains	Occasional	Many	None	None	None
Digestion dental remains	Light	Moderate	None	Moderate	Great
Digestive corrosion	Light	None	Occasional	Great	Moderate
Rounding	Great	Moderate	Moderate	Great	Moderate
Polishing	None	None	Light	None	None
Tooth marks	Great	None	None	None	None

For abbreviations see Table 2.2, page 18

Table 4.20. Comparison of the anatomical composition, breakage patterns, digestion and tooth marks on leporid remains between the honey badger and small carnivore scat assemblages

Leporid predator comparisons	**Honey Badger** *Mellivora capensis*	**Coyote** *Canis latrans*	**Fox** *Vulpes vulpes*	**Lynx** *Lynx pardinus*	**Geoffroy's Cat** *Leopardus geoffroyi*
Reference	Present study	Schmitt and Juell (1994)	Lloveras *et al.*(2012)	Lloveras *et al*. (2008a)	Álvarez *et al.* (2012)
Number of remains (n)	384	840	265	1522	294
Average survival (%)	20	.	25.6	42.9	34
Maximum survival (%)	50	.	83.3	86.9	.
Identifiable remains (%)	14.2	.	.	36.1	.
Survival > 50	fem, cra, hum	Dent	fem, cra, sca, hum, tib	man, cra, fem, pel, dent, hum, uln, sca	cra, phl, c/t ¢
Survival < 20	man, dent, thor, caud, rib, rad, autopodium	hindlimb ¢	Dent, autopodium	c/t, rib, vert	man, pel, tib ¢
Survival = 0	UPC, uln	-	mtc	-	.
Avg max fragment size (mm)	10.9	27.5*	9.1	7.1	.
Complete remains (%)	11.7	7.1	12	43	15
Complete long bones (%)	-	-	-	2.5	.
Articulated remains (%)	8.6	-	-	9.7	.
Digested remains (%)	91.9	.	99.5	97.2	.
Intensity digestion bones	Light	Heavy	Heavy	Heavy	.
Intensity digestion dental	Light	Heavy	Heavy	Heavy	.
Teeth marks (%)	43.5	.	3	0.26	1.6

For abbreviations see Table 2.2, page 18 (.) data not available for comparison. (¢) percentages not available. (*) In the coyote no average value of fragment size was available so we present the maximum fragments size recorded

CHAPTER 5

DISCUSSION AND CONCLUSIONS

This study investigated feeding and bone modification patterns of two captive caracals and two captive honey badgers when presented with domestic rabbit carcasses at the Johannesburg Zoo, South Africa. The caracals were fed on five occasions while the honey badgers were fed on three. On all the feeding occasions, the rabbit carcasses replaced the normal feed, but feeding times were kept to the regular schedule. Similar protocols of refuse and scat collection, bone retrieval from scats and analyses were maintained for both sets of carnivores and throughout the feeding experiments.

5.1. Feeding Patterns in the Caracal and Honey Badger

Feeding patterns differed between the two carnivore species. The honey badger was recorded to preferentially open a carcass at the belly and consume the carcass from the inside through this opening, leaving a partial skin sometimes turned inside out and various bone fragments, some of which remained in articulation. The caracal, on the other hand, was often observed to start feeding from the head or anterior part of the carcass. The caracals would frequently discard low yield skeletal parts like articulated distal appendages. This pattern resembles refuse seen in other wild and captive carnivores such as the coyote, and appears to reflect a natural behaviour during times of abundant resources (Schmitt and Juell, 1994).

5.2. Refuse Assemblages of the Caracal and Honey Badger

The survival of remains in the caracal refuse assemblage was lower than survival in the honey badger's. This is in spite of the greater size (number of carcasses and number of remains) of the caracal refuse assemblage (Table 5.1). The best represented elements in the caracal assemblage were the cranium and autopodial while the pelvis, femur and some dental remains were lowly represented. The refuse remains from caracal feedings closely resembled refuse from wild and captive coyotes and captive red fox (Schmitt and Juell, 1994; Lloveras *et al.* 2012). In the honey badger, on the other hand, the femur, pelvis and dentition were the best

represented elements (Table 5.2). This representation is similar to that observed in experimental feedings of captive Geoffroy's cat (Álvarez *et al.* 2012). Both the caracal and honey badger displayed a preferential consumption of high yield parts of the carcass, such as the scapula, humerus, vertebra and rib elements. Completeness of remains, particularly in the long bones was lower in the honey badger than in the caracal. However crania in both carnivores show distinct patterns of damage to the posterior and basicranium, which allowed the carnivores to access the brain. Cruz-Uribe and Klein (1998) described hyrax crania from eagle nests with the occipital removed. They concluded that the loss of the occipital in these skulls was a post depositional factor due to the naturally loose attachment of the occipital to the rest of the skull, a characteristic also observed in rabbit crania, and the presence of complete occipital elements in the eagle nests. In the case of the rabbit crania from the caracal and honey badger feedings it is clear that the loss of the posterior parts of the cranium including the occipital was not a post depositional character but was the result of carnivore feeding.

5.3. Scat Assemblages of the Caracal and Honey Badger

Survival of skeletal elements in the honey badger scats was greater than in the caracal's (Table 5.3). The honey badger scatological assemblage was five times as large as that of the caracal, despite originating from half as many scats and fewer feedings. The honey badger scat assemblage had a particularly large amount of very tiny unidentifiable bone fragments. Average fragment size was only noted in identifiable remains, and the very small fragments in the honey badger scats were excluded from analysis. Thus the average fragment size of identifiable skeletal elements was almost the same in the honey badger and caracal and was highly consistent with small carnivores' feeding on mesomammals (Lloveras *et al.* 2008a; 2012; Schmitt and Juell, 1994). On the other hand, it is known that skeletal elements from microfauna in a carnivore assemblage are often more complete than remains from larger prey animals, as smaller prey are sometimes swallowed whole (Andrews, 1990; Montalvo *et al*. 2007). Thus the level of completeness or the average fragment size in a know size prey animal could indicate the size range of carnivore responsible for the scatological accumulation.

The scatological assemblages of the caracal and honey badger were characterised by high survival in the femur and cranium and low survival in the autopodium, dentition, vertebra, rib and ulna (Table 5.4). Comparison of the survival of skeletal parts against the bone mineral density of those parts indicates that there is no correlation between the density of remains and their survival. There was a low frequency of complete remains in the scat assemblages of the caracal and honey badger and breakage patterns were very similar with fragmentary long bones and most skeletal elements represented by their most robust parts. The honey badger is distinct in having a high representation of remains from the scapular blade and acromion.

Digestive corrosion was overall light in both the caracal and honey badger, unlike other small carnivores (Lloveras *et al.* 2008a; 2012; Schmitt and Juell, 1994; Montalvo *et al*. 2007). When comparing individual digestive modifications it is apparent that digestion was greater in the caracal. For instance, surface etching, corrosive pitting and rounding of edges were more abundant and severe in the caracal, than in the honey badger. On the other hand, the honey badger displayed a greater frequency of transparent skeletal elements and a darker intensity of staining. In both the caracal and honey badger corrosive holes were abundant, along with excavated foramina and slimming, while other digestive modifications like undulations, cupules and desquamation were rare. These digestive modifications, in this investigation, provide little information with regards to the possible identification of a carnivore accumulator, but are merely indicative of digestive corrosion. On the other hand, Esteban-Nadal *et al.* (2010) discovered that polishing was the most frequent modification, followed by rounding, porosity and angularity in wolf scats, indicating that these modifications can be useful in identifying carnivores in some situations. Digestion in dental remains in the caracal was predominantly heavy, distinct from the honey badger dental remains which were lightly digested. Articulation of remains from the scats was present in low levels in the caracal and honey badger, and was slightly more common in the latter. Articulation was also observed in the lynx and puma scats but always in low frequencies (Lloveras *et al.* 2008a; Montalvo *et al*. 2007).

Tooth marks were almost twice as abundant in the honey badger scat assemblage than in the caracal's. The most common tooth marks in both the caracal and honey badger were crushes, scours, pits and crenulated edges while notches and punctures were rare. Autopodial

remains had few tooth marks in both the caracal and honey badger. In the caracal assemblage, most tooth marks were observed on the postcranial axial skeleton while in the honey badger the appendicular skeleton was extensively tooth marked. The positioning of tooth marks on remains from the scats was irregular in both carnivores. Tooth marks in the caracal and honey badger were extremely small, with overlapping size ranges.

5.4. Bone Modifications of Small Carnivores

5.4.1. Refuse assemblages of small carnivores

Refuse remains of mesomammals in most small carnivores' feeding, including the caracal and honey badger, are characterised by high numbers of complete remains, especially in the long bones (Lloveras e*t al.* 2012; Álvarez *et al.* 2012). Refuse remains from small carnivores feeding on larger prey are likewise characterised by a high frequency of complete remains (Stoddart, 1979). High yield, low density skeletal elements like the rib cage, vertebra and scapula were preferentially consumed by all small carnivores (Lloveras e*t al.* 2012; Álvarez *et al.* 2012; Schmitt and Juell, 1994; Stoddart 1979). Crania in the caracal and honey badger refuse show characteristic damage to the posterior parts of the cranium that was not observed in other small carnivores, but was described in other caracal refuse and in medium sized felids (Grobler 1981; Brain 1981). The destruction of the occipitals and basicranium is likely the result of efforts by the carnivore to access the brain. Damage to the cranium in order to devour the brain is also known in other carnivores like brown hyena (*Parahyaena brunnea*), however crania in hyena kills are more likely to be crushed (Stoddart, 1979).

5.4.2. Scat assemblages of small carnivores

In scat assemblages, on the other hand, low density elements like the autopodium and ribs have poor survival while high density elements like the femur have greater representation. This pattern is observed in the fox, lynx, caracal and honey badger feedings on mesomammals, as well as feedings by herpestids, genets and the pine martin on microfauna (Lloveras *et al.* 2008a; 2012; Andrews and Evans, 1983). However the puma and Geoffroy's cat scat assemblages displayed high survival in low density remains (Montalvo *et al.*2007; Álvarez *et al.* 2012).

Carnivore scatological assemblages have low frequencies of complete remains, most of which were limited to small compact bones, with long bones always fragmented. The exception was the lynx, which had higher average survival of remains than other carnivores, as well as a high number of complete remains including some long bones (Lloveras *et al.* 2008a). Cranial remains had high survival in these carnivores, possibly linked to very high levels of fragmentation in this element and many cranial parts were represented (Lloveras *et al.* 2008a; 2012).

The caracal and honey badger were distinct from other carnivores in displaying light digestive corrosion on bone and dental remains of mesomammals (Lloveras *et al.* 2008a; 2012; Montalvo *et al.* 2007; Schmitt and Juell, 1994). Similarly, the herpestines, viverrids and the small mustelids displayed light digestive modifications on microfauna (Andrews and Evans, 1983). Recovery of articulated remains in the scats was observed in several small carnivores (lynx, puma, caracal and honey badger) but was always infrequent (Lloveras *et al.* 2008a; Montalvo *et al.* 2007). Articulated remains were recovered from carnivores which display overall heavy digestive corrosion and the presence of articulated remains cannot be considered an indication of a lack of digestive action. Rather articulated remains appear to be the result of protection of small elements by skin and fur. The coyote is the only carnivore other than the caracal and honey badger in which staining was recognised (Schmitt and Juell, 1994). This modification is of questionable importance in a palaeontological context as post depositional factors can mask or result in staining of bone remains. Many of these analyses utilised varying characteristics to describe or quantify digestive modifications making comparisons between studies challenging. This investigation revealed that it was most informative to quantify and describe each digestive modification individually as this allowed for more accurate comparison between carnivores.

The honey badger and caracal scat assemblages were frequently tooth marked compared to assemblages from the lynx, fox and Geoffroy's cat (Lloveras *et al*. 2008a; 2012; Álvarez *et al.* 2012). The researchers in these studies investigated the presence of tooth marks under magnification (X40), as was done in this investigation. Lloveras *et al*. (2008a) attributed the low number of tooth marks in the lynx assemblage to high levels of digestion destroying evidence of tooth marks. The existence of tooth marks in the caracal and honey badger refuse

assemblage was not investigated, however it would be beneficial in the future to assess the frequency and position of tooth marks in carnivore refuse assemblages independent of scatological remains, as this might provide information with regards to feeding patterns or behaviour. In the fox scat assemblage tooth marks were common on the appendicular skeleton, while tooth marks in the caracal and honey badger were more common on the axial skeleton and modifications were irregularly placed on bones in all carnivores. Tooth marks in the caracal and honey badger were much smaller than previously recorded for carnivores on larger prey (bovids) remains (Delaney-Rivera *et al.* 2009) Krajcarz and Krajcarz (2012) found small sized tooth marks equivalent to those of the caracal and honey badger in refuse from fox dens, but they attribute the very small tooth marks to juvenile foxes. The small size of tooth marks in the caracal and honey badger on mesomammals may be a result of less effort being required to extract flesh from mesomammals than in larger prey.

There has been some criticism over the use of captive carnivores in experimental studies of bone modification (Krajcarz and Krajcarz, 2012). Captive carnivores which are regularly fed may suffer from satiation and will not consume and process a carcass at the same intensity as a wild carnivore (Krajcarz and Krajcarz, 2012). Thus modification patterns in these carnivores would not provide a good reference for taphonomic studies. This investigation shows that captive carnivores do not display satiation as all meat from the carcasses fed to the caracal and honey badger was consumed. In addition refuse and scatological assemblages from wild carnivores and experimental data from captive carnivores compares favourably in many species (Schmitt and Juell, 1994; Lloveras *et al*. 2008a; 2012; Álvarez *et al.* 2012).

5.5. Small Carnivore Taphonomy in Fossil Assemblages

Small carnivores have been implicated as accumulators of a variety of different prey including mesomammals in fossil assemblages (Andrews, 1990; Castel, 1999; Fernández-Jalvo, 1995). Andrews (1990) applied his actualistic research of carnivore modification on microfauna to the Westbury fossil deposit in Somerset, UK. The majority of the micromammal assemblage was accumulated by raptors, however some units present bone modification patterns consistent with accumulation by a mammalian carnivore. These units were considered

characteristic of a mammalian carnivore assemblage as bone remains displayed extreme breakage, with no complete bones. There was a high representation of isolated dentition and autopodial elements and digestion was moderate with extensive rounding. Andrews identified the accumulator of this unit as a mustelid the size of the modern stoat, however a definite identification of the small carnivore responsible was not possible as his mustelid data set was too small for comparison. Combe Saunière in France has a large assemblage mostly made up of ungulate remains, but with a high representation of mesomammals (hares) and small carnivores, such as foxes and mustelids (Castel, 1999). A large portion of the small carnivore remains were from juvenile individuals. The assemblage was for the most part accumulated by humans, however many of the mesomammal remains had small sized tooth marks and lacked evidence of human interference. In addition, small sized tooth marks were observed on large ungulates along with human induced modifications. Castel thus concluded that the mesomammal remains were accumulated by fox and that this carnivore also fed on the remains from human kills. In the Gran Dolina deposits of Atapuerca, Spain, Llona and Andrews (1999) identified a small mustelid as the accumulating agent of amphibian remains, based on data from comparative actualistic studies. Amphibian remains, from stratigraphic levels TD4 and TD5 displayed high levels of breakage and digestion and the researchers concluded that these remains were accumulated from scats of a small carnivore occupying the cave. However, previous taphonomic research of microfauna in TD4 and TD5 identified the presence of owls (long-eared owl, eagle owl and tawny owl) as accumulators (Fernández-Jalvo, 1996). These microfaunal assemblages had a high abundance of skeletal elements with low to moderate breakage and digestion. Finally, Matthews (1999) investigated the Elands Bay Cave assemblage. Stratigraphic levels 3b, 3c, 3d and 6 had high levels of breakage with low completeness of crania, mandibles, femora and humeri. Dental remains were few and there was a high frequency of incisor etching, all indicative of accumulation by a mammalian carnivore. Matthews identified the accumulator as a viverrid, most likely either the small or large grey mongoose (*Galerella pulverulenta* or *Herpestes ichneumon*).

Mesomammals and small carnivores are commonly recovered in fossil deposits of the *Cradle of Humankind* (Brain, 1981; De Ruiter, 2003; Watson, 1993). They are very abundant in

the Cooper's D locality, particularly the small carnivores (De Ruiter *et al*. 2009). Taphonomic studies in the *Cradle of Humankind* have implicated large carnivores like leopard and hyena as accumulators in many deposits, including Sterkfontein, Swartkrans and Kromdraai (Brain, 1981; Kibii, 2007; Newman, 1993). Microfaunal assemblages in these deposits appear to be the result of activity by nocturnal birds of prey (Avery, 2001). Despite the very large faunal accumulation of the Cooper's D fossil deposit, little taphonomic research has been undertaken in this locality. De Ruiter *et al*. (2009) identified the probable presence of hyena and jackal but a full taphonomic analysis of the deposit has yet to be published. Small carnivores like herpestids are commonly preyed upon by many larger carnivores (Skinner and Chimimba, 2005) and their presence in fossil assemblages has been used to infer the action of a large carnivore accumulating agent (Brain, 1981). Investigation of carnivore dens has shown that remains of the accumulating carnivore, particularly juveniles is common in dens or lairs, and can be considered an indication of the presence of a carnivore accumulator (Krajcarz and Krajcarz, 2012). Additionally many small carnivores have been known to utilise rock crevices or caves as shelters (Estes, 1991; Skinner and Chimimba, 2005). The high frequency of mesomammals and small carnivores in Cooper's D suggests the presence of a small carnivore accumulator.

Little is known with regard to the potential of the caracal or honey badger as accumulators of fossil assemblages. The caracal is associated with open country and open savanna woodland (Skinner and Chimimba, 2005) and it has a preference for plains and rocky hills (Kingdom, 1997). According to Shortridge (1934) caracals will occasionally put up by day either on the open plains or among rocks, away from trees or thick bush cover. Young are born in some secure shelter, like a cave, hollow tree or aardvark burrow (Kingdom, 1977). The caracal is a solitary and generally nocturnal hunter, predominantly terrestrial but also adept at tree climbing (Skinner and Chimimba, 2005). When hunting the caracal approaches its prey to the nearest concealment and then may wait a long period before making a very fast dash (Kingdom, 1977). Prey is killed with either a throat bite or with a bite to the nape of the neck (Skinner and Chimimba, 2005). Smithers (1983) described how a captive female caracal would kill hare prey with a bite to the nape of the neck and if the prey continued to struggle she would

throw herself on the ground and rake the prey with her hindlegs until subdued. The female caracal utilised in this study showed similar behaviour when first presented with a whole rabbit carcass. She took the carcass into the enclosure where she would bite it on the nape of the neck and then would throw herself and the ground and roll with the carcass. She did this several times before starting to consume the carcass. Later feedings did not excite such 'play' behaviour. Skinner and Chimimba (2005) stated that prey were usually eaten where killed and rarely dragged away to cover. However Kingdom (1977) stated that caracal would usually carry its prey back to cover immediately or carry prey up into the forks of trees. Grobler (1981) described how a partially consumed kill was cached covered in grass. It would appear that in protected areas caracal will cache and return to kills, sometimes over several days (Skinner and Chimimba, 2005). While mesomammals often make up the majority of the diet in caracal, this carnivore has been known to take large prey including sitting ostrich and roosting eagles (Kingdom, 1977). The caracal is considered a common species in many parts of its range, despite its solitary and nocturnal habits (Skinner and Chimimba, 2005). The caracal thus has good potential as an accumulator of remains in caves of the South African Plio-Pleistocene. It frequents and even takes shelter in rocky areas where caves are frequent. Like the leopard it is known to take prey remains into the forks of trees (Kingdom, 1977) and may even return to these remains over a period of time.

The honey badger is also a solitary and generally nocturnal predator (Kingdom, 1977). It has catholic habitat preferences and is widespread (Skinner and Chimimba, 2005), but is commonest in open woodland (Kingdom, 1997). Honey badgers are accomplished diggers that will excavate refuges for themselves or adapt existing disused holes to their requirements. When not active the honey badger will lie up by day in such burrows or in rock shelters and in hilly country will lair as a rule in the cool shelter of caves and between crevices (Shortridge, 1934). Thermoregulation appears to be an important factor in choice of lair (Skinner and Chimimba, 2005). In addition honey badgers will explore any hole or cavity they encounter (Kingdom, 1977). Honey badgers climb easily even near vertical rock faces and usually rely on their toughness to get down by simply tumbling (Shortridge, 1934). The honey badger is normally terrestrial when hunting, which they do by broad-spectrum opportunistic foraging

(Kingdom, 1997) rather than stalking, but they are known to climb trees in search of prey or honey (Kingdom, 1977). Honey badgers are opportunistic omnivores and the majority of prey is dug up (Kingdom, 1997; Skinner and Chimimba, 2005; Kruuk and Mills, 1983). They will however take larger prey opportunistically if young or vulnerable (Kingdom, 1997) and it has been recorded that honey badgers will dig out and eat other mammals (Shortridge, 1934). The honey badger will readily scavenge or pirate prey from other (larger) carnivores and Kingdom (1977) describes accounts of honey badger killing young and adult Kudu, even running large prey to exhaustion. There are also descriptions of buffalo and waterbuck from the Kruger National Park who have died from blood loss after being attacked in the scrotum by honey badger (Kingdom, 1977). As Kingdom (1977) amusingly puts it "it is logical that an animal with more aggression than inches should attack what it can reach". Despite their strength honey badgers are described as dainty feeders (Kingdom, 1977). Grubs are extracted individually with the incisors from combs or cocoons which are held between the claws, in addition small animals are often skinned carefully and only the softer parts are eaten, leaving the head and skin. Sheep kills have been described as eviscerated through a hole (Kingdom, 1977). These feeding patterns correlate well with feeding behaviours observed in this study. The honey badgers opened the rabbit carcasses at the belly and fed from that opening leaving a skinned carcass. Bone remains from the feedings where stripped of flesh with only minor damage to the bones. Kingdom (1977) provides several accounts from beekeepers of honey badgers taking surplus honey combs and hiding them some distance away and when raiding chicken houses, chickens are removed and hidden or buried some distance away. Shortridge (1934) observed how extra honey combs were carried off to the lair. Most members of the Mustelidae leave their faeces and urine on elevated or conspicuous sites, however the honey badger will deliberately defecate into crevices or holes, even digging a hole for this purpose (Kingdom, 1977). Presumably this placement is more likely to be explored by other honey badgers. Thus feeding and scatological remains from honey badgers have a high potential for inclusion into a cave environment and the honey badger has good potential as an accumulator of fossils in caves of the South Africa Plio-Pleistocene.

Investigation of the mesomammal assemblage of Cooper's D is ongoing and currently only the craniodental remains have been identified (Table 5.5), postcranial remains have not been analysed. Survival of the Cooper's D mesomammal craniodental material is very similar to survival in the caracal and honey badger. Cranial survival is highest of the remains analysed, as seen in caracal and honey badger and falls (38.1%) between the values found in these carnivores (Table 5.6). Mandibular remains in the Cooper's assemblage had almost the same survival (21.4%) as observed in the caracal assemblage. Dental remains especially upper postcanines (0.8%) had poor survival in the Cooper's assemblage. The lower postcanines had the greatest survival of the dental remains of 3.6% and the incisors had 2.1% survival. The overall poor survival of the dentition and preferential survival of the upper postcanine compares favourably with the caracal and honey badger. Breakage patterns in the craniodental remains are consistent with accumulation by a small carnivore (Table 5.7). The Cooper's mesomammals differ from the caracal and honey badger in the preservation of maxillary remains and the lack of neurocranial fragments. The absence of neurocranial remains in the Cooper's assemblage may be a factor of post depositional forces destroying fragile remains. Like the caracal, most mandibular remains in the Cooper's assemblage are limited to parts of the mandibular body. The majority of isolated dental remains were complete in the Cooper's remains as observed in the caracal and honey badger. Thus the craniodental remains of mesomammals from Cooper's D bear a strong resemblance in terms of survival and breakage patterns to the caracal and honey badger assemblages. The Cooper's material is more similar to the caracal, and caracal remains have been identified at Coopers (Table 1.1) however until the postcranial material is analysed it is not possible to identify which small carnivore might have contributed to the accumulation of Cooper's D.

In conclusion mesomammals and small carnivores are often overlooked in fossil assemblages, even where they are commonly recovered remains and their taphonomy is often poorly understood. These taxa, however, occupy an important ecological niche and their presence and history in a fossil assemblage must be considered when undertaking palaeoecological reconstructions. The first step towards a taphonomic investigation of

mesomammals and small carnivores in any fossil assemblage is to undertake actualistic studies to provide a dataset of modification patterns. A small dataset of such research exists and has been outlined in this dissertation, however most of this research has been undertaken in Europe and the Americas and currently very little is known of African small carnivores and mesomammal taphonomy. Thus future research into small carnivore and mesomammal taphonomy in South Africa will have many implications and influences on palaeoecological reconstructions and interpretations from fossil deposits in South Africa, Africa and the rest of the world.

Table 5.1. Anatomical composition and breakage in the caracal and honey badger refuse assemblages

Leporid predator comparisons	**Honey Badger** *Mellivora capensis*	**Caracal** *Caracal caracal*
Carcasses fed to carnivore (n)	6	10
Carcasses collected (n)	5	9
Number of remains (n)	318	406
Average survival (%)	24.8	12.5
Maximum survival (%)	59.7	40
Survival > 40%	dent, pel, fem,	mps, phl
Survival < 20%	hum, lumb, sca, pat	man, LPC, I, pel, fem, rad, uln
Survival = 0%	vert (except lumbar) and rib	vert, rib, sca, hum, tib
Complete remains (%)	78.4	95.9
Complete long bones (%)	29.4	100

For abbreviations see Table 2.1, page 18

Table 5.2. Survival (%) in the caracal and honey badger refuse assemblages

	Caracal (%)	Honey badger (%)
Cranium	30.5	47.1
Mandible	10	33.3
Upper Postcanine	26.7	59.7
Lower Postcanine	8	45
Incisor	8.3	44.4
Vertebra indet.	-	-
Cervical	-	-
Atlas	-	-
Axis	-	-
Thoracic	-	-
Lumbar	-	11.9
Sacrum	-	33.3
Caudal	-	-
Rib	-	-
Scapula	-	16.7
Humerus	-	8.3
Radius	20	33.3
Ulna	20	25
Pelvis	5	50
Femur	5	50
Tibia	-	25
Carpal	30	33.3
Tarsal	40	33.3
Metacarpal	30	33.3
Metatarsal	40	35.4
Phalange	39.8	34.3

Table 5.3. Anatomical composition, breakage, digestion and tooth marks on leporid remains from the caracal and honey badger scatological samples

Leporid predator comparisons	**Honey Badger** *Mellivora capensis*	**Caracal** *Caracal caracal*
Scats collected (n)	23	42
Total number of remains (n)	2708	534
Identifiable remains (n)	384	223
Unidentifiable remains (%)	85.8	58.6
Average survival (%)	20	9.9
Maximum survival (%)	50	30
Survival > 20%	cra, vert (except thor and caud), sca, hum, pel, fem, tib,	cra, man, atl, axs, pel, fem
Survival < 10%	dent, thor, rib, autopodium	dent, vert, rib, sca, hum, rad, uln, tib, mps, phl
Survival = 0%	UPC, ulna	c/t
Avg max fragment size (mm)	10.9	10.7
Complete remains (%)	11.7	15.7
Complete long bones (%)	0	0
Digested remains (%)	91.9	99.9
Intensity digestion bones	Light	Light
Intensity digestion dental	Light	Heavy
Teeth marks (%)	43.5	28.4

For abbreviations see Table 2.1, page 18

Table 5.4. Survival (%) in the caracal and honey badger scat assemblages

	Caracal (%)	Honey Badger (%)
Cranium	30	50
Mandible	20	16.7
Upper Postcanine	6.7	-
Lower Postcanine	15	8.3
Incisor	10	5.6
Vertebra indet	1.7	4.5
Cervical	4	26.7
Atlas	20	33.3
Axis	20	33.3
Thoracic	2.3	9.0
Lumbar	7.1	31
Caudal	1.9	13.5
Rib	5.8	8.3
Scapula	10	33.3
Humerus	5	50
Radius	5	16.7
Ulna	5	-
Pelvis	25	33.3
Femur	20	50
Tibia	10	41.7
Carpal / Tarsal	-	6.9
Patella	10	8.3
Metapodial	1.7	8.3
Phalange	1	10

Table 5.5. Craniodental mesomammal remains from Cooper's D

	Cranium (MNE)	Mandible (MNE)	Isolated dentition (MNE)	MNI
Leporidae				
Leporidae sp.	7	7	2	11
Hystricidae				
Hystrix africaeaustralis	0	1	8	6
Hystrix makapanensis	0	1	2	2
Pedetidae				
Pedetes capensis	1	0	6	2
Total	**8**	**9**	**18**	**21**

Table 5.6. Comparison of the anatomical composition of the Cooper's D mesomammals against the caracal and honey badger rabbit assemblages

	Caracal			Honey Badger			Cooper's mesomammals		
Skeletal Element	**NISP**	**MNE**	**Survival (%)**	**NISP**	**MNE**	**Survival (%)**	**NISP**	**MNE**	**Survival (%)**
Cranium	22	3	30	17	3	50	8	8	38.1
Mandible	7	4	20	2	2	16.7	9	9	21.4
Upper Postcanine	8	8	6.7	0	0	0	3	3	0.8
Lower Postcanine	15	15	15	5	5	8.3	13	13	3.6
Incisor	6	6	10	2	2	5.6	4	4	2.1

Table 5.7. Comparison of breakage patterns in the Cooper's D mesomammals and the caracal and honey badger assemblages

	M		ZA		NC	
Cranium	**n**	**%**	**n**	**%**	**n**	**%**
Honey badger	-	-	-	-	17	100
Caracal	-	-	4	18.2	18	81.8
Cooper's mesomammals	6	75	2	25	-	-
	MBI		**MB**		**CP**	
Mandible	**n**	**%**	**n**	**%**	**n**	**%**
Honey badger	1	50	-	-	1	50
Caracal	2	28.6	3	42.9	2	28.6
Cooper's mesomammals			8	100		
	C		**F**			
Incisor	**n**	**%**	**n**	**%**		
Honey badger	2	100	-	-		
Caracal	5	83.3	1	16.7		
Cooper's mesomammals	1	25	3	75		
	C		**F**			
Upper Postcanine	**n**	**%**	**n**	**%**		
Caracal	7	87.5	1	12.5		
Cooper's mesomammals	3	100	-	-		
	C		**F**			
Lower Postcanine	**n**	**%**	**n**	**%**		
Honey badger	3	60	2	30		
Caracal	14	93.3	1	6.7		
Cooper's mesomammals	13	100	-	-		

For abbreviations and explanations see Table 2.1, page 18

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