CHAPTER 6

Discussion

Hyaena hyaena assemblages

Jordan

The faunal remains from five striped hyaena dens in Jordan were collected and analysed in May and June of 2001 (Kuhn, 2001, 2005, unpublished). Three areas in the eastern desert known as the Badia were surveyed, one near the bronze age city of Jawa, one near Al-Arteen, and the third at Dhahik, near the Saudi Arabian border. Jawa and Al-Arteen are in the core of the black basalt desert and lay approximately 20 km from one another. Dhahik, some 90 km to the south of Al-Arteen, is outside of the basalt desert and is part of the limestone desert that covers most of Jordan and extends into Saudi Arabia (Figure 7).

The Badia region receives approximately 200 mm of rainfall per annum (Allison *et. al.*, 1998) and is made up of a series of wadis (valleys) and depressions. Jawa and Al-Arteen are both wadi systems while Dhahik is a large depression where the surrounding wadis deposit any rainfall. Outside of the wadis and depressions there is little to no vegetation, thus most wildlife in the region can be found near the numerous wadis and depressions. In the past the region had a plethora of wildlife roaming free, while today the native onager (*Equus onager hemippus*) is extinct and the Arabian Oryx (*Oryx leucoryx*) and ostrich (*Struthio camelus*) are limited to the Shaumari Reserve. While the majority of larger game species are either extinct or have been reintroduced onto nature reserves there are still a number of wild species in

the region, aside from a great number of smaller mammals, birds and reptiles. These include rheem gazelles (*Gazella subguttursa marica*), dorcas gazelles (*Gazella dorcas*), golden jackals (*Canis aureus*), Arabian wolves (*Canis lupus arabs*) and striped hyaenas (*Hyaena hyaena syriaca*).

Figure 11: Map of Jordan showing the study areas

Of five dens analysed, 24.5% of 3,755 remains were identified to species (See Table 40) and 41.2% identified to skeletal element (See Chart 73). The dens were individually broken down to Jawa 4, Jawa 7, Al-Arteen 11, Al-Arteen 13 and Dhahik 32. With the exception of Dhahik 32 all of the dens were natural caves (see Plates 28 & 29). The assemblages of each were analysed for species, skeletal element, fusion

data, carnivore damage and weathering. The percentage of remains identifiable to species or class size for the five dens ranged between 13.5% and 38.3%.

SPECIES/DEN	Al-Arteen 11	Al-Arteen 13	Dhahik 32	Jawa 4	Jawa 7	Total NISP
Camelus dromedarius	16	12	185	125	11	349
Camel/horse size	1	2	33	26	0	62
equid	4	0	8	14	0	26
Equus caballus	1	1	4	22	0	28
Bos spp.	1	0	0	2	0	3
canid (jackal size)	19	7	26	40	0	92
Equus asinus	19	6	20	53	0	98
Fox	4	0	4	1	0	9
Hyaena hyaena	0	0	0	1	0	1
Sus scrofa	3	0	0	0	0	3
Capra hircus	11	0	3	17	3	34
Ovis/Capra	18	9	15	72	2	116
sheep/goat/gazelle size	15	4	6	42	0	67
Ovis aries	4	0	4	3	0	11
Gazelle	2	0	1	13	0	16
Erinaceus spp.	0	0	0	6	0	6
hare/small fox size	0	0	0	2	0	2
Lepus spp.	3	0	0	2	0	5
Small mammal	2	0	0	42	0	44
Struthio camelus	0	0	1	0	0	1
large bird	0	0	1	1	0	2
small bird	1	0	0	13	0	14
small reptile	0	0	0	3	0	3
Total	124	41	311	500	16	992

Table 40: Species NISP per Den, Jordan

Carnivore activity documented for the Jordan dens was limited to punctates, scouring, acid etching and crenulated edges and any combinations thereof. Striations were not noted individually during the Jordanian fieldwork and therefore are not discussed when looking at the striped hyaena dens or comparing striped hyaenas to the other hyaena species in this study.

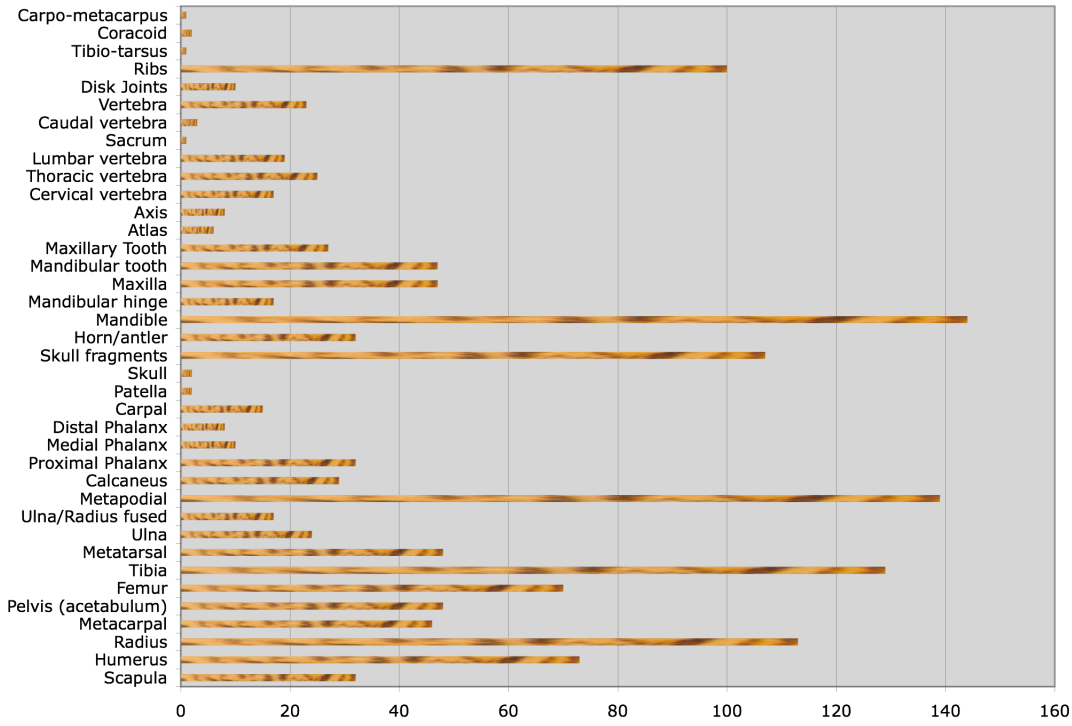

Chart 73: Elements, Striped Hyaena Dens

Jawa den 4 consisted of 1,791 specimens, of which 27.9% were identified to species and had an MNI of 62. Of the 62 individuals, carnivores (hyaena, fox and dog) contributed 29%, the remainder were camel, equid, bovid, avian, reptile and small mammal. Fragment length ranged from <1.0-54 cm, with shaft splinters being the predominant pattern recorded at 74.4% (See Chart 74) followed by one end plus shaft at 9.5%. Carnivore damage was found on 56.2% of the entire assemblage with crenulated edges and punctates being the most prevalent type of damage recorded (See Chart 75). All long bones and small compact bones were represented in the assemblage. Proximal and distal ends of long bones were equally represented with the exception of humerus, which were predominantly distal ends.

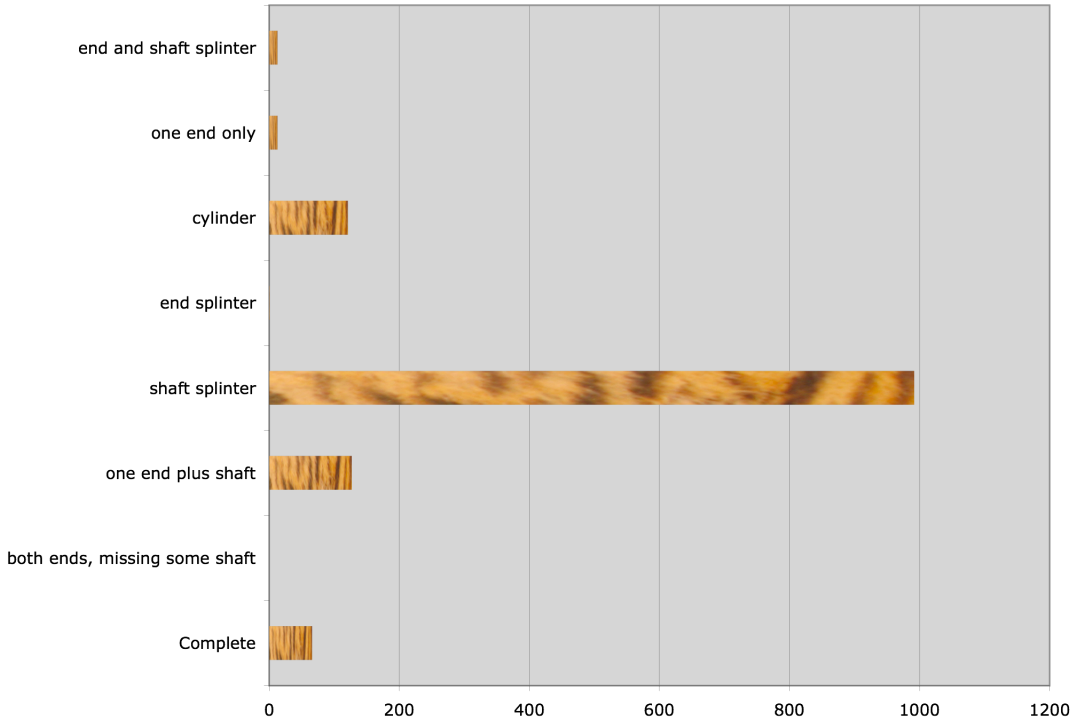

Chart 74: Fragmentation, Jawa Den 4

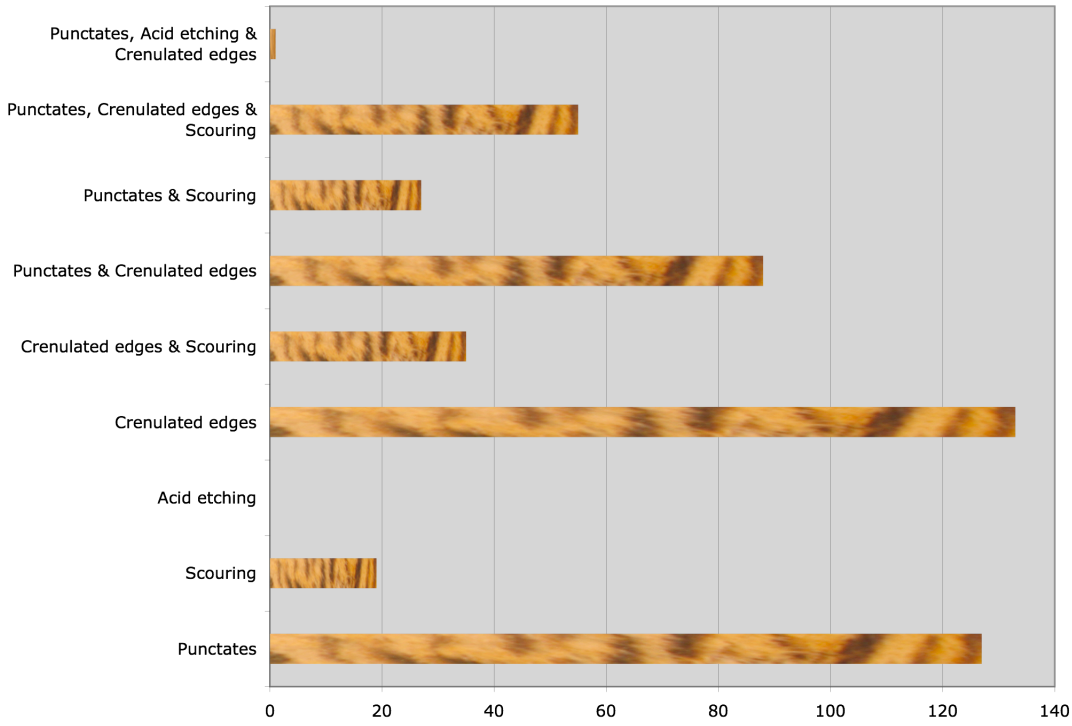

Chart 75: Canivore Damage, Jawa Den 4

Jawa Den 7 consisted of 119 remains, of which 13.5% were identified to species. With an MNI of 4, all of the identified individuals were 'prey' species and carnivore remains were absent from the assemblage. Length of measured fragments ranged from 1.0-45 cm and shaft splinter was the most abundant type of fragmentation pattern recorded (See Chart 76). Carnivore gnawing was noted on 23.5% of the examined remains; specifically of note is the absence of scouring except in combination with punctates and crenulated edges. Absent from the assemblage were scapula, radius, pelvis, and femur; small bones were represented by a single calcaneus and single proximal phalange.

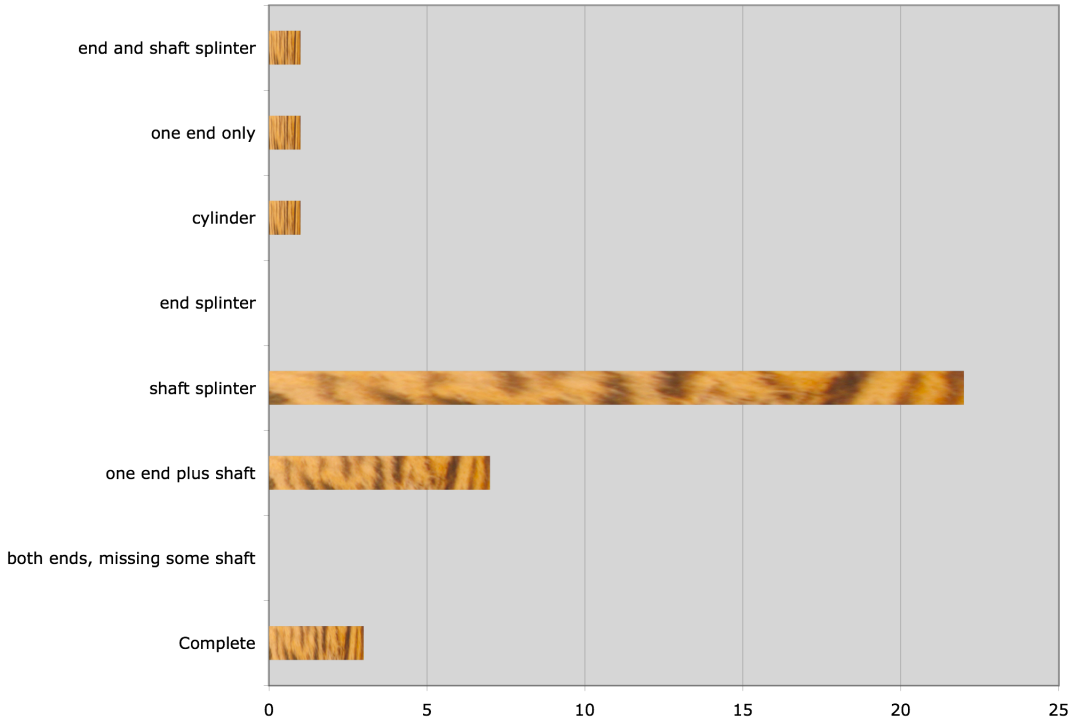

Chart 76: Fragmentation, Jawa Den 7

Al-Arteen Den 13 had 107 specimens in the assemblage, of which 38.6% were identified to species. Of the MNI of 7, 28.6% were carnivore and the remainder were

from ‘prey’ species (horse, camel, donkey and sheep/goat). Fragment length ranged from 2-38 cm, with shaft splinter being the most recorded type of fragmentation (See Chart 77). Carnivore gnawing was found on 39.3% of the assemblage and crenulated edges made up 33.3% of the recorded damage. Punctates constituted 9.5%, scouring 4.8% and there were no examples of acid etching recorded. The combinations of punctates and crenulated edges as well as punctates, crenulated edges and scouring made up 7.1% of the damaged assemblage respectively. Femur was absent from the assemblage as were all small bones except for a single calcaneus. Other long bones were equally represented both proximally and distally except humerus, which were mostly represented by distal ends.

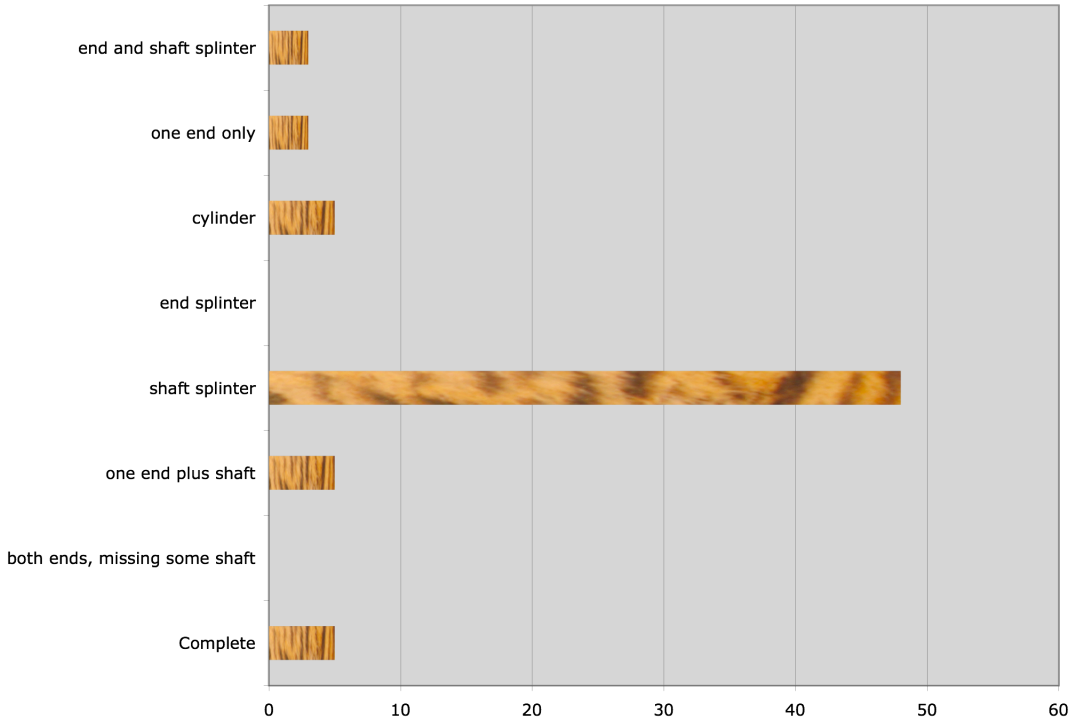

Chart 77: Fragmentation, Al-Arteen Den 13

The den at Al-Arteen 11 consisted of 361 faunal remains, 34.4% of which were identified to species. The den yielded an MNI of 26, of which 26.9% were carnivores

including striped hyaena, fox, and canids. The remaining species consisted of sheep/goat, camel, small mammals, cow (*Bos spp*.), pig *(Sus scrofa*) and gazelle. Length of fragments ranged from 2.0-33 cm and shaft splinter was the predominant type of fragmentation recorded (See Chart 78). Carnivore damage was noted on 41.6% of the assemblage, breakdown of damage is shown on Chart 79. All long bones are present in the assemblage as are the small compact bones. All of the humerus were distal ends; the remaining long bones were represented equally between proximal and distal ends and complete bones.

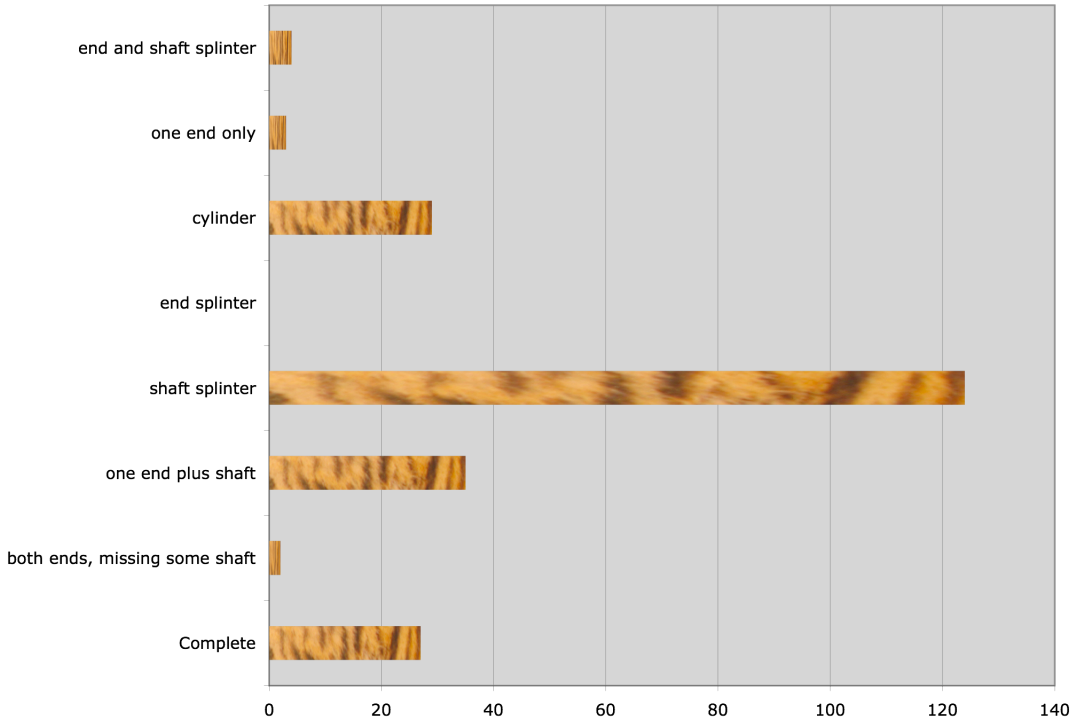

Chart 78: Fragmentation, Al-Arteen Den 13

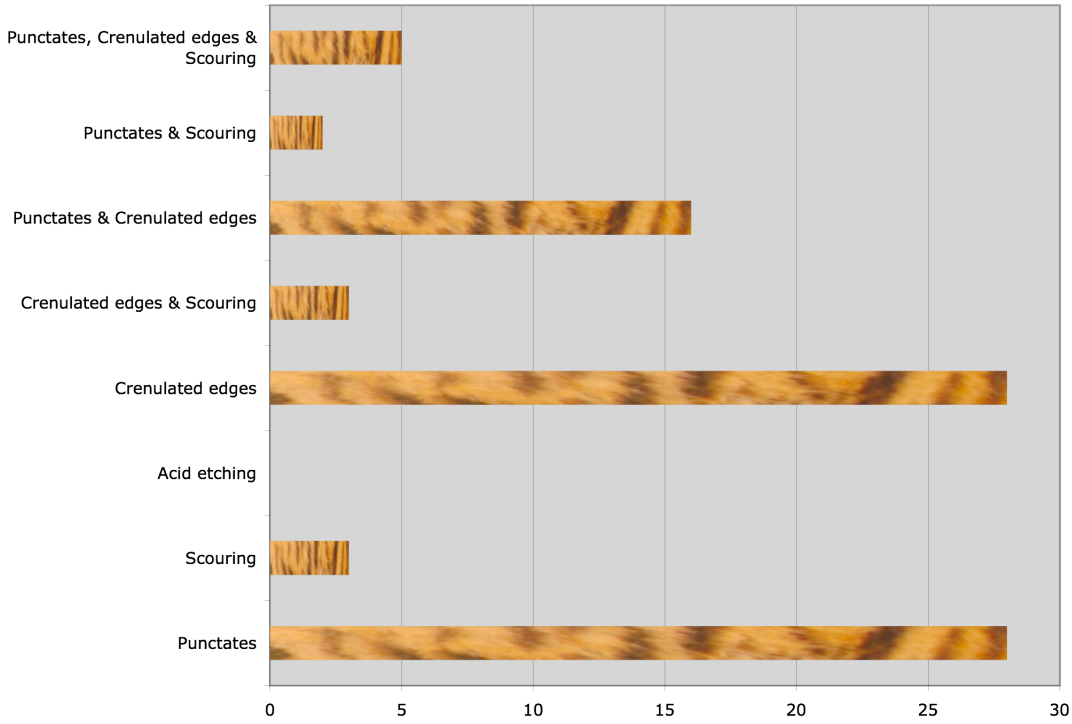

Chart 79: Carnivore Damage, Al-Arteen Den 13

The Dhahik den, Dhahik Den 32, consisted of 1,377 faunal remains, of which 22.5% were identified to species. The den yielded an MNI of 36, of which 19.4% were carnivore (canine and fox) while the remaining individuals were camel, sheep/goat and a single horse. Fragments ranged in length from 2.0-51 cm and shaft splinters predominated the recorded types of documented fragmentation patterns (See Chart 80). Carnivore damage was documented on only 6% of the entire assemblage, with 28 examples of crenulated edges, 20 punctates, no scouring or acid etching a single example of the combination punctates and crenulated edges and two examples of scouring and crenulated edges. Of note is the fact that nearly 80% of the assemblage was weathered heavily, suggesting a range since death of 4-15 yrs. All long bones and small compact bones were represented in the assemblage, with humerus being made up of distal ends and ulnas consisting of only proximal ends.

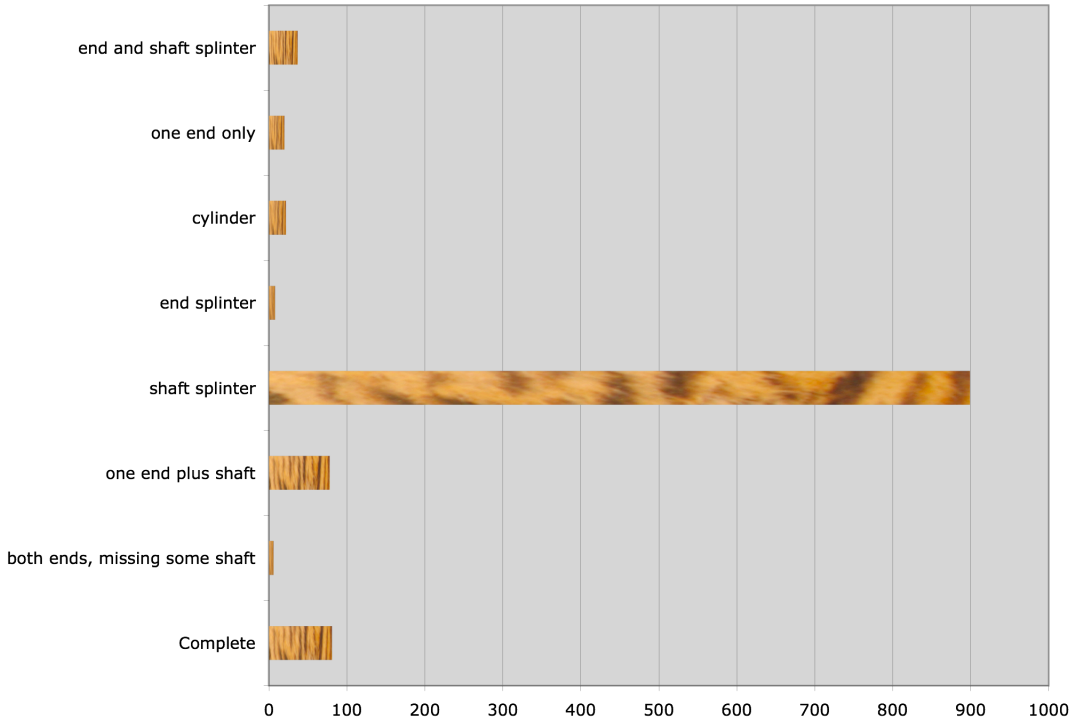

Chart 80: Fragmentation, Dhahik Den 32

Brief summation

The size of the assemblages from striped hyaenas ranged from 107-1,791 specimens. While the size range is similar to that of striped hyaena dens studied by Leakey *et. al.* (1999) it is larger than previous work by Skinner *et. al.* (1980) and smaller than a den excavated by Kerbis-Peterhaus & Horwitz (1992) in Israel. With the exception of the smaller assemblages of Jawa Den 7 and Al-Arteen 13 all major skeletal elements are represented in the assemblages. Elements from the skull and shaft fragments from long bones are the most abundant type of skeletal element identified in the assemblages. With the exception of Jawa Den 7 all the humerus remains examined were mostly from the distal end. This is seen with 2/3 of the humerus from Jawa Den 4, all humerus recovered from Al-Arteen Den 11 and Den 13 and 3/4 of the humerus from Dhahik Den 32. Small compact bones were represented in some form in all five

dens. Of the 2,983 fragments measured to length (for all five dens) 37.1% are shorter than 5 cm and 8.7% are longer than 20cm, thus just over half of the measured remains are between 5 and 20 cm. The assemblages represent the fauna occurring in the region as well as a relative abundance of mammalian fauna within the region. This was also the case with striped hyaena dens in Kenya (Leakey *et. al.*, 1999) and Israel (Kerbis-Peterhans & Horwitz, 1992). When broken down by carnivore MNI per den, Jawa Den 4 had a carnivore MNI of 29%, Jawa Den 7 0%, Al-Arteen Den 11 26.9%, Al-Arteen Den 13 28.6% and Dhahik Den 32 19.4% (mean of 20.1% carnivore). Fragmentation patterns for the five Jordan dens showed a ratio of 3-1 or greater of shaft splinter to other types of fragmentation. Carnivore damage was noted on a range of 6% to 56.2% of the examined remains (a mean of 33.3%). Of the documented damage punctates and crenulated edges were equally distributed in four of the five dens, the lone den (Al-Arteen 13) having a greater number of crenulated edges (33.3% compared to 9.5% punctates). The combination of punctates and crenulated edges was documented in all five dens, but was not in any greater abundance than other recorded combinations of damage.

Crocuta crocuta assemblages

Mashatu

The assemblage from Mashatu Den 1 was identified to species at the 64.5% level and to skeletal element at 74.3% (25.7% unidentifiable). All major skeletal elements are present, including all long bones as well as the small compact bones such as carpals, tarsal, and all phalanges. Ribs and skull fragments made up the bulk of the identified elements. Proximal and distal ends are equally represented in all of the long bones,

with no significant difference in numbers for proximal, distal or complete portions. Length of fragments ranged up to 44 cm and complete bones was the most common type of fragmentation pattern recorded (37.3%) followed by shaft splinter (30.7%). Carnivore damage was recorded from 32.2% of the entire assemblage. Crenulated edges were the most common type of carnivore damage documented (46.4%) and the combination of punctates and crenulated edges were the most common type of multiple damage recorded (26.1%). Of note is the complete lack of carnivore remains from this assemblage, all identified remains belong to bovids, small mammals, and reptiles.

Of the 58 faunal remains from Mashatu Den 2, 65.5% were identified to the species or class size and 67.2% were identified to skeletal element. Thus, 32.8% of the collected materials were unidentifiable. The only significant element absent from the assemblage is scapula; all other major skeletal elements are present. This includes six humerus and five femurs, plus many small compact bones such as the distal, medial and proximal phalanges. Three of the six humerus were distal ends, while the other three were mid-shaft segments. Three of the five femurs were proximal ends; one was a distal end and one a mid-shaft segment. Complete, distal and proximal ends of metapodials are equally represented. Fragment length was measured between 2-36 cm with one end and shaft being 27.8% of the recorded fragmentation patterns. Complete, cylinder and end and shaft fragment types were 22.2% of the assemblage. Carnivore damage was found on 53.5% of the entire assemblage, of which crenulated edges made up 87.1% and punctates 29%. The combinations of punctates and crenulated edges made up 19.4% and crenulated edges and striations 6.5%. Of the

MNI (11), bovids made up 54.6%, hyrax 9.1%, baboons 9.1%, spotted hyaenas 9.1% and equids 9.1%.

Mashatu Den 3 consisted of 93 specimens, of which 59.1% were identified to species and 72% identified to element. Thus 28% of all remains were unidentifiable. Ulna is the only long bone absent from the assemblage, all other major skeletal elements are represented, including the small compact bones such as phalanges and carpals. Of the six humerus, two are distal ends, three are shaft splinters and one is a complete bone. There are no examples of proximal end only in the assemblage. Metapodials are equally represented by proximal, distal, complete and shaft splinters. Fragments measured 3-35 cm in length, with shaft splinters being the most recorded type of fragmentation with 58.2% of fragment data. Carnivore damage was identified on 42% of the entire assemblage. Of this, 51.3% of the documented damage was crenulated edges. Scouring was found on 28.2% and punctates on 20.5% of the gnawed assemblage. The combinations of punctates and crenulated edges were recorded from 23.1% of the damaged assemblage, punctates and striations as well as punctates and scouring occurred on 2.5% of the assemblage respectively. Of note is the absence of any carnivore remains in the assemblage. Of an MNI of 14, two were hyrax, two baboons, and one elephant; the remaining fauna belong to bovids and equids.

Mashatu Den 4 consisted of 611 specimens, of which 51.1% were identified to species and 67.8% to skeletal element. Thus 32.2% of the assemblage was unidentifiable. All long bones were present as well as many small dense bones such as calcaneus, astragalus, and phalanges. Of the long bones humerus was most abundant, and 53.4% of humerus were distal ends, as oppose to 7.1% being proximal ends. All

other long bones were equally distributed between distal and proximal ends. Measured remains ranged from less than 1.0-46 cm, the bulk of fragments consisting of shaft splinters (38%). Complete bones made up 26.2% and one end plus shaft constituted 21% of the fragment types recorded. Carnivore gnawing was recorded on 39.1% of the entire assemblage, of this 58.6% were crenulated edges. Punctates made up 16% while the combination of punctates and crenulated edges was documented on 25% of the gnawed assemblage. Of the 44 minimum species identified, with the exception of one leopard, one porcupine, 3 baboons and 4 hyraxes, all were bird, bovid or equid.

Gobabeb

Gobabeb Den NN-1 was previously collected and published by Henschel *et. al.* in 1979. In total 296 bone and bone fragments were collected from the outside of the den. Identified in the remains were a minimum of seven gemsbok, one equid, one steenbok or klipspringer, four domestic goats and one ostrich. Of the total identified remains (numbers not published) 74.6% were from gemsbok, 13.4% from steenbok or klipspringer, 8.9% from domestic goat, 1.5% from equid and 1.5% from ostrich. Damage noted by Henschel includes 'a splintering of bones by adults with their powerful premolars and gnawing of bones by juveniles'. Fragmentation patterns were not published, nor fragment size.

The current study collected 685 specimens, from which only two species were identified. There was a minimum of one gemsbok and one goat in the assemblage, and 94.1% unidentifiable to species. Long bones and small compact bones were

identified with equal abundance, in contrast to earlier work that suggested leg and skull bones predominate the assemblage. Shaft splinter made up the bulk of fragmentation patterns at 73% and crenulated edges were documented on 79 of the specimens with only a single example of punctates. The single gemsbok left distal humerus from NN-2 had evidence of carnivore gnawing with punctates on the distal end and crenulated edges along the distal shaft. Of note is the complete absence of carnivore bones in either the earlier collection or the current study.

Brief summation

The faunal assemblages of spotted hyaena dens investigated had a range of 1-685 specimens. The size range of the assemblages in question were similar to previous research on spotted hyaena dens (Hughes, 1954, 1961: Mills & Mills, 1977; Henschel *et. al.*, 1979; Skinner *et. al.,* 1986). Looking at the Gobabeb dens and the previous research at den NN-1, one could conclude that spotted hyaena assemblages tend to consist of less than 1,000 bones or bone fragments with a high percentage of unidentifiable remains consisting of mostly shaft fragments with crenulated edges. The identified remains would be that of prey species representative of the region, be they bird (ostrich), bovid or equid and no carnivore remains. The Mashatu dens are consistent with the Gobabeb Dens in that the sizes of the assemblages are less than 1,000 remains, and for the most part consist of prey species within the region. Exceptions are the single leopard skull from Mashatu Den 4 (carnivore MNI 2.3%) and the two spotted hyaena bones from Mashatu Den 2 (carnivore MNI 9.1%). Sutcliffe (1970) stated that bone assemblages of spotted hyaena should consist of distal humerus, proximal radius and ulna, complete metapodials, teeth, complete horns, and upper parts of skulls. The previous collection of Gobabeb NN-1 by

Henschel *et. al.* (1979) is in complete agreement with the stated premise. While in this study Mashatu Den 4 does show a predilection for more distal humerus than proximal, none of the other dens have an over abundance of distal humerus. As for the proximal radius and ulna, none of the Mashatu dens have an excess of either, nor do the dens consist of an over abundance of complete metapodials. Of the 976 remains collected from Mashatu, 742 were measured to length. Of these 33% were 5 cm or less while 14.8% were 20 cm or greater. When the specimens measured from Gobabeb are included the number changes to 57.7% at 5 cm or shorter and 9.1% that are 20 cm or longer. Shaft splinters were the most common type of fragmentation on three of the six dens, while one end plus shaft was predominant on two of the dens and complete bones on one of the dens. Carnivore damage was found on a range of 21-100% of the remains per den, the 100% coming from Gobabeb Den NN-2 that consisted of a single gemsbok humerus with both punctates and crenulated edges. The mean of the remaining five dens with carnivore gnawing was 37.6% (ranged from 21-53.5%). Crenulated edges were the most common type of damage recorded from all four Mashatu dens and Gobabeb Den NN-1.

Parahyaena brunnea assemblages

Rietvlei

Rietvlei Den R01 yielded 27 specimens, of which 74.1% were identified to species and 81.5% to skeletal element, leaving 18.5% unidentifiable. Humerus is absent from the assemblage as are any small bones such as carpals or phalanges. Of the long bones present, both proximal and distal ends are equally represented in the assemblage. Fragments ranged in length from 4-47 cm with shaft splinters constituting 36.4% of

all fragmentation patterns. Complete bones were the next most abundant type of fragmentation with 32%. Carnivore damage was documented on 88.9% of the assemblage. Of this crenulated edges were found on 46% of the damaged remains. Three combinations of damage were noted in the assemblage. Punctates and crenulated edges were found on 21% of the damaged specimens, crenulated edges and striations yielded 12.5% and punctates, crenulated edges and striations were documented on 8.3% of the gnawed material. Of the minimum number of individuals comprising this assemblage, all but a single brown hyaena bone were either equid or bovid.

Of the 12 specimens logged from Rietvlei Den R02 16.7% were unidentifiable, with 83.3% being identified to both species and skeletal element. There were no small bones such as phalanges in the assemblage, also absent were tibia, femur and ulna. The two humerus were medial fragments and the lone radius was a distal end. Length of fragments ranged from 4-35cm with complete bones comprising 55.6% of the assemblage and shaft splinters 22.2%. Carnivore damage was noted on 92% of the assemblage with crenulated edges making up 55% of this. Three combinations of damage types were also documented, these include punctates and crenulated edges (18%), crenulated edges and striations (9%) and punctates and striations (9%). Of an MNI of six, all but one are bovid or equid, the lone exception being from a jackal.

All seven specimens from Rietvlei Den R03 were identified to both species and skeletal element. There were no examples of small bones in the assemblage, also absent were ulna, femur and scapula. Long bones were represented by a complete radius, distal humerus, distal metacarpal and proximal tibia. Fragments ranged in

length from 14-26 cm, of which 50% were one end plus shaft, 25% were complete and 25% were shaft splinters. All specimens had evidence of carnivore damage, 28.6% of the damaged remains were crenulated edges and 14.2% were punctates. The combination of punctates and crenulated edges was documented on 57% of the assemblage. All identified remains (MNI of 7) were bovids.

Brown Hyaena Project Namibia

Den D-P 1 yielded 241 specimens of which 31.1% were identified to species and 89.2% to skeletal element. Thus 10.8% of the examined remains were unidentifiable. All long bones were present in the assemblage as were numerous small compact bones such as astragalus, calcaneus, carpals and phalanges. Proximal and distal ends as well as complete bones and medial shafts equally represented all long bones except humerus. There were no examples of distal humerus, a single complete bone and four proximal ends. Fragment size ranged from <1.0-17 cm and complete bones comprised 30% of the recorded fragmentation patterns and shaft splinters made up 25.6%. Carnivore damage was noted on 31.5% of the entire assemblage, of these 66.7% had crenulated edges. The combinations of punctates and crenulated edges were recorded on 20% of the damaged assemblage, crenulated edges and striations were found on 2.7% and punctates, crenulated edges and striations were found on 1.3% of the damaged remains. Of the 13 minimum number of individuals identified, only three were bovid, three were seals and six were other carnivores.

Den D-P 2 consisted of 256 specimens of which 26.2% were identified to species and 74.2% were identified to skeletal element, leaving 25.8% unidentified. All long bones are represented in the assemblage as well as small compact bones such as calcaneus,

carpals, proximal phalanges and medial phalanges. Proximal and distal ends of long bones were equally represented in the assemblage. Length of fragments ranged from <1.0-15 cm and shaft splinters made up 54.7% of the fragmentation patterns recorded. Complete bones comprised 18% of the recorded fragmentation types. Carnivore damage was documented on 39.5% of the entire assemblage, of these 68.3% had crenulated edges. The combinations of punctates and crenulated edges were noted on 14.8% of the damaged assemblage, crenulated edges and striation on 4.9% and punctates, crenulated edges and striations on 3.9%. Of the seven minimum identified individuals, two were bovid, two seal, one bird and two were other carnivores.

Den D-P 4 consisted of 1,865 specimens, of which 20.7% were identified to species and 81.2% to skeletal element. Thus 18.8% of the assemblage was unidentifiable. All long bones are represented in the assemblage as well as small bones such as proximal, medial and distal phalanges, calcaneus and tarsals. Complete, proximal and distal ends of all long bones were equally represented in the assemblage. Lengths of fragments ranged from <1.0-23 cm with shaft splinters comprising 50.2% of the recorded fragmentation patterns. Complete bones made up 23.6% of the fragmentation types. Carnivore damage was documented on 26% of the entire assemblage, of which 73.6% had crenulated edges. Combinations of punctates and crenulated edges occurred on 14% of the damaged remains, crenulated edges and striations on 2.9% and punctates, crenulated edges and striations on 0.8% of the carnivore gnawed remains. Of the MNI identified (47) 13 are seals, four are avian, 20 are from other carnivores and ten are bovid.

Yielding a total of 5,935 specimens, den D-P 9 was the largest assemblage analysed during this study. Of the total remains examined 40% were identified to species and 94.6% were identified to skeletal element, leaving 5.4% unidentifiable. All major elements of the skeleton were represented, including all long bones and small compact bones. Both proximal and distal ends of all long bones were equally represented in the assemblage. Fragment lengths ranged from <1.0-36 cm with complete bones comprising 41.5% of the fragment types and one end plus shaft making 24.6%. Carnivore damage was documented on 22.1% of the entire assemblage and of this crenulated edges made up 67.4% of the documented damage. The combinations of punctates and crenulated edges were found on 18.7% of the damaged remains, crenulated edges and striations were on 3.4% and punctates, crenulated edges and striations were documented on 0.8% of the carnivore gnawed remains. Bovids, birds and hare combined to make up 24 of the MNI of 133. There were 66 seals, 41 other carnivores, one fish and a single cetacean also identified.

Den D-P 11 consisted of 117 faunal remains, of which 24.8% were identified to species and 80% to skeletal element. Leaving 20% of the examined remains unidentifiable. All long bones are represented in the assemblage as well as smaller compact bones such as phalanges, carpals, astragalus and calcaneus. Fragments ranged in length from <1.0-13 cm and complete bones made up 43% of the measured remains while shaft splinter made up 36%. Carnivore damage was documented on 61.4% of the assemblage with crenulated edges being found on 84.3% of the gnawed remains. The combinations of punctates and crenulated edges were found on 8.6% of the damaged remains and crenulated edges and striations were documented on 1.4%

of the gnawed assemblage. No bovids were amongst the five species identified in the MNI.

Den D-P 16 consisted of 1,287 specimens, 17.9% of which were identified to species, 84.4% identified to skeletal element and 15.6% unidentifiable. All long bones were present in the assemblage as were small bones such as phalanges, carpals and astragalus. Proximal and distal ends of long bones were equally represented with the exception of radius that had a high number of proximal ends when compared to distal ends or complete bones. Length of fragments ranged from <1.0-19 cm and shaft splinter was the most common type of fragmentation with 48.7% of the recorded fragment patterns. Complete bones made up 18.1% of the recorded fragmentation types. Carnivore gnawing was found on 58.8% of the examined remains. Crenulated edges were the most common type of gnawing and were noted on 87.4% of the gnawed remains. The combinations of punctates and crenulated edges were recorded on 6.9% of the gnawed remains and crenulated edges and striations were found on 1.5%. Bovids, birds, small mammals, equids, reptile and fish comprised eight of the MNI of 26, seals contributed to six individuals and other carnivores 11 individuals.

Of the 1,811 faunal remains examined from den D-P 18 36.1% were identified to species and 86.3% to skeletal element, leaving 13.7% unidentifiable. All major skeletal elements were represented, including all long bones and small bones such as phalanges, astragalus, calcaneus and carpals. Of note is the over abundance of proximal radius in the assemblage, when compared to distal ends and complete bones. Fragment length ranged from <1.0-14 cm and complete bones made up 43.7% of the measured fragment types. Shaft splinter made up 27.8% of the fragmentation patterns

recorded. Carnivore gnawing was documented on 64.4% of the assemblage; of these crenulated edges was the most prominent type of damage being on 87.4% of the gnawed remains. The combinations of punctates and crenulated edges were noted on 7.2% of the damaged remains, crenulated edges and striation on 1.1% and punctates, crenulated edges and striation on 0.7%. Seals comprised 14 of the MNI of 36, other carnivores accounted for six individuals, birds seven, reptiles one, fish one and 'prey' species (bovid, equid, small mammal) six individuals.

Den D-SPG 1 yielded 3,252 faunal remains, 46% of which were identified to species and 97.9% were identified to skeletal element. Thus 2.1% of the examined remains were unidentifiable. All long bones and small compact bones are represented in the assemblage and there was no over abundance of proximal or distal ends for any of the long bones. Length of fragments ranged fro <1.0-32 cm with complete bones making up 57.5% of the fragment patterns and one end plus shaft comprising 21% of the fragmentation types documented. Carnivore gnawing was noted on 31.4% of the assemblage with crenulated edges noted on 83% of the gnawed remains. The combination of punctates and crenulated edges made up 11% of the damaged assemblage. There were no other combinations documented for this assemblage. Of the 79 minimum individuals making up the assemblage, 71 are seals, four are other carnivores, three are avian and one is a horse. Of note is the complete absence of bovid in this assemblage.

The Bakers Bay den, D-BB 1, consisted of 1,351 specimens, of which 37.5% were identified to species and 75.9% to skeletal element. Thus 24.1% of the examined remains were unidentifiable. All long bones and small compact bones were

represented in the assemblage and there was no over abundance of any proximal or distal ends of long bones. Fragment lengths ranged from <1.0-48 cm and shaft splinter made up 43.4% of the fragmentation patterns recorded, with complete bones making up 20.2%. Carnivore gnawing was noted on 66% of the assemblage with crenulated edges noted on 81.5% of the gnawed remains. The combinations of punctates and crenulated edges were found on 9.4%, crenulated edges and striations on 2% and punctates and striations on 0.1% of damaged remains. Seals were 29 of the MNI of 55, other carnivores were 10 individuals, avian six, small mammal one, baboon one and bovids seven.

Skinner Collection

The Skinner collection is currently housed at the Bernard Price Institute, University of Witwatersrand, Johannesburg and is a set of faunal remains collected by Skinner *et. al.* in Diamond Area No. 1 in the 80's and early 90's (Skinner & van Aarde, 1991; Skinner *et. al.,* 1998). The current collection had 5,466 faunal remains that were re-examined. Published data indicated that 14,585 remains were collected between 1982 and 1996. Of the 5,466 specimens re-examined 50.4% were identified to species and 85.6% to skeletal element, leaving 14.4% unidentifiable. All long bones and small compact bones were represented in the assemblage with no predilection for either proximal or distal ends of any of the long bones. Length of measured fragments ranged from <1.0-28 cm with complete bones making up 56.1% of the fragment types recorded and shaft splinter yielding 15.3%. Carnivore gnawing was noted on 43.2% of the complete assemblage, 82.8% of which had crenulated edges. The combinations of punctates and crenulated edges were noted on 9.7%, crenulated edges and striations

1.5% and punctates, crenulated edges and striations were noted on 0.7% of the gnawed remains. Of the total MNI of 125, 76 were seal, 16 penguins, 11 avian, 10 other carnivores, six bovid, one ostrich, one horse, one cetacean, one hare, one small mammal, one amphibian and one human. With the exceptions of equid, amphibian and human remains documented during the re-examination of the assemblage, all other species and ratios between species were the same as the previously published works.

Gladysvale

Seventeen specimens were collected from the dens sites near Gladysvale, of which 94.1% were identified to species and 100% to skeletal element. Of the long bones femur, ulna and scapula were absent in the assemblage. Of the small bones only a single calcaneus was present. Fragment length ranged from 7-22 cm and shaft splinter was the most common type of fragmentation pattern. Carnivore gnawing was noted on 94% of the remains, with crenulated edges comprising 50% of the documented damage. The combinations of crenulated edges and striations were found on 25% of the damaged remains, punctates and striations on 12.5% and punctates, crenulated edges and striation s on 6.3% of the gnawed material. All but two of the identified individuals (MNI 8) were bovid, the two exceptions being jackal.

Brief summation

The accumulations of faunal remains ranged from 7-5,935 specimens. The high number of faunal material is consistent with previous research by Skinner & van Aarde (1991) and Skinner *et. al.* (1998), while the lower number of remains is consistent with published work by Lacruz & Maude (2005). With the exception of

the very small assemblages (those with less than 27 examined specimens) all long bones were represented, as were numerous small compact bones such as carpals, phalanges, calcaneus and astragalus. Of the long bones there was no significant predominance for proximal or distal ends. When measured to length 35.7% of the remains are 5 cm or shorter and 2.7% are 20 cm or longer. In seven of the 14 examined assemblages complete bones were the most common type of fragmentation recorded. Shaft splinter was the most common fragmentation pattern in six of the 14 assemblages and in one assemblage one end plus shaft was the most common type of fragmentation documented. The percentage of assemblages that had carnivore gnawing ranged from 22.1% to 100% (a mean of 58.5%). This is similar to the range of carnivore gnawed material from brown hyaena dens in the Makgadikgadi Pans of northern Botswana (Lacruz & Maude, 2005). Crenulated edges were the predominant type of gnawing recorded for all 14 dens examined in this study. The combination of punctates and crenulated edges was the most common multi-type gnawing documented and was noted on 13 of the 14 assemblages. The assemblages were representative of the fauna found in the local regions. Of the inland dens, carnivore made up 14.8% of the total MNI (0% for Rietvlei Den 03, 16.7% for Rietvlei Dens 01 and 02 respectively and 25% for Gladysvale). With the coastal dens the fact that seal make up the majority of remains identified and that seals are the preferred food item by the hyaenas in the region (Goss, 1986; Wiesel, 2006) as well as the fact that seals are carnivores themselves gives a very high MNI for carnivores in the assemblages with a mean of 73.8% carnivore. Removing seals from the total MNI and carnivore MNI, the percentage of carnivores is 43.4%.

Comparative between the three hyaenids

Direct comparisons between species of hyaenids are few in the published record. Skinner recently (2006) published a review of hyaena bone collecting; Skinner & van Aarde published an ecological comparison of brown hyaenas and spotted hyaenas in 1981; Skinner & Ilani published an article on striped hyaenas with a comparison to brown hyaenas in 1979; and there is an unpublished manuscript by Cooper *et. al.* that compares fieldwork with spotted hyaenas to published works on both brown hyaenas and striped hyaenas. Nearly all published works to date concentrate on one species and compare findings with those of previously published studies.

Hyaena assemblages examined in this study can range from a single specimen to over 5,000 faunal remains at a single den site. Assemblages attributed to spotted hyaenas tend to have less remains associated with them, in this study less than 700 remains. Both striped hyaenas and brown hyaenas examined in this study were capable of collecting large faunal assemblages, at times well over 1,000 remains, as well as assemblages of less than 10 specimens. Thus if one locates an unknown assemblage of less than 1,000 remains in a region where hyaenids overlap, small size alone will not determine which hyaena was responsible. This is of course further complicated in the fossil record where all three extant hyaenas overlap along with other extinct hyaenids which may or may not have accumulated faunal assemblages.

All three species in this study utilised natural caves and crevasses as well as modifying the burrows of other animals for their prospective dens. Although all four Mashatu dens that were collected were natural caves, there were two other den sites

located that were modified aardvark burrows. The other spotted hyaena dens located in the Namib Desert were both natural cave sites. With the lone exception of D-SPG 4, brown hyaena dens in and around Diamond Area No. 1 were natural caves. While all the dens of brown hyaenas in the Rietvlei Nature reserve were modified aardvark burrows. In Jordan the Dhahik den was a modified burrow and the dens of the Jawa and Al-Arteen regions were natural caves.

It has been well established that spotted hyaenas are efficient hunters that feed mainly at the site of a kill and bring few faunal remains back to den sites (Kruuk, 1966; Sutcliffe, 1970; Kruuk, 1972; Bearder, 1977; Skinner *et. al*, 1986; Skinner & Chimimba, 2005; Cooper *et. al*., unpublished). In contrast, both brown hyaenas and striped hyaenas are poor hunters in general and rely upon foraging and scavenging alone, or in the case of the Namibian coast, killing of seal pups, and both species bring large quantities of faunal remains back to den sites and resting sites (Mills, 1973, 1990; Mills & Mills, 1977; Skinner, 1976; Owens & Owens, 1978; Yom-Tov & Medelssohn, 2002; Maude, 2005; Maude & Mills, 2005; Skinner & Chimimba, 2005; Wiesel, 2006; pers. obs.). While brown hyaenas have been observed foraging amongst seal colonies in large numbers (eight were observed at one time during the present study), they forage alone and, aside from the occasional greeting or attempts to steal another hyaenas kill, they work completely independently of one another (Wiesel, 2006).

As Figure 1 illustrates, both brown hyaenas and striped hyaenas are separated geographically, but both fill similar niches within their given ranges which tend to be environmentally arid where they survive primarily by scavenging. Both brown hyaena

and striped hyaenas also share a portion of their extant ranges with spotted hyaenas. Little has been documented about the interaction between striped hyaenas and spotted hyaenas, but considering how six Arabian wolves dominated four adult striped hyaenas in Israel on one occasion, while three hyaena were dominant over three wolves on another occasion (Skinner & Ilani, 1979) is suggestive that spotted hyaenas would be the dominant species whenever the two meet at a carcass. Similarly in regions where spotted hyaenas and brown hyaenas overlap, due to the behavioural differences and size differences it is certain that brown hyaenas would be dominated by the larger and more social spotted hyaenas (Skinner & van Aarde, 1981). For example, in the Kruger National Park, spotted hyaenas through competitive exclusion have exterminated brown hyaenas; on the other hand, both species co-exist in the Kgalagadi Transfrontier Park because only a small number of spotted hyaena clans survive in such rigorous climatic conditions (Skinner, J.D., unpublished).

The species represented in the faunal assemblages will naturally vary according to the fauna that inhabit the various regions. Thus, in the case of the striped hyaena, which has the largest range by far (Kruuk, 1976), it would be expected to have very different bone assemblages if one compared dens in the Middle East to those of dens on the Indian sub-continent or Africa. But it is reasonable to hypothesize that the taphonomic signatures left by *Hyaena* in the deserts of Jordan should be similar to those left by the same species in India or Africa and may be related to fossil assemblages associated with *Hyaena* (*makapani*) remains in southern Africa. Additionally, the fact that all three extant hyaena species have latrine areas that are regularly used, both inside and outside of dens, where large quantities of coprolites are deposited is a positive indicator for the presence of hyaenas (Skinner, 1976; Owens & Owens, 1979;

pers. obs.). This factor has been routinely ignored in the archaeological literature with the noted exceptions of Klein (1986), Klein *et. al.* (1999) and more recently Berger (unpublished).

Examining the patterns of fragmentation for the species the Skinner collection and the assemblage from Gobabeb NN-1 were not included due to the assemblages being collected previously and the researcher not knowing for sure what, if any, faunal remains were not collected. As Chart 81 illustrates, shaft splinters predominate the collections of striped hyaenas, while in collections by spotted hyaenas and brown hyaenas shaft splinters are a major type of fragmentation but do not dominate the assemblage. In this study the assemblages of spotted hyaenas and brown hyaenas are actually quite similar in fragmentation patterns. The noted exception being that there are more complete bones in brown hyaena assemblages and less shaft splinters when compared to assemblages of spotted hyaenas. Both the spotted hyaena and brown hyaena assemblages have a similar number of one end plus shaft, which is double the amount found in the assemblages of striped hyaenas. All three species have similar numbers of both ends present, some shaft missing. A very small number of end splinters were found in the assemblages of spotted hyaenas and striped hyaenas, while there were more end and shaft splinters found amongst the assemblages of spotted hyaenas. End and shaft splinters were equally represented between brown hyaenas and striped hyaenas. One end only was equally represented in spotted hyaena and brown hyaena assemblages, while approximately 50% were noted in the assemblages of striped hyaenas. Cylinders were found more often amongst brown hyaena assemblages, followed by striped hyaenas and spotted hyaenas. Of note is the fact that not all of the dens follow the patterns established for species, for instance the three

Rietvlei dens in this study each had a different type of fragmentation than that which predominated the coastal brown hyaena assemblages. Den R01 was 36.5% shaft splinter, Den R02 was 55.6% complete and Den R03 was 50% one end plus shaft. The same is true for the Mashatu dens, two were predominantly shaft splinter, one complete and one was one end plus shaft. Only with striped hyaenas were the fragmentation patterns uniformly shaft splinters across all five dens.

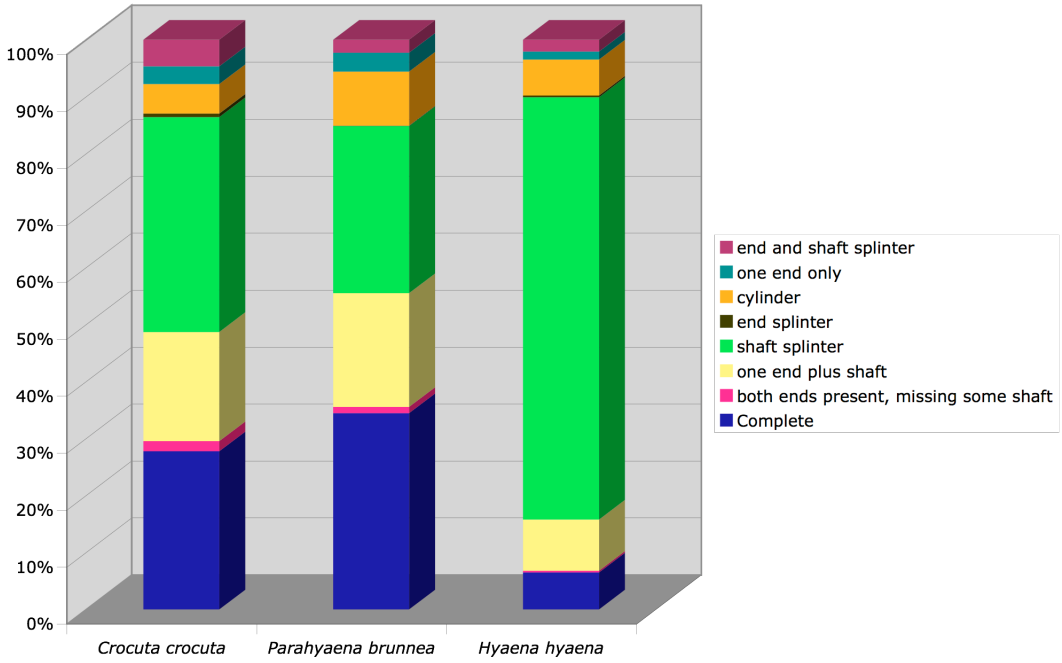

Chart 81: Fragmentation by Species

In this study the damage due to gnawing upon the faunal remains ranges from 33.3% in striped hyaenas to 48% in spotted hyaenas and 58.5% in the case of brown hyaenas. The gnawing damage done to the examined elements by hyaena species is illustrated in Chart 82. Crenulated edges were the most prevalent type of damage found in brown hyaena and spotted hyaena assemblages, while both crenulated edges and punctates were equally noted on gnawed material from striped hyaena assemblages. Punctates made up a considerable portion of the damage done by striped hyaenas, but in spotted

hyaenas punctates alone were found on less than 20% of the assemblage and in the case of brown hyaenas that number declines to just over 5%. Of note is that the combination of punctates and crenulated edges are more prevalent in both spotted hyaena and brown hyaena assemblages than punctates alone, while in the striped hyaena assemblages in Jordan this was not the case. Scouring (See Plate 26), or scooping out to use Maguire (1980), was noted on a small percentage of spotted hyaena and striped hyaena assemblages. Of note were the combinations of scouring with other forms of gnawing documented on 23.2 % of the striped hyaena assemblages. This is contrary to a study done by Leakey *et. al.* (1999) where they state that this form of damage is uncommon in striped hyaena assemblages and Sutcliffe (1970) where he states that this form of damage is common in spotted hyaena damaged remains.

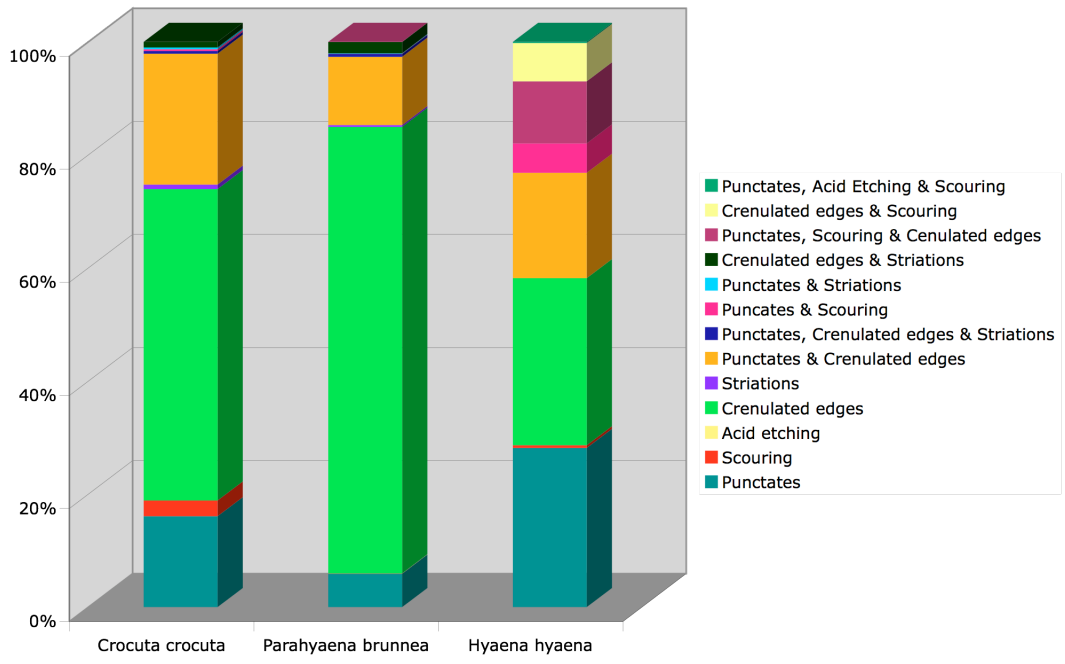

Chart 82: Carnivore Damage by Species

Analysing the gnawed long bones by proximal and distal ends per species in this study indicates that in spotted hyaena and striped hyaena assemblages there is an abundance of distal humerus. Spotted hyaena assemblages also have an abundance of proximal ulnas. All other long bones that have been gnawed are equally represented when broken down by species.

Criteria for distinguishing between hyaena or hominid

Of the published works attempting to distinguish between hyaena collected assemblages and those collected by hominids the research by Stiner (1991) and Cruz-Uribe (1991) has suggested criteria that rely upon 'tendencies' of hyaena collection activity. The lone contribution by Stiner states that 'a purported pattern of excessive proportions of horn or antler in hyaena-accumulated assemblages' is indicative of hyaena den occupation. Of the 25 dens/assemblages examined for the present study, none had an over abundance of horn or antler. Cruz-Uribe suggested the following criteria to confirm hyaenas as collecting agents: 1)'A purported absence or low occurrence of small, hard, compact bones such as sesamoids, carpals, smaller tarsals, and phalanges in hyaena-accumulated assemblages'. In the current study the three dens from Rietvlei would agree with this criterion, as there were no small, compact bones recovered from any of these dens. Data from the other 22 dens examined in this study is contrary to this particular criterion as even the smaller assemblages had small compact bones well represented. 2)'A purported tendency for smaller ungulates to be better represented by cranial bones and for larger ungulates to be better represented by post-cranial bones' suggests a hyaena assemblage. This does not appear to be the case in the 25 assemblages examined for this study, as there were a number of larger skulls from camel, kudu and gemsbok noted from dens of all three

hyaena species as well as numerous lower limb bones from smaller ungulates. 3) 'A purported tendency for bovid mortality profiles to be attritional in hyaena-accumulated assemblages'. As Pickering (2002) indicated, the assumptions needed to validate this particular criterion are not justified. That being said, the majority of fusion data for bovid remains indicated that the animals were adult at the time of death, and pathology from remains taken from the Mashatu dens indicate that at least one kudu was old enough for arthritic conditions to have developed (Franklin, unpublished). 4)'A relative abundance of carnivores (≥20 percent of the total MNI) in hyaena-accumulated assemblages'. This particular criterion has been refuted by Pickering (2002), Lacruz & Maude (2005) and Kuhn (2005). The data from Kuhn (2005) comes from the striped assemblages covered here and the percent carnivore (MNI) ranged from 0-29% with a mean of 20.1% carnivore. Spotted hyaena assemblages in this study had a range of 0-9.1%, with a mean of 1.9% carnivore. The question regarding brown hyaena assemblages and percent carnivore has been touched upon previously, the problem being that dens on the coast have a high number of seal remains and seals are carnivores. Thus the brown hyaena dens surveyed in this study had a range from 0-95% carnivore with a mean with seals counted of 73.8% and a mean with out seals at 43.4%. 5)'An abundance of limb bones with relatively complete shafts, but are lacking epiphyses, in hyaena-accumulated assemblages'. While not the most common type of fragmentation for any of the species in this study, cylinders did represent 23.2% of fragment types in spotted hyaena assemblages, 18.7% in striped hyaena assemblages and 12.1% in brown hyaena assemblages. 6) 'Hyaena-inflicted bone surface damage in hyaena-accumulated assemblages'. Obviously, hyaena-inflicted damage is indicative of hyaena activity on a given assemblage. The question remains what distinguishes

hyaena from other carnivores, be they extant or extinct. Pickering (2001) noted hyaena-inflicted damage on assemblages ranged from 38% to 100%, the present study indicated damage ranging from as low as 33% for striped hyaena assemblages to 56% for brown hyaena assemblages (with spotted hyaena assemblages being 48% gnawed).

CHAPTER 7

Conclusion

Trends of hyaenid assemblages

The history and importance of hyaenids as potential collectors of palaeontological bone assemblages has been well established in the literature and this study. In addition to establishing the background and reasoning for this particular study a number of questions were specifically asked at the outset of this study (see page 7):

Question 1) Are there observable differences in assemblages of striped hyaenas, brown hyaenas and spotted hyaenas? It was found in this study that the assemblages of striped hyaenas tend to have a greater proportion of shaft splinters when compared to the other species' assemblages. Striped hyaena assemblages also had a greater incidence of scouring, usually combined with other types of damage (see Chart 82). In contrast, the bone assemblages of brown hyaenas and spotted hyaenas were quite similar in their fragmentation patterns, while brown hyaena assemblages showed no evidence of scouring and individual bones exhibited predominantly crenulated edges, presumably from gnawing.

Question 2) Do spotted hyaenas create smaller assemblages than either striped hyaenas or brown hyaenas? In general the assemblages attributed to spotted hyaenas in this study were much smaller than the larger assemblages of either striped hyaenas or brown hyaenas. A pair of spotted hyaena assemblages, however, comprised over 600 remains, and were larger than many striped hyaena and brown hyaena

assemblages examined in this study (see chapter 5). Thus in this study a small assemblage was not diagnostic for a particular species of hyaenid.

Question 3) Are the bone fragments left after gnawing by spotted hyaenas consistently smaller than those of striped or brown hyaenas? While the fragments from the Rietvlei dens were seldom smaller than four centimetres, all of the brown hyaena sites in Namibia had numerous fragments smaller than one centimetre. This was also true of the striped hyaena material examined from the Jordanian sites. The environment possibly influences fragment size, as fragment size in this study was constantly smaller in the more arid environments.

Question 4) Are the striped hyaenas and brown hyaenas truly similar in their collecting behaviours as suggested by independent studies of the two species (Owens & Owens, 1978; Skinner, 1976; Kruuk, 1976; Bearder, 1977; Skinner *et. al.,* 1980, 1991; Leakey *et. al.,* 1999; Kuhn, 2001, 2005 and Lacruz & Maude, 2005)? Or will there be distinctive patterns established to differentiate between the two species? Contrary to some of the previous studies, it was noted in this study that both striped hyaenas and brown hyaenas scavenge species from small mammals up to the largest animals inhabiting the prospective regions (camels in the case of striped hyaenas and buffaloes in the case of brown hyaenas). The differences noted in this study between the collecting behaviour of these two species may be seen in the patterns of fragmentation and percentages of specific damage done to the faunal remains. Specifically, bones within the striped hyaena assemblages tend to have relatively equal numbers of crenulated edges and punctates while in contrast, bones within brown hyaena assemblages tend to have large numbers of crenulated edges. Remains

within striped hyaena assemblages also show scouring (Chart 82), albeit usually in conjunction with some other form of gnawing, while brown hyaena assemblages lack scouring.

Question 5) Are there noticeable differences in the collecting behaviours and den usage of the three hyaena species in question? All three species in this study made use of both natural caves and crevasses as well as modified burrows of other animals. There were no obvious differences in the assemblages associated with any type of den.

6) Are there differences between populations of the same species from different environments? Aside from the difference in prey species available, there were differences noted between brown hyaena populations from inland sites at Rietvlei and the coastal sites of Namibia as well as spotted hyaena populations in Mashatu and Gobabeb. Specifically, the brown hyaenas of Rietvlei did not leave many smaller fragments (nothing smaller than four centimetres), plus these populations did not exhibit the large assemblages typically associated with brown hyaenas, possibly due to a more abundant food supply through out the year (surrounding farms routinely drop domestic carcasses, especially chicken, in the reserve) thus less dependence upon bone material in their diet. The spotted hyaenas of the Namib-Naukluft Desert left behind a greater number of shaft splinters and a higher number of small fragments than the spotted hyaenas of Mashatu, possibly attributed to a greater utilization of bone in their diet as a direct reflection of environmental conditions and fewer prey species.

Question 7) Do spotted hyaenas bring back larger faunal remains than either striped hyaenas or brown hyaenas as hypothesised by numerous previous researchers (Kruuk, 1972; Bearder, 1977; Skinner *et. al*, 1986; Cooper *et. al.*, unpublished)? It was shown in the present study that all three species are capable of bringing back remains from the largest species available in their prospective regions. Striped hyaenas in Jordan scavenged from adult camels, brown hyaenas from Rietvlei had buffalo remains in the assemblages, brown hyaenas from the coast had adult seal remains as well as adult gemsbok in the assemblages while spotted hyaenas in Mashatu even had an elephant bone in the assemblage. Gemsbok was common in the assemblages from the Namib-Naukluft Desert.

Question 8) Which species leaves behind more distinctive taphonomic signatures, and which of these signatures is more prevalent? In this study the bone assemblages of brown hyaenas showed a greater percentage of carnivore gnawed remains in the combined assemblages, striped hyaenas the least. Crenulated edges were the most common type of damage left behind on bone by both brown hyaenas and spotted hyaenas. Crenulated edges and punctates were equally represented in the assemblages of striped hyaenas. Some of the punctates left behind by striped hyaenas were very deep, in one case transgressing a mid-line metapodial of a camel.

Question 9) Are there distinguishing taphonomic signatures of hyaenids that separate them from other carnivore collectors such as leopards? Deep punctates like the one found through the camel metapodial by a striped hyaena (most likely indicative of hyaena jaw strength) could be characterised as hyaena activity. In addition, Richardson (1980) and Richardson *et. al.* (1986) indicate that hyaena 'damage and

destroy' more bones than lions, leopards, dogs or jackals. While spotted hyaenas have been labelled as having the strongest jaws and are the 'most effective extant bone cracking carnivore' (Marean & Spencer, 1991). It is worth noting that striped hyaenas produced a larger percentage of shaft splinters of the three hyaena species examined in this study. Additionally much of the 'hyaena' damage, such as ragged-edged chewing/crenulated edges, pitting, punctates, striations and acid etching have been identified in modern collections in North America where it is believed that canids, most probably coyotes (*Canis latrans*) were the carnivore responsible for the damage (Lyman, 1994). Additionally Njau and Blumenschine (2006) found that crocodiles (*Crocodylus niloticus*) produce similar taphonomic signatures as large mammalian carnivores as well as bite marks unique to crocodiles. With this in mind it is perhaps better to use the ratios of fragmentation patterns and damage types that have been found here for the given species and not just the type of damage for determining if hyaenids are responsible for various unknown assemblages.

In addition to the above cautionary note, porcupine activity was recorded in the present study (see Chapter 5) in 10 of the 25 dens examined. In addition a black-backed jackal family was observed in residence at a previously identified hyaena den on the Luderitz Peninsula (D-P 10). The jackals in question remained at the den for over seven days and did not appear to be disturbed by human presence. This brings into question a number of variables, such as: have porcupines contributed to the faunal assemblages by bringing material into the dens, or have the porcupines gnawed on material that hyaenas have collected? If porcupines were contributing to the assemblages, how would their contributions affect the rate of accumulation?

Additionally what sort of damage do the jackals do to the faunal remains and how does one differentiate this damage from hyaena inflicted damage?

Although no census of current fauna was conducted, from what was observed on a daily basis it appears that all of the bone assemblages were direct reflections of the fauna inhabiting the region. Furthermore, the ratios of faunal remains reflect the ratios found between the local fauna of the given regions. The clearest examples were from the coastal den sites in Namibia where Cape fur seal (*Arctocephalus pusillus)* predominated the bone assemblages and are by far the most abundant mammals inhabiting the region at this particular time.

Criteria for distinguishing between hyaena or hominid

Of the seven criteria for distinguishing assemblages of hyaenids from hominids put forth by Stiner (1991) and Cruz-Uribe (1991), only two by Cruz-Uribe are substantiated by the current study. These are 'An abundance of limb bones with relatively complete shafts, but are lacking epiphyses, in hyaena-accumulated assemblages' and, 'Hyaena-inflicted bone surface damage in hyaena-accumulated assemblages'. A third criterion, 'A relative abundance of carnivores (≥20 percent of the total MNI) in hyaena-accumulated assemblages' has been refuted by the present study when one examines spotted hyaena assemblages, seriously questioned when examining the assemblages of striped hyaenas, but supported by and large in the bone assemblages of brown hyaenas. Even within the data set for brown hyaenas, however, all three dens examined at Rietvlei had less than 20%carnivore remains (two had 16% carnivore and one had 0%). Of the five dens examined from striped hyaenas two had

less than 20% carnivore. Thus, as Lacruz & Maude (2005) as well as Kuhn (2005) stated, using this criterion alone to determine hyaenids as the accumulator of an unknown assemblage should be done only with caution. As mentioned previously, other carnivores can produce what has previously been considered uniquely 'hyaena damage' features, such as crenulated edges. Thus combining the types of damage, along with percentages of damage and fragmentation types as well as assemblage make up (MNI percentages) may be better suited for determining an unknown collector.

Further research

While there has been a fair amount of research to date concerning bone collections and taphonomy of potential faunal accumulators, it is clear from the results of the present study that more needs to be done, especially on known accumulators such as leopards. Recognition of specific types of fragmentation and carnivore damage, as well as what percentage of each type of damage is found in a given assemblage needs to be examined, preferably over a large geographic range. In addition, the percentage of unidentifiable fragments left behind by other carnivores should be documented. Additionally more research needs to be done on the issue of multiple collectors and the issue of other 'non-collecting' carnivores such as jackals and their use of and impact on bone assemblages in 'hyaena dens'.