International Journal of Osteoarchaeology
Int. J. Osteoarchaeol. (2008)
Published online in Wiley InterScience
(www.interscience.wiley.com) DOI: 10.1002/oa.996

Examining Criteria for Identifying and Differentiating Fossil Faunal Assemblages Accumulated by Hyenas and Hominins using Extant Hyenid Accumulations

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ABSTRACT Numerous authors have put forth criteria for distinguishing between assemblages collected by hyenas and hominins. Of the seven most recognised criteria used to distinguish hyenid from hominin assemblages, it has recently been suggested that four be rejected and three retained. The four rejected criteria are: an excessive proportion of horns and horn cores in hyena accumulated assemblages; the absence of small, hard, compact bones; mortality profiles; and the ratio of cranial bones to postcranial bones. The three criteria previous researchers suggested be retained are: a carnivore MNI ratio of $\geq$20%; an abundance of cylinder fragments; and hyena-inflicted damage upon the bones. In this examination of over 27,000 faunal remains associated with all three species of extant bone-collecting hyenids from four countries and two continents, six of the seven previously established criteria and reconsiderations of criteria have been evaluated. The results of the present study indicate that of the six criteria examined, none, as written, are indicative of hyenid activity on bone assemblages of unknown origin. Copyright © 2008 John Wiley & Sons, Ltd.

Key words: hyena; taphonomy; bone assemblages; faunal analysis

Introduction

Interpretations of how fossil assemblages were accumulated have ranged from Dart's theory of predatory, carnivorous, tool-wielding, bone-collecting hominins (Dart, 1957, 1958) to non-hominin bone collectors, from birds (Mayhew, 1977; Berger & Clarke, 1995; Cruz-Uribe & Klein, 1998) to rodents (Kerbis Peterhans & Singer, 2006) to large mammals (Henschel *et al.*, 1979; Skinner & Ilani, 1979; Brain, 1981; Skinner & van Aarde, 1991; de Ruiter & Berger, 2000, 2001; Kuhn, 2005; Lacruz & Maude, 2005; Skinner, 2006). In order to understand and interpret the fossil assemblages one needs to be able to determine, with a degree of certainty, the mode or modes of collection for any particular accumulation. As Maguire *et al.* (1980) stated with regards to the Makapansgat Limeworks Grey Breccia in South Africa, 'Hominids, hyaenas,

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Received 17 January 2008
Revised 7 April 2008
Accepted 16 April 2008

hystricids or hill wash?' (1980: 73), noting that these are just four possible modes of collection for this specific site. In particular, hyenas are considered critically important taphonomic agents in the fossil record since they are among the most prolific extant bone accumulators (Henschel *et al.*, 1979; Skinner & Ilani, 1979; Skinner *et al.*, 1980; Skinner & van Aarde, 1991; Lam, 1992; Leakey *et al.*, 1999; Kuhn, 2005; Lacruz & Maude, 2005; Skinner, 2006). Determining whether hyenids played a role in the accumulation of fossil material allows one to interpret not only the relationship of the fauna represented in the accumulation to the external environment, but may also shed light upon the relationship between hominins and hyenids in ancient landscapes, thereby exploring potential evolutionary adaptations in our lineage.

To date, a number of diagnostic criteria have been put forward by various scientists, all attempting to differentiate between hyena- and hominin-collected bone assemblages. These have included studies of modern human populations (Brain, 1967), modern hunter-gatherer accumulations compared with those of spotted hyena (*Crocuta crocuta*) accumulations (Bunn, 1983), spotted hyena bone modifications (Hill, 1989), studies of both extant and extinct hyena morphology (Brain, 1981) and presumed archaeological hyena den sites (Klein, 1975; Scott & Klein, 1981). Subsequently, specific criteria have been published that are proposed to distinguish between hyena- and hominin-collected bone assemblages (Maguire *et al.*, 1980; Hill, 1984; Binford *et al.*, 1988; Blumenschine, 1988; Cruz-Uribe, 1991; Stiner, 1991; Marean *et al.*, 1992; Marean & Bertino, 1994; Pickering, 2002; Kuhn, 2005; Lacruz & Maude, 2005; Faith *et al.*, 2007; Pokines & Kerbis Peterhans, 2007). Stiner (1991) proposed a single criterion and Cruz-Uribe (1991) put forth six criteria, that together made seven specific criteria that were hypothesised to distinguish whether or not hyenids or hominins were responsible for any particular fossil faunal accumulation. However, Cruz-Uribe (1991) was specific in indicating that no one criterion on its own was diagnostic of hyena activity. The seven criteria and Pickering's suggested retention or rejection are shown in Table 1.

Table 1. Criteria by Cruz-Uribe (1991) and Stiner (1991), and subsequent evaluation by Pickering (2002)

The criteria	Author	Pickering's re-evaluation (2002)
Carnivore-ungulate ratio. Cruz-Uribe (1991) hypothesised that the MNI (minimum number of individuals) of carnivore remains in a hyena-accumulated assemblage will be $\geq$20% of the ungulate plus carnivore MNI, while in hominid accumulations this number will always be $<$13%.	Cruz-Uribe (1991)	Retain
Damage to bone surfaces. This includes distinctive hyena damage, which includes striations, pitting, grooves, scooping and acid etching. Cruz-Uribe (1991) hypothesised that damage will occur on at least 50% of bones in modern assemblages, but much less in fossil ones.	Cruz-Uribe (1991)	Retain
Bone breakage. Cruz-Uribe (1991) hypothesised that hyena accumulations will be characterised by many bone cylinders, while hominid collections will have more broken shafts and complete epiphyses, highlighting that broken shafts alone are not diagnostic of hominid collections.	Cruz-Uribe (1991)	Retain
Cranial/postcranial ratio. Cruz-Uribe (1991) hypothesised that this ratio will decrease with the size of the ungulate; therefore smaller ungulates are better represented by cranial bones and larger ungulates by postcranial elements.	Cruz-Uribe (1991)	Rejected
Representation of small hard bones. Cruz-Uribe (1991) hypothesised that the small hard bones of prey species will be absent or at the very least uncommon in hyena accumulations.	Cruz-Uribe (1991)	Rejected
Age profiles. Cruz-Uribe (1991) hypothesised that hyena accumulations will have an attritional mortality profile, thus there will be more young and old specimens in an assemblage and very few prime adults.*	Cruz-Uribe (1991)	Rejected
Stiner (1991) stated that excessive proportions of *horn or antler* in an assemblage is indicative of hyena as the accumulator.	Stiner (1991)	Rejected

*This particular criterion was not examined in the present study.

DOI: 10.1002/oa

Considering that the previous criteria by Cruz-Uribe (1991) and Stiner (1991) were based on assumed fossil assemblages, and the subsequent reconsiderations by Pickering (2002) were based upon assumed fossil hyena accumulations and quoted specific examples from modern hyena behavioural studies (Pickering, 2002: 129), we decided to conduct an independent examination of accumulations from all three extant bone-collecting species of hyenids over a broad geographical range. The present study examined over 27,000 bones from more than 24 dens of extant spotted hyenas, striped hyenas and brown hyenas located in South Africa, Namibia, Botswana and Jordan. The results presented here provide a substantial modern analogue with which to test the previously hypothesised criteria. The present study also gives further insight into the viability of discriminating and identifying hyenid activity upon assemblages, both ancient and modern.

Materials and methods

For the present study we examined the faunal remains recovered from five active striped hyena dens in the eastern desert of Jordan (Kuhn, 2001, 2005). We additionally examined faunal remains recovered from four active spotted hyena dens in the Mashatu Game Reserve, Botswana and examined the remains from two spotted hyena dens in the Namib-Naukluft Park, Namibia. We also collected and examined the faunal remains from three active brown hyena dens in the Rietvlei Nature Reserve, South Africa, as well as from multiple active dens near the Gladysvale palaeontology site on the John Nash Reserve, South Africa. The faunal remains from nine active brown hyena dens in and around Diamond Area No. 1, Namibia, were examined *in situ* (Figure 1) (Kuhn, 2006). In addition, previous collections by Skinner (Skinner & van Aarde, 1991; Skinner *et al.*, 1998) from modern brown hyena dens on the coast of Namibia were also re-examined.

With the exception of the material in Namibia where the research had to be conducted *in situ*, all of the faunal remains were collected, labelled, crated and transported to laboratory facilities for analysis and identification. Material collected from South Africa and Botswana was taken to the Bernard Price Institute for Palaeontological Research (BPI), University of the Witwatersrand,

Figure 1. Map showing study sites in southern Africa.

DOI: 10.1002/oa

Johannesburg. Material collected in Jordan was transported to the Council for British Research in the Levant offices in Amman, Jordan. With the exception of the Skinner collections (Skinner & van Aarde, 1991; Skinner *et al.*, 1998) which are stored at the BPI, material in Namibia was gathered, identified and analysed at each den locality in accordance with protocols set by the Namibian Ministry of Environment and Tourism (MET) and the NAMDEB diamond company.

Approximately 25% of the total surface area of three of the five dens examined in Jordan was sieved to a depth of 5 cm through a 5mm mesh (Kuhn, 2005). Digging, and therefore sieving, of any of the dens in Namibia was not allowed in the protocols set by MET, nor was it allowed in the reserves or national parks of South Africa or Botswana as the dens used were active. Extra care was taken at the dens where sieving could not take place, with the researchers shifting substrate by hand over the entire collection area in order to recover as many small bones and bone fragments as possible. The sieved dens did not yield a greater abundance of small bones or bone fragments than the other dens examined for this study. The substrates associated with the unsieved sites in Jordan were stone, thus making sieving impossible. The same was true for the dens examined by Skinner and van Aarde (1991) and Skinner *et al.* (1998). Sieving increased the database by 3.6%. While the presence of coprolites was noted, they were not counted nor examined in detail for this study.

For this analysis the identification and abundance of skeletal elements, body side, taxa, epiphysial fusion, specific carnivore damage and fragmentation patterns were recorded. All specimens were identified to element and species or class size (following Brain, 1981) where possible. Fragments that could not be positively identified were recorded as such and included in the analysis. In keeping with the methodology of Cruz-Uribe (1991), all macroscopic damage was noted with the naked eye, following Lyman (1994). From this the number of identified specimens (NISP) and minimum number of individuals (MNI) were calculated. Long bone and mandible body sides were used to determine MNI. The percentage carnivore MNI is the percentage of carnivore from the ungulate–carnivore MNI, in order to compare the results with those of Cruz-Uribe (1991). While seals belong to the family Carnivora, the question arose as to whether to assimilate them into the terrestrial carnivore MNI. As inclusion might bias certain coastal sites to exhibit higher carnivore percentages, we decided to report the numbers and percentages as excluding and including seal remains in the results where relevant. In the current study, phalanges, carpals, tarsals and sesamoids were included as small, hard bones. A cylinder fragment is defined here as a bone diaphysis with both epiphyses missing and a portion of the original diameter present (after Binford, 1981). All specimens recovered are included in the analysis.

The data from the present study are here used to re-examine six of the seven criteria established by Cruz-Uribe (1991) and Stiner (1991). The age mortality criterion from Cruz-Uribe (1991) is not examined in this study. While more rigorous statistical analyses are reported in the results, these particular analyses are not included in the discussion comparing the extant accumulations with the specific criteria reported by Cruz-Uribe (1991) and Stiner (1991) and re-evaluated by Pickering (2002).

Results

Table 2 shows the percentage carnivore MNI for each den and the mean value for each hyenid species. Spotted hyena accumulations range in sample size from 58 to 686 specimens per den and all have a carnivore MNI of less than 13% (a mean value of 3.1%). Three of the five dens in question yielded a carnivore MNI of zero. Striped hyena accumulations ranged in size from 107 to 1792 specimens. The carnivore MNI for striped hyena dens averaged 19.4%, and ranged from 0–32.2%. Brown hyena accumulations ranged in sample size from seven to 5955 recorded specimens. The carnivore MNI for brown hyena dens ranged from 0–100% and had a mean value of 48.7% (64.4% when seals are included). When more rigorous statistical methods are applied, a significant relationship exists between sample size and percentage carnivores when looking at hyenids as one group ($r = 0.554$, $P = 0.005$) and brown

DOI: 10.1002/oa

Table 2. Percentage carnivore of ungulate-carnivore MNI (numbers including seals in parentheses)

Collector	Den	Sample size	NISP	Ungulate + carnivore MNI	Carnivore MNI	%MNI carnivore	Mean
Crocuta crocuta	Mashatu Den 1	214	138	11	0	0%	
	Mashatu Den 2	58	37	8	1	12.5%	
	Mashatu Den 3	93	55	9	0	0%	
	Mashatu Den 4	611	312	31	1	3.2%	
	Gobabeb NN-1 & NN2	686	41	3	0	0%	3.1%
Parahyaena brunnea	Rietvlei Den 1	27	20	6	1	16.7%	
	Rietvlei Den 2	12	10	6	1	16.7%	
	Rietvlei Den 3	7	7	5	0	0%	
	BHP D-P 1	241	75	9 (12)	6 (9)	67% (75%)	
	BHP D-P 2	256	67	4 (6)	2 (4)	50% (66.7%)	
	BHP D-P 4	1865	377	27 (40)	19 (32)	70.1% (80%)	
	BHP D-P 9	5955	2383	45 (111)	38 (104)	84.4% (94%)	
	BHP D-P 11	117	29	2 (4)	2 (4)	100% (100%)	
	BHP D-P 16	1287	220	15 (21)	10 (16)	67% (76.1%)	
	BHP D-P 18	1811	653	9 (23)	6 (20)	66.7% (87%)	
	BHP D-SPG 1	3253	1493	5 (76)	4 (75)	80% (99%)	
	BHP D-BB 1	1351	510	17 (46)	10 (39)	59% (85%)	
	Skinner Collection	5466	2757	17 (93)	10 (86)	59% (92.5%)	
	Gladysvale	17	16	8	1	12.5%	48.7% (64.4%)
Hyaena hyaena	Jawa Den 4	1792	500	59	18	32.2%	
	Jawa Den 7	119	16	6	0	0%	
	Al-Arteen Den 11	361	124	28	6	21.4%	
	Al-Arteen Den 13	107	41	9	2	22.2%	
	Dhahik Den 32	1377	311	28	6	21.4%	19.4%

hyena assemblages ($r = 0.658$, $P = 0.0005$), but not for striped hyena assemblages ($r = 0.484$, $P = 0.016$). Spotted hyenas have a negative correlation that is not significant ($r = -0.396$, $P = 0.0554$). Looking at the log of the sample size and percentage carnivores illustrates that sample size may affect the percentage carnivores for brown hyena and striped hyena accumulations, but appear to have a negative correlation for spotted hyena accumulations (Figure 2).

Juvenile hyena remains were documented from at least some of the dens of all three species of hyena. Table 3 shows the MNI of juvenile hyenas from specific dens. Juvenile hyena bones were recovered from one of the five dens associated with spotted hyenas, one of five dens associated with striped hyenas, and nine of the 14 brown hyena accumulations.

Carnivore gnawing is documented for each den or collection and is illustrated in Table 4. The percentage of carnivore-chewed specimens from spotted hyena dens ranged from 29–53.5%, with a mean value of 39.2%. For the assemblages attributed to brown hyenas, the percentage of carnivore-gnawed material ranged from 22.1–100% with a mean value of 58.5%. For striped hyenas the range was 6–56.2% carnivore-gnawed, with a mean value of 40.2%. The den yielding only 6% (Dhahik Den 32) had extreme weathering associated with over 90% of the assemblage, thus the results from this den were not included in the mean value. Figure 3 illustrates that when one looks at the log of the sample size compared with percentage carnivore gnawing, there is a direct correlation between sample size and observed gnawing for hyenids in general, spotted hyenas and brown hyenas. The opposite is true for striped hyenas; in this case the percentage carnivore-gnawed increased with the sample size.

In addition to general carnivore gnawing, the abundance of bone cylinder fragments was documented (Table 5). Accumulations attributed to spotted hyenas averaged 6.5% cylinder fragments. Cylinder fragments made up 10% of brown hyena assemblages and 6% of striped

DOI: 10.1002/oa

hyena assemblages. Types of carnivore damage and combinations of damage recorded for each species are illustrated in Figures 4–6. Acid or gastric etching was only recorded on 11 specimens: one from striped hyena, four from brown hyena, and six from spotted hyena assemblages. Considering that coprolites were not examined and neither striped hyenas nor brown hyenas regurgitate, the low numbers for these two species is not surprising. Spotted hyenas do regurgitate in and around den sites, thus the low number from these accumulations was of note.

The cranial/postcranial ratios for large, medium and small ungulates as well as small canids were calculated for each species of hyena, and the results can be seen in Table 6. For spotted hyenas, larger prey species are better represented by postcranial elements and smaller ungulates by cranial elements. The ratio of cranial to postcranial elements increases as the size of prey

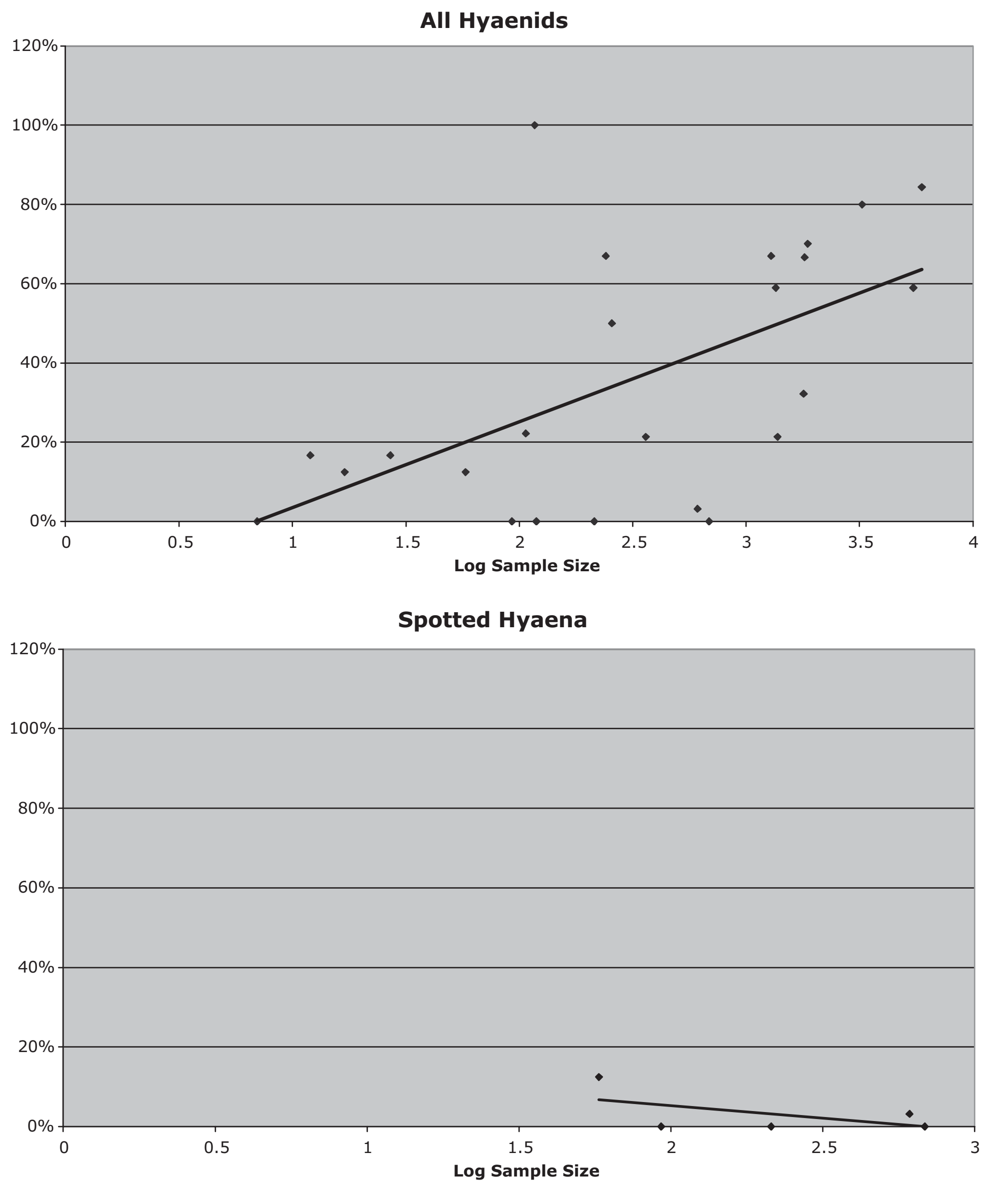

Figure 2. Log of sample size compared to % carnivore for all hyenids and each species separately.

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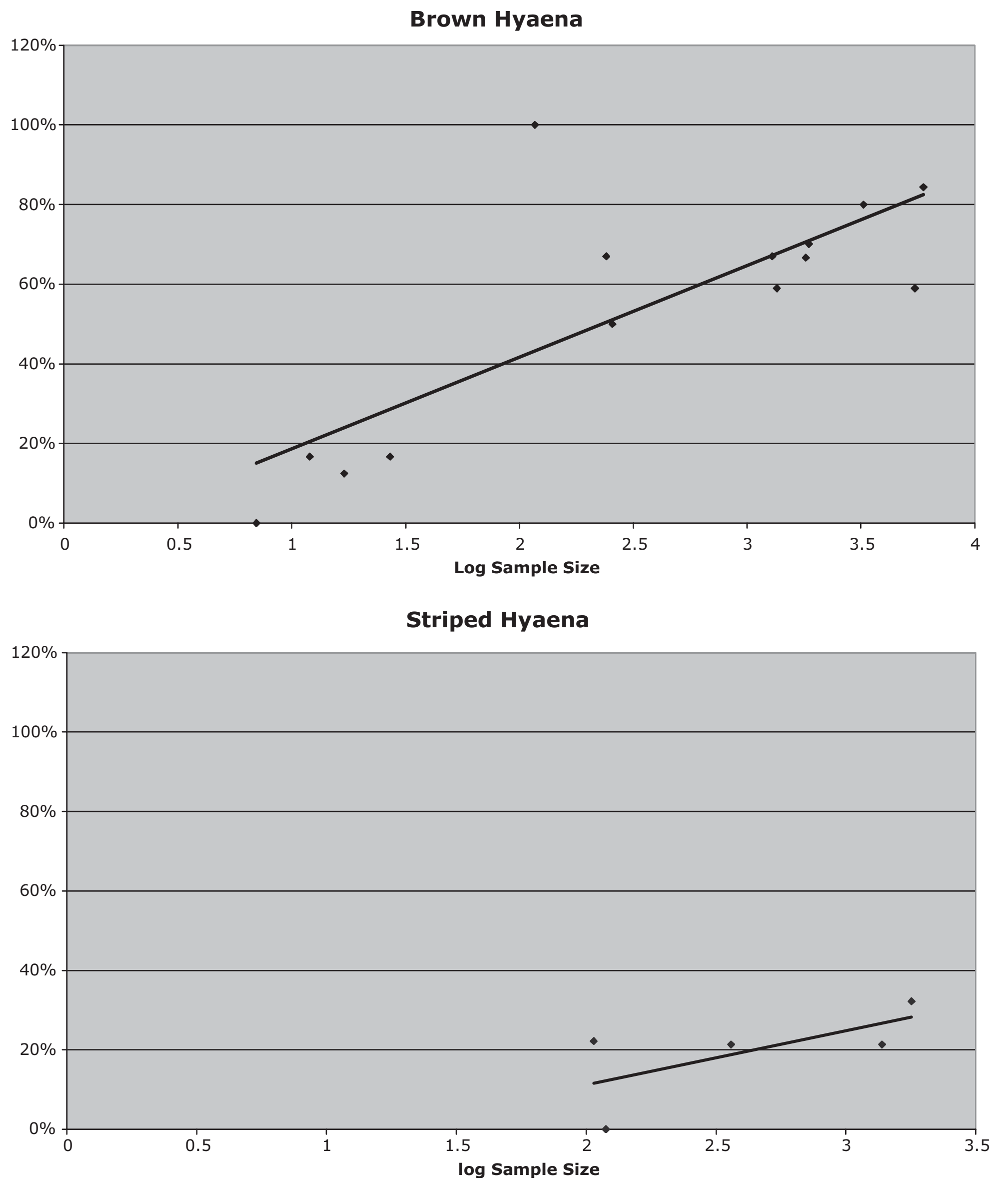

Figure 2. *Continued*

species decreases. For both the striped hyenas and brown hyenas the ratios of large to small ungulates are not as clear as that recorded for spotted hyenas. In both of these cases the ratio of cranial to postcranial remains increases as prey size goes from large to medium-sized ungulates, but decreases again as prey size goes from medium to small ungulates. Applying a chi-square test for the three species indicates that the abundance of cranial to postcranial bones is significant when compared across body size for spotted hyenas ($\chi^2 = 0.029$, $p = 0.864$) and striped hyenas ($\chi^2 = 0.013$, $p = 0.91$), but not significant for brown hyenas ($\chi^2 = 0.839$, $p = 0.359$). Thus for spotted hyenas and striped hyenas the patterns differ significantly from what can be expected from sampling error.

The abundance of small hard bones in relation to all postcranial bones can be seen in Table 7. Small hard bones make up as little as 0% and as

DOI: 10.1002/oa

Table 3. Juvenile hyena MNI per den

Hyena species/den	MNI
Hyaena hyaena	
Jawa Den 4	1
Parahyaena brunnea	
Skinner Collection	1
D-P 1	1
D-P 4	1
D-P 9	2
D-P 16	3
D-P 18	1
D-SPG 1	1
D-BB 1	2
Rietvlei Den 1	1
Crocuta crocuta	
Mashatu Den 2	1

much as 34% of the postcranial remains. In four of the accumulations, three from brown hyena dens and one from a striped hyena den, no small hard bones were recovered. The three brown hyena dens in question yielded very small assemblages (fewer than 30 total specimens), while the striped hyena den yielded over 100 specimens and was sieved. The relative abundance of small hard bones from spotted hyena dens ranged from 13.7–34%, while for brown hyenas it ranged from 0–23.2% and for striped hyenas the abundance of small hard bones ranged from 0–10.6%. Figure 7 illustrates that sample size has little effect upon the percentage of small compact bones. A chi-square test comparing small bones from sieved dens with those that were not sieved indicates that the difference is not significant ($\chi^2 = 2.33$, $p = 0.126$).

Table 8 illustrates the abundance of horn recovered from each den in relation to the minimum number of elements (MNE) for limb bones. The numbers of horn recorded are the maximum number recovered with no correction for fragmentation. Even with the horn values inflated there are only four examples of an overabundance of horn in the dens examined. All four of these assemblages had very low limb bone MNE, either due to small assemblage size or severe fragmentation.

Table 4. Percentage of assemblage with carnivore gnawing

Collector	Den	Sample size	% carnivore gnawed	Mean
Crocuta crocuta	Mashatu Den 1	214	32.2	
	Mashatu Den 2	58	53.5	
	Mashatu Den 3	93	42	
	Mashatu Den 4	611	39.1	
	Gobabeb NN-1 & NN-2	686	29	39.2%
Parahyaena brunnea	Rietvlei Den 1	27	88.9	
	Rietvlei Den 2	12	92	
	Rietvlei Den 3	7	100	
	BHP D-P 1	241	31.5	
	BHP D-P 2	256	39.5	
	BHP D-P 4	1865	26	
	BHP D-P 9	5955	22.1	
	BHP D-P 11	117	61.4	
	BHP D-P 16	1287	58.8	
	BHP D-P 18	1811	64.4	
	BHP D-SPG 1	3253	31.4	
	BHP D-BB 1	1351	66	
	Skinner Collection	5466	43.2	
	Gladysvale	17	94	58.5%
Hyaena hyaena	Jawa Den 4	1792	56.2	
	Jawa Den 7	119	23.5	
	Al-Arteen Den 11	361	41.6	
	Al-Arteen Den 13	107	39.3	
	Dhahik Den 32*	1377	6*	40.2%*

*Dhahik Den 32 had extreme weathering, and thus is not included in the mean value.

DOI: 10.1002/oa

Discussion

Re-evaluating previously established criteria

Carnivore-ungulate ratio

'The MNI of carnivores will be ≥20% in hyena accumulations' (Cruz-Uribe, 1991: 475).

Examining the results from the present study supports the statement by Cruz-Uribe (1991) that the 20% or greater carnivore MNI does not hold for spotted hyenas. Three of the five spotted hyena dens examined yielded no carnivore remains at all, with the remaining dens yielding MNI of 12.5% and 3.2%. The data from the

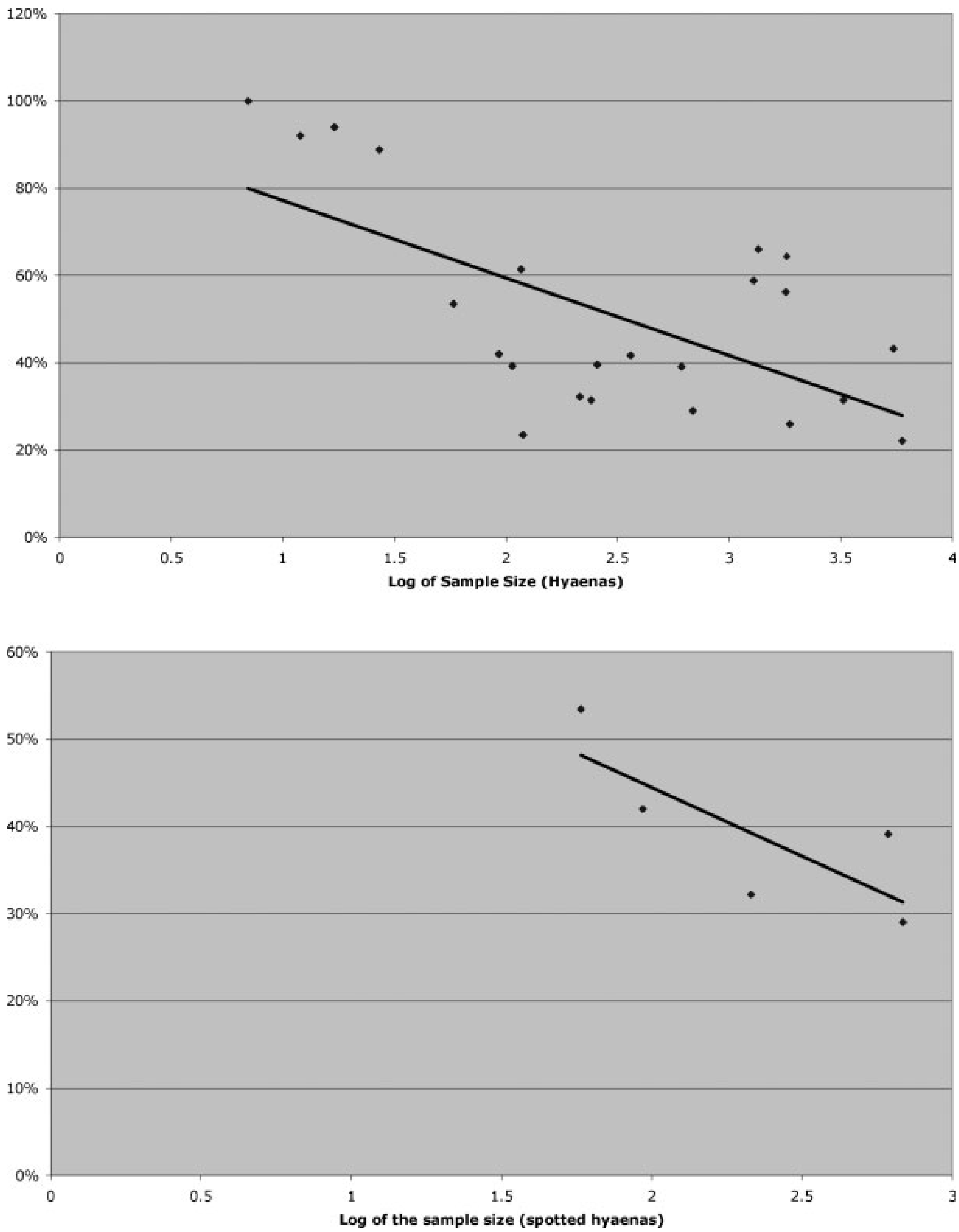

Figure 3. Log of sample size compared with % carnivore-gnawed for hyenas as a species as well as for each individual species. *Note*: Dhahik Den 32 removed from striped hyena and overall hyena data due to extreme weathering.

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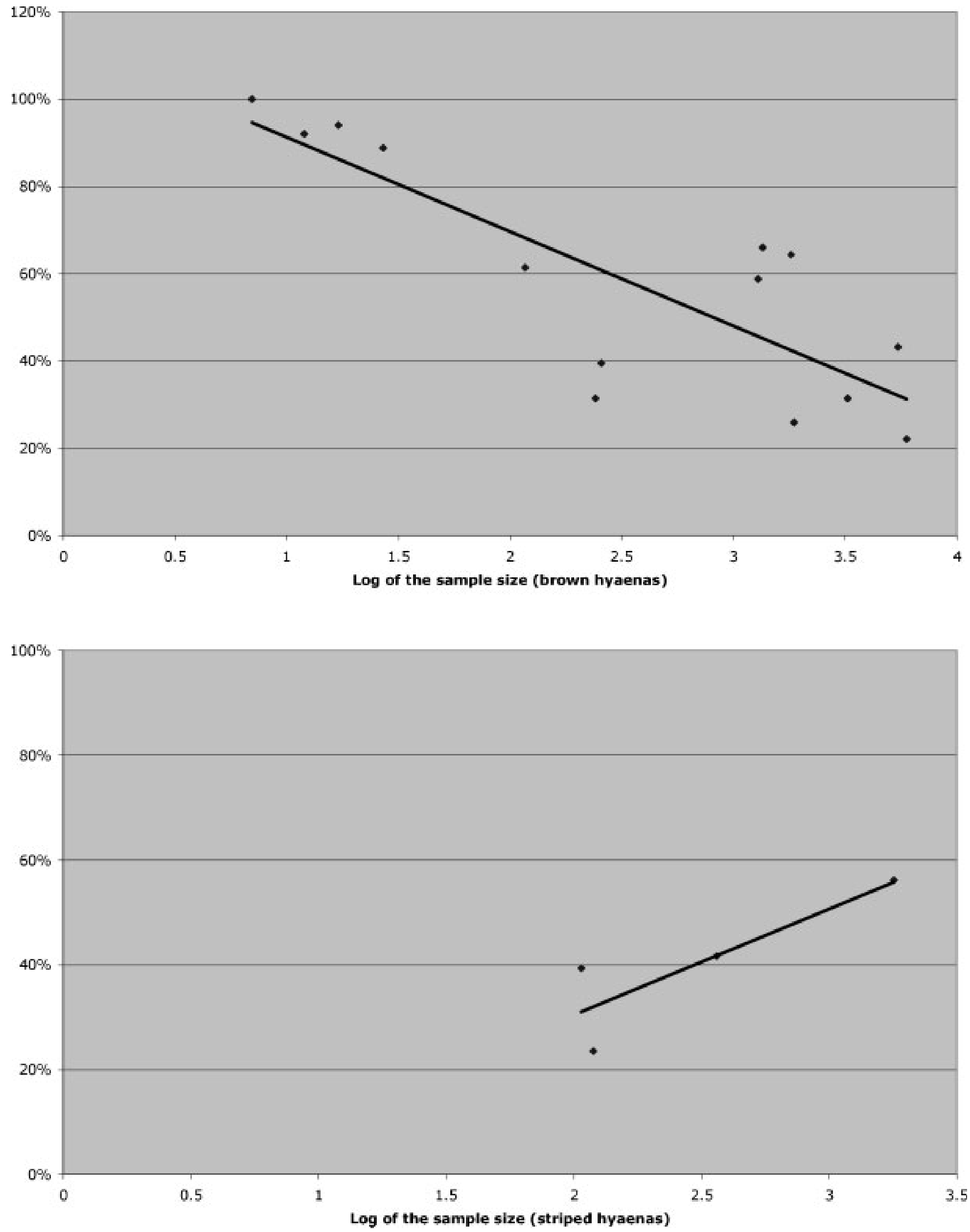

Figure 3. *Continued*

present study indicate that a carnivore MNI of 20% or greater may not always be true for brown hyenas or striped hyenas either. While the mean values of carnivore MNI for brown hyenas is greater than 20%, four of the dens examined had carnivore MNI of less than 20%. When examining the data from the striped hyena dens, while the mean value was 19.4%, one of the dens yielded no carnivore remains at all. The current study thus shows a wide range of variation, not

DOI: 10.1002/oa

Table 5. Percentage of cylinder fragments per den

Hyenid species	Den	% cylinder	Mean
Crocuta crocuta	Mashatu Den 1	2.7	
	Mashatu Den 2	22.2	
	Mashatu Den 3	2	
	Mashatu Den 4	5.3	
	Gobabeb NN-1	0	
	Gobabeb NN-2 only had 1 specimen		6.5%
Parahyaena brunnea	Rietvlei Den 1	4.5	
	Rietvlei Den 2	11	
	Rietvlei Den 3	0	
	BHP D-P 1	16.3	
	BHP D-P 2	14	
	BHP D-P 4	8	
	BHP D-P 9	10.6	
	BHP D-P 11	5.4	
	BHP D-P 16	9.1	
	BHP D-P 18	5.9	
	BHP D-SPG 1	10.6	
	BHP D-BB 1	20	
	Skinner Collection	9.8	
	Gladysvale	14.3	10%
Hyaena hyaena	Jawa Den 4	9.5	
	Jawa Den 7	2.9	
	Al-Arteen Den 11	12	
	Al-Arteen Den 13	3	
	Dhahik Den 32	2.7	6%

only over a large geographical range but also within hyenid species over a relatively small geographical range. The striped hyena dens near the Bronze Age city of Jawa were less than 200 m apart, yet one exhibited a high carnivore MNI of 32.2% while the other had a carnivore MNI of zero. A similar, although less dramatic example can be observed in our results from the spotted

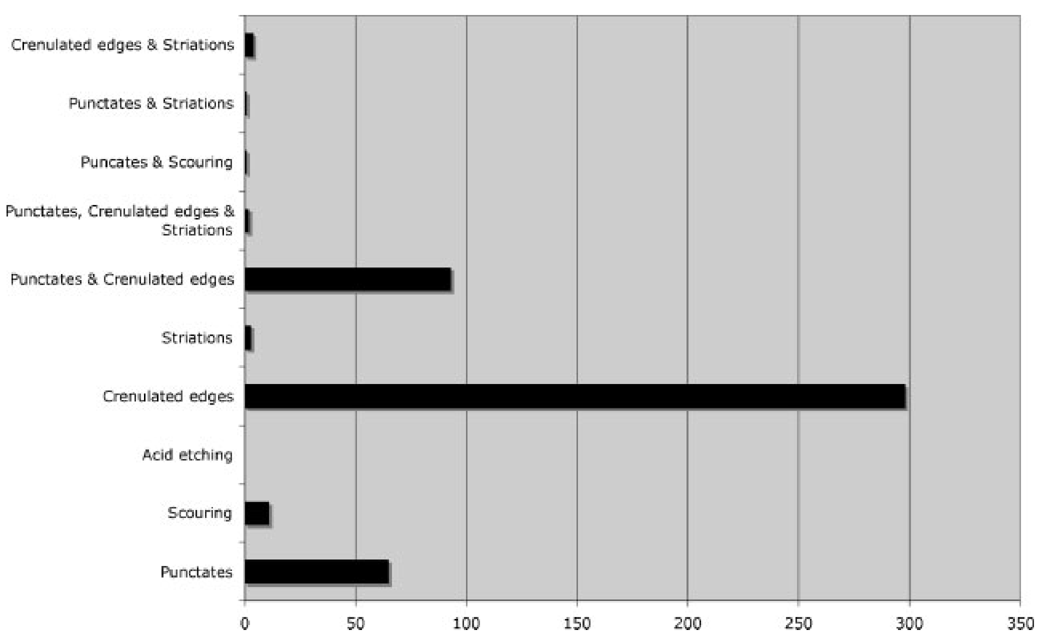

Figure 4. Carnivore damage from spotted hyena dens.

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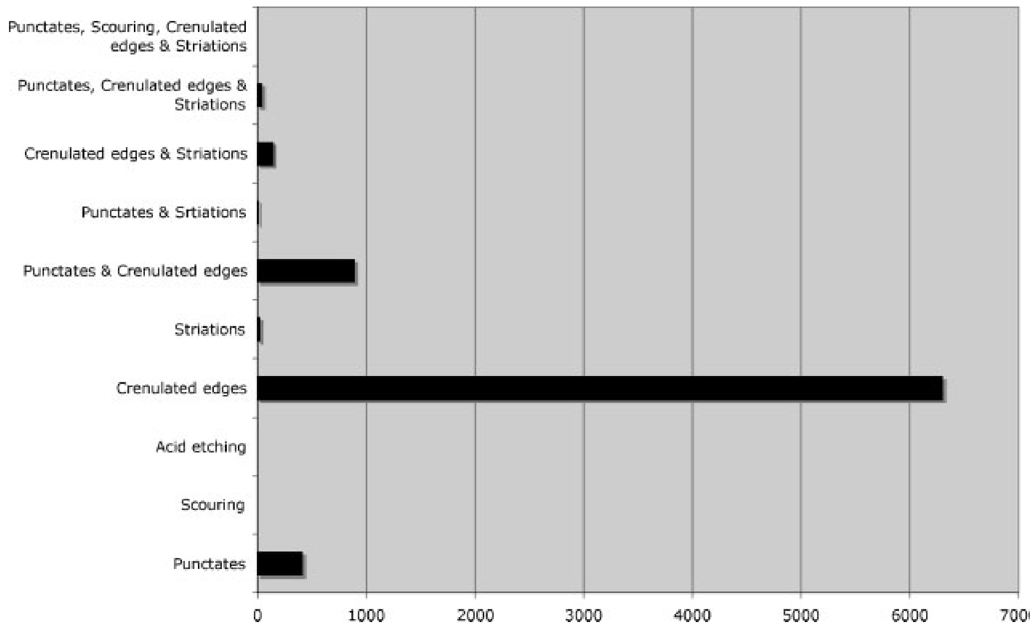

Figure 5. Carnivore damage from brown hyena dens.

hyena dens of Mashatu. All of these dens are within 20 km^2 and yet two had no carnivore remains identified, one had a carnivore MNI of 12.5% and the last presented a carnivore MNI of 3.2%. The only region where the carnivore MNI was consistently greater than 20% was on the Namibian coast, where the carnivore MNI ranged from 50–100% excluding seals. When the seal data are added the carnivore MNI ranged from 67–100%. The spotted hyena Mashatu Den 2 had

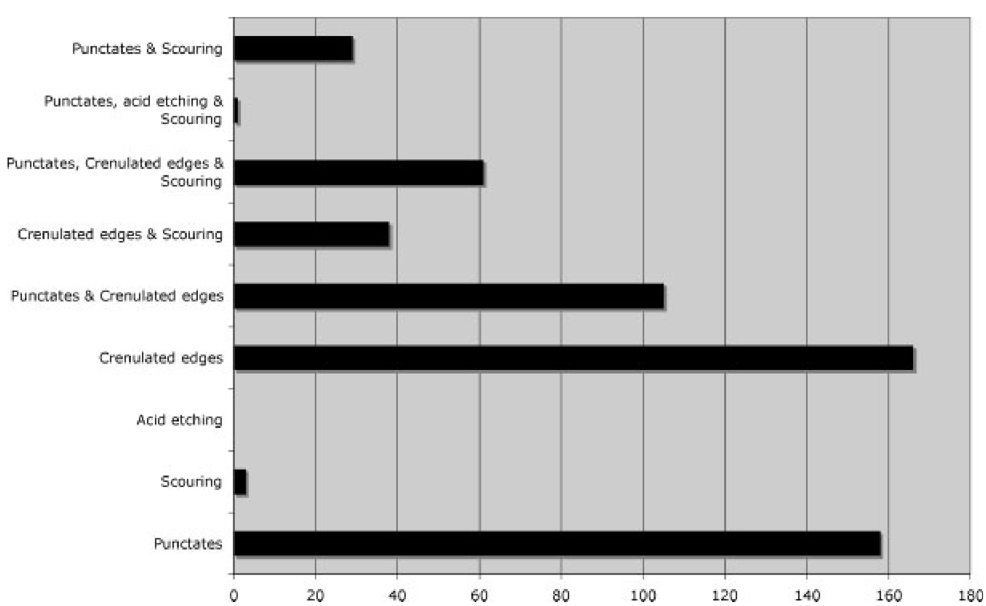

Figure 6. Carnivore damage from striped hyena dens.

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Table 6. Cranial/postcranial MNI ratio

Prey, by hyenid species	Den	Collected species (size)	Cranial MNI	Postcranial MNI	Ratio
Large ungulates					
Crocuta crocuta	Mashatu Den 4	Zebra, cow	1	4	0.25
	Mean				0.25
Parahyaena brunnea	Rietvlei Den 1	Zebra	1	1	1
	Mean				1
Hyaena hyaena	Jawa Den 4	Horse, camel, cow	8	14	0.57
	Jawa Den 7	camel	1	3	0.33
	Al-Arteen Den 11	Horse, camel	1	2	0.5
	Al-Arteen Den 13	Camel	1	1	1
	Dhahik Den 32	Horse, camel	5	20	0.25
	Mean				0.53
Total			18	44	0.41
Medium ungulates					
Crocuta crocuta	Mashatu Den 1	III	2	3	0.67
	Mashatu Den 3	III	1	2	0.5
	Mashatu Den 4	III	1	10	0.1
	Gobabeb NN-1	III	1	1	1
	Mean				0.57
Parahyaena brunnea	Rietvlei Den 2	III	1	1	1
	BHP D-P 1	III	2	1	2
	BHP D-P 9	III	4	2	2
	Skinner Collection	III	1	1	1
	Mean				1.5
Hyaena hyaena	Jawa Den 4	Donkey	17	5	3.4
	Al-Arteen Den 11	Donkey	2	2	1
	Al-Arteen Den 13	Donkey	1	1	1
	Dhahik Den 32	Donkey	2	3	0.67
	Mean				1.52
Total			35	32	1.1
Small ungulates					
Crocuta crocuta	Mashatu Den 1	I, II	6	5	1.2
	Mashatu Den 2	II	3	4	0.75
	Mashatu Den 4	I, II	7	11	0.64
	Gobabeb NN-1	II	1	2	0.5
	Mean				0.77
Parahyaena brunnea	Rietvlei Den 1	II	1	2	0.5
	BHP D-P 1	II	1	2	0.5
	BHP D-P 2	II	1	1	1
	BHP D-P 9	I, II	3	3	1
	BHP D-P 16	II	3	1	3
	Skinner Collection	I, II	1	3	0.33
	Gladysvale	II	3	2	1.5
	Mean				1.12
Hyaena hyaena	Jawa Den 4	II	5	7	0.71
	Al-Arteen Den 11	II	6	7	0.86
	Al-Arteen Den 13	II	2	1	2
	Dhahik Den 32	II	2	4	0.5
	Mean				1.02
Total			45	55	0.82
Canids					
Parahyaena brunnea	BHP D-P 1	Dog, jackal	1	2	0.5
	BHP D-P 2	Dog	1	1	1
	BHP D-P 4	Dog, jackal, fox	5	9	0.56
	BHP D-P 9	Dog, jackal, fox	17	33	0.52
	BHP D-P 11	Dog, jackal	2	3	0.67
	BHP D-P 16	Dog, jackal, fox	16	7	2.29

(*Continues*)

DOI: 10.1002/oa

Table 6. (Continued)

Prey, by hyenid species	Den	Collected species (size)	Cranial MNI	Postcranial MNI	Ratio
	BHP D-P 18	Dog, jackal, fox	1	4	0.25
	BHP D-SPG 1	Dog, jackal	2	3	0.67
	BHP D-BB 1	Dog, jackal, fox	4	8	0.5
	Skinner Collection	Dog, jackal, fox	10	8	1.25
	Mean				0.82
Hyaena hyaena	Jawa Den 4	Dog	17	2	8.5
	Al-Arteen Den 11	Dog, fox	5	5	1
	Al-Arteen Den 13	Dog	2	1	2
	Dhahik Den 32	Dog, fox	4	6	0.67
	Mean				2.59
Total			87	92	0.95

58 specimens yet had a carnivore MNI of 12.5%, whereas Mashatu Den 4 had 611 specimens but a carnivore MNI of only 3.2%. Mashatu Dens 1 and 3 had sample sizes of 214 and 93 respectively, but carnivore MNIs of zero. The inland brown hyena dens were all relatively small in size, but three of the four had carnivore MNI percentages of 16.7%, 16.7% and 12.5%, in line with the numbers reported by Lacruz and Maude (2005) for the same species, while the fourth den had a carnivore MNI of zero. The same can be said of striped hyena dens; while Jawa Den 7 had only 119 specimens and a carnivore MNI of zero, Al-Arteen 13 had 107 specimens and a carnivore MNI of 22.2%.

More recent research by Lacruz and Maude (2005) supported the criterion of carnivore MNI $\geq$20% for brown hyenas but not for spotted hyenas or striped hyenas, indicating that research conducted over a wide geographical area may

Table 7. Relative abundance of small hard bones in relation to postcranial bones

Collector	Den	Sample size	Postcranial bones	Small hard bones	% small hard bones of postcranial bones
Crocuta crocuta	Mashatu Den 1	214	125	21	16.8%
	Mashatu Den 2	58	28	4	14.3%
	Mashatu Den 3	93	51	7	13.7%
	Mashatu Den 4	611	336	49	14.6%
	Gobabeb NN-1 & NN-2	686	53	18	34%
Parahyaena brunnea	Rietvlei Den 1	27	18	0	0%
	Rietvlei Den 2	12	7	1	14%
	Rietvlei Den 3	7	7	0	0%
	BHP D-P 1	241	175	9	5.1%
	BHP D-P 2	256	137	9	6.6%
	BHP D-P 4	1865	1224	55	4.5%
	BHP D-P 9	5955	4962	492	10%
	BHP D-P 11	117	73	17	23.2%
	BHP D-P 16	1287	787	17	2.2%
	BHP D-P 18	1811	1285	127	9.9%
	BHP D-SPG 1	3253	2652	180	6.8%
	BHP D-BB 1	1351	789	23	3.0%
	Skinner Collection	5466	3652	482	13.20%
	Gladysvale	17	8	0	0%
Hyaena hyaena	Jawa Den 4	1792	497	29	4.2%
	Jawa Den 7	119	11	1	5%
	Al-Arteen Den 11	361	186	9	7.3%
	Al-Arteen Den 13	107	40	0	0%
	Dhahik Den 32	1377	340	36	10.6%

DOI: 10.1002/oa

yield considerable variation. Subsequently Pokines and Kerbis Peterhans (2007) have reported that only striped hyena and brown hyena accumulations consistently yield a carnivore MNI of ≥20%.

The presence of Juvenile hyena remains

In the present study 62 hyena remains (with an MNI of 15 juveniles) were identified from 11 separate dens from all three hyena species (Table 3). Juvenile remains ranged in abundance from a single element up to 20 documented juvenile hyena bones from a single den. The current study supports Pickering (2002) in stating that the presence of juvenile hyena remains is a strong indicator that the assemblage is indeed that of hyenas.

Damage to bone surfaces

'Distinctive hyaena damage, which includes striations, pitting, grooves, scooping and acid

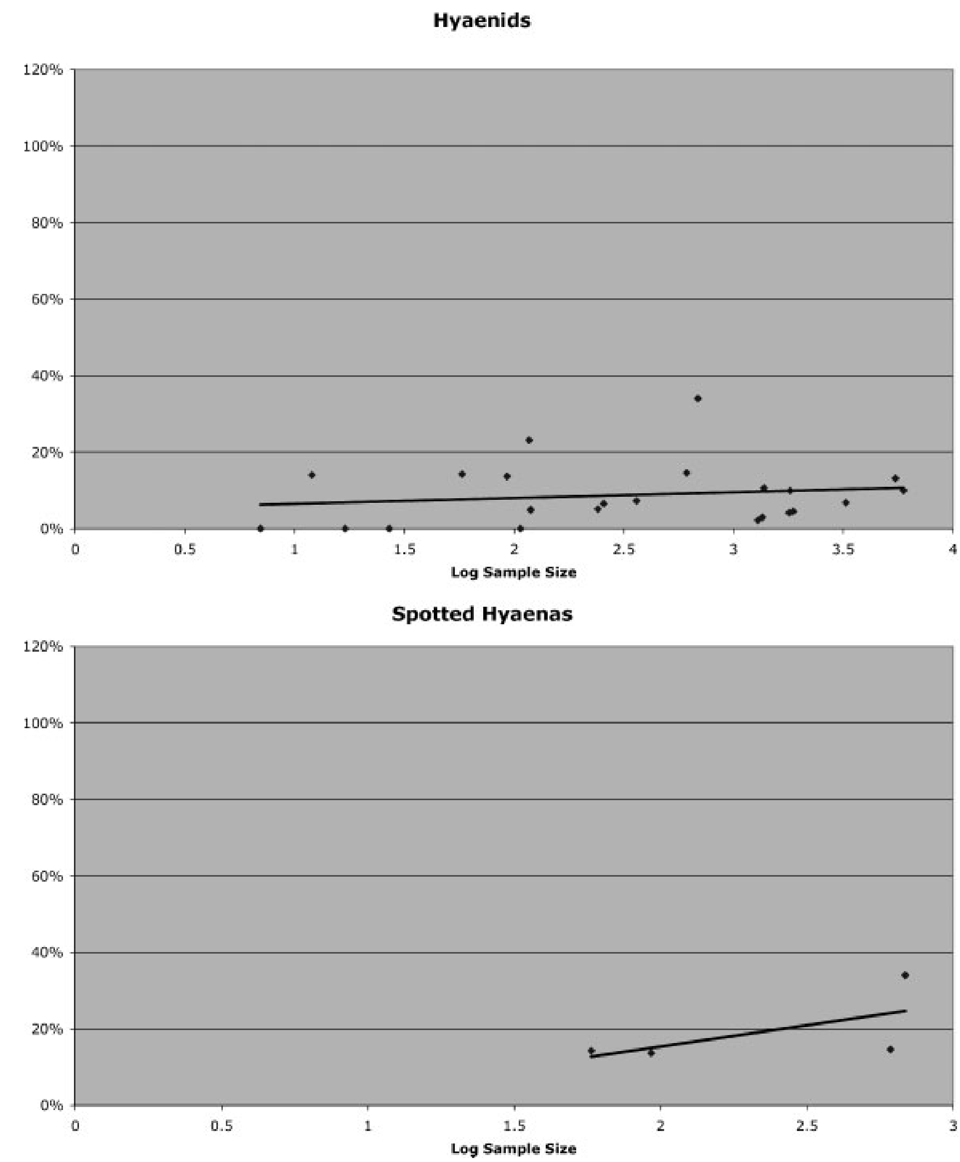

Figure 7. Log of sample size compared to % small compact bones for all hyenas and individual species.

DOI: 10.1002/oa

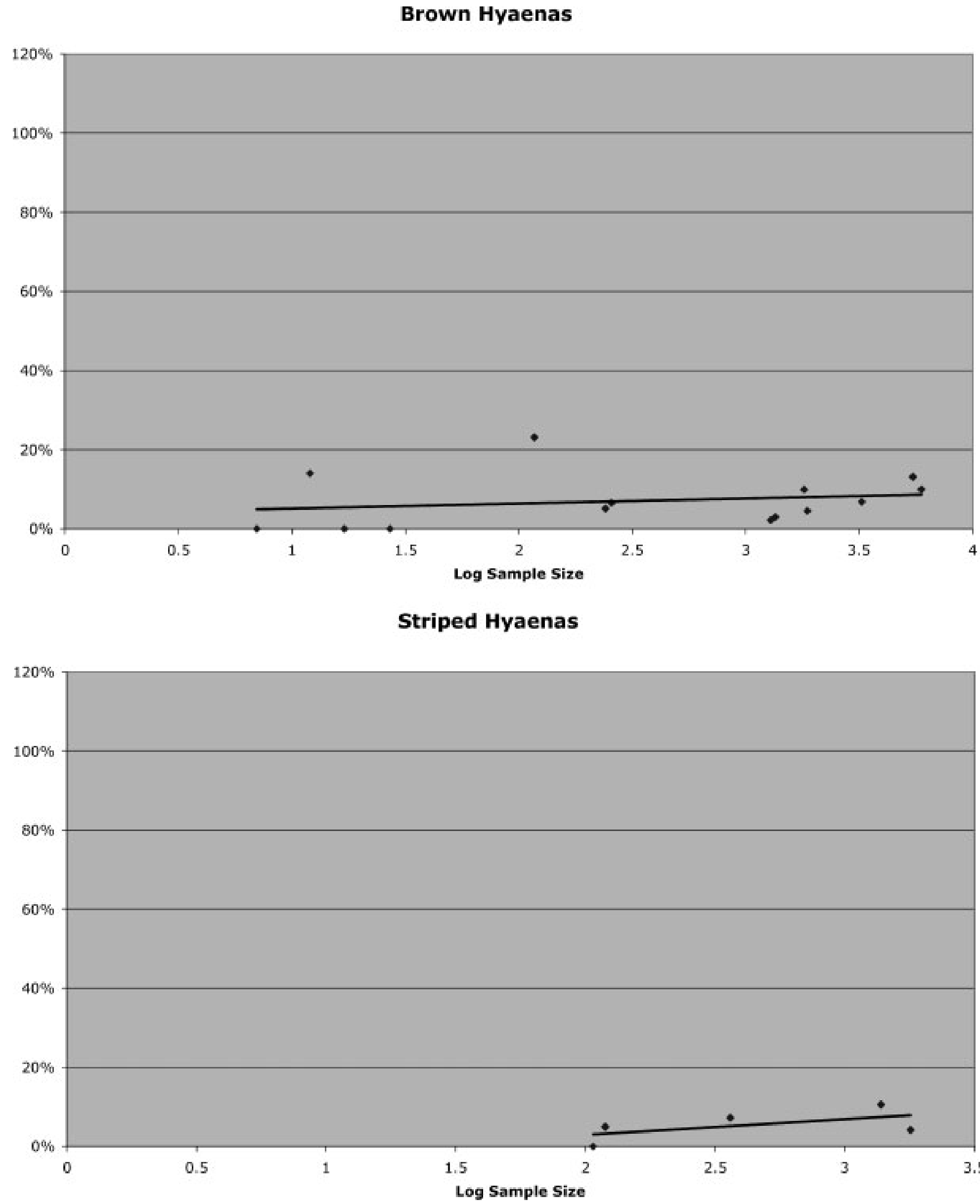

Figure 7. *Continued*

etching. Such damage will occur on at least 50% of bones in modern assemblages, but much less in fossil ones' (Cruz-Uribe, 1991: 476).

While examples of all of these particular types of damage were recorded in the present study, the issue is that numerous other carnivores have since been identified as producing the same or very similar types of damage (Lyman, 1994; Dominguez-Rodrigo, 1999; Pickering, 2002; Njau & Blumenschine, 2006). Results in Table 4 indicate that hyena damage may be on much less than 50% of the faunal remains recovered from any given den. While brown hyena assemblages average greater than 50% carnivore gnawed, the mean value for both spotted hyenas and striped hyenas were below the prescribed 50%. Eight of 14 brown hyena assemblages had carnivore gnawing on at least 50% of the assemblage.

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Table 8. Horn abundance in relation to limb bone MNE

Collector	Den	Sample size	Limb MNE	Horn	% limb MNE
Crocuta crocuta	Mashatu Den 1	214	56	0	0%
	Mashatu Den 2	58	18	0	0%
	Mashatu Den 3	93	30	0	0%
	Mashatu Den 4	611	188	1	0.5%
	Gobabeb NN-1 & NN-2	686	5	2	40%
Parahyaena brunnea	Rietvlei Den 1	27	15	2	13%
	Rietvlei Den 2	12	5	1	20%
	Rietvlei Den 3	7	7	0	0%
	BHP D-P 1	241	54	0	0%
	BHP D-P 2	256	55	1	1.8%
	BHP D-P 4	1865	335	0	0%
	BHP D-P 9	5955	1664	1	0%
	BHP D-P 11	117	21	0	0%
	BHP D-P 16	1287	270	0	0%
	BHP D-P 18	1811	350	0	0%
	BHP D-SPG 1	3253	1262	0	0%
	BHP D-BB 1	1351	425	18	4.3%
	Skinner Collection	5466	1464	3	0.2%
	Gladysvale	17	8	0	0%
Hyaena hyaena	Jawa Den 4	1792	371	23	6.2%
	Jawa Den 7	119	9	3	33.3%
	Al-Arteen Den 11	361	102	2	1.2%
	Al-Arteen Den 13	107	30	0	0%
	Dhahik Den 32	1377	271	4	2%

Lacruz and Maude (2005) also supported the criterion for hyena-inflicted damage to be found upon the bones in a hyena accumulation. In their study of brown hyenas they found hyena damage on an average of 63.6% of all the remains examined. For both spotted hyenas and striped hyenas, only one of five assemblages had carnivore gnawing on more than 50% of the bones. Recent research by Faith (2007) suggests that spotted hyenas leave tooth marks on >70% of the remains examined. It is worth noting here that the current study examined all of the remains collected at the various dens, while the material used by Faith (2007) was collected previously by other researchers and is limited to mammal material with weathering stages 0-1 (following Behrensmeyer, 1978).

Bone breakage

'Hyaena accumulations will be characterised by many bone cylinders, while hominid collections will have more broken shafts and complete epiphyses, broken shafts alone are not diagnostic of hominid collections' (Cruz-Uribe, 1991: 477).

Both Cruz-Uribe (1991) and Pickering (2002) stated that hyena accumulations will have an abundance of cylinder type fragments in the assemblage. The question is what exactly is an abundance? Neither Cruz-Uribe (1991) nor Pickering (2002) defined what they considered an abundance of cylinder fragments in an assemblage to be. Perhaps, considering that Cruz-Uribe stated that 'hominid accumulations have broken shafts and intact epiphyses' (Cruz-Uribe, 1991; 467), the author considered the presence of cylinders alone as indicative of hyena activity. Table 5 illustrates the abundance of cylinder fragments for each accumulation examined during the present study. In no accumulation were cylinders the most common, or even the second most common type of fragmentation recorded. The mean values for cylinder fragments for all three species is 10% or less of recorded fragmentation patterns. The greatest abundance recorded was 22.2% and came from one of the spotted hyena dens. The greatest abundance for brown hyenas and striped hyenas was 16.3% and 12% respectively. Assuming the presence alone of cylinder fragments is indicative of hyena activity, the problem,

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as stated by Pickering (2002), is that other carnivores, specifically lions (*Panthera leo*) and leopards, leave behind similar cylinder fragments after feeding. Thus the presence of cylinders would be indicative of carnivore involvement, but not specifically hyena involvement.

Cranial/postcranial ratio

'This ratio will decrease with the size of the ungulate; therefore smaller ungulates are better represented by cranial bones and larger ungulates by post-cranial elements' (Cruz-Uribe, 1991: 478).

One reason for this criterion being established by Cruz-Uribe (1991) was that at the time is was thought that hyenas 'cannot transport the skulls of large animals' (Cruz-Uribe, 1991; 478). As Pickering (2002) noted, however, hyenas are very capable of carrying away the skulls of large ungulates and this is corroborated by the presence of large ungulate skulls in accumulations from the present study. During the current study the skulls of male kudus (*Tragelaphus strepsiceros*), wildebeest (*Connochaetes taurinus*) and zebras (*Equus quagga*) were recovered from the dens of spotted hyenas, while complete or nearly complete skulls of zebras and gemsbok (*Oryx gazella*) were recovered from brown hyena dens. Skulls of camels (*Camelus dromedaries*), horses (*Equus caballus*) and donkeys (*Equus asinus*) were recovered in striped hyena dens. More recently, Pokines and Kerbis Peterhans (2007) studied spotted hyena accumulations and suggested Cruz-Uribe's (1991) criterion for using the cranial to postcranial ratios of large, medium and small ungulates be retained, as their data from spotted hyena dens match the criterion published by Cruz-Uribe (1991). Interestingly, Cruz-Uribe (1991) noted at the time that the criterion concerning the cranial/postcranial ratio does not hold for spotted hyenas and is only indicative of hyenas other than spotted hyenas. Examining the ratio of cranial/postcranial bones in comparison to ungulate size in the present study indicates no clear pattern for hyenids in general (Table 6). Moreover, similar to the results reported by Pokines and Kerbis Peterhans (2007), the present study found that only spotted hyenas followed the linear trend suggested by Cruz-Uribe (1991) for indicating hyena involvement in any given accumulation, while striped hyena and brown hyena accumulations do not.

Representation of small hard bones

'The small hard bones of prey species will be absent or at the very least uncommon from hyaena accumulations' (Cruz-Uribe, 1991: 479).

Cruz-Uribe's stated reasoning for inclusion of this criterion was that hyenas can and do swallow bones whole and digest them, thereby removing them from hyena-accumulated assemblages. Cruz-Uribe (1991), in the same paragraph, stated that these small hard bones are 'absent', 'do not survive in high proportions', and 'will always be uncommon' (Cruz-Uribe, 1991; 470). Pickering (2002) indicated that small foot bones are routinely found in the regurgitations of spotted hyenas, whereas Skinner (unpublished) notes that the hooves of small antelope were regurgitated with the hair. Regurgitations and faeces are found both within and outside of dens (Sutcliffe, 1970; Kruuk, 1972; Bearder, 1977; personal observations). In the current study, small hard bones ranged from 0% to 23.3% of the postcranial MNI. The data indicate that small, hard bones are only consistently underrepresented in the dens of striped hyenas, three of which were sieved. Our data overall support Pickering's (2002) rejection of the criterion as being indicative of hyena activity.

Accumulation of horn

The single criterion from Stiner (1991) stated that there would be an excessive proportion of horn or antler in hyena-accumulated assemblages. While Stiner (1991) did not define what excessive proportions are, in the current study horn material makes up very low percentages of accumulations when compared with the MNE of limb bones in the majority of dens. The exceptions to this were dens with relatively small sample sizes or a distinctly low MNE in relation to the sample size. The data from the present study support Pickering (2002) in his rejection of the criterion that an excessive proportion of horn or antler is indicative of at least extant hyena-accumulated assemblages.

DOI: 10.1002/oa

Conclusions

The present study shows that none of the six criteria examined here can be used solely to determine beyond reasonable doubt which assemblages were accumulated dominantly by hyenas, or used to discriminate between assemblages primarily collected by either hominins or hyenas. Our study has shown that a greater than 20% presence of carnivores does not necessarily indicate a hyenid accumulation. We observed a wide variation in carnivore MNI in both brown hyena and striped hyena accumulations, while the data from spotted hyena dens are continually below the 13% threshold that Cruz-Uribe (1991) hypothesised is diagnostic of hominin assemblages. Perhaps this criterion should be used only when other factors indicate dominant hyena involvement. Our data would suggest that such a statement be modified to state that a carnivore MNI of approximately 20% is suggestive of striped hyena accumulations, a carnivore MNI greater than 30% is suggestive of brown hyena accumulations, and a carnivore MNI of less than 13% is suggestive of spotted hyena accumulating behaviour.

Our data support Pickering's (2002) hypothesis that the presence of juvenile and/or subadult hyena remains in a given accumulation is indicative of hyena involvement. Our data, however, also suggest that one should not take the lack of hyena remains to exclude hyena activity, and that one considers the possibility that young hyena remains might be collected by other bone-accumulating animals.

The damage to faunal remains, in particular striations, pitting, grooves, scooping and acid etching, have been found to occur after feeding episodes of other carnivores as well as hyenas (Lyman, 1994; Dominguez-Rodrigo, 1999; Njau & Blumenschine, 2006). Our study supports these types of gnawing as diagnostic of carnivore activity upon a bone, but not necessarily hyena activity. This is also the case with cylinder fragments. As Pickering (2002) indicated, lions and leopards, like spotted hyenas, consume limb bone ends, thus leaving behind cylinders.

As with the carnivore MNI criterion, our study suggests that the cranial to postcranial ratios could be used to indicate spotted hyenas as dominant accumulators of an assemblage as opposed to striped hyenas or brown hyenas, but only when other evidence indicates hyenas as the dominant collector of an accumulation. Despite the statement of Cruz-Uribe (1991) that this particular criterion does not indicate spotted hyena activity, the present study, as well as Pokines and Kerbis Peterhans' (2007) examination of extant spotted hyena accumulations, suggest that this criterion is indeed indicative of spotted hyena activity.

The low abundance of small, hard bones, while not diagnostic of overall hyena activity, may be indicative of either striped hyenas or brown hyenas once hyena activity has been established. The current study yielded no data to lend credence to the criterion stating that an excessive proportion of horn, horn core or antler is indicative of hyena accumulations.

Finally, Cruz-Uribe (1991) stated that the presence of fossil (hyenid) coprolites associated with the fossil assemblages was evidence that hyenas accumulated the assemblages. Pickering (2002: 135) stated that 'two such categories of evidence (in addition to the others discussed above), lumped together here under discussion of bone modification, are digested bone pieces and hyaena coprolites. The presence of these materials in an assemblage indicates the intimate use of the area by hyaenas'. During the course of fieldwork for the current study, hyena coprolites were noted both inside and outside the dens of all three species in question. We concur with Cruz-Uribe (1991) in that no one criterion on its own is diagnostic of hyena activity. Therefore, the current study suggests that of all the criteria previously established and re-evaluated, the only two that can confidently differentiate between accumulations of hominins and hyenas were not actually part of the criteria laid out by Cruz-Uribe (1991) or Stiner (1991) and are the presence of either an abundance of coprolites and/or the presence of juvenile hyena remains in the assemblage.

Acknowledgements

The Palaeoanthropological Scientific Trust (PAST) and the University of Pretoria financed the project in southern Africa. The Council for British

DOI: 10.1002/oa

Research in the Levant (CBRL) and the Institute of Archaeology, University College London, supported the Jordanian portion of fieldwork. Grateful appreciation is accorded to: Rietvlei Nature Reserve, South Africa; Mashatu Game Reserve, Botswana; the Brown Hyaena Research Project, NAMDEB Diamond Company, Gobabeb Desert Research and Training Centre, and the Ministry of Environment and Tourism, all of Namibia; the Higher Council for Science and Technology, Amman, Badia Research and Development Centre, Safawi, and the CBRL offices Amman, all in Jordan. Thanks go to Rodrigo Lacruz, Darryl de Ruiter and two anonymous reviewers for constructive comments on earlier drafts of this manuscript.

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