Variation in tooth mark frequencies on long bones from the assemblages of all three extant bone-collecting hyaenids

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Abstract

Tooth mark frequencies on long bones are examined from the assemblages of all three extant bone-collecting hyaenids. Comparisons are made with a recent study examining tooth mark frequencies and possible sources of variation from a single spotted hyaena (*Crocuta crocuta*) assemblage (Faith, J.T., 2007. Sources of variation in carnivore tooth-mark frequencies in a modern spotted hyena (*Crocuta crocuta*) den assemblage, Amboseli Park, Kenya. Journal of Archaeological Science 34 (10), 1601–1609). The factors that may influence tooth mark frequencies are fragment size, fragments from different sized animals, region of skeletal element and bone density. All four factors are examined in the present study and compared across species and with previous results. The results indicate that there is a great deal of variation in tooth mark frequencies not only between the species but also from the same species.

Keywords: Tooth marks; Striped hyaena; Spotted hyaena; Brown hyaena; Taphonomy

1. Introduction

Variations in carnivore damage found between various carnivore species have been investigated on a broad scale previously (Haynes, 1983). In an attempt to illustrate possible sources of variation in carnivore tooth mark frequencies Faith (2007) conducted an examination of the remains of prey animals previously collected from a spotted hyaena (*Crocuta crocuta*) den in Amboseli Park, Kenya. He examined four specific questions in relation to tooth marks frequency: ‘(1) How does long-bone fragment size impact tooth-mark frequencies? (2) How do tooth-mark frequencies vary across taxa of different body size classes? (3) How does the incidence of tooth-marking vary across portions of different long bone elements? (4) What is the relationship between tooth-mark frequency and bone density?' (Faith, 2007, p. 1602). Faith limits the long bone data set to mammal remains, and appears to exclude anything smaller than springhares (*Pedetes capensis*). In addition the sample set is limited to weathering stages 0–1 (weathering data follow Behrensmeyer, 1978). Faith concludes that there is a positive relationship between per cent tooth marks and the length of fragments, as well as a direct relationship between tooth marks and prey body size. The 2007 study indicates that tooth mark frequencies are highly variable across various portions of the long bone elements. The relationship between bone density and tooth mark percentages, as shown by Faith, is negative for long bone epiphyses and proximal/distal shafts while mid shafts show no relationship with bone density.

Our study looks at the same questions for all three bone-collecting hyaenids from four countries and two continents. In order to make as direct a comparison as possible between our study and the results reported by Faith, our study examined the long bone remains from mammals with weathering stages 0–1. In addition, data without weathering limitations were also examined in order to determine if weathering influences the outcome. In data sets where Faith limits the examination to bovid size class 2–3 (following Brain, 1981), our study gives data for all mammals as well as data limited to bovid size class 2–3. Our study also indicates that, when the assemblages of all three extant bone-collecting hyaenas are examined, the tooth mark frequencies are significantly different between the species as well as different within the species when various limitations are placed upon the data sets.

2. Study sites

For our study hyaena dens were located and the associated faunal remains examined from dens in Jordan, South Africa, Botswana and Namibia. For precise locations of the Jordan dens see Kuhn (2005) and for study site locations in southern Africa see Kuhn et al. (2008). In Jordan the faunal accumulations of five active striped hyaena (*Hyaena hyaena*) dens were collected and examined in three areas of the eastern desert. Four spotted hyaena dens were located and the faunal remains examined in the Mashatu Game Reserve, Botswana and two dens located in the Namib-Naukluft Park, Namibia. In South Africa three active brown hyaena (*Parahyaena brunnea*) dens from the Rietvlei Nature Reserve were collected from and the faunal remains examined. Additional faunal remains from South Africa were collected from active brown hyaena dens near the Gladysvale palaeontology site. The faunal remains from nine brown hyaena dens in the south west of Namibia on the Luderitz Peninsula and in Diamond Area No. 1 were analysed *in situ*. Faunal remains previously collected by Skinner and van Aarde (1991) and Skinner et al. (1998) from Diamond Area No. 1 were reanalysed and included in this study.

3. Materials and methods

Our study examined more than 27 000 bones, 7843 of which were identified as long bones, from the dens of all three extant bone-collecting hyaenas. Only material from terrestrial mammals, excluding species smaller than hyraxes (*Procavia capensis*) was included. Species identified with NISP (number of identified specimens) and MNI (minimum number of individuals) for the three hyaena species can be seen in Table 1. NISP (0–1) and MNI (0–1) refer to material with weathering stages 0–1. MNI was calculated using the body side of long bones for each species. For each specimen data recorded were: skeletal element, taxon, bovid size class, portion of long bone, length of specimen and carnivore tooth marks (presence). Macroscopic tooth marks were noted with the naked eye. Division of skeletal elements followed Marean and Spencer (1991) in dividing the long bones into proximal end, proximal shaft, distal end, distal shaft and middle shaft, for the sake of documenting carnivore tooth marks at specific locations on long bones and long bone fragments. Like Faith, we examine the percentage of tooth marks on long bones in relation to the total number of long bones.

Table 1. *NISP and MNI of faunal remains collected by each species of hyaena*

Taxon	**NISP**	**NISP (0–1)**	**MNI**	**MNI (0–1)**
Striped hyaenas				
Camelus dromedarius	275	127	25	9
Camel/horse size	26			2
Equus caballus	20	18	4	3
Bos spp.	3	3	1	1
Canid	41	22	5	3
Equus asinus	78	43	9	7
Vulpes spp.	5	2	4	2
Capra hircus	16	13	4	3
Ovis/Capra	31	28	5	5
Ovis aries	5	5	2	2
Gazella spp.	12	12	3	3
Hare/small fox size	1	1	1	1
Lepus spp.	4	1	4	1

Taxon	NISP	NISP (0–1)	MNI	MNI (0–1)
Sus scrofa	1	0	1	0
Bovid size 2	1003	839	5	4
Bovid size 3	37	21	6	4
Bovid size 4	1083	371	2	2
Total	2641	1379	56	52
Spotted hyaenas				
Aepyceros melampus	82	19	13	3
Tragelaphus strepsiceros	38	5	4	1
Connochaetes taurinus	8	1	3	1
Papio cynocephalus	4	3	2	1
Phacochoerus africanus	6	3	2	1
Procavia capensis	5	4	2	2
Capra hircus	6	1	1	1
Raphicerus campestris	5	3	2	1
Sylvicapra grimmia	1	1	1	1
Equus burchellii	20	4	3	1
Crocuta crocuta	1	1	1	1
Bovid size 1	2	2	1	1
Bovid size 2	23	17	2	2
Bovid size 3	28	6	4	1
Total	229	70	41	18
Brown hyaenas				
Antidorcas marsupialis	46	9	6	1
Oryx gazella	61	3	7	1
Damaliscus dorcas phillipsi	6	5	1	1
Connochaetes taurinus	2	2	1	1

Taxon	NISP	NISP (0–1)	MNI	MNI (0–1)
Alcelaphus buselaphus	1	1	1	1
Syncerus caffer	2	2	1	1
Oreotragus oreotragus	7	0	2	0
Equus burchellii	5	4	1	1
Canis familiaris	178	9	32	1
Canis mesomelas	121	13	15	3
Vulpes chama	22	1	4	1
Felis (domestic size)	44	3	6	1
Parahyaena brunnea	31	2	7	1
Bovid size 2	6	6	2	2
Bovid size 3	2	2	1	1
Total	534	62	87	17

Analyses of faunal material were completed using reference collections housed at the Council for British Research in the Levant, Amman, Jordan, the Palaeoanthropology Unit for Research and Exploration (PURE), Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa and four publications ([Hillson, 1992], [Peters, 1986], [Schmid, 1972] and [Walker, 1985]). Specimens from South Africa and Botswana were collected, bagged, labelled and transported to laboratory facilities at PURE, the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, for identification and analysis. Analyses of faunal remains in Namibia had to be completed *in situ* at the den sites, complying with protocols set by NAMDEB Diamond Company and the Namibian Ministry of Environment and Tourism.

4. Results

4.1. Tooth marks and length of long bones and long bone fragments

Table 2 illustrates the per cent tooth marks on long bones across 20 mm length intervals. Included in the table are results that, like Faith, limit the data to specimens with weathering stages 0–1 as well as data unlimited by weathering stages. The relationship between the length of long bone and long bone fragment was positive for all three hyaena species, whether the data were limited or not, but only significant for spotted hyaenas and brown hyaenas whereas the correlation was not significant for striped hyaenas with limited data sets (spotted hyaena: unlimited $r = 0.998$, $p = <0.0001$, limited $r = 0.994$, $p = <0.0001$; brown hyaena: unlimited $r = 0.996$, $p = <0.0001$, limited $r = 0.974$, $p = <0.0001$; striped hyaena: unlimited $r = 0.514$, $p = 0.19$. limited $r = 0.278$, $p = 0.50$).

Table 2. *Percentage of tooth marked (%TM) long bones across 20 mm size groupings; N is the total number of long bones for each size grouping*

Length in mm	**Striped hyaena**		**Spotted hyaena**		**Brown hyaena**	
	N	**%TM**	***N***	**%TM**	***N***	**%TM**
Weathering stages 0–1						
0–20.0	201	8.5	10	40.0	0	0.0
20.1–40.0	312	32.4	9	33.3	2	100.0
40.1–60.0	223	63.7	6	33.3	3	66.7
60.1–80.0	196	85.2	10	70.0	2	0.0
80.1–100.0	159	91.8	5	80.0	7	85.8
100.1–120.0	97	95.9	4	75.0	4	75.0
120.1–140.0	62	90.3	5	60.0	7	57.1
>140	214	97.2	19	57.9	27	88.9
Total	1464	70.6	68	56.2	52	59.2
All weathering stages						
0–20.0	205	8.3	11	36.4	3	66.7
20.1–40.0	525	19.2	16	50.0	22	54.6
40.1–60.0	493	29.4	15	60.0	39	35.9
60.1–80.0	313	55.6	16	56.3	53	49.1
80.1–100.0	290	52.4	22	72.3	73	61.6
100.1–120.0	186	54.8	19	52.6	65	69.2
120.1–140.0	123	47.2	16	81.3	88	64.8

Length in mm	Striped hyaena		Spotted hyaena		Brown hyaena	
	N	**%TM**	***N***	**%TM**	***N***	**%TM**
>140	414	57.3	118	55.1	203	69.5
Total	2549	40.5	233	58.0	546	58.9

4.2. Prey body size and tooth mark frequencies

Previous works contend that bovid class size 2 and 3 are the most abundant remains found in modern assemblages. While our study concurs that bovid class size 2 and 3 are the most abundant for spotted hyaenas and brown hyaenas, Table 1 illustrates that bovid size class 1 occurs (though not in great abundance) in accumulations of spotted hyaenas and brown hyaenas and bovid size class 4 occurs in accumulations of brown hyaenas and occurs in equal abundance to bovid size class 3 in striped hyaena accumulations. For matters of direct comparison Table 3 limits the range of data to mid shaft fragments of bovid class size 2 and 3 only. Examining the limited data, as prey size increases the per cent tooth marks increases by 50% for spotted hyaenas and 51% for striped hyaenas, but decreases by 37.5% for brown hyaenas. The unlimited data indicate an increase in tooth mark frequency in relation to increased prey size for striped hyaenas (20.8%) and brown hyaenas (1.7%), while spotted hyaena accumulations exhibit a decrease of 12%. With the exception of the unlimited brown hyaena data, whether the tooth mark frequencies increase or decrease the X^2 are greater than the 6.53 reported by Faith and are significant. Further restricting the data to only include fragments from 20 to 60 mm in length illustrates a negative relation between prey body size and tooth mark frequencies for all three unlimited data sets with each decrease being significant for brown hyaenas and not significant for striped hyaenas or spotted hyaenas (striped hyaena $X^2 = 8.54$ ($p = 0.014$), brown hyaena $X^2 = 0.21$ ($p = 0.90$), spotted hyaena $X^2 = 2.04$ ($p = 0.361$)). The spotted hyaena assemblage limited to length and weathering 0–1 shows an increase in tooth marks as prey body size increases ($X^2 = 0.03$, $p = 0.985$). Prey body size class 3 does not occur in assemblages from striped hyaenas or brown hyaenas when limited to length 20–60 mm.

Table 3. *Mid shaft fragments with per cent tooth marked (%TM) for bovid size class 2 and 3 mammals, weathering stages 0–1 and all weathering stages where N is the total number of specimens*

Striped hyaena (0–1)	***N***	**%TM**	**Striped hyaena**	***N***	**%TM**
Long-bone mid shafts			Long-bone mid shafts		
Size 2	863	49	Size 2	1105	42.4
Size 3	30	100	Size 3	129	63.6
Long-bone mid shafts (fragment length 20.0–60.0 mm)			Long-bone mid shafts (fragment length 20.0–60.0 mm)		
Size 2	576	46.4	Size 2	691	30.1
Size 3	0	0	Size 3	10	20
Brown hyaena (0–1)	*N*	%TM	Brown hyaena	*N*	%TM
Long-bone mid shafts			Long-bone mid shafts		
Size 2	8	87.5	Size 2	58	82.8
Size 3	2	50	Size 3	71	84.5
Long-bone mid shafts (fragment length 20.0–60.0 mm)			Long-bone mid shafts (fragment length 20.0–60.0 mm)		
Size 2	0	0	Size 2	5	80
Size 3	0	0	Size 3	18	72.2
Spotted hyaena (0–1)	*N*	%TM	Spotted hyaena	*N*	%TM
Long-bone mid shafts			Long-bone mid shafts		
Size 2	12	33.3	Size 2	111	63.1
Size 3	6	83.3	Size 3	94	51.1
Long-bone mid shafts (fragment length 20.0–60.0 mm)			Long-bone mid shafts (fragment length 20.0–60.0 mm)		
Size 2	6	16.7	Size 2	17	47.1
Size 3	2	50	Size 3	52	34.6

4.3. Distribution and frequency across long bone elements

Examining specific long bones, tooth marks (by location following Marean and Spencer, 1991) and the relative frequencies of tooth marks were documented for sample sets that include bovid class size 2 and 3 (Table 4), bovid class size 2 and 3 with weathering limited to 0–1 (Table 5), all terrestrial mammals (Table 6) and all terrestrial mammals with weathering limited to 0–1 (Table 7). Specific long bones examined include femurs, tibiae, humeri, radii, and metapodials. Metapodials include metacarpals and metatarsals as well as specimens identified only as metapodials. Frequency of tooth marks and location are recorded as well as the relevant percentages for each specific long bone. The data reported here refer to general tooth mark locations and the percentage in relation to element. While restricting the data to bovid class size 2–3 and weathering 0–1 reduces the incidence of tooth marks in the data set, the relative frequencies of tooth marks across the specific regions of long bones remain consistent for all three species of hyaena.

Table 4. *Anatomical distribution and frequency of tooth marks across long bone elements, bovid size 2–3*

Portion	**Element**									
	Femur		**Tibia**		**Humerus**		**Radius**		**Metapodials**	
	TM	**%**	**TM**	**%**	**TM**	**%**	**TM**	**%**	**TM**	**%**
Striped hyaena										
Proximal end	5	29.4	18	41.9	8	40	17	32.7	14	19.2
Proximal shaft	1	5.9	11	25.6	0	0	8	15.4	5	6.9
Distal shaft	0	0	2	4.7	0	0	7	13.5	2	2.7
Distal end	6	35.1	14	33	10	50	17	32.7	13	17.8
Middle shaft	2	11.8	6	14	0	0	10	19.2	12	16.4
Brown hyaena										
Proximal end	14	67	6	26.1	10	66.7	6	28.6	7	20.0
Proximal shaft	2	9.5	8	34.8	2	13.3	5	23.8	4	11.4
Distal shaft	5	24	5	21.7	3	20	4	19.1	13	37.1
Distal end	14	66.7	3	13	10	66.7	6	28.6	6	17.1
Middle shaft	2	9.5	2	8.7	4	26.7	1	4.8	6	17.1
Spotted hyaena										
Proximal end	9	34.6	4	18.2	13	33.3	2	10.5	5	12.2
Proximal shaft	4	15.4	2	9.1	8	20.5	1	5.3	8	19.5
Distal shaft	5	19.2	3	13.6	9	23.1	4	21.1	3	7.3
Distal end	10	38.5	0	0	11	28.2	3	15.8	6	14.6
Middle shaft	1	3.9	3	13.6	3	7.7	0	0	3	7.3

Table 5. *Anatomical distribution and frequency of tooth marks across long bone elements, bovid size 2–3, weathering 0–1*

Portion	Element									
	Femur		Tibia		Humerus		Radius		Metapodials	
	TM	%	TM	%	TM	%	TM	%	TM	%
Striped hyaena										
Proximal end	6	54.6	17	46.0	6	40.0	17	34.7	14	29.2
Proximal shaft	1	9.1	11	29.7	0	0	8	16.3	5	10.4
Distal shaft	0	0	3	8.1	1	6.7	7	14.3	1	2.1
Distal end	8	72.7	14	37.8	9	60	17	34.7	12	25.0
Middle shaft	2	18.2	6	16.2	1	6.7	11	22.5	12	25
Brown hyaena										
Proximal end	2	100	1	20	4	100	0	0	3	25.0
Proximal shaft	1	50	1	20	1	25	2	50	2	16.7
Distal shaft	1	50	1	20	0	0	1	25	5	41.7
Distal end	1	50	0	0	3	75	1	25	2	16.7
Middle shaft	1	50	2	10	3	75	1	25	4	33.3
Spotted hyaena										
Proximal end	3	27.3	0	0	2	33.3	0	0	2	25
Proximal shaft	4	37	1	14.3	2	33.3	1	12.5	2	25
Distal shaft	2	18	1	14.3	3	50	1	12.5	0	0
Distal end	3	27.3	0	0	2	33.3	1	12.5	1	13
Middle shaft	0	0	1	14.3	0	0	0	0	1	12.5

Table 6. *Anatomical distribution and frequency of tooth marks across long bone elements, all terrestrial mammals*

Portion	**Element**									
	Femur		**Tibia**		**Humerus**		**Radius**		**Metapodials**	
	TM	**%**	**TM**	**%**	**TM**	**%**	**TM**	**%**	**TM**	**%**
Striped hyaena										
Proximal end	11	19.6	37	30.6	34	50.0	25	22.9	48	21.2
Proximal shaft	1	1.8	15	12.4	1	1.5	17	15.6	8	3.5
Distal shaft	2	3.6	4	3.3	2	2.9	8	7.3	5	2.2
Distal end	12	21.4	22	18.2	38	55.9	23	21.1	49	21.60
Middle shaft	3	5.4	11	9.1	6	8.8	16	14.7	22	9.9
Brown hyaena										
Proximal end	33	47	30	27.3	29	35.8	10	11.5	8	4.1
Proximal shaft	11	16	38	34.6	27	33.3	13	14.9	8	4.1
Distal shaft	14	20	15	13.6	10	12.4	15	17.2	17	8.6
Distal end	32	45.7	19	17.3	26	32.1	15	17.2	6	3
Middle shaft	3	4.3	4	3.6	6	7.4	2	2.3	9	4.6
Spotted hyaena										
Proximal end	12	32.4	5	15.2	15	31.9	4	13.8	4	6.9
Proximal shaft	7	18.9	4	12.1	10	21.3	1	3.5	9	15.5
Distal shaft	7	18.9	3	9.1	10	21.3	5	17.2	3	5.2
Distal end	13	35.1	3	9.1	12	25.5	4	13.8	5	8.6
Middle shaft	1	2.7	3	9.1	3	6.4	1	3.5	2	3.5

Table 7. *Anatomical distribution and frequency of tooth marks across long bone elements, all terrestrial mammals, weathering 0–1*

Portion	**Element**									
	Femur		**Tibia**		**Humerus**		**Radius**		**Metapodials**	
	TM	**%**	**TM**	**%**	**TM**	**%**	**TM**	**%**	**TM**	**%**
Striped hyaena										
Proximal end	10	40.0	32	45.1	31	73.8	24	27.9	48	39.3
Proximal shaft	1	4.0	15	21.1	0	0	17	19.8	8	6.6
Distal shaft	2	8.0	4	5.6	1	2.4	10	11.6	4	3.3
Distal end	12	48.0	21	29.6	34	81	22	25.6	48	39.3
Middle shaft	3	12.0	12	16.9	5	11.9	16	18.6	21	17.2
Brown hyaena										
Proximal end	3	33	3	37.5	4	57.1	0	0	3	15.8
Proximal shaft	3	33	1	12.5	2	28.6	2	22.2	1	5.3
Distal shaft	2	22	1	12.5	0	0	2	22.2	5	26.3
Distal end	2	22.2	1	12.5	3	42.9	1	11.1	2	10.5
Middle shaft	0	0	1	12.5	1	14.3	1	11.1	4	21.1
Spotted hyaena										
Proximal end	4	25.0	0	0	3	37.5	1	9.1	2	18.2
Proximal shaft	6	38	1	9.1	2	25	1	9.1	2	18.2
Distal shaft	4	25	1	9.1	1	12.5	1	9.1	1	9.1
Distal end	4	25.0	1	9.1	3	37.5	2	18.2	1	9.1
Middle shaft	0	0	1	9.1	0	0	1	9.1	1	9.1

4.4. Correlation between tooth mark frequency and bone density

The per cent tooth marks in relation to bone density have been plotted in Fig. 1, Fig. 2, Fig. 3, Fig. 4, Fig. 5, Fig. 6, Fig. 7, Fig. 8 and Fig. 9 for all three species of hyaena, illustrating data sets with all mammal remains and no limitations, all mammal remains with weathering limited to 0–1, bovid size class 2–3 and bovid size class 2–3 with weathering limited to 0–1. Bone densities used are the mean value (BMD_1) for wildebeest (*Connochaetes taurinus*) (Lam et al., 1999). All fragments identified as metatarsals, metacarpals and metapodials are combined (identified as Mp3 in the figures) and the densities averaged for the analysis.

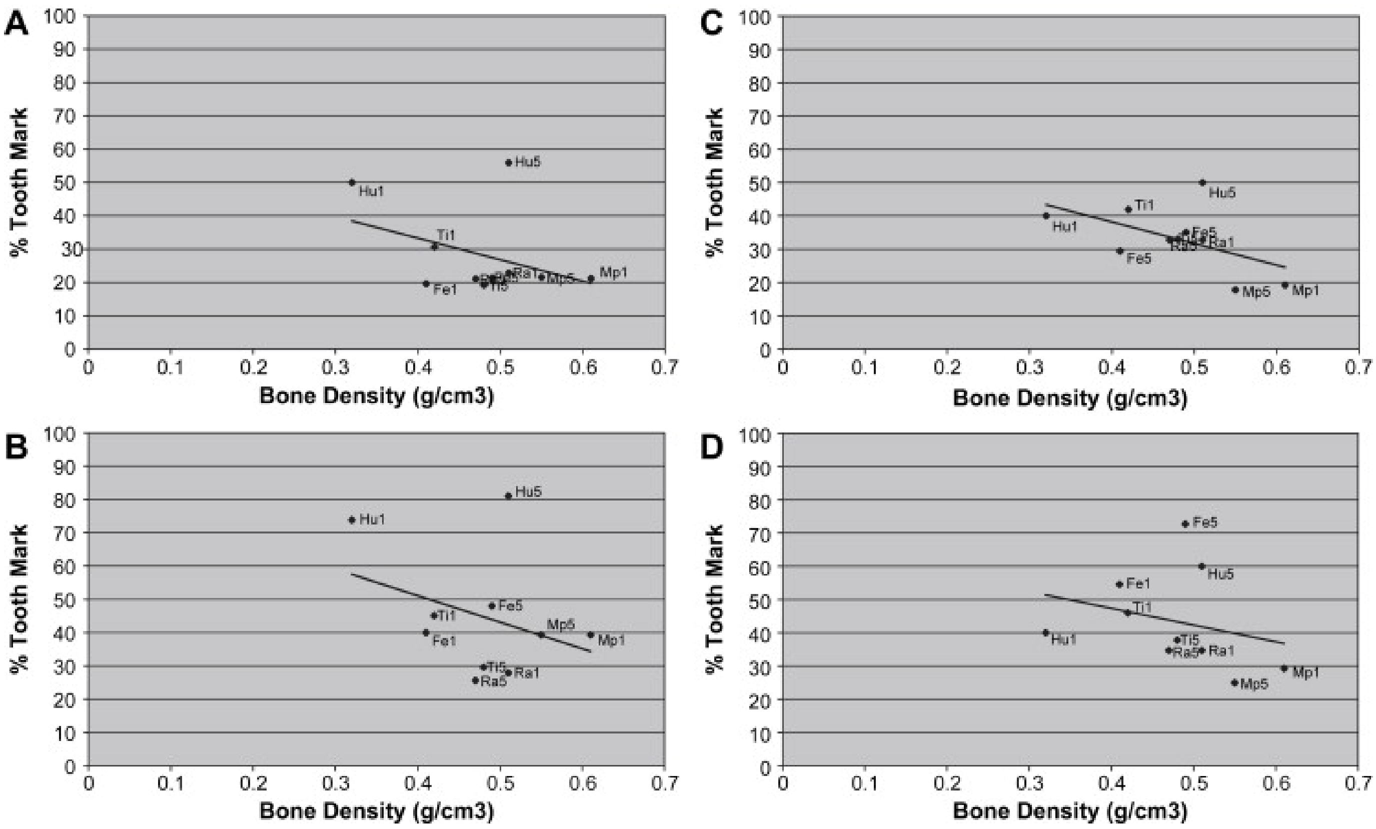

Fig. 1. *(A) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long bone epiphyses (r = −0.384, p = 0.137) from striped hyaena dens including all mammals without weathering limitations. (B) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long bone epiphyses (r = −0.353, p = 0.158) from striped hyaena dens including all mammals with weathering 0–1. (C) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long bone epiphyses (r = −0.530, p = 0.057) from striped hyaena dens, bovid size 2–3, no weathering limitations. (D) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long bone epiphyses (r = −0.271, p = 0.224) from striped hyaena dens, bovid size 2–3, weathering 0–1.*

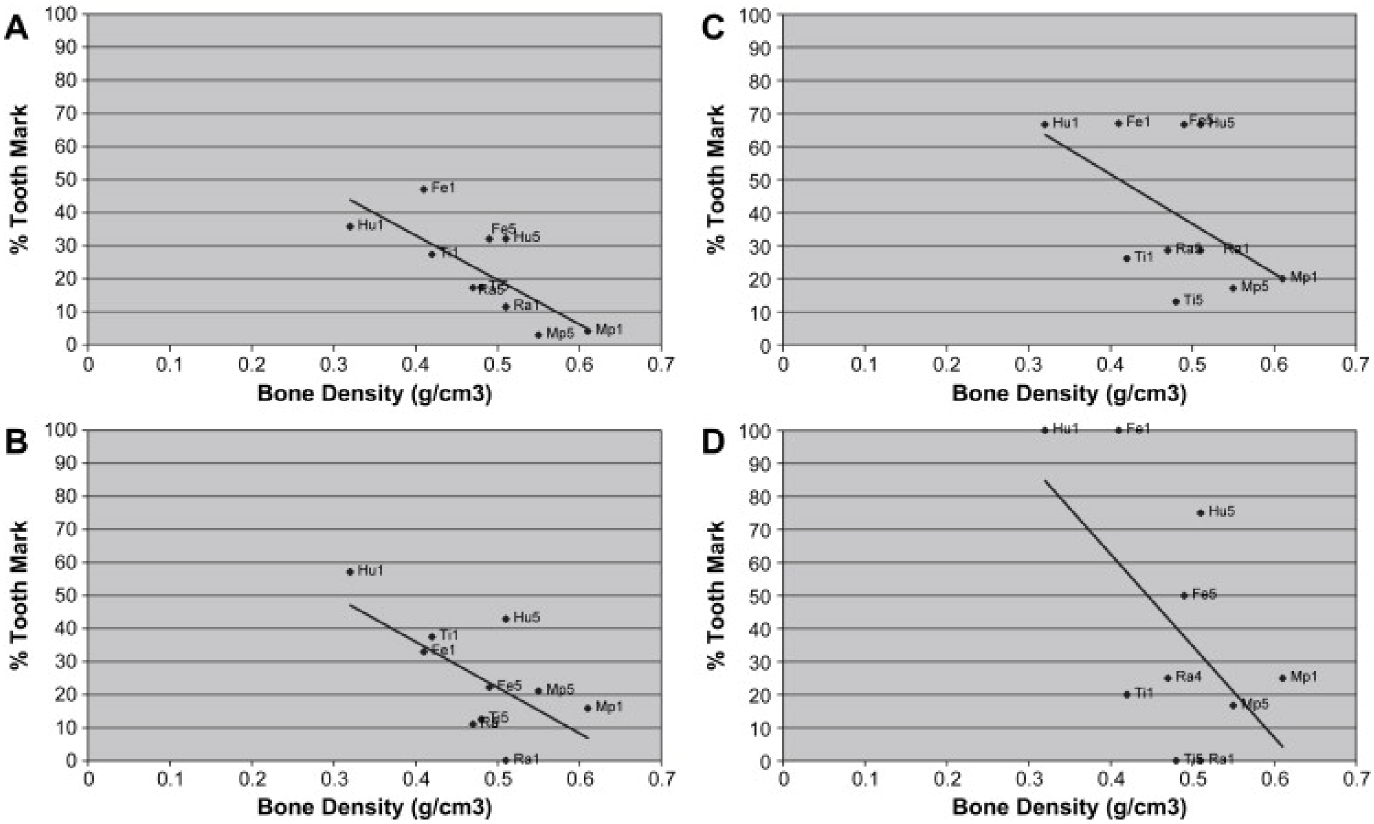

Fig. 2. *(A) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long bone epiphyses (r = −0.746, p = 0.006) from brown hyaena dens including all mammals without weathering limitations. (B) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long bone epiphyses (r = −0.647, p = 0.022) from brown hyaena dens including all mammals with weathering 0–1. (C) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long bone epiphyses (r = −0.512, p = 0.065) from brown hyaena dens, bovid size 2–3, without weathering limitations. (D) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long bone epiphyses (r = −0.583, p = 0.039) from brown hyaena dens, bovid size 2–3, weathering 0–1.*

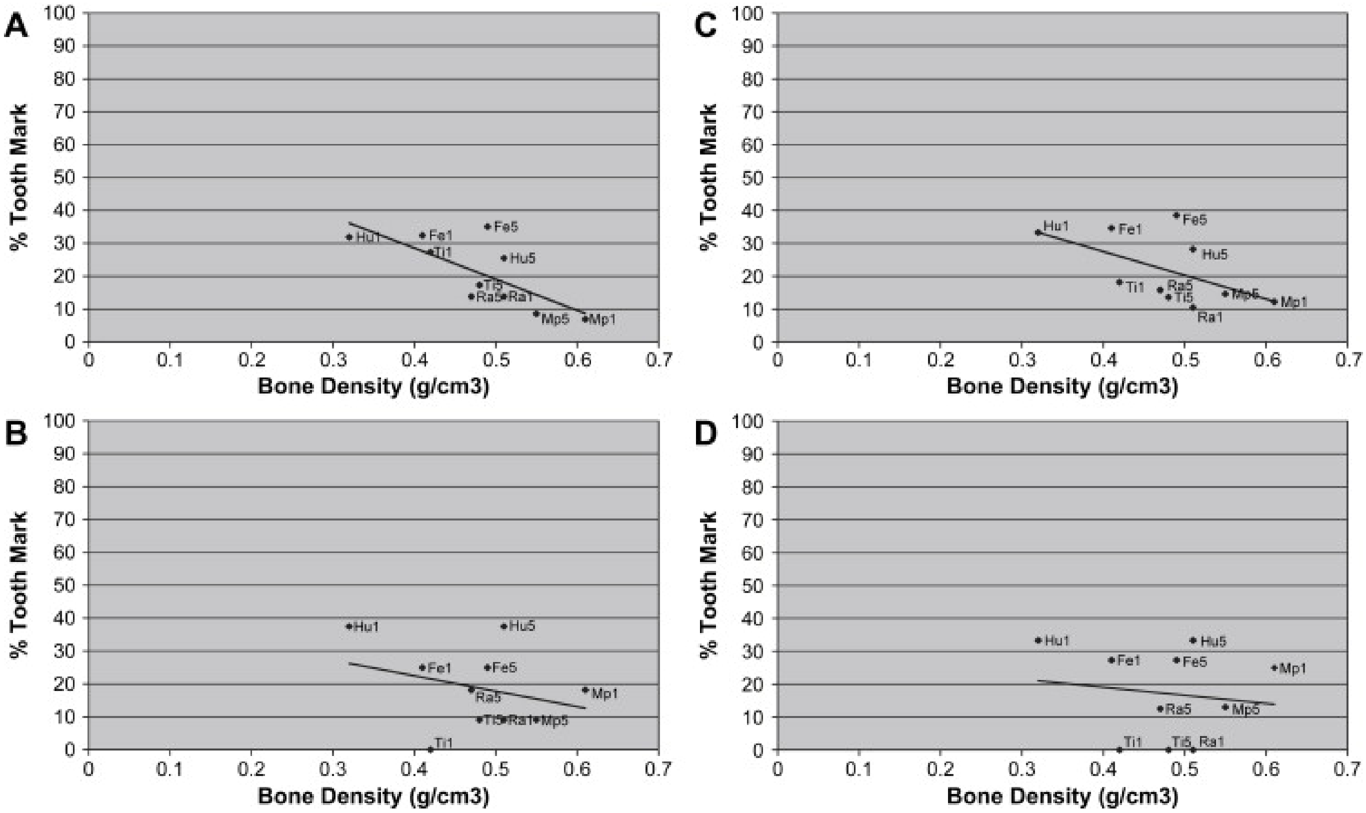

Fig. 3. *(A) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long bone epiphyses (r = −0.729, p = 0.008) from spotted hyaena dens including all mammals without weathering limitations. (B) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long bone epiphyses (r = −0.300, p = 0.199) from spotted hyaena dens including all mammals, weathering 0–1. (C) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long bone epiphyses (r = −0.549, p = 0.050) from spotted hyaena dens, bovid size 2–3, without weathering limitations. (D) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long bone epiphyses (r = −0.142, p = 0.348) from spotted hyaena dens, bovid size 2–3, weathering 0–1.*

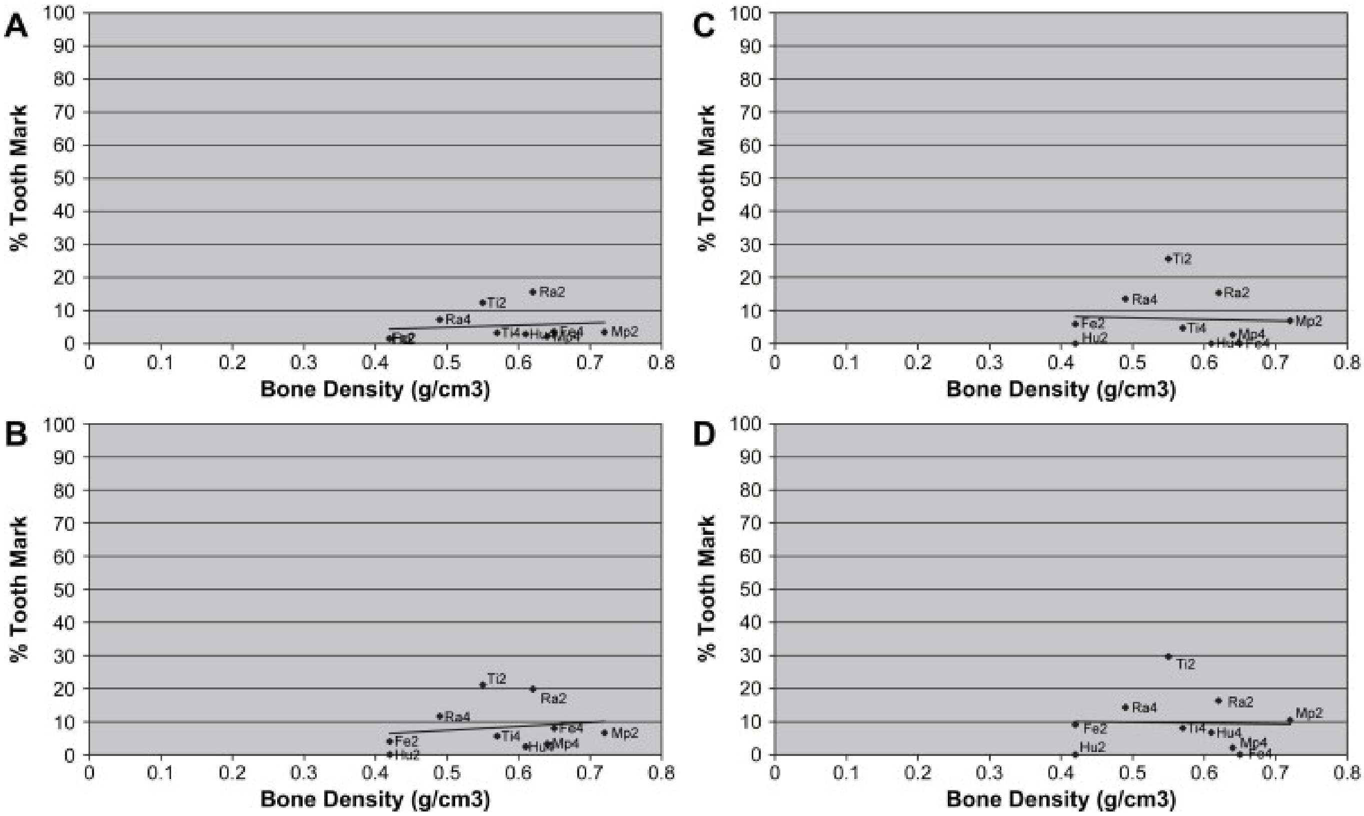

Fig. 4. *(A) Correlation between tooth mark per cent and bone density (wildebeest* [Lam et al., 1999](#)*) for long bone proximal and distal shafts (r = 0.135, p = 0.355) from striped hyaena dens with all mammals, no weathering limitations. (B) Correlation between tooth mark per cent and bone density (wildebeest* [Lam et al., 1999](#)*) for long bone proximal and distal shafts (r = 0.167, p = 0.322) from striped hyaena dens with all mammals, weathering 0–1. (C) Correlation between tooth mark per cent and bone density (wildebeest* [Lam et al., 1999](#)*) for long bone proximal and distal shafts (r = −0.054, p = 0.441) from striped hyaena dens, bovid size 2–3, no weathering limitations. (D) Correlation between tooth mark per cent and bone density (wildebeest* [Lam et al., 1999](#)*) for long bone proximal and distal shafts (r = −0.027, p = 0.471) from striped hyaena dens, bovid size 2–3, weathering 0–1.*

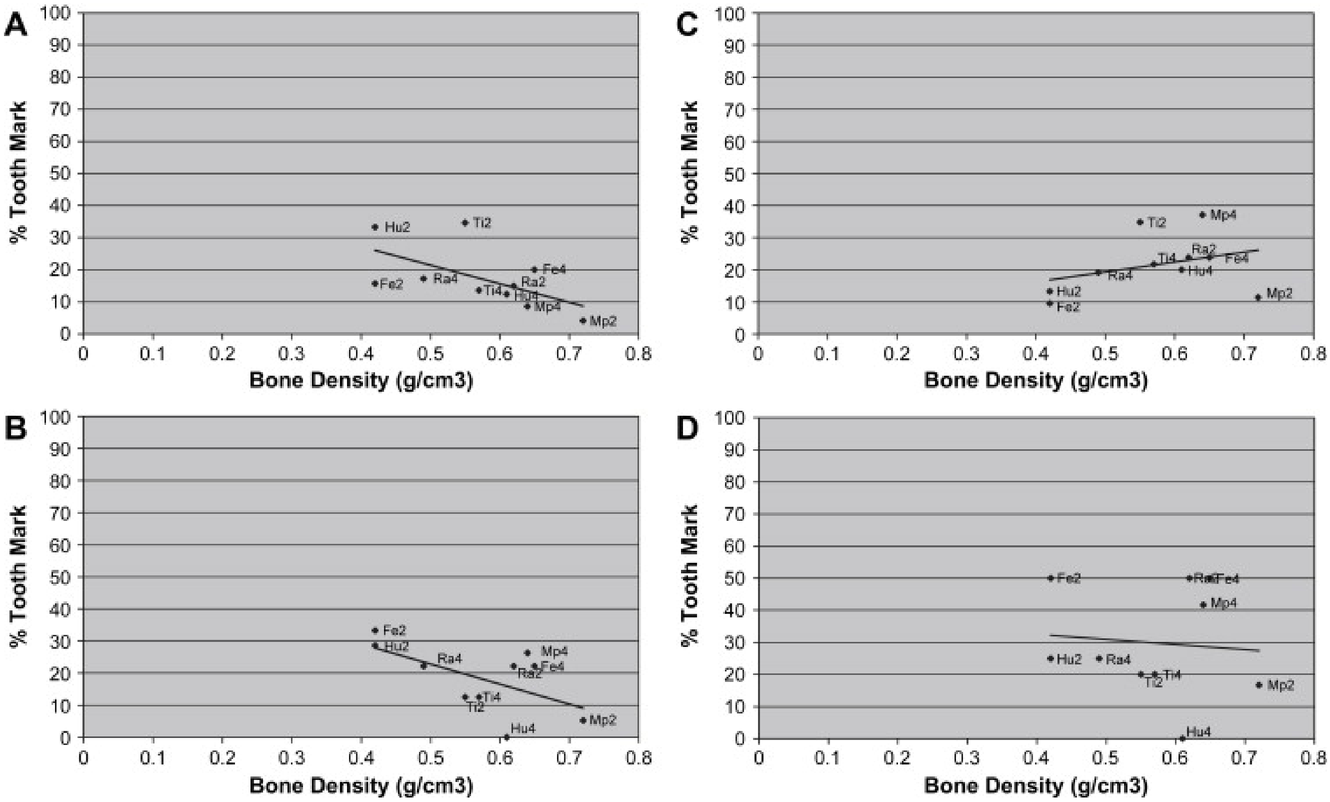

Fig. 5. *(A) Correlation between tooth mark per cent and bone density (wildebeest [Lam et al., 1999]) for long bone proximal and distal shafts (r = −0.591, p = 0.036) from brown hyaena dens with all mammals and no weathering limitations. (B) Correlation between tooth mark per cent and bone density (wildebeest [Lam et al., 1999]) for long bone proximal and distal shafts (r = −0.588, p = 0.037) from brown hyaena dens with all mammals, weathering 0–1. (C) Correlation between tooth mark per cent and bone density (wildebeest [Lam et al., 1999]) for long bone proximal and distal shafts (r = 0.337, p = 0.171) from brown hyaena dens, bovid size 2–3, no weathering limitations. (D) Correlation between tooth mark per cent and bone density (wildebeest [Lam et al., 1999]) for long bone proximal and distal shafts (r = −0.092, p = 0.4) from brown hyaena dens, bovid size 2–3, weathering 0–1.*

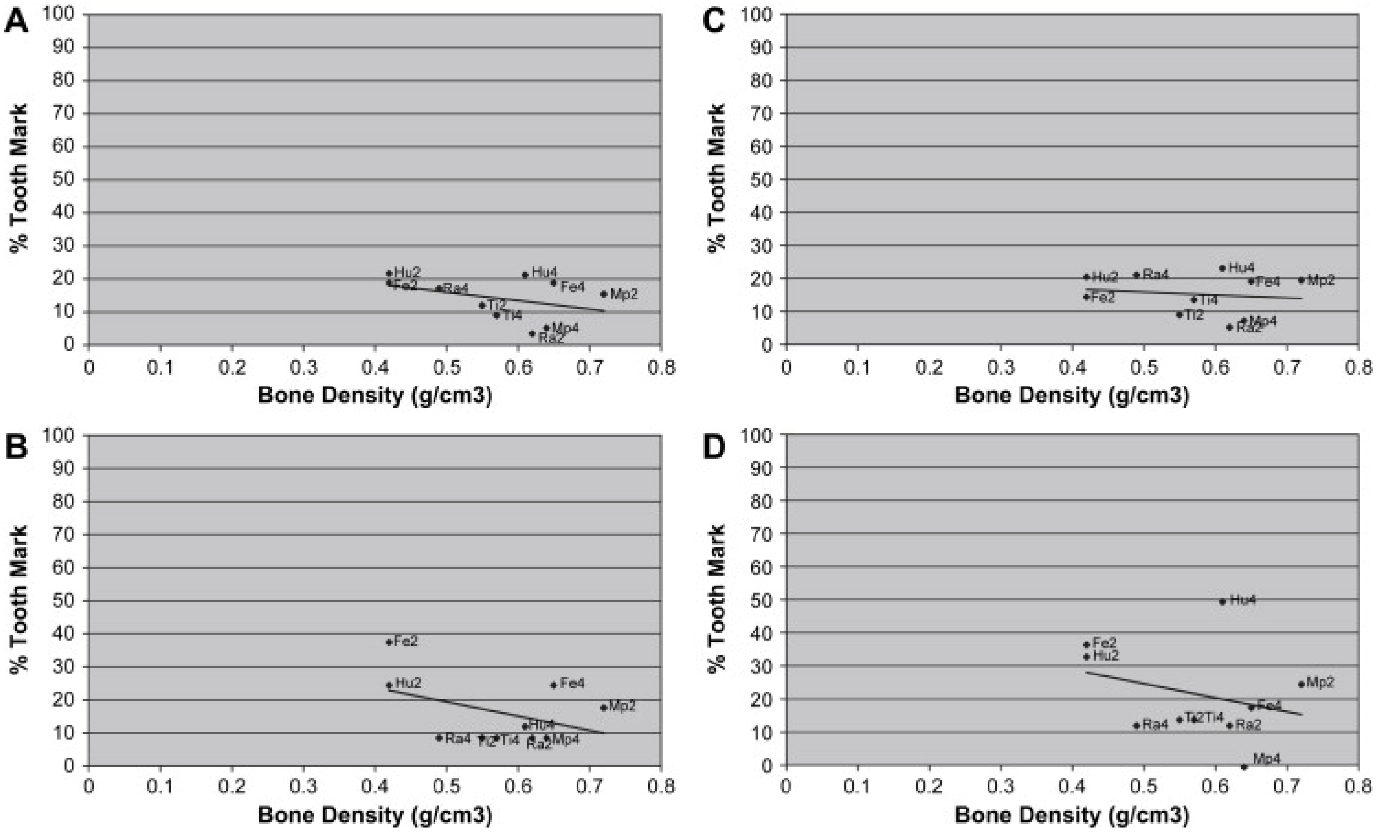

Fig. 6. *(A) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long bone proximal and distal shafts (r = −0.389, p = 0.133) from spotted hyaena dens with all mammals, no weathering limitations. (B) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long bone proximal and distal shafts (r = −0.431, p = 0.107) from spotted hyaena dens with all mammals, weathering 0–1. (C) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long bone proximal and distal shafts (r = −0.139, p = 0.351) from spotted hyaena dens, bovid size 2–3, no weathering limitations. (D) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long bone proximal and distal shafts (r = −0.288, p = 0.21) from spotted hyaena dens, bovid size 2–3, weathering 0–1.*

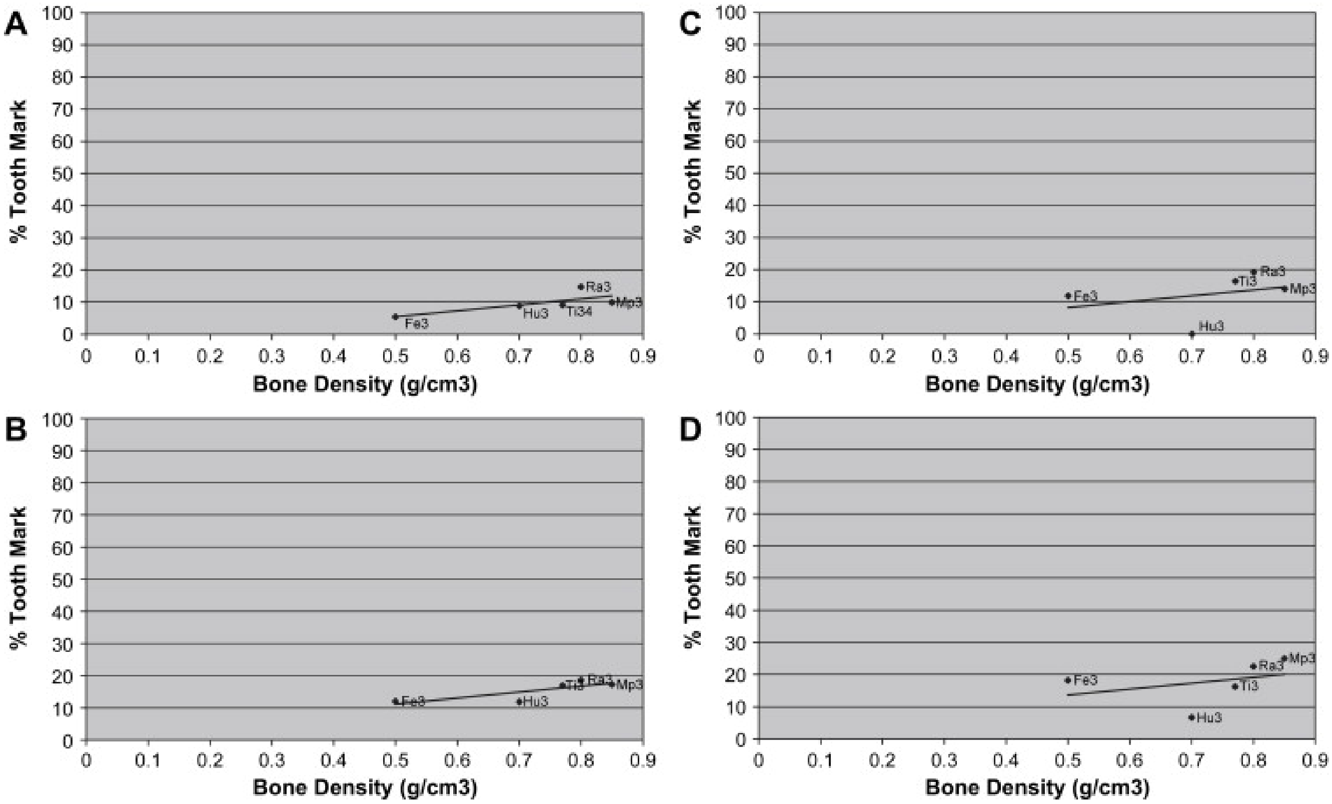

Fig. 7. *(A) Correlation between tooth mark per cent and bone density (wildebeest [Lam et al., 1999]) for long-bone mid shafts (r = 0.747, p = 0.044) from striped hyaena dens with all mammals and no weathering limitations. (B) Correlation between tooth mark per cent and bone density (wildebeest [Lam et al., 1999]) for long-bone mid shafts (r = 0.806, p = 0.026) from striped hyaena dens with all mammals, weathering 0–1. (C) Correlation between tooth mark per cent and bone density (wildebeest [Lam et al., 1999]) for long-bone mid shafts (r = 0.330, p = 0.252) from striped hyaena dens, bovid size 2–3, no weathering limitations. (D) Correlation between tooth mark per cent and bone density (wildebeest [Lam et al., 1999]) for long bone mid (r = 0.354, p = 0.246) from striped hyaena dens, bovid size 2–3, weathering 0–1.*

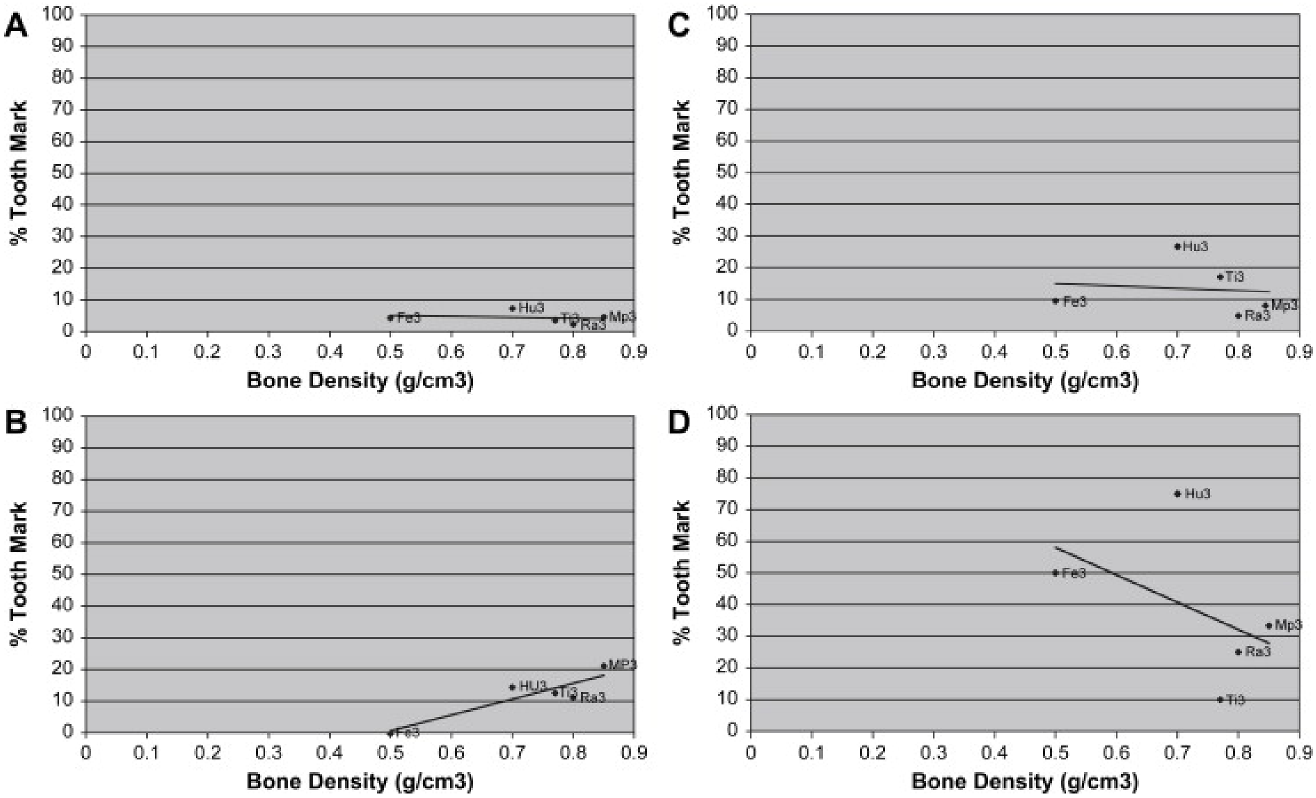

Fig. 8. *(A) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long-bone mid shafts (r = −0.215, p = 0.341) from brown hyaena dens with all mammals and no weathering limitations. (B) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long-bone mid shafts (r = 0.896, p = 0.008) from brown hyaena dens with all mammals, weathering 0–1. (C) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long-bone mid shafts (r = −0.11, p = 0.418) from brown hyaena dens, bovid size 2–3, no weathering limitations. (D) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long-bone mid shafts (r = −0.473, p = 0.172) from brown hyaena dens, bovid size 2–3, weathering 0–1.*

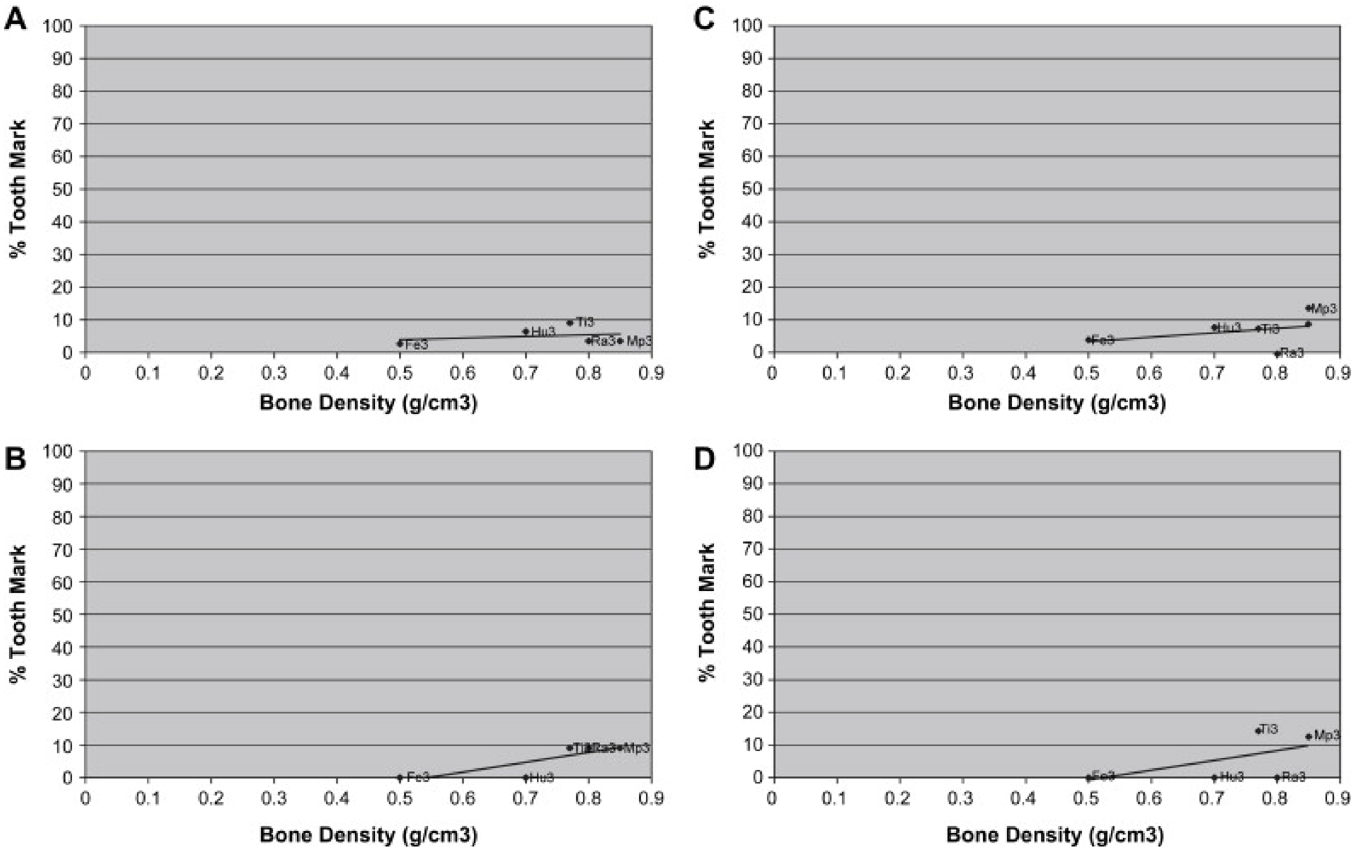

Fig. 9. *(A) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long-bone mid shafts (r = 0.252, p = 0.315) from spotted hyaena dens with all mammals and no weathering limitations. (B) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long-bone mid shafts (r = 0.829, p = 0.021) from spotted hyaena dens with all mammals, weathering 0–1. (C) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long-bone mid shafts (r = 0.36, p = 0.242) from spotted hyaena dens, bovid size 2–3, no weathering limitations. (D) Correlation between tooth mark per cent and bone density (wildebeest Lam et al., 1999) for long-bone mid shafts (r = 0.555, p = 0.127) from spotted hyaena dens, bovid size 2–3, weathering 0–1.*

Fig. 1, Fig. 2 and Fig. 3 illustrate the per cent tooth marks and bone density for the epiphyses of long bones. For all three hyaena species and for all four data sets the relationship is negative, meaning that as the bone density increases the per cent tooth marks decreases. For striped hyaenas the only data set where this is significant is the one looking at bovid class size 2–3 and no weathering limitations (Fig. 1C). All four data sets from brown hyaenas were significant (Fig. 2A–D), and the two spotted hyaena data sets without weathering limitations are also significant (Fig. 3A and C).

Examining the correlation between proximal and distal shaft densities and per cent tooth marks for each species and all four data sets are illustrated in Fig. 4, Fig. 5 and Fig. 6. For striped hyaenas, when one examines the data using all mammal remains, the relationship is positive (meaning that as the bone density increases the per cent tooth marks increases) but non-significant (Fig. 4A and B). The relationship is negative and non-significant when one examines data limited to bovid class size 2–3 (Fig. 4C and D). Examining the data sets from the brown hyaenas illustrates negative and significant relationships when examining data from all mammals (Fig. 5A and B). When examining the data set limited to bovid class size 2–3 (Fig. 5C) the relationship is positive and non-significant, whereas when the weathering limitation is added to the bovid class size 2–3 data set the relationship is negative and non-significant (Fig. 5D). All four data sets for spotted hyaenas have negative relationships and are non-significant (Fig. 6A–D).

Examining the figures for long bone mid shaft fragments for striped hyaenas illustrates that the relationship for all four data sets is positive, but only significant when examining the data sets for all mammals (Fig. 7A and B) and non-significant for the data sets limited to bovid class size 2–3 (Fig. 7C and D). For the brown hyaena data sets the unlimited data (Fig. 8A) and the data limited to bovid class size 2–3 (Fig. 8C and D) have a negative relationship that is non-significant. The data set with all mammals and limited to weathering 0–1 has a positive and significant relationship (Fig. 8B). The relationship between tooth marks and mid shafts for spotted hyaenas is positive for all four data sets. The relationship is non-significant for the two data sets without weathering restrictions (Fig. 9A and C) and significant for the data sets limited to weathering 0–1 (Fig. 9B and D).

5. Discussion

When examining the question of fragment length and per cent tooth marks our study supports Faith and previous work by Pobiner et al. (2002), that there is a direct correlation between fragment length and tooth mark frequencies. This relationship is evident for all three hyaena species known to collect bones. One problem, as pointed out by Faith, is that other factors such as trampling and weathering, can drive down the per cent of observed tooth marks. Our study shows that weathering overall does indeed affect the per cent of observed tooth marks.

Our study indicates that the relationship between prey body size and frequency of tooth marked bones is not as straightforward as Faith suggested. If one were to examine striped hyaena assemblages one would concur with the previous study that as prey body size increases so does the per cent of tooth marks. However, as illustrated in Table 3, for brown hyaenas the per cent of tooth marks declines when the data are limited to weathering 0–1 as well as data not limited to weathering but constrained to size 20–60 mm and only increases by less than 2% when the data are not limited. Spotted hyaena assemblages show a marked increase in the per cent tooth marks in relation to size for data limited to weathering 0–1 but this percentage decreases when unlimited data are examined, this is further evidence that weathering reduces the observed frequency of tooth marks.

Percentages of tooth marked portions of long bone specimens differ between skeletal elements as well as between hyaena species. This can be explained in part by the relationship between bone density and tooth mark frequencies. Comparing the data from spotted hyaenas to the spotted hyaena trends reported by Faith for the three distinct regions of long bones support his data; the relationships for epiphyses and proximal/distal shafts are negative while the relationship for mid shafts is positive. This is true for all four data sets reported here for spotted hyaenas. For brown hyaenas the data limited to weathering 0–1 and bovid size class 2–3 follow the same patterns as those of spotted hyaena accumulations reported here as well as Faith's results. The variation occurs for data limited to bovid size class 2–3 for proximal and distal shafts and data reported for mid shafts. For the proximal and distal shafts the relationship is positive, while the relationships for three of the four mid shafts are negative. The data for striped hyaenas show a similarity to both spotted hyaena and brown hyaena data sets when examining the relationships of tooth marks and the long bone epiphyses and similar to spotted hyaena data for mid shaft fragments. In this instance the variation occurs when the bovid size class restrictions are removed. When the data sets are limited to bovid size class 2–3 the relationship is negative like that of spotted hyaenas, but when the bovid size class limitation is removed the relationship between bone density and tooth mark frequency is positive.

6. Conclusion

Examining the questions originally cast by Faith: ‘1) How does long-bone fragment size impact tooth-mark frequencies? 2) How do tooth-mark frequencies vary across taxa of different body size classes? 3) How does the incidence of tooth-marking vary across portions of different long bone elements? 4) What is the relationship between tooth-mark frequency and bone density?’ (Faith, 2007, p. 1602) and comparing them to our study we find that: (1) Fragment size is related to tooth mark frequency for all three species, the analysis indicates that the relation is significant for all but one of the data sets examined. (2) Examining prey body size and tooth mark frequencies across the three hyaena species reveals that brown hyaenas leave behind different frequency patterns than the other two species of hyaenas. (3 and 4) When looking at something which appears to be fairly straightforward, like tooth mark frequency across various portions of long bones and tooth mark frequency in relation to bone density one finds variation not only between the hyaena species but also within the species when various limitations are placed on the data sets. It is the limitations placed upon the data examined which has consequences that need to be answered before we can attempt to correct for the variation. Like Faith and Lupo and O'Connell (2002) suggest, the study of tooth mark frequencies is not a simple matter. This further supports the previous work by Haynes (1983) documenting variation between species and exposes variations that are found within a species. Our study clearly shows that tooth mark frequencies of a single species of hyaena are not representative of the other extant species, not to mention extinct species. When examining the relationship between bone density and tooth marks our study indicates variation between and within species that warrants more research be done before any sort of corrections for variation suggested by Faith can be implemented with any confidence.

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