Bone-collecting habits of spotted hyaenas *Crocuta crocuta* in the Kruger National Park

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An examination of 18 *Crocuta crocuta* dens in the Kruger National Park, showed that this species can be responsible for bone assemblages at dens, more so at permanent sites such as granite or calcrete caves than at temporarily occupied aardvark holes or road culverts. Because of the facultative nature of food-transporting behaviour, the rate at which bones are accumulated at dens varies, ranging from no bones collected to nine food items collected per month. The relative abundance of ungulate species represented in the large assemblages resembles that of ungulates living in the region surrounding a den.
S. Afr. J. Zool. 1986, 21: 303 – 308

Agtien *Crocuta crocuta* lêplekke is in die Nasionale Krugerwildtuin ondersoek. Uit die resultate blyk dat hierdie spesie soms bene in sulke gate versamel, veral in permanente graniet- of kalkreetgrotte en minder dikwels in tydelike erdvarkgate of stormwaterslote. Die tempo waarteen hierdie beenversamelings groei varieer van geen tot nege items per maand, hoofsaaklik te wyte aan die onvoorspelbare wyse waarop hiënas die oorskotte van prooidiere versprei. Die relatiewe voorkoms van prooispesies in die beenversamelings vergelyk goed met die voorkoms van prooidiere in die onmiddellike omgewings van die lêplekke.
S.-Afr. Tydskr. Dierk. 1986, 21: 303 – 308

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Received 23 October 1985; accepted 22 April 1986

Whether or not spotted hyaenas *Crocuta crocuta* accumulate bones at den sites has long been a subject of dispute (Hughes 1954; Brain 1981). Originally, part of this controversy arose because of interspecific behavioural differences between hyaenids. It has now been established beyond doubt that both *Hyaena hyaena* and *H. brunnea* are important bone-collecting agents (Kruuk 1976; Skinner 1976; Mills & Mills 1977; Skinner, Davis & Ilani 1980; Skinner & van Aarde in press) and that the porcupine *Hystrix africaeaustralis* is an important secondary agent which frequently serves to confound the analysis of bone assemblages (Brain 1976; Maguire 1976).

In the present paper, we contribute to the ongoing discussion on the role of spotted hyaenas as agents responsible for bone accumulations (see Mills & Mills 1977; Henschel, Tilson & von Blottnitz 1979; Brain 1981) by presenting results of an analysis of bone assemblages at 18 dens in the Kruger National Park. Because brown hyaenas are extremely rare in this park (Mills 1985), this analysis presents a good opportunity to analyse the bone-collecting habits of spotted hyaenas with little chance of confusing them with those of brown hyaenas.

Apart from documenting the nature of the assemblages and the type of cavity used by spotted hyaenas, factors which can be useful for determining the probable collecting agent at palaeontological sites (Brain 1981), this study presents notes on the rate of bone accumulation by spotted hyaenas. Furthermore, the hypothesis that ancient ungulate fauna can be reconstructed from an analysis of bones found in ancient hyaena dens is tested by comparing the species compositions of bones found at three of the present study sites with those of living ungulates in the region.

Methods

Eighteen spotted hyaena dens were examined along the length of the park (Table 1). Whenever possible, bones were examined and identified on site, but others were removed for later analysis. At one den, observations were conducted on the rate of bone accumulation over a one-month period. Other observations of hyaenas of one clan transporting animal remains, were made over a two-year period.

Data on the abundance of ungulates of impala (*Aepyceros melampus*) size and bigger during six consecutive years (1979 to 1984) in the vicinities (31,5 – 50,4 km^2) of three den sites were obtained from the National Parks Board data bank of aerial censuses conducted once annually between May and July.

Table 1 Location of spotted hyaena dens examined

Den No.	Location	Longitude	Latitude
1	Olifants Rest Camp	31°46'E	24°46'S
2	Nwatimhisi (Olifants)	31°40'E	24°00'S
3	Mbangari (Roodewal)	31°37'E	24°12'S
4	Nhlanganini (Letaba)	31°33'E	23°57'S
5	Josiaspruit (Pafuri)	31°18'E	22°28'S
6	Mananga (Satara)	31°48'E	24°20'S
7	Witpens (Satara)	31°44'E	24°21'S
8	Olifants Trails Camp	31°45'E	24°00'S
9	Kingfisherspruit	31°27'E	24°27'S
10	Orpen	31°26'E	24°29'S
11	Punda Milia	30°55'E	22°43'S
12	Manangananga	31°03'E	22°49'S
13	Olifants River Bridge	31°42'E	24°04'S
14	Tshokwane	31°52'E	24°48'S
15	Tshokwane	31°44'E	24°42'S
16	Pretoriuskop	31°16'E	25°09'S
17	Napi Plots	31°24'E	25°06'S
18	Nghotsa	31°43'E	24°13'S

Results

Den descriptions

Four types of dens were used by spotted hyaenas in the Kruger National Park. These were granite caves formed by weathering, eroded calcrete limestone cavities, earthen holes probably excavated by aardvark (*Orycteropus afer*), and concrete culverts under macadamized roads (Table 2; Figure 1; Figure 2). All 18 hyaena dens examined had more than one entrance. The sizes of all dens were such that adult hyaenas could enter for some distance, but all natural caves, except one granite and two earthen dens, had smaller side tunnels which could only be entered by cubs. The entrances of granite and calcrete caves were high (0,6 – 1,4 m), but the caves usually narrowed down to less than 0,2 m. Earthen dens were sometimes intricate systems, with numerous entrances and a network of tunnels, the height of the main tunnel being 0,3 – 0,5 m.

Three of the four granite caves examined showed signs of porcupine occupation, judging by the number of quills and porcupine faeces found inside. Except for den No. 6, where an aardvark resided at one end of the system, while hyaenas made use of three other entrances, no evidence of co-habitation was found at any of the earthen dens. Culverts were also used by warthogs, porcupines, bats and jackals, but no evidence of co-habitation with spotted hyaenas was found.

Bone assemblages

The number of bones found at different dens varied substantially (0 – 626; $\bar{x}$ = 48,67 ± 145,73; Table 2). Granite and calcrete caves usually had large assemblages ($\bar{x}$ = 158,40 ± 262,67), while earthen dens and culverts seldom had more than an occasional bone ($\bar{x}$ = 6,46 ± 11,89). Six dens (1, 2, 3, 5, 6 & 13) had more than 28 bones, but others had less than nine.

The results of the three biggest collections at Dens 1, 3 and 5 are summarized in Table 3. Although all three dens were also inhabited by porcupines, only 1,3%, 13,6% and 15,0%

Figure 1 Entrances of natural hyaena den sites utilized by spotted hyaenas in the Kruger National Park at: (a) Olifants Site 1; (b) Mbangari Site 3; (c) Pafuri Site 5; (d) Satara Site 6.

Table 2 Descriptions of spotted hyaena dens examined in 1983 and 1984. Source of information for last occupation by spotted hyaenas are: o = own observation; r = ranger report; f = footprint; s = hyaena scat; h = hyaena hair identified by cross-sectioning (Keogh 1979); maximum tunnel height was measured at a position 2 m into a den

No.	Substratum	Origin	Number of Entrances	Tunnel Height	Bones	Last occupied	Source
1	Granite	Wind?	2	80 cm	626	pre-1984	r,s
2	"	Water	2	100 cm	41	pre-1984	r,s
3	"	"	2	60 cm	44	pre-1984	r,s,f
4	"	"	2	35 cm	4	1983	o
5	Calcrete	"	2	24 cm	77	pre-1983	r,f,h
6	Earth	Aardvark	3	30 cm	36	1984	o
7	"	"	2	50 cm	2	1983	o
8	"	"	8	30 cm	0	1984	o
9	"	"	4		8	1982	r
10	"	"	2		0	1981	r
11	"	"	2		0	1984	r,f
12	"	"	4		1	1983	r
13	Culvert	Man	2		29	1982	o
14	"	"	2		0	1983	o
15	"	"	2		0	pre-1984	r
16	"	"	2		5	pre-1984	r
17	"	"	4		0	1984	o
18	"	"	2		3	1984	o

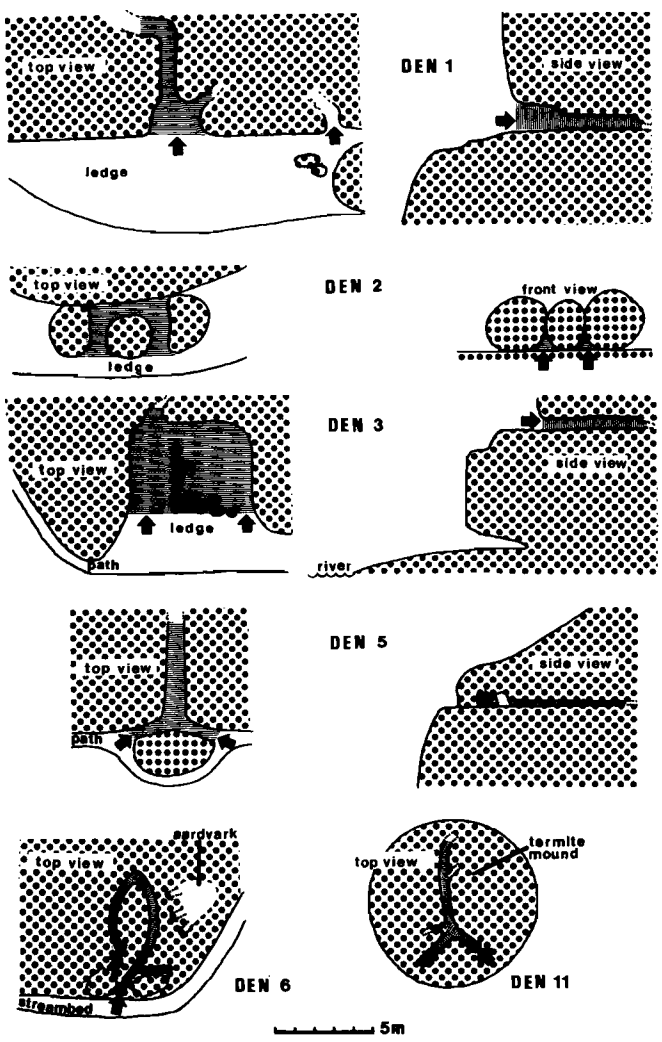

Figure 2 Schematic drawings of horizontal sections (top view), vertical sections (side view), or front view of six natural spotted hyaena dens (shaded). Arrows indicate den entrances.

respectively of the bones were gnawed by porcupines, while all showed signs of crushing or gnawing by hyaenas. These assemblages consisted mostly of long bones (Table 3; Appendix). Of the 41 bones found at Den 2, 39 were unidentified chips and two were impala leg bones. The 29 bones at Den 13 comprised 6 of impala, 3 of zebra, 1 of giraffe and 19 unidentified chips.

The relative abundance of the major prey species in the assemblages at Dens 1, 3 and 13 was compared to the relative mean abundance of ungulates in the areas surrounding these dens (Figure 3). The values of Spearman Rank correlation coefficients were highly significant ($P < 0{,}01$; r_s = 0,84, 0,77 and 0,89 for Den 1, 3 and 13 respectively), although by visual analysis, giraffe seemed to be more abundant in the assemblage at Den 3 than would be expected from the surrounding fauna. This was probably related to the large size of the giraffe bones, which enhanced their survival rate. These results indicate that the bone assemblages gave a fairly accurate representation of the surrounding medium-to-large ungulate populations.

Rate of accumulation

The rate of bone accumulation was monitored at an earthen den (No. 6) which hyaenas had adapted from an actively used aardvark den. During a month-long period of observation at this den, where a female hyaena had given birth to a cub, the dam carried ungulate remains to the den on eight occasions, and her adult male companion did so once. All nine items were complete fleshy legs, scapula (or humerus) to hoof or femur to hoof, and in one case the intact hindquarters of a zebra foal was taken to the den (Table 4). In three instances these items were carried from carcasses which were more than 5 km from the den. The dam fed on all of these items at the den, while other hyaenas occasionally partook of them. When the dam died violently after a month, examination of the den revealed the dismembered remains of seven of these items inside or within 10 m of the den (Table 4).

Table 3 Species distribution of bones inside (i) and within a 10 m radius outside (o) of three dens in the Kruger National Park; totals (t) and percentages (%) are indicated

	Den sites											
	1				3				5			
Species	i	o	t	%	i	o	t	%	i	o	t	%
Giraffa camelopardalis	15	3	18	2,9	8	5	13	29,6				
Syncerus caffer	17	2	19	3,0	6	0	6	13,6	3	0	3	3,9
Equus burchelli	19	2	21	3,4	1	2	3	6,8	2	1	3	3,9
Kobus ellipsiprymnus					1	0	1	2,3				
Connochaetes taurinus	12	4	16	2,6	1	1	2	4,6				
Tragelaphus strepsiceros	8	5	13	2,1	3	0	3	6,8	1	1	2	2,5
Tragelaphus angasii									2	0	2	2,5
Tragelaphus scriptus	2	1	3	0,5					1	0	1	1,2
Aepyceros melampus	62	23	85	13,6	3	0	3	6,8	18	5	23	28,8
Phocochoerus aethiopicus									3	1	4	5,0
Potamochoerus porcus									1	0	1	1,2
Raphicerus campestris									0	1	1	1,2
Crocuta crocuta	1	0	1	0,2								
Carnivora									2	0	2	2,5
Crocodylus niloticus					2	2	4	9,1				
Unidentified chip	69	381	450	71,9	5	4	9	20,5	24	14	38	47,5
Total	205	421	626		30	14	44		54	19	80	
Percent	33	67			68	32			70	30		
Porcupine quills			156				409				113	
% Porcupine gnawed				1,3				13,6				15,0
% Skull bones and horns*				18,8				20,0				14,3
% Leg bones and hooves*				71,0				45,7				59,5
% Vertebrae, ribs & pelvis*				10,2				34,3				26,2

*Unidentified chips were excluded in these calculations.

Table 4 Items carried to den Site 6 during one month and the remains found inside and within 10 m of the den at the end of this period

Date	Species	Part	Remains	Pieces
08/06/84	Kudu	back leg	none	
10/06/84	Buffalo	front leg	hoof-radius	1
10/06/84	Buffalo	back leg	hoof-tibia	1
17/06/84	Zebra adult	front leg	hoof-radius	1
18/06/84	Zebra adult	front leg	none	
27/06/84	Zebra foal	hindquarters	hooves-vertebrae	29
30/06/84 –	Impala	back legs	metatarsals	2
07/07/84	Kudu	front leg	hoof-scapula	1
	Kudu	front leg	hoof-scapula	1
Total				36

Transport of animal remains

Of 134 carcass pieces, comprising soft parts (29,2%), long bones (55,9%), vertebrae and skulls (14,9%), which were observed to be carried away from carcass sites by spotted hyaenas, 12,7% were taken further than 1 km (Table 5). Usually this had the effect of reducing interference competition for available food, as pieces were removed to be consumed at leisure in relative safety and peace. On 18 occasions such items were cached at different sites, usually in grass clumps under bushes and once in water. Eleven cached items were later observed to be retrieved. This behaviour of spotted hyaenas usually had the effect of dispersing animal remains, but because it was neccessary for a female with cubs to spend much time at the den, she sometimes took food items there rather than to a different place, with the result that bones could accumulate at a den site, but nowhere else.

Discussion

The bone accumulations found in the Kruger National Park support previous findings that spotted hyaenas may sometimes play an important role as agents in the establishment of bone assemblages. Porcupines cannot be precluded as possible agents that could have contributed to some of the collections. However, they could not have played a major role, because of the low proportion of bones with gnaw marks, and the large size of many of the bones at the dens. In contrast, the type of damage seen on many of the bones was characteristic of the splintering, gnawing and partial digestion (prior to

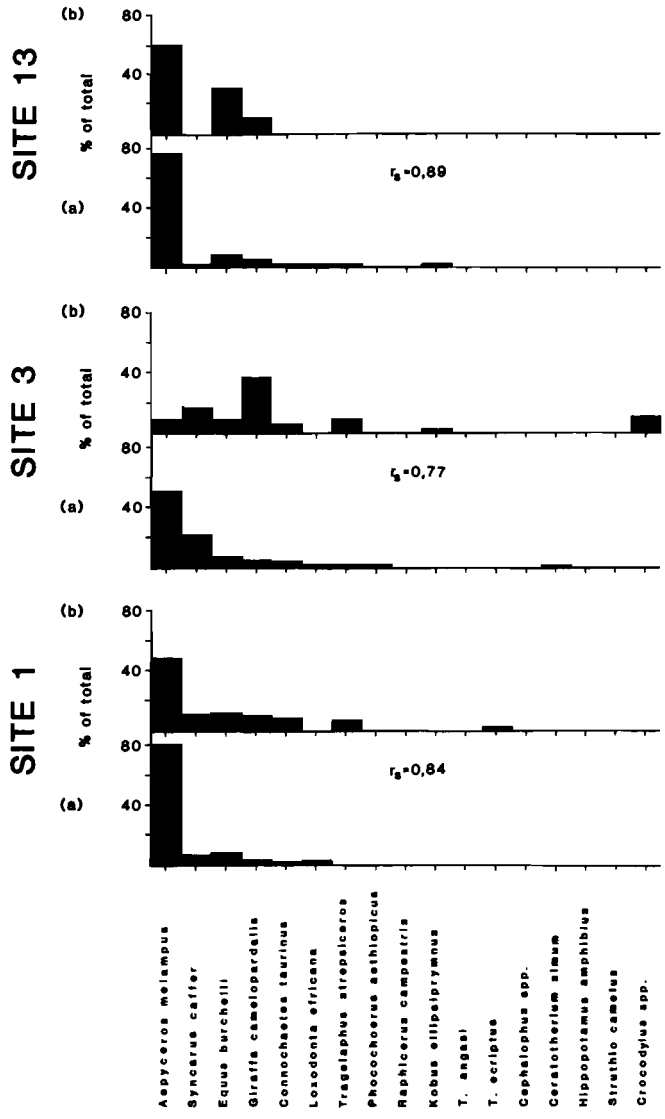

Figure 3 Histogram depicting the relative abundance of prey species: (a) counted in the immediate vicinities (31,5 – 50,4 km^2) of den sites during six successive annual aerial censuses (1979 – 1984) and (b) represented in bone accumulations at den sites.

Table 5 Transport of bones by spotted hyaenas away from carcass sites

Distance	Frequency	Percent
< 100 m	65	48,5
100 – 1 000 m	52	38,8
1 – 2 km	10	7,5
2 – 6 km	7	5,2
Total	134	100,0

regurgitating), caused by spotted hyaenas (Sutcliffe 1970). Furthermore, the preponderance of long bones can be explained from direct observations of spotted hyaena behaviour in the present study, and compares well with previous studies of spotted hyaena assemblages (Henschel *et al.* 1979; Hill 1980b).

Casual observations at culverts and earthen dens indicated that these were seldom used for a long period of time. On the other hand, granite and calcrete caves provide more permanent protection, have existed much longer than man-made structures, such as roads with culverts, and are repeatedly used. It is therefore not surprising to find that most bones accumulated at granite or calcrete caves. We have no idea over what time-span the 626 bones at Den 1 were accumulated. However, judging from their texture and odour, many of the bones were of very recent origin.

The debate concerning the role of spotted hyaenas as bone-collecting agents was a result of the facultative nature of their food transporting behaviour. Unlike *Hyaena hyaena* and *H. brunnea, Crocuta crocuta* does not provide its cubs with meat (Kruuk 1972), except for one observation recorded by Hill (1980a). However, we observed hyaenas moving food frequently from one locality to another as a means of avoiding interference competition. This can sometimes result in an accumulation forming at a den, depending on the inclinations of certain individuals. In a similar way, the close proximity of a human settlement could be a disturbance that leads hyaenas to carry food remains to their lairs, as was described by Sutcliffe (1970) in an East African region.

The examination of various den sites by different authors has contributed to differing interpretations of the role of *Crocuta* as bone-accumulating agents. Some of the dens we examined had quite large bone accumulations, similar to dens examined by previous authors (Mills & Mills 1977; Henschel *et al.* 1979; Hill 1980b), while others had few or no bones, similar to dens examined by Hughes (1954; 1961). However, the number of bones found in *Crocuta* assemblages does not compare to the large number found at *Hyaena* dens in Israel (Skinner *et al.* 1980) or Namibia (Skinner & van Aarde in press). Both the latter species collected a larger proportion of bones of smaller prey species and *Crocuta* assemblages contained a greater proportion of bone chips, reflecting the more powerful crushing ability of *Crocuta* jaws.

Conclusion

Four types of dens are used by spotted hyaenas in the Kruger National Park. The more permanent granite and calcrete caves could serve many generations of hyaenas, while aardvark holes and road culverts are not only more temporary, but the bones are exposed to more weathering. Assemblages are formed on a facultative basis by *Crocuta* and reflect their tendency to move food away from carcass sites. The assemblages thus formed show a predominance of long bones over vertebrae, the representation of species resembling the local ungulate populations. These results support the validity of describing ancient medium-to-large ungulate fauna from an analysis of ancient hyaena dens.

Acknowledgements

We are grateful to the warden and staff of the Kruger National Park for their assistance, interest in, and encouragement of our research on hyaenas. Dr. A. Turner commented on an earlier draft and Mrs. A. Nel kindly drew the figure.

References

BRAIN, C.K. 1976. Some criteria for the recognition of bone-collecting agencies in African caves. *Berg Wartenstein Symposium No. 69.* Wenner-Gren Foundation, N.Y.

BRAIN, C.K. 1981. The hunters or the hunted? An introduction to African Cave Taphonomy. The University Press, Chicago.

HENSCHEL, J.R., TILSON, R. & VON BLOTTNITZ, F. 1979. Implications of a spotted hyaena bone assemblage in the Namib desert. *S. Afr. archaeol. Bull.* 34: 127 – 131.

HILL, A. 1980a. Hyaena provisioning of juvenile offspring at the den. *Mammalia* 44: 594 – 595.

HILL, A. 1980b. A modern hyaena den in Ambolesi National Park, Kenya. *Proc. 8th PACPQS*, Nairobi.

HUGHES, A.R. 1954. Hyaenas versus australopithecines as agents of bone accumulation. *Am. J. Phys. Anthrop.* 12: 467 – 486.

HUGHES, A.R. 1961. Some ancient and recent observations of hyaenas. *Koedoe* 1: 105 – 114.

KEOGH, H.J. 1979. An atlas of hair from southern African mammal species with reference to its taxanomic and ecological significance. D.Sc. thesis, University of Pretoria, Pretoria.

KRUUK, H. 1972. The spotted hyaena. University of Chicago Press, Chicago.

KRUUK, H. 1976. Feeding and social behaviour of the striped hyaena (*Hyaena vulgaris* Desmarest). *E. Afr. Wildl. J.* 14: 91 – 111.

MAGUIRE, J.M. 1976. A taxonomic and ecological study of the living and fossil Hystricidae with particular reference to southern Africa. Ph.D. thesis, University of Witwatersrand, Johannesburg.

MILLS, M.G.L. 1985. Hyaena survey of the Kruger National Park: August-October 1984. *I.U.C.N. Hyaena Specialist Group Newsl. 2*: 15 – 25.

MILLS, M.G.L. & MILLS, M.E.J. 1977. An analysis of bones collected at hyaena breeding dens in the Gemsbok National Park. *Ann. Trans. Mus.* 30: 145 – 155.

SKINNER, J.D. 1976. Ecology of brown hyaenas *Hyaena brunnea* in the Transvaal with a distribution map for southern Africa. *S. Afr. Sci.* 72: 262 – 269.

SKINNER, J.D., DAVIS, S. & ILANI, H. 1980. Bone collecting by striped hyaenas *Hyaena hyaena* in Israel. *Paleont. afr.* 23: 99 – 104.

SKINNER, J.D. & VAN AARDE, R.J. (in press) Bone collecting by brown hyaenas *Hyaena brunnea* in the central Namib desert. *J. Archeol. Sci.* (1987).

SUTCLIFFE, A.J. 1970. Spotted hyaena: crusher, gnawer, digester and collector of bones. *Nature (Lond.)* 227: 1110 – 1113.

Appendix Skeletal parts identified at Dens 1, 3 and 5.
1 = horn; 2 = skull; 3 = maxilla; 4 = mandible; 5 = tooth; 6 = vertebra; 7 = pelvis; 8 = rib; 9 = scapula; 10 = tubercle; 11 = humerus; 12 = radius/ulna; 13 = femur; 14 = tibia/fibula; 15 = astralagus; 16 = metatarsal/metacarpal; 17 = phalange; 18 = hoof.

	Skeletal parts																
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Den 1																		
Giraffe		1	3		2					1	1	2	1	2	1	4		
Buffalo						1	2		1		1	3	3	4	1	1		2
Zebra					1	6	1					1		3		7		2
Wildebeest	3					2	2				1	2	2	1		3		
Kudu			2									3		2	1	2		3
Bushbuck								1			1					1		
Impala	12	1		6	1		3		4	1	5	11	1	6		18		16
Hyaena					1													
Den 3																		
Giraffe						4	3		2	1	1			2				
Buffalo						2	1		2		1							
Zebra											1	1		1				
Waterbuck											1							
Wildebeest														1		1		
Kudu	1						2											
Impala	2								1									
Crocodile			2	2														
Den 5																		
Buffalo						1			1					1				
Zebra						1					1							1
Kudu												2						
Nyala														1		1		
Bushbuck																1		
Impala	1	2		1		5	2	2			2	2		2	1	3		
Warthog				1	1							1				1		
Bushpig																1		
Steenbok									1									
Carnivore														1			1	