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ABSTRACT

Differences in bone collecting behaviour of three species of hyaena and porcupines are discussed. Observations on feeding behaviour of striped hyaenas are described as well as their habit of carrying pieces away particularly if feeding cubs at maternity dens. At one maternity den near Arad the floor of the main cavern was littered with bones which covered an area of 40 m^2 . Of this 2,0 m² was sampled and found to contain 267 bones and bone fragments from no fewer than 57 individuals, mainly of domestic species such as camel, donkey, caprovines and dogs.

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INTRODUCTION

Whether or not hyaenas accumulate bones at den sites has long been a subject of dispute. Some of the confusion has undoubtedly arisen from differences in behaviour between the three species of hyaena and from differences in behaviour of the same species in different geographic regions. Thus, Hughes (1954a, b) and Dart (1957) concluded that hyaenas are not important accumulators of bones, rather feeding where they find their food. On the other hand, Sutcliffe (1970) describes bone accumulations in East Africa which he ascribes to Crocuta, and Kruuk (1972) alleges that Crocuta does not expressly carry food back to the den to feed its young although they frequently carry objects back to their dens to chew. More recently Bearder (1977) reported bone remains in six Crocuta dens in the eastern Transvaal and thereby demonstrated the definite involvement of this species in accumulating bone fragments.

Recent studies (Skinner 1975, Mills and Mills 1977, Mills 1978, Owens and Owens 1978) have shown that brown hyaenas, *Hyaena brunnea*, carry food items away from the site of discovery either to cache them or more frequently to feed their young in maternity dens. Preliminary studies of striped hyaenas, *Hyaena hyaena*, in East Africa (Kruuk 1976) have indicated that they are similar in this regard. The present paper describes bone accumulations at a cave in Israel which have been attributed to *Hyaena hyaena*, and some observations on the feeding behaviour of this species.

PROCEDURE

During studies on *Hyaena hyaena* in Israel in December 1977 and January 1978, the opportunity arose to visit at least three maternity dens and four other lairs of this species. The dens were all situated in the Judean and Negev deserts.

The most significant maternity den was discovered in 1974 by a Bedouin goat herd. It was sited some 3,5 km south-west of Arad about 200 m above the valley floor and some 100 m from the top of the plateau. There are at least two entrances. The first is through a round hole nearly half a metre in diameter which opens out after some ten metres into a large, totally dark cavern about 100 m² and over 1,5 m from floor to ceiling at its highest point. Leading off this cavern are five short passages into small caverns and at least one long passage to another large cavern some 20 m away on a higher level. Another exit from this second cavern seemed to be used primarily as a latrine.

The Arad maternity den was occupied by a mother and cubs at the time of this investigation, and the main cavern was reserved as an eating place. Hundreds of bone fragments, including

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skulls, covered the floor of this cavern over an area of 40 m². Because we were reluctant to disturb this extraordinary deposit we sampled two 1 m² areas (A and B) 10 m apart, and the bones were taken to the Hebrew University for identification.

We also made nightly observations on the feeding behaviour of Hyaena hyaena using mounted and hand-held floodlights to which the hyaenas were habituated and floodlights at feeding sites established by the Nature Reserves Authority at En Gedi and Sde Boger. Five dead donkeys were placed one at a time at one of these feeding sites. There was competition with other carnivores at both sites. At En Gedi at least four individual hyaenas were identified plus a pack of six wolves Canis lupus, and about 20 foxes Vulpes vulpes. At Sde Boger the site was visited by at least three individual adut and three subadult hyaenas plus three wolves, about six foxes, a caracal, Felis caracal, and at least 20 griffon vultures.

RESULTS

Striped hyaenas feed one at a time except the subadult siblings which may feed together. A donkey carcass is opened at the anus and the flesh on the buttocks devoured. The ribs are "scissored" using the carnassial shear. After two nights of eating the first donkey was completely dismembered, devoured or carried away. All that was left was the earless head, the masseter muscle on the one side and a few neck vertebrae and the pelvic girdle stripped of flesh, the latter being the only remaining skeletal part after three nights. Although no exact measurements were made, it was estimated that adult hyaenas would consume 7-10 kg of soft flesh at a "meal", and subadults, which were only about 5,0 kg lighter, each consumed about 5,0 kg.

Usually after consuming as much soft flesh as they wanted, a carcass would be slowly dismembered as each hyaena tore off limbs or large pieces and carried them away. It took an adult hyaena 30 minutes of intense effort to tear off a hind leg from an adult donkey. Three individual hyaenas between them removed both hind limbs and tore out the stomach of the third donkey and carried them away. The head and forequarters were all that remained after one night, and the following day the vultures devoured the remaining soft flesh and left only the head for the hyaenas.

A characteristic of all the dens visited was that one area was used exclusively for feeding. It was here that the bones had accumulated, and these consisted mostly of cranial and mandibular pieces, metacarpals, hoof and horn sheaths and bone flakes from domestic ungulates. At no den was there a very large accumulation of bone fragments; this mostly ranged from 20-30 bone fragments per den.

The hyaenas occupying the den at Arad had recently brought in a domestic goat, Capra hircus. The rest of the sample (tables 1 and 2) contained 267 bones and bone fragments that represented at least 57 individuals, mainly camel (38%), donkey

(25%), caprovines (18%) and dogs (16%). Although not weighed and measured, a large proportion of the bone-fragments appeared to be over 50 g. There was no evidence of porcupine gnawing on a large sample of randomly selected bones.

TABLE 1

Bones collected from the Arad cave from 2,0 m² of a 40 m² area covered by bones. The areas sampled, A and B, were of equal size, and the earth beneath was sampled to a depth of 20 cm, but no identifiable bones or rodent bones were found in this.

AREA A					
SPECIES	LISTING BY A	NATOMICAL PARTS			
Camel:	Left side Right side				
Skull 1 and 1 maxilla (pa	alate + both der	ntal arcades)			
Mandible	4	6			
Scapula	3				
Humerus proximal		i di seconda di second			
Humerus shaft	near Arad U-				
Humerus distal	i ^a , Of this 2,0 4,	4			
Humerus complete		2			
Radius proximal	3	2			
Radius shaft	2	3			
Radius distal	$2(1 = u^*)$	2(1 = u)			
Radius complete	1	1			
Metacarpus proximal	3	INTRODUC			
Metacarpus shaft	3	1UCLION PROCEDUL			
Metacarpus distal	1	1.ST.IUSER			
Metacarpus complete	1	DISCUSSIO			
Acetabulum	Vit	2			
Femur proximal	DOEMENT S.	ACKNON			
Femur shaft	3	REFERENCE			
Femur distal	3(f)	1(u)			
Femur complete	-				
Tibia proximal	± 00001	Hall of the second second			
Tibia shaft	hyaenas a c	Whether or pli			
Tibia distal	been a subre	4(l=u)			
Tibia complete	as undoubre	of the confusion [
Metatarsus proximal	5	2 2			
Metatarsus shaft	5	2 and bes see and			
Metatarsus distal	4	same species in di			
Metatarsus complete		To in 291994 and and			
Calcaneum	and Dart (1)	1 (f)			
Astragalus	iportant <u>arc</u> i	hyaenas are not In			
Phalanx 1	re mey me	rather recoming which			
Phalanx 2	$\frac{1}{10} (0) R(1) = 0$	other hand, Suteli			
Phalanx 3	Africa whi ch	mulations in East			
Shafts of camel size	8	ada, and Kruuk (
o the den to feed its.	1 axis + 2 cerv	rical vertebrae			
Bos:	ev frequently	vourie although th			
Mandible	chew Mor	to their dens to			
Humerus distal	I anisona an	(1977) reported bo			
Donkey:					
Skull 1					
Maxilla 1 complete pa		maxillary arcades (6			
max. teeth $+ 4$ mand.	teeth)	angun sone gauna			
Mandible	Skinner 199	3			
Radius complete	Owens and	1977, Mills 19781			
Femur distal	hyaenas, I	4word that mode			
Femur shaft	m the site of	4			
Femur proximal	e frequences	2 (1=horse?)			
Tibia distal	2 2	6 (2=horse?) (1=u)			
Tibia complete	2	2			
Tibia shaft	2	6			
Metacarpus complete	I'm ann ba	Imput sym (over			
Metatarsus complete	_	1 = horse			
Phalanx 3	2				
*Epiphysis:					
u = unfused					
f = fused					

Goat/ibex/sheep:	that d	e.veld in southern Am2.3.1	Donkey:	ave	focumulated homes there.		
	de) + 2 cores without horn	Mandible 1 2					
Complete palate with b			Humerus	T	5		
Single max. arcades	3	3	Radius complete	1			
Mandible (+ post.	0	Figure 1989 and that	Radius shaft	3	2		
parts)	9	3	Radius proximal	3	2		
Acetabulum	Э		Femur distal Femur shaft	1	Columna Columnia and		
Humerus	1	Nin man I the lower of Class V will	Tibia distal	1	2		
Astragalus Metatarsus shaft	1	1	Tibia shaft	2	2		
Metatarsus complete (g	roat) 1		Tibia complete	1	2		
Ibex O' skull	soat) I	1 (with maxilla)	Acetabulum	5	3		
Gazelle O' skull		1 (without maxilla)	Metacarpus proximal		3		
Dog:			Metacarpus distal		3		
Skull 1			Metacarpus shafts		4 (1 = complete)		
Mandible	2	4	Metatarsus proximal	3	3		
Maxilla/palate —			Metatarsus distal	2	3		
complete	2	show <u>a</u> preference for	Metatarsus shafts	2	3		
Scapula	2	—	Metatarsus complete	2	3		
Humerus distal	01 800	prising that the bones in	Calcaneum	-	2		
Humerus proximal	umulai	In were not gnawed by	Astragalus	1	ave been absent them this		
Humerus shaft	l po	1 amount louils and bones	Phalanx 1		1		
Radius complete	in cav	floor home were needen	Phalanx 3	,	2		
Pelvis complete	1	1 (=1 pelvis girdle)	4 max teeth shafts — n	/0 +	l rib		
7 vertebrae			Capra:				
Hystrix:	Pho al			s + 2	horn cores i.e. total of 4 cores		
1 palate with both max	illae		Maxilla	2	3		
Pig:			Mandible	2	ub slupper begoleveb llew		
Teeth — few			Scapula				
Radius proximal	Inon	traction-montheatteration	Humerus distal Tibia	1	-+2 shafts		
Man:	reque		Acetabulum	1	-+1 shaft		
mandible	IST STOR	l (l complete		1	de Londuzzoad Automita di		
		lower jaw)	Radius proximal	1	HHE X MAT ISTET HORISI		
AREA B Camel:		knowed is accounting bo	Dog: Skull complete		said the eastern. Trains		
Mandible	2	5 (+ 1 palate with)	Maxilla	8	6		
		both dental arcades)	Mandible	5	6		
Scapula	3	2	Acetabulum	5	0		
Humerus proximal	handaha	something bet determination	Fox:	1.10	that warry food to a cache		
Humerus shaft	nte Ma	timber meterseren meters	Maxilla	1	sterioscilli Landvitterinite		
Humerus distal	ST. are	infinition I monoral s auformore and	Gazelle:		Konselected 29 and Maller mod		
Humerus complete	1	the trates de con horrier ? (hale	Horn		Owenstand Games 101 Stor		
Radius proximal	trad 1	2					
Radius shaft	100 C	2					
Radius distal	10 <u>100</u> 4.3	-1 HISTATION SISW INSTREMEN					
Radius complete	<u>-</u> 13	HEPELLER HE BURGER HE SHERE					
Metacarpus proximal	19 -4 998	B Number 19 sememored to					
Metacarpus shaft	1 36 hel	3	0.08360 EXECTED STATES				
Metacarpus distal	Attendo	als icensities produced the most	I apable of dayour-				
Metacarpus complete	-	a bolo 2 - and a a taxeto an	Although preda	tion	by spotted hyaenas has		
Acetabulum	2	tion see 4 south me of generality	been discussed at	leng	th during the past fifteen		
Femur proximal	oldo Ver	resting, polytopinde relice	years (Eloff 1964, 1	Kruu	k 1972), brown and striped		
Femur shaft	575346	M.J. Mortall' Suffrance and			as ineffective hunters that		
Femur distal	7.619	Gravestar Jan Ballio 95 - 50			g only the smallest of prey		
Femur complete	1()	and they bring back me			Owens 1978, Kruuk 1976,		
Tibia proximal	1(u)	_			press). This difference in		
Tibia shaft		2			due to the fact that Crocuta		
Tibia distal	1100	2					
Tibia complete	2	8			Hyaena (Skinner 1976, Skin-		
Metatarsus proximal	5	8			and to social behaviour be-		
Metatarsus shaft	4	issuoury and an Analist			t and feed in clans (Kruuk		
Metatarsus distal	1	INTERCONCEPTION OF THE STATE OF	19/2), whereas Hy	aena	forage alone or at most in		
Metatarsus complete	Indeed	$\frac{1}{2(n)} \pm 10(0)$			1976, Mills 1978, Owens		
Calcaneum	17190	2(u) + 1R(f)	and Owens 1978,	Mac	Donald 1978, Skinner and		
Astragalus Phalany 1	1	2	Ilani in press). Th	nis so	ocial behaviour may be re-		
Phalanx 1 Phalanx 2		THE SOMERAND FOR SUC	lated to brain ca	pacit	y (Oboussier 1979), since		
Phalanx 2		White told ab within the			ain and evolved later than		
					in a storted fater tildi		
Phalanx 3 Shafts of camel size		14	Hygeng (()boussier	hers	comm.). However there are		
Shafts of camel size Cervical vertebrae		14			comm.). However, there are ences in social behaviour		

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TABLE 2

A quantitative faunal list of mammalian species present in the Arad cave.* A + B COMBINED

						A	+ B COMBI	NED
				No. of			No. of	2) Stationery
	Bone	counts	indiv	iduals	Bone counts	%	individuals	%
	А	В	A	В				
Camel	49	52	6	8	101	38	14	25
Donkey	24	43	6	5	67	25	11	19
Cow	2	0	1	0	2		1	
Caprovines	31	17	9	5	48	18	14	25
Dog	17	27	4	8	44	16	12	21
Fox	. 0	1	0	1	without maxilla)		1 1	
Hystrix	1	0	1	9	1		1	
Gazelle	1	0	1	0	1		1	
Pig	1	0	1	0	1		1	
Man	1	0	1	0	1		_1	
							57	or a total of 1 140 indi- viduals over the 40 m ²
								area
*Counts not exhaustive but for est	timating the minimum numbe	rs of animal species	s represented and	for comparing a	reas A and B.			

which are not yet fully understood; for example, the *Crocuta* female is larger than the male, has a well developed penile clitoris and is dominant (Racey and Skinner 1979), but in *Hyaena* sexual dimorphism favours the male. There are also interesting differences in the behaviour of *Crocuta* clans in different geographic regions such as East Africa (Kruuk 1972), the Kalahari desert (Eloff 1964), and the eastern Transvaal lowveld savanna (Bearder 1977). These seem to be related to the presence and behaviour of lions.

However, Hyaena are best known as scavengers that carry food to a cache or to their dens, particularly when they have cubs (Harrison 1968, Kruuk 1972, Mills and Mills 1977, Mills 1978, Owens and Owens 1978). The present study confirms this behaviour. Not only does Hyaena feed singly (Ilani 1975, Kruuk 1976, Mills 1978, Skinner and Ilani in press), but, after filling their stomachs, their whole strategy is aimed at dismembering the carcass and carrying away large parts. The amount they appear capable of devouring at one meal (7–10 kg) is half that which Crocuta can devour at one time (Bearder 1977).

Although Sutcliffe (1970) and Bearder (1977) support the view that *Crocuta* does accumulate bones at den sites, it is probable that the accumulations reported by Sutcliffe also resulted from foraging activities of *Hyaena hyaena*, since he made no attempt to separate the activities of various scavengers. Morever, Brain (1976) has emphasised that any cave which has been open for thousands of years will contain bones brought to it in a variety of different ways. Bearder (1977) examined the bones for evidence of porcupine gnawing but found only two examples in a sample of 409. Brown hyaenas are extremely rare in Bearder's study area and probably made no contribution to the bone accumulations he ascribed to *Crocuta*.

On the other hand evidence has shown that *Hyaena brunnea* usually collects bones at maternity

dens (Skinner 1975, Mills and Mills 1977, Mills 1978, Owens and Owens 1978). Bone collections of 20–30 fragments seen at *Hyaena hyaena* dens in the present study were very similar to those described by Mills and Mills (1977) for *Hyaena brunnea*.

However, it frequently happens that vacant dens are used by other species such as aardvarks, warthogs and porcupines. Porcupines have long been known to accumulate bones in quite large quantities in their dens in the Kalahari sandveld (Brain 1976). Indeed, Brain suspects that porcupines carry more bones to African caves than any other species, but he does find this behaviour unusual for a vegetarian rodent. Examining the Nossob porcupine bone collections, Brain (1976) found that the great bulk (70 per cent) of the 1 708 individual specimens weighed between 0-50 g and 77 per cent were between 1-15 cm in length. Furthermore, Brain (1976) suggests that bone collecting by porcupines (Hystrix africae-australis) "has to do with the wearing down of the incisor teeth rather than with nutrition". As in other rodents the incisors are open-rooted, grow throughout life and through attrition are kept at usable length. While resting, porcupines select objects and gnaw on them for this purpose. Moreover, Brain (1976) believes collecting behaviour has become compulsive, and they bring back more objects than they require; for example, only 55,2 per cent of the bones from the Nossob collection showed signs of gnaw-

ing. This remarkable behaviour of porcupines is apparently unique amongst other species with similar incisor teeth, even those of similar size and weight such as *Lepus* or *Procavia*. Indeed, the necessary attrition takes place through the wear of upper against lower incisors as well as when gnawing food. Furthermore, the porcupines in Israel, *Hystrix indica*, do not gnaw bones (Mendelssohn *pers. comm.*): In fact Mendelssohn ascribes bone chewing to phosphorus deficiency.

It is well known that the veld in southern Africa is deficient in phosphorus, particularly in the sandy areas of the Kalahari savanna (Du Toit and Bisschop 1929, Du Toit, Malan, Louw, Holzapfel and Roets 1932, 1935a, b, Henrici 1928) and that this results in osteophagia which in turn caused widespread cattle deaths from botulism as early as the eighteenth century in Namaqualand (le Vaillant 1796 cited by Henning 1949). Throughout this region phosphates are given to domestic livestock to compensate for this deficiency. The reason why porcupines do not die of botulism can be ascribed in part to Brain's (1976) observation that no more than 15 bone fragments in the Nossob collection showed appreciable traces of fattiness. In other words porcupines show a preference for weathered bones.

It is therefore not surprising that the bones in the Arad cave accumulation were not gnawed by porcupines. Although porcupine quills and bones were present on the cave floor, these were probably from individuals eaten by Hyaena, as Hyaena are known to kill porcupines when the opportunity arises (Skinner and Ilani in press). There are possibly three reasons why porcupines have not been a factor in the Arad collection. First, it is not a phosphorus deficient area (Mendelssohn pers. comm.), and osteophagia hardly occurs in herbivores in those areas. Secondly, there may be species differences in porcupine behaviour, or compulsive collecting as suggested by Brain (1975) may have evolved in a phosphorus deficient area. Thirdly, the Arad cave is very high and may be inaccessible to porcupines.

The Arad cave has been used by *Hyaena* as a den, perhaps exclusively for maternity purposes, for many years, perhaps for hundreds of years. This does not preclude the possibility that other

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agents may also have accumulated bones there. Nevertheless, it is a unique deposit because the bone accumulations have largely been protected from weathering as a result of the narrow tunnel openings to the cave. Moreover, it has been protected from incidental scavenging and vultures because of its size and seclusion. Only carnivores seeking such seclusion would find it.

CONCLUSION

We suggest that the Arad collection is largely, perhaps exclusively, that of *Hyaena* and we believe that other agents are unlikely to have been responsible. Primitive man is unlikely to have entered a dark cavern through such a narrow tunnel. "Civilised" man in this region was and still is so suspicious of hyaenas (Harrison 1968) that if he had known of the cave he would probably have avoided it. Leopards have been absent from this area in living memory, and porcupines are not implicated. The collection reflects the present large mammal composition of the surrounding area, and the collection is probably the remains of individuals scavenged by hyaenas and brought to the den to feed cubs.

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other words porcupines show a preference for weightered hones. It is therefore not surprising that the bones in the therefore not surprising that the bones in porcuping Athough porcupine quills and bones were present on the cave floor, these were postably from individuals eaten by from a 25 them all there in the cave floor, these were postatistic over the present on the cave floor, there were postatistic over the present on the cave floor, there were postatistic over the present on the cave floor, there were postatistic over the present on the cave floor, there were postatistic over the present of the cave floor there were postting there increases subrive or there were postatistic over the present floor there were postting there increases and conference is a transment floor a difference in efficient over the present floor a difference in the transmess is difference in the phosphenese relation in the relation of the difference in the accessible to present the control of the difference in the present of the present her control of the difference in the phosphenese relation of the difference in the bones of the difference in the transmess is difference in the phosphenese relation of the difference in the bones accessible to phonese and the control of the difference in the present of the transmession of the floor of the difference in the present of the transmession of the difference in the present of the transmession of the difference in the present of the transmession of the difference in the accessibility of the state of the transmession of the transmession of the transmession of the difference in the transmession of the transmession of the difference in the transmession of the transmession of the difference in the transmession of the difference in the transmession of the transmession of the difference in the transmession of the difference in the transmession of the transmession of the difference in the transmession of the transmession of the difference in the difference in the transmession of th

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