

CARNIVORE DAMAGE TO ANTELOPE BONES AND ITS ARCHAEOLOGICAL IMPLICATIONS

by

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ABSTRACT

The rates of survival, damage, fragmentation and degree of articulation of the bones of 89 bovids eaten by a variety of carnivores in the Transvaal are presented and evaluated. These results are entirely predictable considering the size, density, shape and mode of attachment of the bones. With the exception of the brown and spotted hyaenas the extent of damage to these bones can be directly related to the sizes of the bovids and the carnivores concerned. The hyaenas have disproportionately high abilities to crush bones, particularly the long limb bones. The bones all had fairly uniform survival rates except the ribs, carpals, tarsals, phalanges and caudal vertebrae, which are easily eaten or removed. Mandibles and scapulae had exceptionally low articulation rates, and long bones, crania and ribs had the highest fragmentation rates. Small bovid bones were far more susceptible to damage by trampling than those of larger bovids.

Certain differences between carnivore and hominid damage to bones are mentioned. These relate primarily to hominids using their hands to dismember and damage bones selectively, particularly long bones which are broken in half to extract the marrow. A different pattern of survival of long bone epiphyses resulting from hominid activity can be predicted from that caused by carnivores, especially hyaenas. The pattern of survival of epiphyses at Makapansgat is that predicted for hominids, whereas the pattern at Swartklip I, an accepted hyaena site, is the opposite. It is therefore suggested that australopithecines were the primary bone collectors at Makapansgat. Further data on the differences between carnivore and hominid damage are also presented.

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INTRODUCTION

A major field of interest at present is the reconstruction of australopithecine behaviour at various sites in the Transvaal. However, numerous difficulties are experienced because of the great number of variables involved in the accumulation and subsequent preservation of the bones found at

these localities. Analysis of the bones may be directed at establishing faunal composition or the survival rates of particular bones. The former helps to elucidate past environmental conditions and hunting methods (Klein 1977, 1978, Vrba 1974), but the latter may give more information on the identity of the primary accumulating agents

(Klein 1975). Hominids, hyaenas, leopards and porcupines are all accepted as potential contributors. However, because definitive examples of bones accumulated and damaged by these agents have not and possibly cannot be described, the same bone assemblages are often subject to quite different interpretations.

Brain (1969a) has shown that the bones of goats eaten by Hottentots and their dogs in the Namib desert had a very similar pattern of survival to the Makapansgat sample on which Dart (1957) based his Osteodontokeratic culture of *Australopithecus prometheus*. In view of this similarity and the widely different environmental conditions that characterise each site, he suggested that the survival rate of bones is quite predictable in terms of their durability alone and does not necessarily relate to selective hominid accumulation and usage. During a recently completed study of the feeding behaviour of carnivores on all sizes of antelope, I collected data on the survival rates of the bones of these antelope. These data are used here to examine Brain's interpretation.

CARNIVORE DAMAGE TO BONES

Method

Between July 1976 and November 1978 I put out or found 89 carcasses of various bovids, equids or giraffe ranging in size from springbok lambs (~12 kg) to giraffe bulls (~1 200 kg). Because of their similar bone structure, they will all henceforth be referred to as "bovids". The sites used were three farms and three reserves in the Transvaal and a reserve in Zimbabwe. The brown hyaena occurred on the farm Olifantshoek, and a pair of feral dogs appeared temporarily on another. Lions, spotted hyaenas, jackals and five species of vultures occurred on all the reserves. Only jackals and griffon vultures were common throughout. The carcasses were left in fairly open sites and were observed from hides. The survival, damage, articulation and fragmentation of all the major bones of the carcasses were recorded at intervals between feeding bouts and after the final feeding bout of scavengers or predators. Subsequent observations were made whenever these sites were revisited weeks or months later.

The survival of bones was recorded on a presence or absence basis and related to the maximum number of bones of its type for each species. The atlas and axis vertebrae were recorded together. The carpals, tarsals, phalanges and sesamoids were all recorded, but, because of their similar survival rates, they have been grouped together as "small bones". Left and right bones were recorded but have also been grouped together.

Bones were recorded as being damaged or undamaged and photographs were taken to supplement these observations.

The percentage articulation for each bone type was calculated as the number of intact joints divided by the maximum number possible. The maximum numbers of articulation surfaces were

derived as follows: the cranium has one surface to the atlas; the mandibles have three surfaces, two to the cranium and one to each other; all vertebral types except the last caudal have one more surface than their own numbers to account for articulation at either end; the same applies to the long bones of each limb; the sacrum has four surfaces, two to the lumbar and caudal vertebrae and two to the innominates; the innominates have five surfaces, two to the femora, two to the sacrum and one to each other; the small bones each have one surface. This method gives details for each bone type, indicates exactly where disarticulation has occurred, and, since the same bias applies to all carcasses, the few duplications of articulation surfaces between bone types will not affect the relative frequencies between carcasses.

The fragmentation ratio gives an average indication of how many pieces each bone yielded when broken. It was calculated by counting the number of bone pieces that were found and dividing them by the number of bones from which they came. It was often difficult to determine the exact origin of long bone chips; in this case the number of bones was over- rather than under-estimated. The ratio was expressed as a percentage. The relative fragmentation ratios of whole carcasses were calculated by using only the long bones, cranium and ribs because these are the bones which fragment most readily.

The carcasses were divided into three weight classes which directly relate to the upper three classes described by Klein (1977). Since I did not have any very small antelope and only a few springbok lambs, a very small class was not warranted. The classes were as follows:

Small: 10–100 kg — Springbok, Blesbok, Impala;
Medium: 100–300 kg — Kudu, Zebra, Cattle;
Large: >300 kg — Eland, Buffalo, Giraffe.

Results

The results of damage caused by carnivores at the end of the initial feeding bouts are recorded in Figure 1. The sample size is not 89 because these observations could not be made at every carcass. Because of the range in size of both the carcasses and the carnivores involved, these results indicate only general trends. However, certain features are still quite evident.

Survival

The survival rates of all the bone types are remarkably similar. The only notable observation is that the largest types, crania, and smallest bones, especially caudal vertebrae, have the highest and lowest survival rates respectively. Being small and at an extremity, the caudal vertebrae are readily eaten by all carnivores.

Damage

The softer, thinner and more prominent bones are the ones most susceptible to damage. However, because one of the primary aims of this study was to record any possible differences between carni-

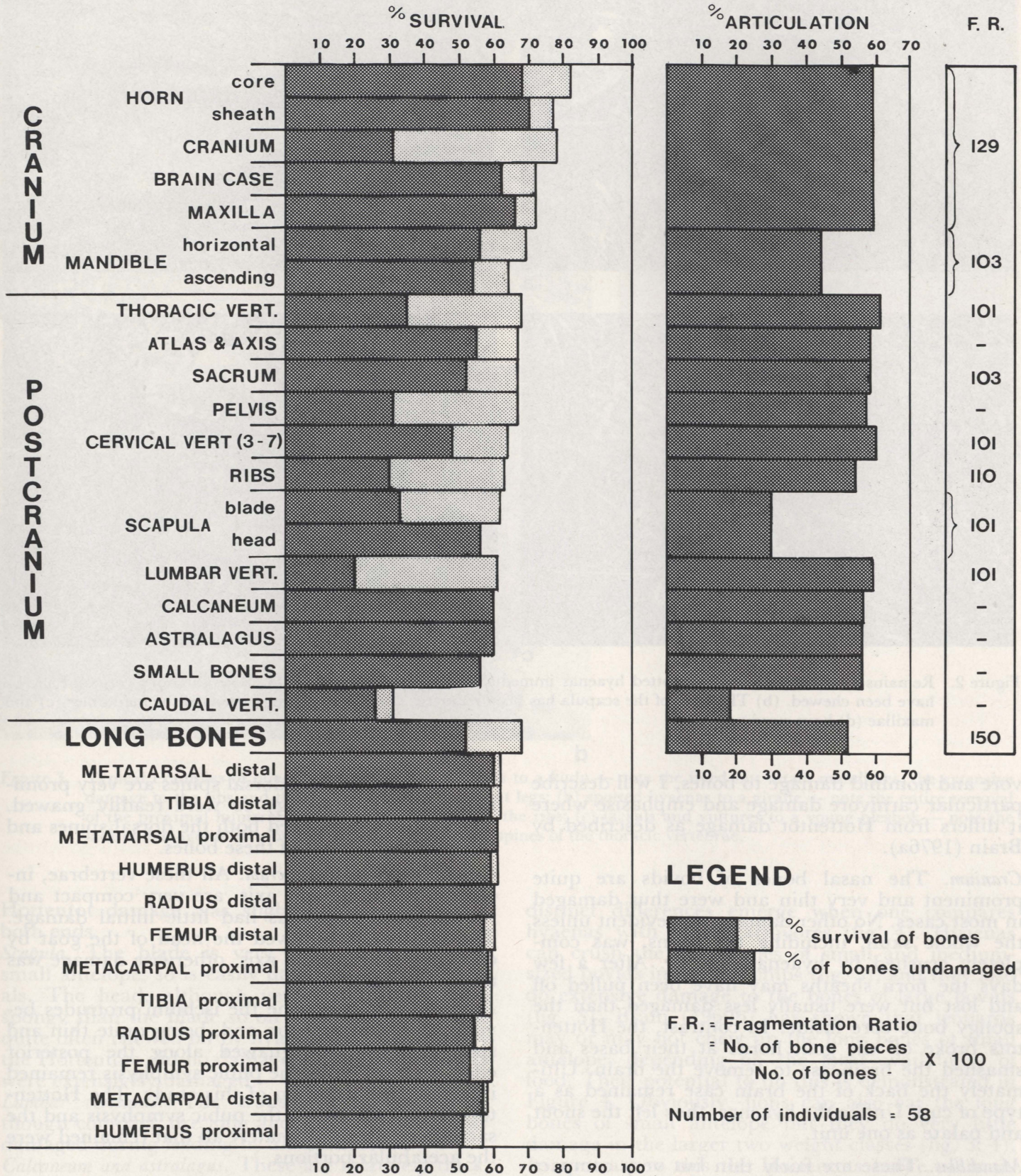


Figure 1. Percentage survival, damage, articulation and fragmentation of parts of bovid skeletons once carnivores have finished feeding.

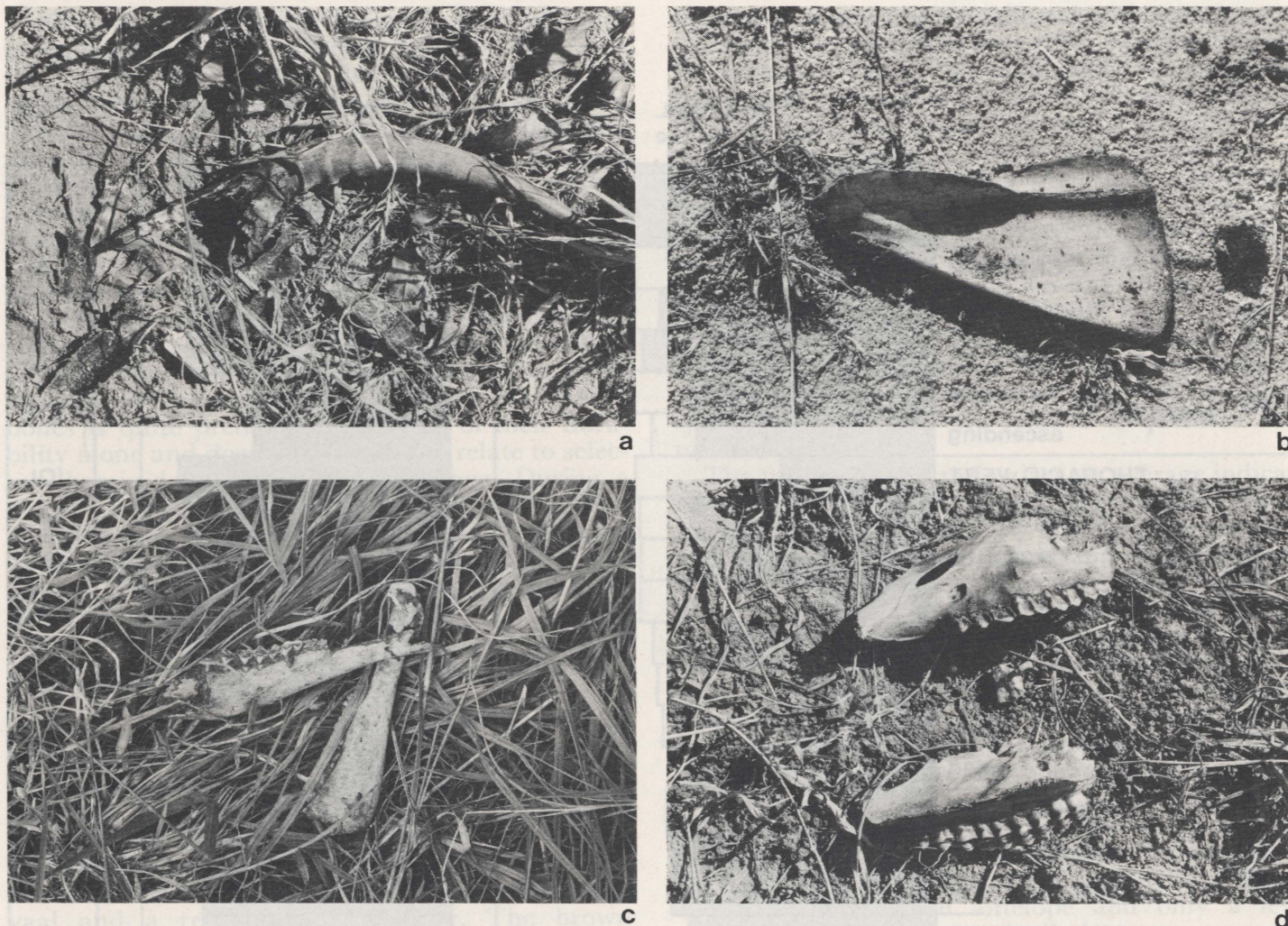


Figure 2. Remains of an impala left by spotted hyenas immediately after their first feed. (a) Both the horn core and sheath have been chewed. (b) The head of the scapula has been removed. Only the densest portions of the mandibles (c) and maxillae (d) have survived.

vore and hominid damage to bones, I will describe particular carnivore damage and emphasise where it differs from Hottentot damage as described by Brain (1976a).

Cranium. The nasal bones of bovids are quite prominent and very thin and were thus damaged in most cases. No other damage was evident unless the whole skull, including the horns, was completely crushed by hyenas (fig. 2). After a few days the horn sheaths may have been pulled off and lost but were usually less damaged than the spongy bone core inside. In contrast, the Hottentots broke off the goat horns at their bases and smashed the braincase to remove the brain. Ultimately the back of the brain case remained as a type of cup. Unlike the hyenas, they left the snout and palate as one unit.

Mandibles. These are fairly thin but very compact bones and so were less damaged than the crania. The ascending ramus is thinner and more protruding than the horizontal ramus and consequently had a lower survival rate (fig. 2). They suffered no damage with the initial feeding of Hottentots.

Thoracic vertebrae. The dorsal spines are very prominent and quite spongy so were readily gnawed. The Hottentots gnawed both the dorsal spines and the lateral processes of these bones.

Cervical vertebrae and sacrum. All these vertebrae, including the atlas and axis, are very compact and robust bones and thus had little initial damage. The Hottentots removed the head of the goat by chopping through the axis, otherwise damage was also very slight.

Innominate. In this bone the ischium protrudes beyond the clean skeleton and, being quite thin and spongy, was often gnawed along the posterior edge. In most cases the pubic symphysis remained intact for the duration of this study. The Hottentots chopped through the pubic symphysis and the sacroiliac joints. Ultimately all that remained were the acetabular portions.

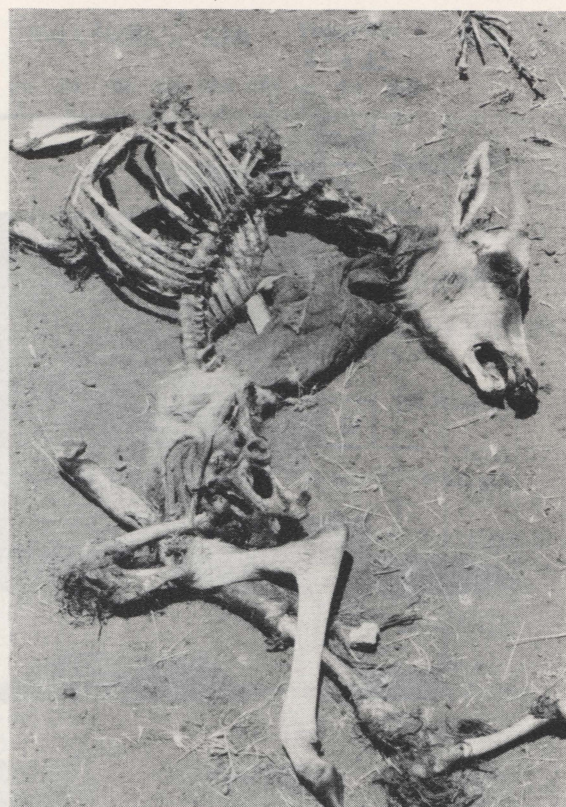
Ribs. These are thin, flat bones which are spongy in the centre, so the distal ends are easily damaged while carnivores feed on the thoracic contents. They may also be eaten by the larger carnivores and are then extensively damaged (fig. 3). Initial



a



b



c

Figure 3. Typical examples of bone damage done by: (a) lions to a kudu — note the freed but intact mandibles, the extensive damage to the ribs and the disappearance of the front legs; (b) spotted hyaenas to a giraffe — note the entire removal of the proximal humerus and the severe damage to the ribs; (c) jackals and vultures to a young blesbok — note the lack of damage to the ribs and the prominent dorsal spines of the thoracic vertebrae.

Hottentot damage was slight but later included both ends.

Scapula. The blade is very thin, particularly in small antelope, so is easily damaged even by jackals. The head, although very compact, is more spongy than the blade so on smaller antelope was quite often chewed off by hyaenas (fig. 2). Initially the Hottentots did no damage, but later the blades were extensively damaged.

Lumbar vertebrae. The transverse processes, although compact, are long and very thin and easily damaged during feeding by all carnivores.

Calcaneum and astragalus. These are relatively thick, compact bones which were either eaten completely or left undamaged. The same applied to the other small bones, so I did not record their damage.

Long bones. These bones were only very slightly damaged by the carnivores as a whole. However,

distinct differences emerge when one compares hyaenas with other carnivores (fig. 4). Hyaenas can crush the long bones of small and medium-sized bovids into small chips (fig. 5), and they also do extensive damage to the bones of large bovids (fig. 3). Brain (1969b) has shown that leopards may or may not chew up the long bones of small antelope, depending on the local availability of food. Their potential to do this is demonstrated in Figure 4. Obviously, lions can also eat the long bones of small antelope but they do very little damage in the larger two weight classes (fig. 3, 4). In contrast to this the Hottentots broke all marrow-containing bones, using two rocks as hammer and anvil. They then chewed the softer epiphyses. Thus the Hottentots broke all the long bones but left most of the epiphyses with varying degrees of damage.

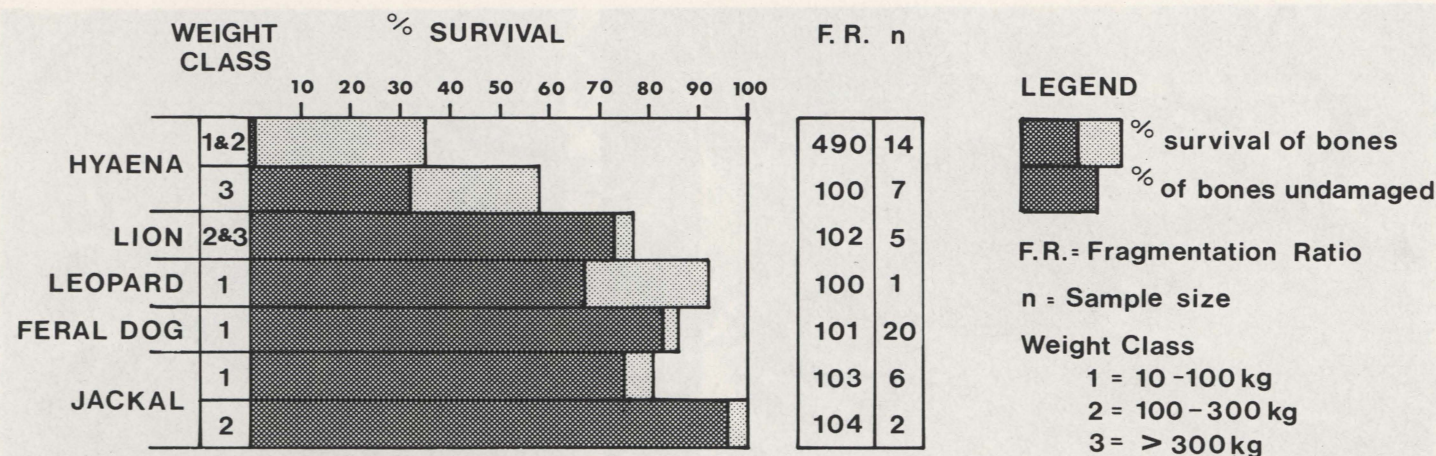


Figure 4. Total percentage survival, damage and fragmentation of bovid long bones when fed on by various carnivores.

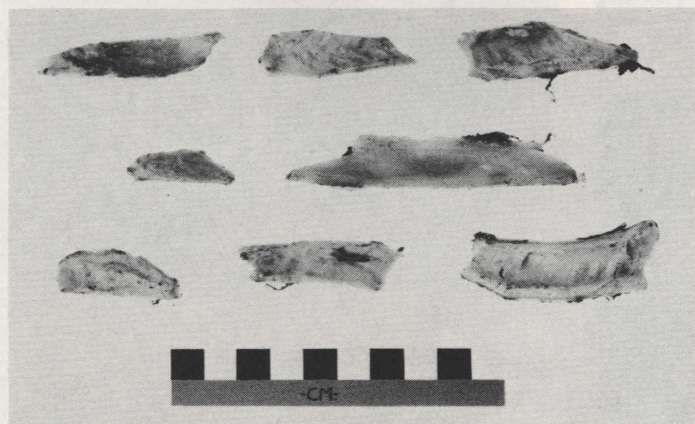


Figure 5. Some of the long bone chips that remained after a brown hyaena had eaten a blesbok.

Articulation

The most obvious and disproportionate disarticulation of bones occurs with mandibles, scapulae and caudal vertebrae (fig. 1). In the latter case this is because they have been eaten. However, in the other two cases this phenomenon obviously relates to their mode of attachment to the rest of the skeleton. The mandibles are only attached to the cranium by means of muscles, so that as soon as the meat and skin of the face have been eaten, they are found loose although they are firmly attached to each other and may remain so for years. Similarly,

the scapulae are only joined by muscle to the axial skeleton and have rather flat articulation surfaces with the proximal humeri. Thus they too are often completely disarticulated once the meat of the shoulder has been removed. Contrary to the hypothesis of Shipman and Phillips (1976) that disarticulated bones are the ones likely to disappear first, mandibles and scapulae had very good survival rates at the kill sites. This reflects their low potential as food sources, both being hard compact bones. The pelvic girdle was very resistant to separation and often remained intact for many months. However, the hind limbs soon became separated as complete units. The first separation in the spinal column usually came between the thoracic and lumbar vertebrae. Although some ribs were always freed, the greater percentage of them remained attached for a surprisingly long time (fig. 3). Subsequent disarticulation of the skeleton was fairly random with small groups of vertebrae, the mandibles and the innominates being the last to separate.

The Hottentots displayed some distinct differences in the dismembering of their goat:

1. the hind limbs were removed with innominates attached;
2. the feet were separated from the legs at the metapodial/phalangeal joints;
3. the ribs were separated from the thoracic vertebrae, which probably accounts for the greater damage caused to the transverse pro-



Figure 6. Some bone remains of a young blesbok that had been eaten by maggots and then jackals, showing how separation can occur within bones that have not yet fused: (a) cranium; (b) sacrum; (c) distal metapodial.

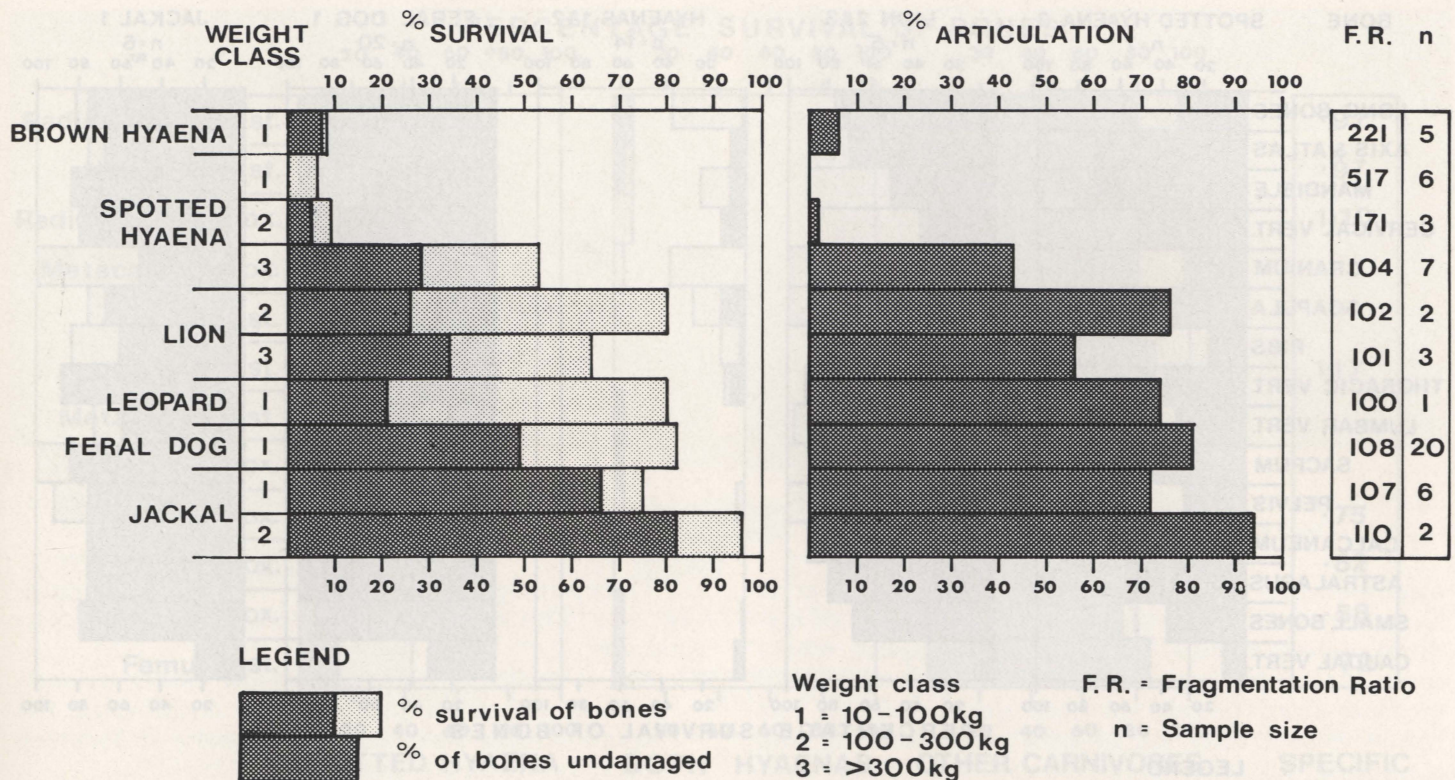


Figure 7. Total percentage survival, damage and fragmentation of bovid bones when fed on by various carnivores.

cesses of thoracic vertebrae by Hottentots than by carnivores.

Fragmentation

Just as a high disarticulation rate does not necessarily reflect a low survival rate, so a high percentage damage does not necessarily mean a high fragmentation ratio. The only bones with appreciable fragmentation ratios were long bones, crania and ribs. When the shafts of long bones were chewed by hyaenas, only numerous small chips were usually found (fig. 5). The cranium separated into maxillae and pieces of brain case. The ribs have a spongy centre and are less likely to chip than long bone shafts and thus were eaten with fewer chips being discarded. Fragmentation of the rest of the bones was almost exclusively caused by hyaenas or resulted from separation within the bone because fusion had not yet occurred in the young animal (fig. 6).

INDIVIDUAL CARNIVORE DAMAGE

One can see a pattern of decreasing damage caused by hyaenas, lions, leopards, dogs and jackals (fig. 7, 3). It is remarkable that hyaenas do more damage to large bovids than lions do to medium-sized ones.

Individual Bones

Spotted and brown hyaenas are grouped together because they caused similar damage to smaller bovids (fig. 8). The results for lion damage to medium and large bovids are put together for similar reasons. The leopard was not included in this analysis because of insufficient data.

There are various discrepancies between hyaena and lion damage in the larger weight classes. However, apart from the long bones these differences probably occurred because of the small sample sizes and varying environmental conditions. The most noticeable feature in both cases is the minor damage caused to the scapulae. This is probably because they are thicker and not subject to incidental damage in larger animals and are only gnawed if the carnivores are really hungry.

In the small weight class it is interesting to note that the mandibles and scapulae still had relatively high survival rates even when hyaenas fed. In this case the survival of long bones is exaggerated because they consisted almost exclusively of bone chips. Although the survival patterns of bones damaged by dogs and jackals were similar, the dogs caused far more damage to all bone types.

Individual Long Bones

If one looks at the individual long bone damage caused by hyaenas and the other carnivores, three distinct patterns emerge (fig. 9):

1. the patterns of damage and survival of all the long bones fed on by the other carnivores were virtually identical, and only the proximal humerus and proximal femur had any noticeable damage;
2. when hyaenas fed on the smaller bovids, there was no predictable pattern of differential survival of bones — almost all the bones were completely chewed up and survival was fortuitous;
3. the predictable pattern of bone survival as described by Brain (1976a) only emerged when hyaenas fed on large bovids.

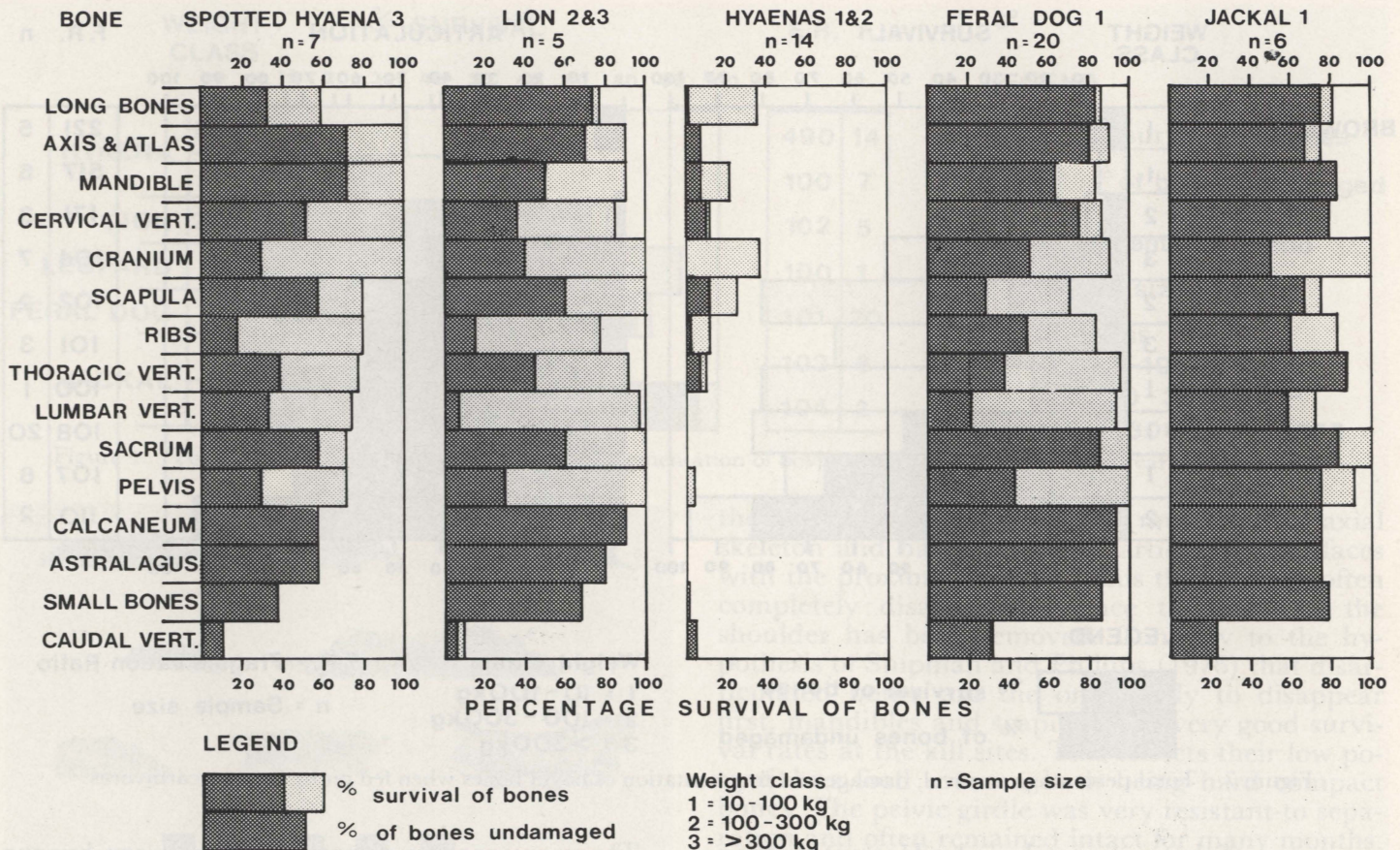


Figure 8. Percentage survival and damage of parts of bovid skeletons when fed on by various carnivores.

If one assumes that the specific gravity of the epiphyses of goat bones (Brain 1976a) applies also to bovids and equids in general, then, with the exception of the distal tibia, the group with the highest specific gravities have the highest survival rates and those with the lowest S.G. the lowest survival rates. Although the proximal radius and ulna have a very high specific gravity, they were often damaged, but the distal ends which have a lower density were not. This is because the olecranon process of the ulna protrudes from the skeleton and thus is easily chewed. Assuming that damaged epiphyses are likely to have lower survival rates than undamaged ones, the undamaged rate was plotted against specific gravity (fig. 10), and the predicted pattern emerges even more clearly ($r = 0.80$). This correlation coefficient is surprisingly high considering that bones were often dragged off in a random manner.

Another factor that can affect the survival and damage of long bones is the age of the bovid concerned because of the different fusion times of the epiphyses to their shafts. In young animals the unfused epiphyses are soft and may disarticulate or be chewed off (Brain 1976a). To confirm this, the four categories of bone damage caused by jackals and vultures to adult and juvenile small antelope are illustrated in Figure 11. In all four categories the bones of the juveniles had greater damage and hence less chance of surviving. Typical examples of separation within the bone are shown (fig. 6).

A final factor which may play a role in the survival of bones is whether fly larvae have fed on the carcass before it is eaten by carnivores. Although I do not have quantitative data, the bones of car-

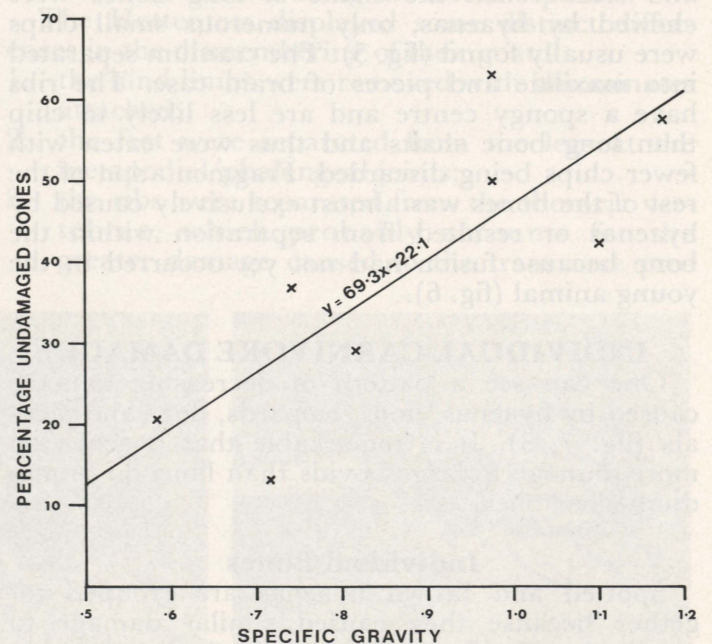


Figure 9. Graphical representation of the relationship between the specific gravity of the epiphyses of large bovid long bones and their rate of damage by spotted hyenas ($r = .798$, $P < 0.05$).

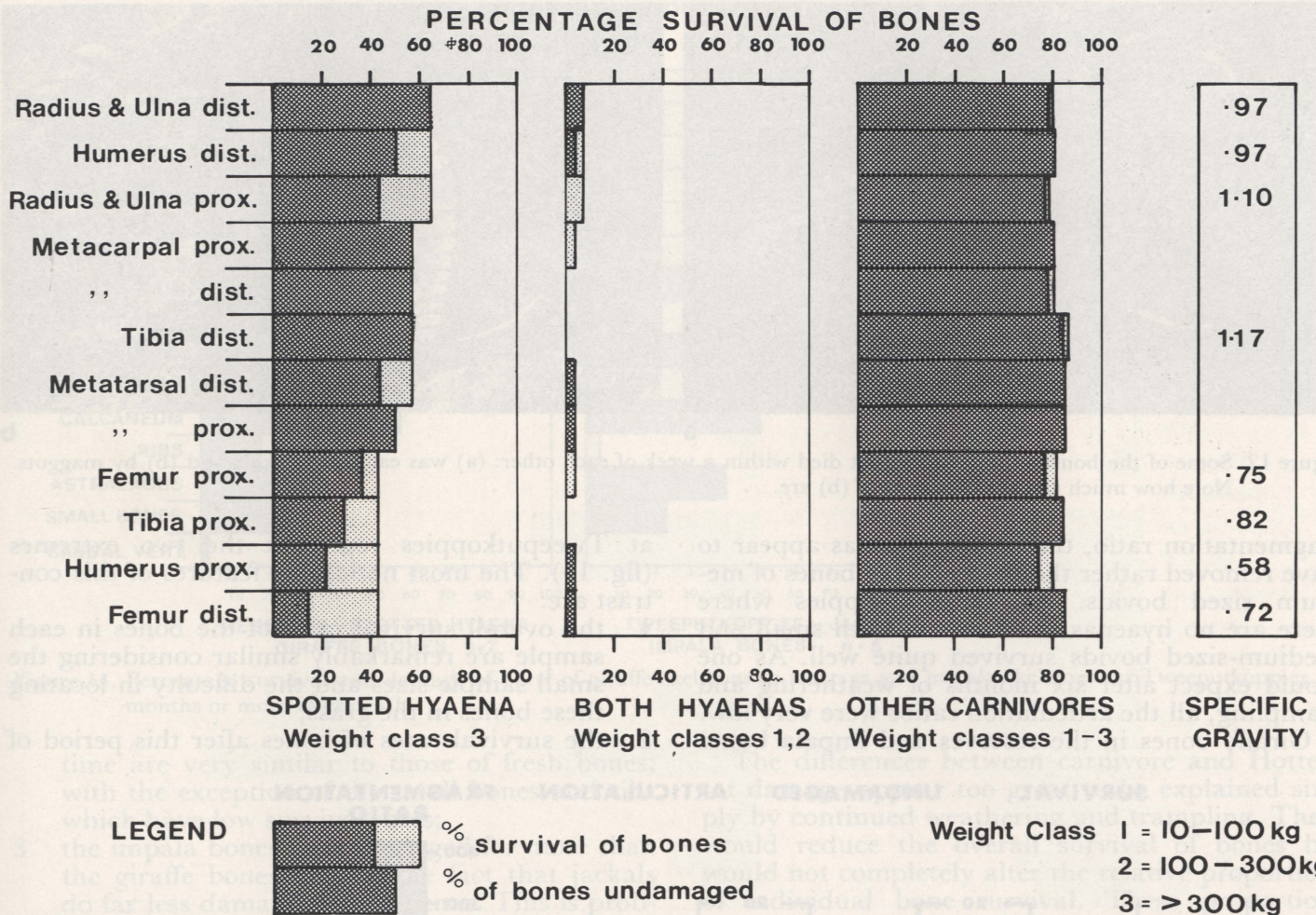


Figure 10. Percentage survival of bovid long bones when fed on by various carnivores.

casses on which maggots had fed disarticulated much more readily and were cleaner than others (fig. 12).

BONE SURVIVAL AFTER SIX MONTHS

To approximate more closely Brain's results relating to goat bones in the desert, the results of the remains of bones that were in the veld for over six months are presented (figs. 13, 14). These bones were those left on the reserves and on two farms

where the bush cover is quite thick, the jackals largely undisturbed and numerous cattle occur which may trample the bones. After six months further bone damage could not be specifically related to particular carnivores but rather to the area and its fauna.

In areas with hyaenas (fig. 13) nearly all the bones of small and medium sized bovids were eaten or removed and only the large bovids were well represented. However, considering the low

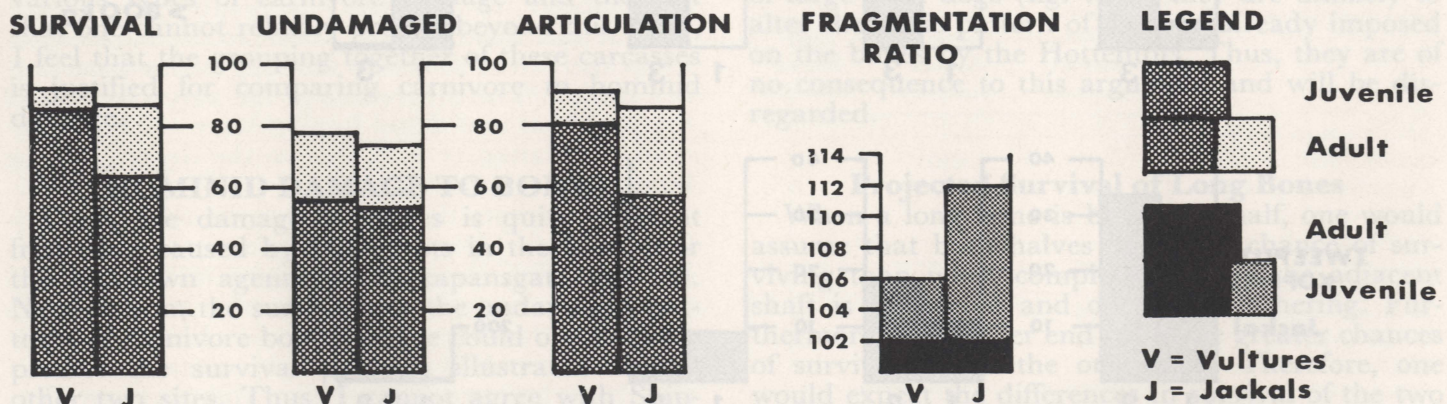
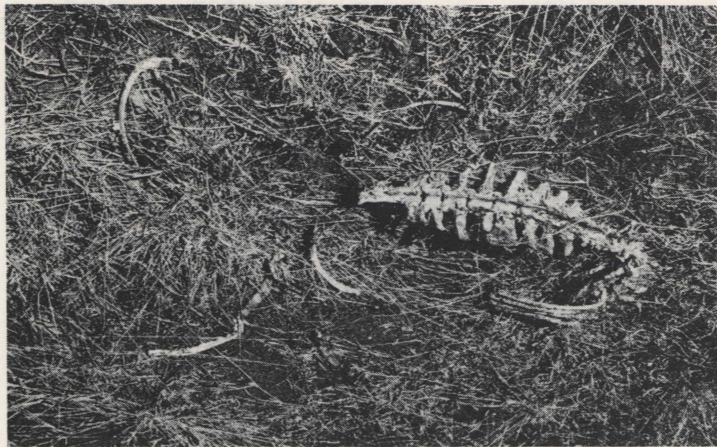


Figure 11. Total percentage survival, damage, articulation and fragmentation of small bovids' bones when fed on by jackals or vultures.



a

b

Figure 12. Some of the bones of two sheep that died within a week of each other: (a) was eaten by jackals and (b) by maggots. Note how much cleaner the bones of (b) are.

fragmentation ratio, the brown hyaenas appear to have removed rather than chewed the bones of medium sized bovids. At Tweeputkoppies where there are no hyaenas the bones of both small and medium-sized bovids survived quite well. As one would expect after six months of weathering and trampling, all the articulation ratios were very low.

Giraffe bones in the reserves and impala bones

at Tweeputkoppies represent the two extremes (fig. 14). The most noticeable features of this contrast are:

1. the overall survival rates of the bones in each sample are remarkably similar considering the small sample sizes and the difficulty in locating these bones in the grass;
2. the survival rates of bones after this period of

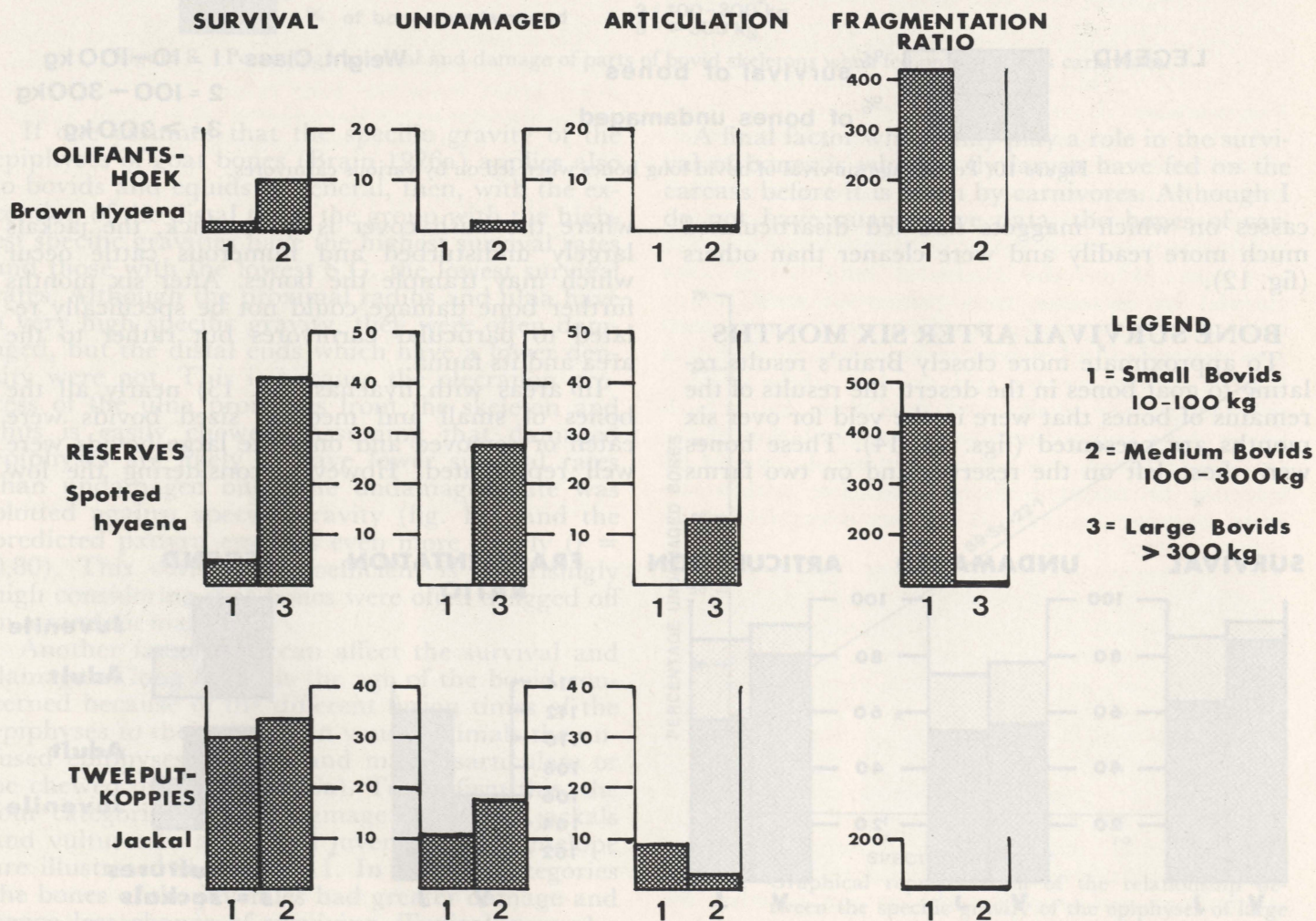


Figure 13. Total percentage survival, damage, articulation and fragmentation of bovid bones six months or more after death in three different areas.

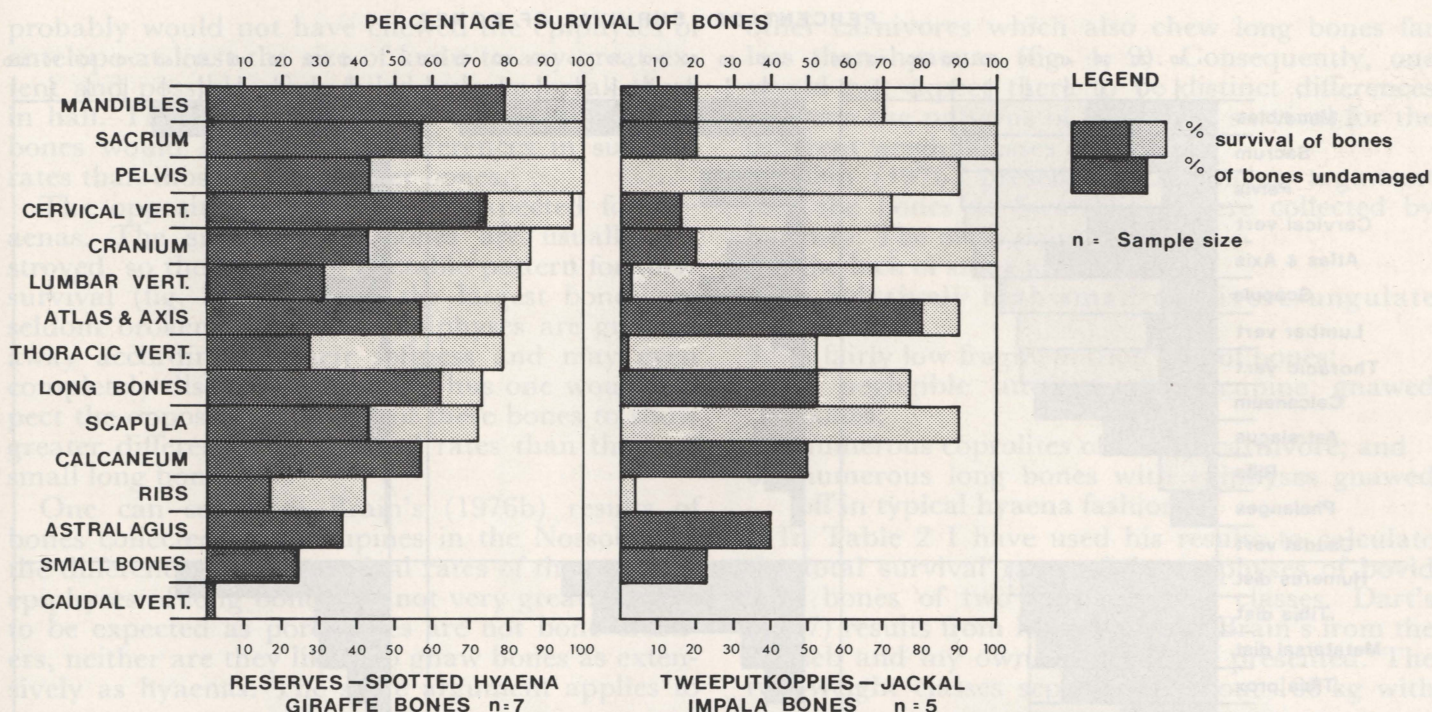


Figure 14. Percentage survival and damage of parts of giraffe skeletons in reserves and impala skeletons on Tweeputkoppies six months or more after death.

time are very similar to those of fresh bones; with the exception of the small bones and ribs which have low survival rates;

3. the impala bones were damaged far more than the giraffe bones despite the fact that jackals do far less damage than hyaenas. This is probably because of the greater susceptibility of impala bones to damage by trampling.

After a certain period of time bones in the veld were no longer disturbed by carnivores, and their survival seemed to remain static. This period was longer for large animals (~12 months) than small ones (~6 months). Once this stage has been reached, only trampling, weathering, burying and removal by porcupines will affect bone survival in natural situations. All of these influences will be difficult to predict. Although I cannot say that all the carcasses had reached this "post-carnivore influence" stage, many of them appeared to have done so. In view of the eventual similarity of the various types of carnivore damage and the fact that one cannot reliably predict beyond this stage, I feel that the grouping together of these carcasses is justified for comparing carnivore to hominid damage.

HOMINID DAMAGE TO BONES

Carnivore damage to bones is quite different from that caused by Hottentots in the Kuiseb or the unknown agents at Makapansgat (fig. 15). Neither from the survival nor the undamaged patterns of carnivore bone damage could one possibly predict the survival patterns illustrated at the other two sites. Thus, I cannot agree with Shipman and Phillips-Conroy (1976) that recent hyaena damage resembles that at Makapansgat.

The differences between carnivore and Hottentot damage appear too great to be explained simply by continued weathering and trampling. These would reduce the overall survival of bones but would not completely alter the relative proportions of individual bone survival. These proportions probably developed not only because of the hardness of the bones but also because of the initial damage inflicted by the Hottentots. The greatest difference in initial damage is to the long bones which the Hottentots always broke in half to extract the marrow while leaving the epiphyses somewhat damaged but intact. This is in complete contrast to what any carnivore does.

Brain (1976a) emphasises the fact that, after the Hottentots have chewed the bones, they are given to their dogs which do further damage. However, in view of the differences between carnivore and Hottentot damage and because these jackal sized dogs are unlikely to do more damage than the pair of large feral dogs (fig. 7, 8), they are unlikely to alter the basic pattern of damage already imposed on the bones by the Hottentots. Thus, they are of no consequence to this argument and will be disregarded.

Projected Survival of Long Bones

When a long bone is broken in half, one would assume that both halves have less chance of surviving than when complete because the adjacent shaft is splintered and open to weathering. Furthermore, the harder end will have greater chances of surviving than the other end. Therefore, one would expect the differences in survival of the two opposite ends of long bones to be far greater when they have been broken in half than when complete.

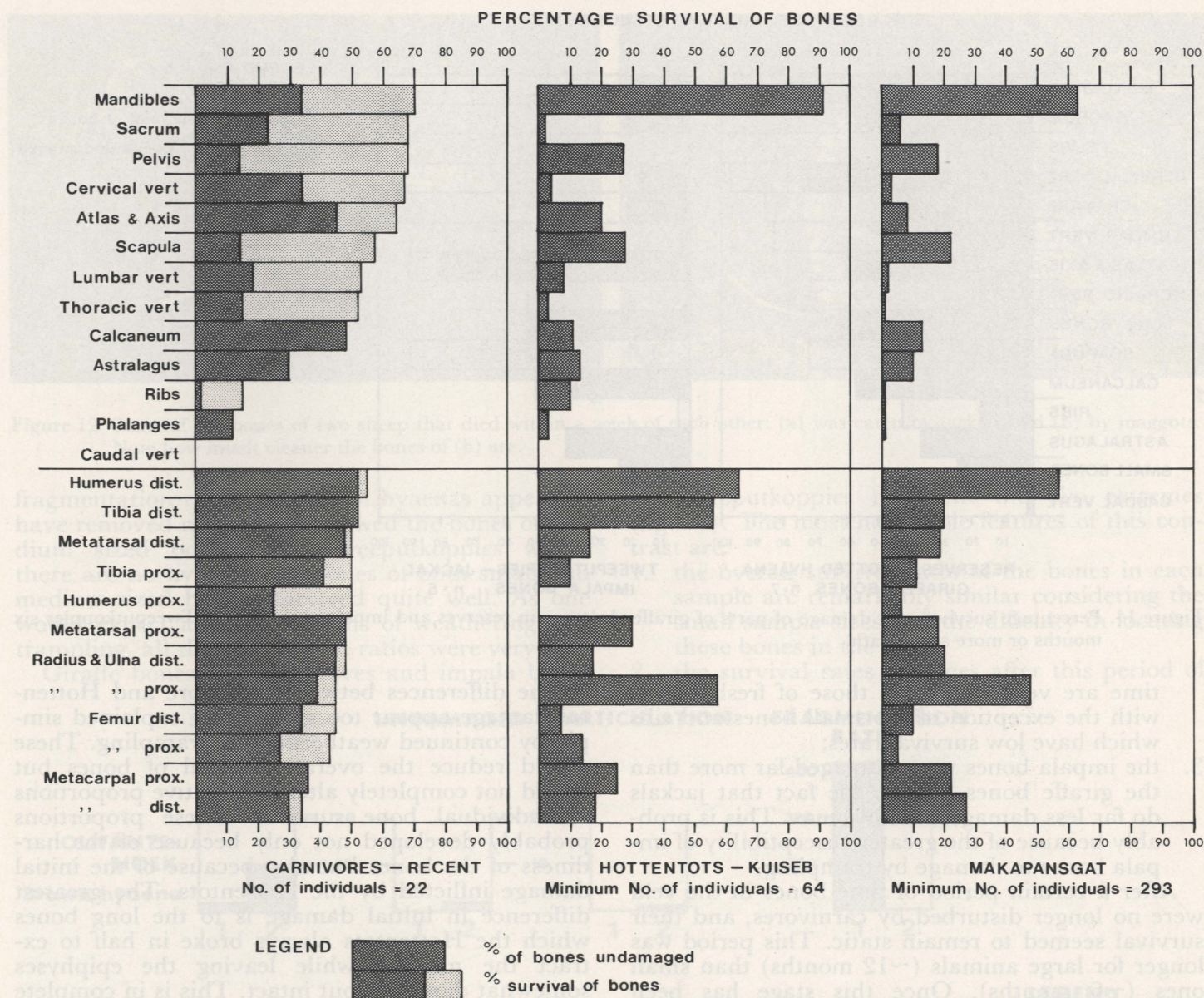


Figure 15. Percentage survival of parts of bovid skeletons at Makapansgat, in Transvaal reserves and farms and of goat skeletons in the Kuiseb.

TABLE 1
Differential survival and damage of long bones at three northern German levels

	<i>Ham- burgian Stellmoor</i>	<i>Ahrens- burgian Stellmoor</i>	<i>Ham- burgian Meiendorf</i>
Minimum number individuals	41	650	71
Complete long bones	73	720	0
Loose epiphyses	58	1 494	233
A: % of epiphyses separated	28	51	100
Proximal humerus	14	163	6
Distal humerus	15	441	32
B: Distal/Proximal humerus	1,07	2,7	5,3
Correlation coefficient of A vs. B: $r = 0,995$; $df = 1$; $p < 0,1$			

This argument is supported by the results obtained from three separate archaeological bone accumulations in Germany presented by Read-Martin and Read (1976). These accumulations differ in the extent to which the long bones were broken in half. The differences in the survival rates of the proximal and distal humeri have a strong positive correlation ($r = 0,955$) to the degree of long bone breakage (table 1).

If one accepts this argument, the relative survival rates of epiphyses of long bones can be predicted. There is a big difference in the survival rates of the opposite epiphyses of goat long bones when they have been broken and chewed by Hottentots (Brain 1976a). Although australopithecines may have had greater chewing abilities than Hottentots, one would still expect them to inflict more damage on small bones than large ones. They

probably would not have chewed the epiphyses of antelope at least the size of kudu to any great extent and possibly often failed even to break them in half. Therefore the opposite epiphyses of these bones would have smaller differences in survival rates than those of the smaller bones.

The opposite pattern can be expected for hyaenas. The smaller long bones are usually destroyed, so there is no predictable pattern for their survival (fig. 9). Although the largest bones are seldom broken in half, the epiphyses are gnawed away according to their softness and may even completely disappear (fig. 3). Thus one would expect the opposite epiphyses of these bones to show greater differences in survival rates than those of small long bones.

One can see from Brain's (1976b) results of bones collected by porcupines in the Nossob that the differences in the survival rates of the opposite epiphyses of long bones are not very great. This is to be expected as porcupines are not bone crushers, neither are they likely to gnaw bones as extensively as hyaenas. The same argument applies to

other carnivores which also chew long bones far less than hyaenas (fig. 4, 9). Consequently, one would not expect there to be distinct differences between the patterns of long bone survival for the different weight classes of bovids.

Klein (1976) presents a convincing argument that the bones at Swartklip I were collected by hyaenas. The main points are:

1. the lack of stone artefacts;
2. a relatively high small-carnivore/ungulate ratio;
3. a fairly low fragmentation rate of bones;
4. a negligible amount of porcupine gnawed bones;
5. numerous coprolites of a large carnivore; and
6. numerous long bones with epiphyses gnawed off in typical hyaena fashion.

In Table 2 I have used his results to calculate the total survival rates of the epiphyses of bovid long bones of two major weight classes. Dart's (1957) results from Makapansgat, Brain's from the Kuiseb and my own are similarly presented. The two weight classes separate at about 100 kg with

TABLE 2
Differential survival rates of long bone epiphyses at Makapansgat, in the Kuiseb, Swartklip I and for recent hyaena damage

	S.G.	HOMINID PATTERN						HYAENA PATTERN												
		Makapansgat			Kuiseb			Swartklip I			Fresh		6 months							
		I No.	% diff	II No.	% diff	χ^2	I No.	% diff	No.	II % diff	χ^2	I No.	II No.	I No.	II No.					
proximal	0,58	7		26		*	33		6			1	6	0	11					
Humerus			95		27	82,7		82		78										
distal	0,97	291		45			336		48		87	0,80	2	9	0	13				
proximal	1,10	103		74			279		38				2	9	0	10				
Radius & Ulna			17		29	0,99		42		17		16								
distal	0,97	73		41			114		28		50	3,69	2	9	0	10				
proximal		109		20			129		38				1	8	0	6				
Metacarpal			13		3	0,84		11		7		14	0,22	0	8	0	6			
distal		142		19			161		44		74		0	8	0	6				
proximal	0,75	11		17			28		12				1	6	0	8				
Femur			35		32	0,02		33		48		43	0,05	1	6	0	9			
distal	0,72	23		33			56		34		20		1	6	0	9				
proximal	0,82	26		38		*	64		28				0	6	0	9				
Tibia			55		12	20,8		30		30		63	† 5,45	0	8	0	11			
distal	1,17	89		30			119		52		62		0	8	0	11				
proximal		89		18			107		58				1	7	0	8				
Metatarsal			4		16	1,11		1		5		6	0,54	1	8	0	9			
distal		97		13			110		52		36		1	8	0	9				
Sum of differences Total No. of bones Total No. of bones Minimum No. individuals		41		22			38		25		33		17		7		0		5	
		4,2		9,6			5,2		4,5		11,5		3		11,3		0		12,2	
Minimum No. individuals		254		39			293		98		39		4		8		1		9	
Actual No. individuals													11		10		5		9	

Weight classes: I = < 100 kg, II = > 100 kg, No. = number, S.G. = specific gravity, Difference = $|x_{\text{proximal}} - x_{\text{distal}}|$,
 $\% \text{ diff.} = \frac{|x_{\text{proximal}} - x_{\text{distal}}|}{x_{\text{proximal}} + x_{\text{distal}}} \times 100$, Statistical significance indicated as follows: * $P < 0,001$ † $P < 0,05$,

wildebeest and kudu being the smallest species in the larger class. I have chosen these two weight classes because in all the samples the survival rates of long bones in the upper class were more than double those in the lower class. I also found that both spotted and brown hyaenas fragmented bones far more in the lower class (fig. 4, 13). Unfortunately Klein has not given the actual numbers of bones but the minimum numbers of individuals represented by each bone type. For this table and subsequent graphs I have simply doubled the figures where appropriate to account for left and right sides. Although this will over-represent some bones, this will probably not seriously affect my interpretations, since I am primarily concerned with relative proportions.

The pattern of long bone survival at Swartklip I is that expected for hyaenas. The opposite epiphyses of the large weight class long bones generally have greater differences in survival rates than those of the small weight class. Tested individually these differences are only statistically significant in the case of the tibia. This is to be expected because it has the biggest difference in specific gravity between opposite ends and thus is most likely to indicate selective chewing of the softer end. The pattern of survival of the radius and ulna corresponds to my own results for hyaenas (fig. 9) with the slightly harder but very prominent proximal end having the lower survival rate. Conversely, the pattern at Makapansgat is that expected for hominids. Here the differences in survival rates tend to be greater in the lower weight class and are significantly different in both the tibia and humerus. It was not possible to test the Kuiseb sample and my own data, but they are also indicative of hominid and hyaena damage respectively.

Cranial and postcranial representation

Further differences between the bone assemblages at Makapansgat and Swartklip I can be seen in the minimum numbers of different sized bovids represented by cranial and postcranial material. Klein (1975) did not compare these two sets of data on a one-to-one basis because of the irregular size categories used by Dart (1957). However, apart from *Redunca arundinum* (reedbuck) which Dart classified as small and not medium, Klein's data can fit into the size classes used by Dart. In Table 3 I have circumvented this problem by first classifying reedbuck as medium and then as small. In both cases the pattern for medium sized bovids at Swartklip I is the opposite of that at Makapansgat.

If one takes only the chewing abilities of the various agents into consideration, then one would expect the harder cranial material to survive better than the postcranial material. This difference should be particularly evident in the smaller weight classes and should disappear in the large class where the postcranial bones are big enough not to be destroyed. The change-over between these two extremes will depend on the chewing

TABLE 3
Minimum numbers of different sized bovids represented by cranial and postcranial material at Makapansgat, Swartklip I and for recent carnivore data

		Very Small	Small	Medium	Large
Makapansgat	Cranial	28	100	62	30
	Postcranial	—	27	126	39
Swartklip I	Cranial	—	29(67)	69(31)	29
	Postcranial	—	14(24)	30(20)	39
Hyaenas	Cranial			4	8
— fresh	Postcranial			2 11*	9 10*
Hyaenas	Cranial			1	9
— 6 months	Postcranial			— 5*	9 9*
Carnivores	Cranial			6	12
— 6 months	Postcranial			5 10*	12 12*

Typical animals of each class are:

Very small — *Cephalophus*, duiker; Small — *Raphicerus*, grysbok; Medium — *Damaliscus*, blesbok; Large — *Tragelaphus*, kudu. If *Redunca arundinum* (reed buck) is classed as small as in Dart (1957), then the minimum numbers of individuals represented at Swartklip I change to those in parentheses. The actual numbers of individuals for the recent carnivore data are indicated with asterisks (*).

abilities of the agent concerned. For hyaenas (Swartklip I and my own data) this change-over only occurred in the large weight class. At Makapansgat it occurred in the medium class. This suggests that the agents concerned could not chew medium sized postcranial bones as successfully as hyaenas. However, one must also consider that cranial and postcranial bones may not have been collected at the same rates. The representation of material at Swartklip I suggests that it was collected at much the same rate, but postcranial material was then selectively chewed. At Makapansgat the extremely high representation of individuals in the medium sized class by postcranial material suggests that these bones were selectively collected but not extensively chewed. Here again these factors suggest hominids were responsible.

Other bones

Further evidence supporting the hypothesis that hominids were the primary bone accumulators at Makapansgat can be seen in Figure 16 which compares the survival rates of bones at Makapansgat, Stellmoor, Meiendorf, Swartklip I and my results for recent carnivore damage. With the exception of vertebrae and mandibles the results from Stellmoor closely approximate those at Makapansgat. The differences that exist are magnified at Meiendorf and are even further magnified in the Transvaal carnivore data. My explanation for this pattern is that at Makapansgat the australopithecines did extensive and selective damage to bones, particularly long bones. At Stellmoor and Meiendorf hominids did less selective damage as shown by their decreasing long bone breaking habits (table 1). Typical carnivore damage is at the end of the scale where the damage is not selective but depen-

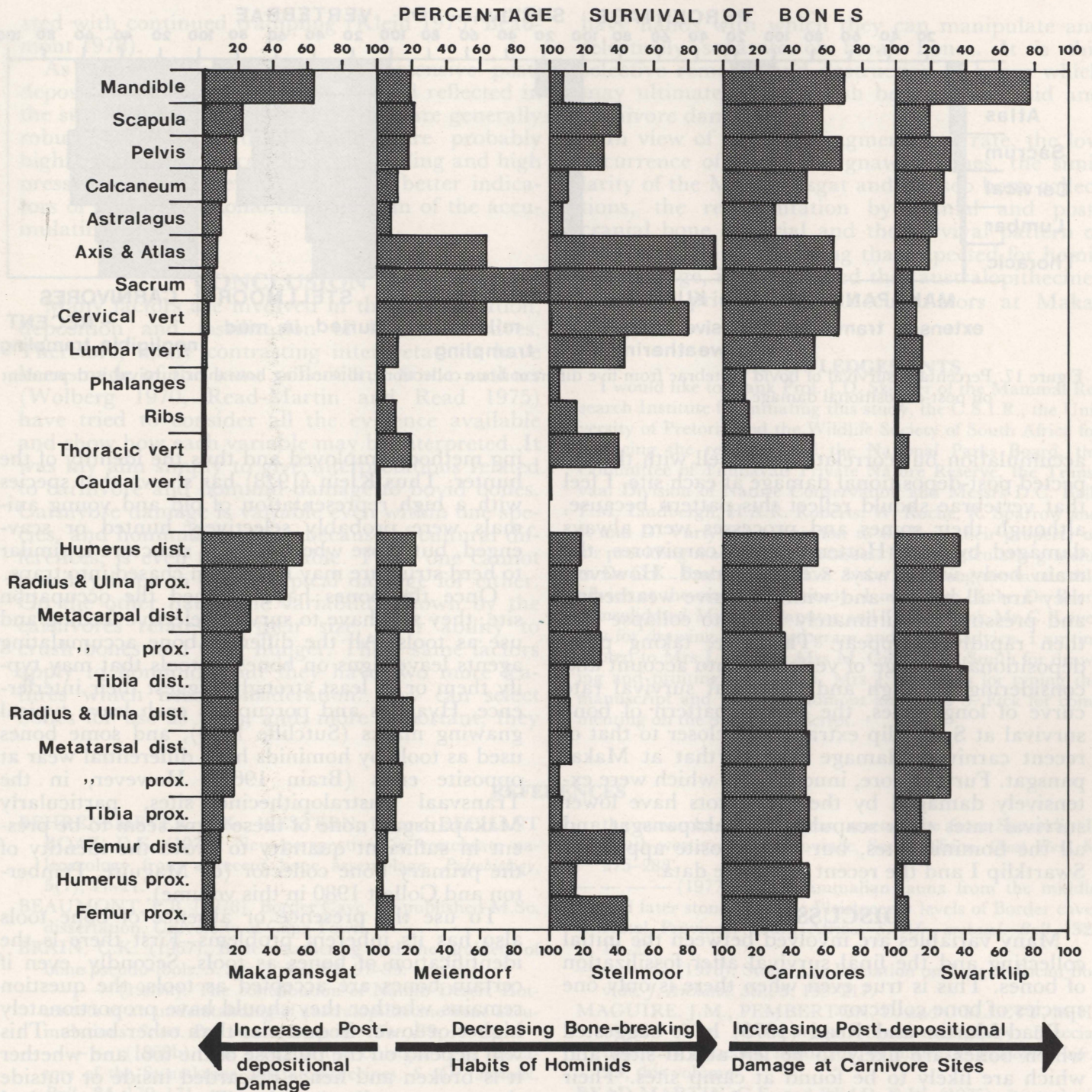


Figure 16. Percentage survival of parts of bovid skeletons from five different bone collections, illustrating how survival depends on both the bone-breaking habits of hominids and on post-depositional damage.

dent on the size, hardness and friability of the bones.

The results from Swartklip I appear at first to refute this argument because the pattern of bone survival appears to differ more from the recent carnivore pattern than from the Makapansgat pattern. However, I believe this difference can largely be accounted for by post-depositional damage. Although the bones at Swartklip were not very highly fragmented (Klein 1975), they probably experienced far higher post-depositional damage than those in my study or those at the two German

sites where they were buried in mud (Read-Martin and Read 1975). The disproportionately high survival rate of mandibles and the fact that the site must have been occupied for a long time to have accumulated that number of bones support this argument. By the same reasoning post-depositional damage must have been even greater in the Kuiseb, where trampling and weathering were severe (Brain 1976a) and at Makapansgat, where fragmentation was high (Dart 1958).

The patterns of survival of vertebrae at these sites (fig. 17) have nothing to do with the agents of

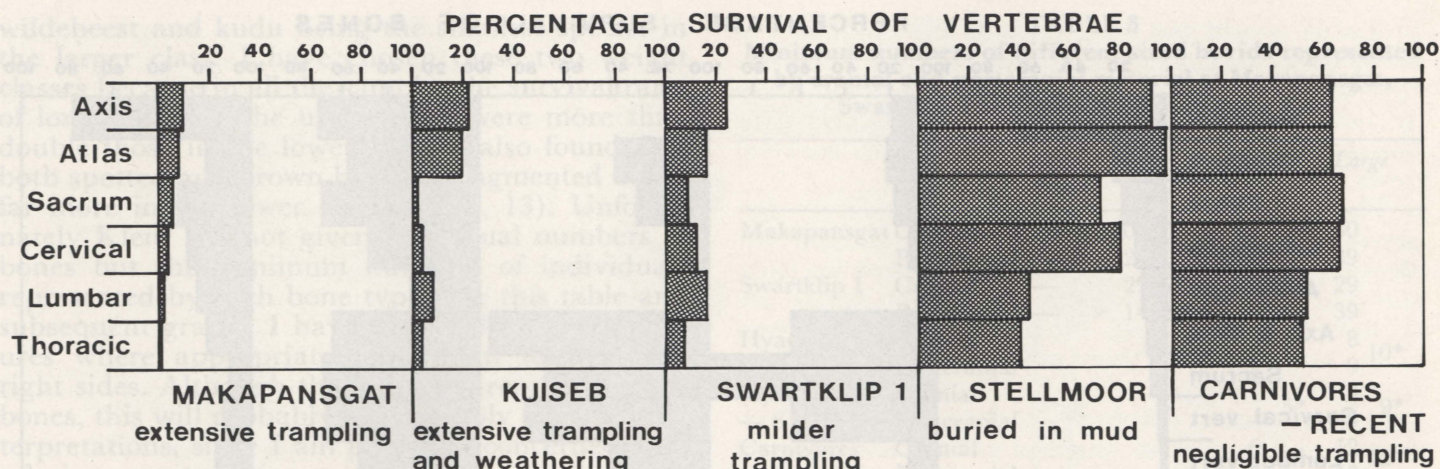


Figure 17. Percentage survival of bovid vertebrae from five different bone collections, illustrating how their survival is dependent on post-depositional damage.

accumulation but correlate quite well with the expected post-depositional damage at each site. I feel that vertebrae should reflect this pattern because, although their spines and processes were always damaged by both Hottentots and carnivores, the main body was always well preserved. However, they are all hollow and with extensive weathering and pressure are ultimately likely to collapse and then rapidly disappear. Therefore, taking post-depositional damage of vertebrae into account and considering the high and fairly flat survival rate curve of long bones, the overall pattern of bone survival at Swartklip extrapolates closer to that of recent carnivore damage than to that at Makapansgat. Furthermore, innominates which were extensively damaged by the Hottentots have lower survival rates than scapulae at Makapansgat and all the hominid sites, but the opposite applies to Swartklip I and the recent carnivore data.

DISCUSSION

Many variables are involved between the initial collecting and the final survival after fossilization of bones. This is true even when there is only one species of bone collector.

Read-Martin and Read (1975) have suggested which bones are likely to be left at kill sites and which are likely to be found at camp sites. Their reasoning is based on the size of the animal, the distance between the camp and the kill site and the usefulness of the bones with or without meat as food or tools. However, when one considers the basic similarity of the bone accumulations at Makapansgat, hyaenas or hominids at a camp site in the Kuiseb, hominids at kill site at Swartklip, hyaenas at camp site and my own data, carnivores at kill site, it will be very difficult to separate the agents of accumulations on these terms. The only generalization that might safely be made is that camp sites, if they are not also kill sites, will have a smaller representation of some or all the bones of large bovids. But this again applies to both hyaenas and hominids. The age structure of the bovids collected can also give indications of the hunt-

ing methods employed and thus the identity of the hunter. Thus Klein (1978) has shown that species with a high representation of old and young animals were probably selectively hunted or scavenged, but those where the age structure is similar to herd structure may have been chased into traps.

Once the bones have reached the occupation site, they still have to survive selective feeding and use as tools. All the different bone accumulating agents leave signs on bones or tools that may typify them or at least strongly suggest their interference. Hyaenas and porcupines each leave typical gnawing marks (Sutcliffe 1970), and some bones used as tools by hominids have differential wear at opposite ends (Brain 1967). However, in the Transvaal australopithecine sites, particularly Makapansgat, none of these signs seem to be present in sufficient quantity to prove the identity of the primary bone collector (cf. Maguire, Pemberton and Collett 1980 in this volume).

To use the presence or absence of bone tools also has its inherent problems. First there is the identification of bones as tools. Secondly, even if certain bones are accepted as tools, the question remains whether they should have proportionately higher or lower frequencies than other bones. This will depend on the purpose of the tool and whether it is broken and hence discarded inside or outside the cave or collecting site. The very low survival rates of mandibles at Stellmoor and Meiendorf suggest that they were used as tools and discarded elsewhere. Kitching (1963) lists numerous ways in which they can be used as tools.

After bones have been collected, chewed and used as tools, they may still have to survive many pressures before they are finally preserved. In this respect smaller animals have lower survival rates than expected from their abundance in the living community (Behrensmeyer, Western and Boaz 1979). Bone fragmentation can to a certain extent be related to initial damage by hominids because of their bone breaking habits with stones (Brain 1970). But really extensive fragmentation seems to result more from slow sedimentation rates associ-

ated with continued trampling (Klein 1975, Beaumont 1978).

As suggested above (fig. 17), extensive post-depositional damage may also be well reflected in the survival rates of vertebrae. These are generally robust bones, but being hollow are probably highly susceptible to continued trampling and high pressures. Thus, they are probably better indicators of post-depositional damage than of the accumulating agents.

CONCLUSION

Many factors are involved in the accumulation, deposition and fossilization of bones in caves. Therefore, many contrasting interpretations have been made of the same collections. Some authors (Wolberg 1970, Read-Martin and Read 1975) have tried to consider all the evidence available and show how each variable may be interpreted. It was my aim simply to give interpretations related to carnivore and hominid damage to bovid bones. Carnivore damage is variable even within one species, and hominid damage, because of cultural differences, is even more variable. Thus, one cannot possibly hope to define typical damage for either. On the other hand, the variability shown by the carnivores relates to their size, their ability to crush bones and their hunger. These same factors apply to hominids, but they have two more features which need consideration: they can select bones for use as tools; and, more important, they

have hands with which they can manipulate and selectively separate or break bones. It is this selective removal and destruction of bones which may ultimately distinguish between hominid and carnivore damage.

In view of the high fragmentation rate, the low occurrence of porcupine gnawed bones, the similarity of the Makapansgat and Kuseb bone collections, the representation by cranial and post-cranial bone material and the survival pattern of long bone epiphyses being that expected for hominid damage, it is suggested that australopithecines were the primary bone accumulators at Makapansgat.

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