

THE NATURAL REMOVAL OF UNGULATE CARCASSES,
AND THE ADAPTIVE FEATURES OF THE SCAVENGERS INVOLVED

by

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ABSTRACT

The natural removal of ungulate carcasses was monitored on a variety of livestock farms and nature reserves in the Transvaal and southern Zimbabwe. 89 carcasses of different sized ungulates were placed or found on these sites, and 30 of these were observed from hides. The rate of decomposition of the carcasses was recorded as well as the behaviour of the scavengers involved.

Carcass removal proceeds much faster on nature reserves because they have a greater variety of scavengers than the farms. Griffon vultures and spotted hyaenas are the primary scavengers on the reserves. The vultures remove most of the soft tissues, while hyaenas remove most of the skin and bone. On the farms griffon vultures are still the most efficient scavengers, but because they are shy, jackals and maggots are able to compete more successfully than in the nature reserves.

The scavenging success of vultures is analysed in terms of their feeding behaviour, and social organization. The griffon vultures and the hooded vulture are considered to be successful scavengers, while lappet-faced and white-headed vultures are suggested as having alternative sources of food other than large ungulate carcasses.

Spotted and brown hyaenas are the only carnivores that regularly and efficiently crush bones. Bone damage by hyaenas and hominids are compared with each other and found to be distinctly different. These differences relate primarily to the survival of long bone epiphyses, and are suggested to persist in fossilized bones. Therefore the agents of accumulation of fossilized bones found in caves should be identifiable from the survival pattern of the long bones.

The roles hyaenas and griffon vultures perform in the nutrient cycle and in the spreading of disease are briefly discussed. The evolution of the major scavengers are considered in terms of their physical adaptations, social organization and foraging strategies.

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CHAPTER 1 : INTRODUCTION

Carcasses - biological components of the ecosystem

A great number of studies have been carried out in Africa on the biology of large herbivores and carnivores (Estes 1976, Kruuk 1972, Schaller 1972, Sinclair 1977). The population dynamics of many of these species have been worked out, but there is still very little quantified data on the exact causes of mortality of the large herbivores (Schaller 1972). Many stock farmers know the extent and causes of mortality to their livestock because they keep a close tally of their numbers and welfare. However when dealing with thousands or millions of head of game, this is not possible, so the information is lost. Thus while there are considerable data available on the important living components of African ecosystems, little is known about mortality factors, and even less about the decomposition of these animals when they die (Coe 1978).

A number of predator-prey studies have been conducted to evaluate the impact of predators on their prey. The conclusions vary, depending on the predator, the prey and local environmental conditions, from the predator having a direct and limiting effect on the prey population, to it being a very minor mortality factor and having little or no effect on the prey species' biology (Hirst 1969, Kruuk 1972, Schaller 1972, Smuts 1978). Houston (1974a) was the first person to try and establish an accurate figure of the number of carcasses that lie in the veld that are not the direct result of predation. Using other scientists figures for the annual mortality of the large herbivores and annual consumption of the carnivores in the Serengeti, Houston concluded that 75% of herbivores that die annually are not eaten by the carnivores. Assuming that a similar situation prevails in southern Africa, it was the primary aim of the present study to determine what happens to this large supply of carcasses that have not died as a result of predation.

Pathways of decomposition

The possibility that over 50% of large herbivores are not consumed by carnivores when they die, opens a new approach to the ecology of these animals. Thus in terms of nutrient cycling, other avenues of carcass decomposition must be utilized.

The potential avenues of decomposition are:

- vertebrate scavengers - carnivores
- vultures
- arthropod scavengers - maggots (blowflies)
- beetles and others
- microbial scavengers
- weathering

In the Transvaal nature reserves and farms the ecological situations are very different from each other and from the Serengeti. Nevertheless, although one does not know the exact proportion of herbivores that die non-violent deaths in these areas, these carcasses do occur and it is pertinent to determine how they are decomposed in the different areas.

To date, few studies have been carried out on the decomposition of carcasses, and the majority of these have concentrated on the arthropod decomposers (Fuller 1934, Bornemissza 1957, Reed 1958, Collins 1970). Interest was focussed on the arthropods because of their importance in two different fields. The first was forensic medicine (Méglin 1894 in Ulllyett 1950). During the last century, entomologists realised that they could potentially age a carcass by studying the faunal composition of the arthropods that inhabit the carcass. Therefore this information could be very useful in solving certain murder cases (Nuorteva 1977). The second field was agriculture, particularly sheep farming. Blowflies are responsible for causing myiasis (strike) in sheep (Zumpt 1965) and can thereby cause millions of Rands worth of damage. As early as the 1920's extensive research was being conducted on the biology of blowflies in an effort to control them (Smit and Du Plessis 1926).

Coe (1978) was the first person to look at the whole spectrum of scavengers (vertebrate and invertebrate) as they utilize carcasses. This was however a special case, as he was examining a mass mortality of elephants, where so much flesh was available that vultures and hyaenas could not cope. Most other studies of the vertebrate scavengers have been concerned more with the scavengers themselves (as a scavenger or a predator) rather than with the carcasses they consumed (Kruuk 1967, 1972, Schaller 1972, Houston 1973). Houston (1974a) calculated the number and availability of carcasses in the Serengeti, however,

he was still primarily concerned with the potential food source for griffon vultures rather than the fate of the carcasses.

The roles played by micro-organisms and weathering in the decomposition of carcasses are very difficult to determine as they are usually in competition with the vertebrate and arthropod scavengers, and are therefore overshadowed by them. Nevertheless, Coe (1978) has published some data on these aspects of decomposition.

Scavenger behaviour

Kruuk (1972) and Schaller (1972) have studied the predator-prey relations of spotted hyaenas (Crocuta crocuta) and lions (Panthera leo) respectively in great detail. From these studies they have data on the prey composition and the proportion of scavenged material in the diets of these carnivores. However, despite this, they have not considered the behavioural adaptations that may increase the success of these species at scavenging, rather regarding scavenged food as being incidentally acquired and not actively sought for in terms of foraging strategy. Similarly most other studies of African carnivores have considered the adaptations of the species as predators, as opposed to their adaptations as scavengers (Kruuk and Turner 1967, Caraco and Wolf 1975, Lamprecht 1978a).

Vultures are some of the few species that have been studied in terms of their adaptations to a scavenging way of life. Kruuk (1967) and Houston (1975) have looked at the feeding behaviour of vultures at carcasses, while Pennycuick (1972) has considered how the flying abilities of these species enable them to cover large areas of land and hence find sufficient carcasses. Nevertheless, none of these authors has adequately considered the availability of carcasses to all the species of vultures as determined by their foraging and feeding behaviour and social organization. These aspects are considered for all the vertebrate species recorded to scavenge carcasses during the present study.

Skeletal remains

The skeletal remains of vertebrate carcasses can provide important clues when

determining past environmental conditions or the biology of particular species. At present there are two taphonomic problems which relate directly to carnivore damage to antelope bones. The first concerns the interpretation of fossil bone remains that have accumulated in caves. By knowing what damage carnivores do to bones in the living community, one can extrapolate for the fossil community and hence suggest which carnivores may or may not have accumulated the bones.

The most controversial problem in this field concerns the fossil bones at Makapansgat. Dart (1957) suggested that these bones were the remains of animals hunted by the australopithecines whose remains have also been found in this cave. However, Dart's interpretation has been questioned (Brain 1969_a, Klein 1975) and it has been suggested that the australopithecines were not the hunters, but rather the hunted, their bones being accumulated by hyaenas or some other agent.

The second problem also relates to carnivore damage to bones, but is concerned with recent bones that lie in the veld. Griffon vulture chicks do not get sufficient calcium for the rapid growth of their bones from the meat provided by their parents (Houston 1973). Their parents therefore supply them with bone fragments that they have picked up at carcasses (Mundy and Ledger 1976).

At present, the Cape vulture (Gyps coprotheres) has a declining population (Siegfried, Frost, Cooper and Kemp 1976) and it has been suggested by Mundy and Ledger (1976) that one of the reasons for this is the high incidence of calcium deficiency (osteodystrophy) in the chicks in cattle ranching areas. They have correlated the occurrence of osteodystrophy to the poor supply of bone fragments brought back to the nests by the adults. The supply of bones has in turn been correlated to the occurrence of large carnivores in the surrounding areas. They suggest that the vultures require large carnivores to break up the bones of carcasses into suitable fragments that they can feed to their chicks. In the absence of large carnivores in cattle ranching areas, the vultures have difficulty in finding bone fragments for their chicks and therefore a number of chicks develop osteodystrophy and subsequently die. This hypothesis can be tested by determining the bone chewing habits of the different carnivores and relating their

presence or absence to the supply of bone chips found in vultures nests.

Aims of the study

The present study was initiated to determine the various factors involved in the decomposition of large carcasses in the veld, and the importance of the different pathways of decomposition under different ecological and environmental conditions.

In order to understand these patterns of decomposition it was felt that it was necessary to determine what physical and behavioural characteristics of the scavenger species are important to their success as scavengers.

As the decomposition of all the tissues of carcasses and the agents responsible were being recorded, it was considered pertinent to record in detail the bone damage caused by different carnivores and thereby to contribute to the interpretation of fossil and recent bone remains.

Various farms and nature reserves of the Transvaal and southern Zimbabwe were chosen as study areas. In this way carcasses in a wide variety of ecological conditions could be monitored. The two biggest variables are : (i) the variety of scavenger fauna - the nature reserves having the large carnivores and more vulture species, and (ii) the change of climate - both seasonally and geographically.

CHAPTER 2 : MATERIALS AND METHODS

GENERAL

The present study was conducted from March 1977 to November 1978 on three farms and three nature reserves in the Transvaal, and on one game ranch in Zimbabwe. The study consisted of observing the state of decomposition of large mammal carcasses in the veld and recording all the agents responsible. Thirty of these carcasses were observed from hides and the feeding behaviour of all the scavengers, particularly vultures, was recorded. Most carcasses were of bovids shot for the study, however any found to have died a natural death (violent or non-violent) were also observed.

The present study was preceded by a less detailed one from March 1976 to February 1977, during which only general observations on the rate of decomposition of carcasses and scavenger behaviour were recorded. Using these observations as a guideline, it was possible to draw up detailed data sheets which were used to record:- (i) the conditions of the site and the carcass (ii) the rate of decomposition of the carcass and the agents responsible (iii) details of bone damage by all the scavengers (iv) scavenger feeding behaviour and interactions at the carcass. These data sheets were then used during the main study.

STUDY AREAS

Locality, altitude, climate and vegetation

The localities of all the study areas are shown in Fig. 1. The climatic conditions and vegetation of these areas vary quite considerably, from the colder Highveld in the west to the hot Lowveld in the east. The most westerly site, Vaalboschfontein $27^{\circ}15'S$, $25^{\circ}42'E$, has the typical Highveld open grassveld vegetation, as well as some stretches of Acacia erioloba savanna. It is situated at an altitude of 1330m and has the coldest climate of all the study areas. The mean daily temperatures at Wolmaransstad for January and July are $22,1^{\circ}C$ and $8,6^{\circ}C$ respectively. Olifantshoek $25^{\circ}52'S$, $27^{\circ}16'E$ is situated immediately south of the Magaliesberg, the farm boundary rising to the escarpment of this range. Most of the study area

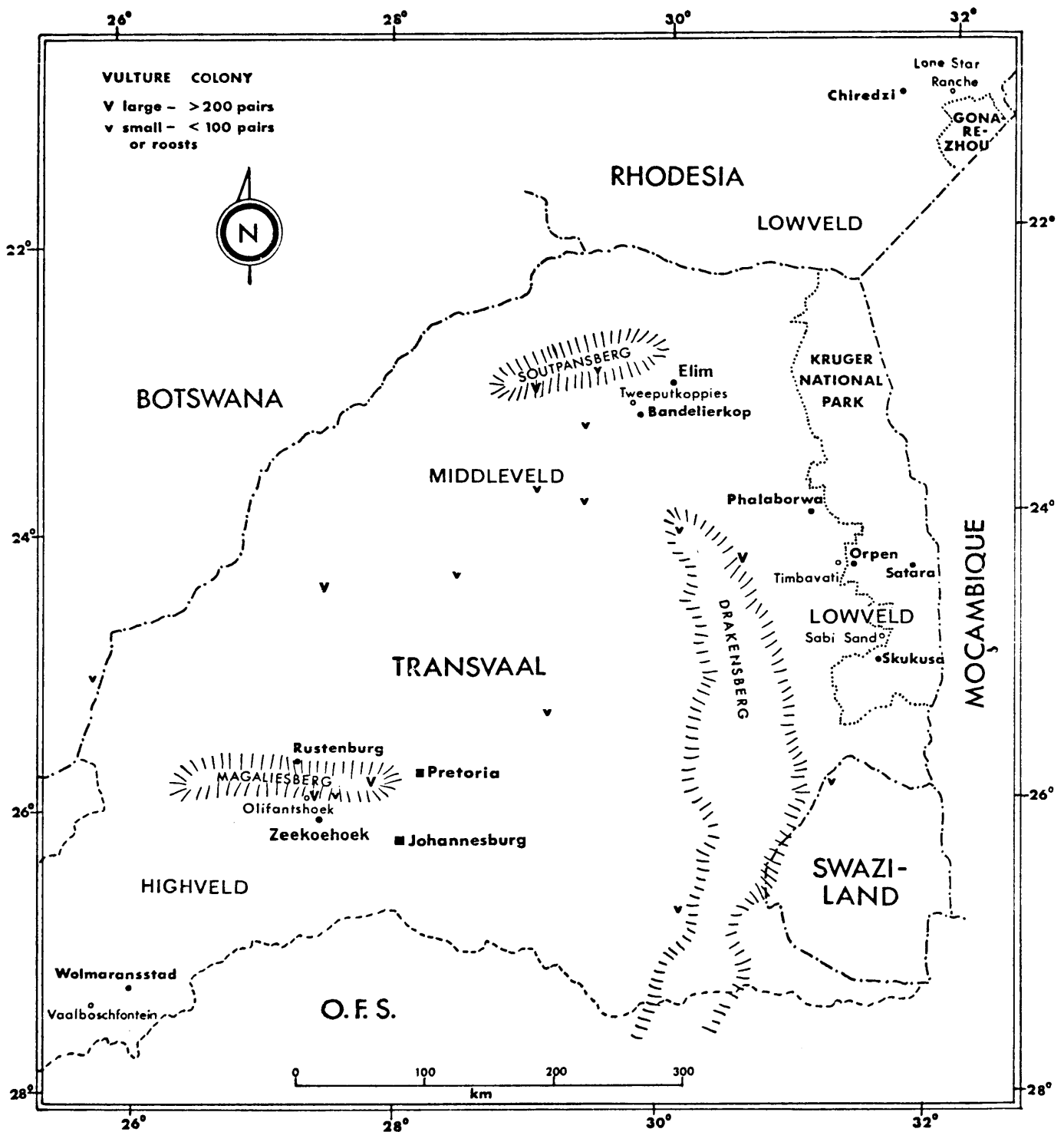


Figure 1 : The Transvaal and southern Zimbabwe showing the study areas, the main Cape Vulture (*Gyps coprotheres*) breeding colonies and roosting sites, and various important geographical features. Vulture colonies after Mundy In litt. 24 March 1980. Study areas indicated by open circles.

is covered by Acacia scrub. The altitude of the site used at the base of the mountain range is 1270m. Being in the shadow of the Magaliesberg the climate is cold in winter and thus similar to that at Vaalboschfontein. The mean daily temperatures at Zeekoehoek for January and July are 21,2⁰ and 8,8⁰C respectively. Tweeputkoppies 23⁰13'S, 29⁰46'E is about 40 km south of the Soutpansberg and was the third farm used as a study area. The whole farm is dominated by Acacia/Combretum scrub savanna. Because it is situated at an altitude of 1030m and is further north it has the warmest climate of the three farms. The mean daily temperatures at Elim for January and July are 22,5⁰C and 14,7⁰C respectively. The three nature reserves, Kruger National Park, Timbavati Private Nature Reserve and Sabi Sand Wildduin are all in the eastern Transvaal Lowveld, the last two occurring along the western boundary of the Kruger National Park. Within Timbavati, two farms, Vlakgezig 24⁰22'S, 31⁰22'E and Birmingham 24⁰32'S, 31⁰16'E were used as study areas. In the Kruger National Park research was carried out about 15 km and 60 km north-east of the Phalaborwa gate 23⁰57'S, 31⁰10'E and about 10 km south of Satara 24⁰24'S, 31⁰46'E. In Sabi Sand Wildduin the two farms Sparta 24⁰49'S, 31⁰30'E and Toulon 24⁰57'S, 31⁰36'E were used. Throughout these areas the vegetation is primarily Acacia and Colophospermum mopane scrub savanna. All these areas are situated at low altitudes, varying from 240m near Satara to 480m at Birmingham. Because of the low altitudes the climate is usually hot. The mean daily temperatures for January and July at Skukuza are 25,9⁰C and 15,5⁰C respectively.

The game ranch in Zimbabwe, Lone Star Ranche 21⁰08'S, 31⁰55'E adjoins the north-western boundary of the Gona re Zhou National Park and has a similar vegetation to that of the eastern Transvaal Lowveld study areas. The altitude is 350m, however being further north, the climate is somewhat warmer.

Scavenger fauna

The species of vertebrate scavengers varied considerably through the study areas. The black-backed jackal (Canis mesomelas) and griffon vultures were present in all

the regions. However the species of griffon vulture varied with the sites. The Cape vulture was the dominant vulture at Olifantshoek and Tweeputkoppies as they breed on the nearby cliffs of the Magaliesberg and Soutpansberg respectively (see Fig. 1). At all the other sites the white-backed vulture (Gyps africanus) was the most plentiful species.

The brown hyaena (Hyaena brunnea) was only encountered at Olifantshoek, although it is endemic but rare in the other Transvaal study areas. Spotted hyaenas and lions occurred only in the nature reserves and on Lone Star Ranche. Similarly, the other three more common African vulture species, the lappet-faced vulture (Torgos tracheliotus), the white-headed vulture (Trigonoceps occipitalis) and the hooded vulture (Necrosyrtes monachus) were all present in these areas. The lappet-faced vulture was the only other vulture seen on the farms. Feral dogs (Canis familiaris) were the only other vertebrate species which played a significant role in this study. A pair of dogs were present for about three months on Vaalboschfontein and during that time they killed about 12 springbok (Antidorcas marsupialis).

Apart from the 10 species mentioned above, some 11 more vertebrate scavengers were encountered during the study. These are considered separately in Chapters 3 and 4.

Nine families of arthropod scavengers were recorded during the study. Although the species within these families may have changed with the study areas, all nine families were present throughout. These are discussed further in Chapter 5.

Shyness of scavengers

The shyness of the various vertebrate scavengers encountered during the study can be directly related to the local farming conditions. In the nature reserves, with the use of adequate hides, all the scavengers fed readily at the carcasses and seemed to be unperturbed by the observers' presence. On the farms this was not the case. The three farms are all run primarily as cattle ranches. However, on Vaalboschfontein about one third of the farm is exclusively used as a game

camp. White-backed vultures breed in this game camp and are protected by the farmer. Consequently they are remarkably bold for vultures in farming areas. Conversely jackals are shy because they are usually shot on sight. The openness of the vegetation further contributes to the shyness of the jackals.

At Olifantshoek the Cape vultures which breed on the farm are also strictly protected by the farmer, however many other farmers shoot and poison them, so these birds are exceptionally shy. Jackals are very seldom shot by the farmer and because of the denseness of the vegetation are also seldom seen. Therefore they were not as shy as those on Vaalboschfontein.

The Cape vultures seen at Tweeputkoppies have a feeding range that covers extensive cattle ranching areas and probably have less contact with man than those in the Magaliesberg. It is probably because of this that they were much bolder than those in the Magaliesberg, although still shyer than the white-backed vultures on Vaalboschfontein. Similarly, because of the large size of the local farms and the denseness of the vegetation, the jackals encountered on this farm were bolder than on any of the others.

CARCASSES

The decomposition of 89 carcasses was recorded during the present study. The numbers of each species observed at each locality are recorded in Table 1. From this table it is apparent that a variety of ungulates were used - Bovidae, Equidae Giraffidae and Suidae. However, because bovids were the most common ungulate used and because the body structure of most of these ungulates are very similar they will henceforth be collectively referred to as bovids.

Weight classes

The carcasses were divided into three weight classes which relate directly to the upper three classes described by Klein (1977). As I used no very small bovids and only a few springbok lambs, a very small class was not warranted.

The classes are as follows :

Table 1 : Carcasses observed in each study area of the Transvaal and southern Zimbabwe

LOCALITY	CARCASS SPECIES		NUMBER
	COMMON NAME	SCIENTIFIC NAME	
VAALBOSCHFONTEIN	Springbok	<i>Antidorcas marsupialis</i>	28
	Blesbok	<i>Damaliscus dorcas</i>	4
	Eland	<i>Taurotragus oryx</i>	3
	Horse	<i>Equus caballus</i>	1
	Cattle	<i>Bos indicus</i>	1
OLIFANTSHOEK	Impala	<i>Aepyceros melampus</i>	4
	Blesbok	<i>Damaliscus dorcas</i>	4
	Cattle	<i>Bos indicus</i>	3
	Sheep	<i>Ovis aries</i>	2
TWEESPUTKOPPIES	Impala	<i>Aepyceros melampus</i>	5
	Mule	<i>Equus sp.</i>	2
	Donkey	<i>Equus asinus</i>	1
	Cattle	<i>Bos indicus</i>	1
TIMBAVATI	Impala	<i>Aepyceros melampus</i>	8
	Giraffe	<i>Giraffa camelopardalis</i>	5
SABI SAND	Kudu	<i>Tragelaphus strepsiceros</i>	1
	Buffalo	<i>Syncerus caffer</i>	1
	Zebra	<i>Equus burchelli</i>	1
KRUGER NATIONAL PARK	Buffalo	<i>Syncerus caffer</i>	3
	Impala	<i>Aepyceros melampus</i>	2
	Giraffe	<i>Giraffa camelopardalis</i>	1
LONE STAR RANCHE	Impala	<i>Aepyceros melampus</i>	3
	Kudu	<i>Tragelaphus strepsiceros</i>	2
	Warthog	<i>Phacochoerus aethiopicus</i>	1
	Bushbuck	<i>Tragelaphus scriptus</i>	1
	Eland	<i>Taurotragus oryx</i>	1

Small : 10 - 100 kg. eg. Antidorcas springbok, Aepyceros impala

Medium : 100 - 300 kg. eg. Tragelaphus kudu, Equus zebra

Large : 300 kg. eg. Taurotragus eland, Giraffa giraffe.

In order to assemble a reasonable sample of carcasses for this study, most of the bovids used were shot. Any other carcasses found were also utilized. These included bovids which had died natural, non-violent deaths (starvation, disease, old age) and predator kills. When bovids were shot and placed near a hide for observation, certain precautions were taken to prevent vultures from seeing them being put out. If the bovid was shot early in the morning, before the vultures had left their roosts (about 09h00), the carcass was put out immediately. If there was a chance of being seen by the vultures (particularly on the farms), it was hidden till the evening and put out just after dark, or early the next morning.

METHODS OF OBSERVATION

Hides

Two basic types of hide were used during the study. On each of the farms a permanent fixed hide was built, whereas in the nature reserves a vehicle was used as a mobile hide. At Olifantshoek and Tweeputkoppies fairly simple hides of wire and hessian were made. The hides were situated on the sides of kopjes with views down to open stretches on the plains below, on which the carcasses were placed. In both cases the hides were placed beneath large trees. Eight gauge wire was strung from suitable branches and rocks to make a roughly square hide beneath the canopy of the tree. Very thick, non-transparent hessian (hemp) was hung over this wire framework and joined to it with thin wire. At Tweeputkoppies extensive use was made of surrounding boulders, so only a roof and two sides of hessian were required.

Along one of the joins in the hessian a large loose flap was left to act as a doorway. In order to observe the carcass a small flap (20 x 7 cm), just large enough to accommodate a pair of binoculars, was cut.

At Vaalboschfontein the farmer made the hide himself. He made a wall of sand around a large existing cement column, then wired down numerous Eucalyptus branches to form a roof between the column and the wall. Within the wall, half flattened 200 litre drums were placed horizontally, so one had a view to the outside through the drums. One had access to the hide via an L - shaped doorway in the outer wall.

These fixed hides had the advantage that they became permanent features of the landscape and therefore vultures were not disturbed by their presence. However their use was limited because they could only be used to observe carcasses specifically placed nearby.

In the nature reserves the scavengers were far less shy than on the farms, so one could use less elaborate hides. A large hessian sack was made which completely covered a Land Rover. Small peepholes were made in this sack which was always hung over the vehicle in the same way, so that these peepholes were placed opposite a side window and the rear window. Other vehicles used as hides were a Volkswagen Kombi and a one and a half ton delivery van. The hide was always adjusted so that there was no excess material which would flap in a wind.

When carcasses were put out, sites were chosen to give maximum camouflage to the hide, yet still giving clear visibility of the carcass. The most suitable conditions for this were flat, short grassy plains bordered by tall, thick vegetation. The vehicle was parked in this tall vegetation and the carcass placed south of it in the open plain. This southward view ensured that one always had the sun behind oneself, thus aiding observation and increasing one's camouflage.

When lion kills were found, these carcasses could not be moved, so one had to park in as suitable a place as could be found within range of vision.

Lighting

Various methods were used to enable the observer to see at night. As far as possible field trips were organised to coincide with the full moon. While the moon was strong, observations were made simply with the aid of 7 x 42 binoculars.

A starlight scope was also used. This was most effective for seeing long distances in open areas on moonlit nights. This scope could also be used for shorter distances on starlit evenings, but its use was severely limited when there was little light available and tall vegetation present, as this appeared to confuse the screen and no distinct patterns were discernible.

On many occasions observations had to be made when there was no moonlight. In the nature reserves, a wide angle spotlight with a 6 candle-power 12 volt bulb was tied to a tree overlooking the carcass. Flex was run from this spotlight at a height of approximately 2 m back to the hide, where it was attached to a spare 12 volt car battery and a rheostat.

This light was left disconnected until any carnivores arrived, when it was connected, but with maximum resistance so that no light emerged. Very slowly the resistance was decreased so that at first the light was just a dull red glow which brightened gradually. During the next ten minutes the light was increased until it was on full power. At this stage the light available was about double that of a moonlit night. This was quite adequate and because of the low candle power, very little power was drawn off the battery, thus enabling one to run the light all night for at least a week.

Once the light was on full, carnivores moved in and out of the lit area apparently quite unperturbed by the light. On some occasions the light was left on all night after being turned on for the first time with the arrival of the first carnivores. On these occasions lions and hyaenas would still come and feed, even though the carcass was well lit when they first arrived. All that seemed to worry them was a sudden change of light intensity. Jackals, even in the farming areas, appeared to be less perturbed by the use of lights than lions and hyaenas.

On the farms this system was not used, because it was felt that the flex leading to the hide would frighten the vultures. Therefore more use was made of the starlight scope. On some occasions when jackals were feeding regularly at a carcass every night, a battery was connected to a three candle-power light which was placed in a tree near the carcass. This light was left on all night.

Inside the hides a three candle-power bulb covered with red cellophane was used for recording at night.

Periods of observation

In order to gain as much information as possible from each carcass, only one carcass was put out at a time. When possible the carcass was watched continuously from a hide until all the soft tissues and skin had been consumed. Thereafter daily observations were made to record what happened to the remains of the skeleton. If another carcass was then being observed within the study area, further observations of the first carcass were made only when it was possible to leave the second carcass. This situation would arise when vultures had consumed all the soft tissues of a carcass and therefore no longer visited it during the day, while hyaenas and jackals still visited it at night to chew the remaining skin and bones. Similarly, if two bovids died within a short period of time, the most accessible was watched from a hide while periodic observations were made at the other. Subsequent observations of carcasses were made when the study area was next visited, weeks or months later.

In the farming areas only those carcasses specifically placed near hides could be observed from the hides. Therefore at any other carcasses found, only daily or less frequent observations could be made.

DATA RECORDED

Estimation of body tissues consumed by different scavengers

In order to determine the importance of the different species as scavengers, one must be able to say how much of each carcass was removed by each species. To achieve this, one must know which specific parts of the carcass have been removed by each species. This information was usually quite easy to record.

During this study the scavengers, to a large extent fed alone, so at the end of each feeding bout one simply recorded all that had been removed. This was aided by the fact that carnivores usually began feeding at one end of the carcass, so it was possible to estimate how much was left when they departed. Whenever a group

of scavengers had finished feeding on a carcass, notes were made of which parts of the carcass had been removed and which parts remained. Whenever possible black and white photographs or colour transparencies were taken to supplement these notes.

By day vultures were generally the only important scavengers, therefore all tissues removed during the day were usually consumed by them. If jackals also fed, they were always in low numbers and one could estimate how much each individual had eaten. Hyaenas fed almost exclusively by night, so all tissues removed overnight could be recorded as having been eaten by hyaenas. Here again individual amounts consumed by jackals could be estimated.

When lions fed at carcasses they usually prevented any other scavengers from feeding, so were responsible for all tissues consumed. Maggots only managed to feed at a carcass when the other scavengers ignored it or when they fed too slowly on a large carcass. Thus here again feeding was largely in isolation and the responsible agents could be determined.

It was usually also possible to monitor the decomposition of carcasses which were not permanently being watched from hides. This was done by using spoor and because of the characteristic manners of feeding the different scavengers have (see Chapters 3,4,5 and 6). However, when carcasses were half decomposed when first found, or if the periods of observation were many days apart, it was often impossible to say specifically which agents were responsible, so they were recorded as unknown.

Body composition of an average bovid

Having determined which parts of a carcass have been removed by a specific scavenger, one needs to know what percentage of the carcass those parts represent, before one can say how much the scavenger has actually eaten. One needs to have these values as a percentage of the total body mass because in this way one can then account for the decomposition of the entire carcass. However Hall-Martin,

von la Chevallerie and Skinner (1977) are the only authors to have published this kind of information for any African ungulates. Unfortunately it is only for giraffe, which have distinct differences from the antelopes.

No other studies on the body composition of bovids account for the whole animal in detail. Huntley (1971) gives a break down of the composition of the cold carcass and then expresses the skin, head, feet, external offal and viscera as a percentage of live weight for blesbok (Damaliscus dorcas) and kudu (Tragelaphus strepsiceros). However he failed to separate these other broad categories into their component parts. Similarly Joubert (1959), Ledger (1968), van Zyl, von la Chevallerie and Skinner (1969) and von la Chevallerie, Erasmus, Skinner and van Zyl (1971) have all studied the body composition of various bovids, all publishing specific pieces of information, but none giving a complete picture of the whole carcass.

In order to calculate how much each scavenger had consumed from each carcass it was decided to draw up a table containing the body composition of an average bovid. This was feasible for two reasons : (i) The very scanty data available in the literature made it impossible to draw up a table for each species studied; (ii) Because of the crude methods involved and the high number of carcasses used (89), it would not have been practical to have had a different table for each species.

A live animal can be said to be composed of three basic parts - warm carcass, external offal (skin, head and feet) and internal offal (intestines, organs and stomach plus contents) (Hall-Martin et al. 1977). When this animal is slaughtered into these component parts there is a loss in the total weight of the cold components. This is largely due to loss of blood and body fluids (van Zyl et al. 1969), so when a bovid dies and is consumed by scavengers, it is suggested that there will be a similar wastage of fluids. Furthermore none of the vertebrate scavengers eat the stomach contents of bovids, so this must also be deducted from the liveweight of the bovid in order to determine its edible mass.

The one figure that is invariably quoted in the literature, is the cold carcass as a percentage of liveweight (dressing percentage). This is because the cold carcass is the most important part of the body in terms of meat production.

When calculating the body composition of an average bovid it is desirable to see how large the variation is between certain species. As the cold carcass usually represents over 50% of the liveweight and because it is the most quoted figure it is the obvious parameter to use for this comparison. However for the purposes of this study, one wants to compare the carcass as a percentage of edible liveweight and therefore the stomach contents and weight loss due to loss of blood must be removed from the calculations.

Ledger (1968) is the only author to have quoted figures on the body composition (including stomach contents as a percentage of liveweight) of a wide variety of African ungulates. Unfortunately he does not quote weight loss during slaughtering. Nevertheless, because his are the only available figures and because this weight loss appears to be fairly constant (van Zyl et al. 1969), his figures are used in this comparison. At this stage weight loss in slaughtering will be disregarded.

$$\text{Carcass as \% of Edible liveweight} = \frac{\text{Carcass as \% of liveweight} \times 100}{(100 - \text{stomach contents as \% of liveweight})}$$

Impala ram :

$$\text{Carcass as \% of Edible liveweight} = 58,1 \times \frac{100}{(100 - 9,9)} = 64,48\%$$

Similarly the figures for other antelope are :

Buffalo <u>Syncerus caffer</u> :	♂ : 59,6%	♀ : -
Wilbeest <u>Connochaetes taurinus</u>	♂ : 64,7%	♀ : 64,3%
Lesser kudu <u>Tragelaphus imberbis</u>	♂ : 68,4%	♀ : -
Impala <u>Aepyceros melampus</u>	♂ : 64,5%	♀ : 65,8%

These figures for the carcass as a percentage of edible liveweight are remarkably similar and bear a closer relationship to each other than as a percentage of real liveweight. Because the impala ram appears to represent a reasonable mean and because it was widely used throughout the study (see Table 1) the values for an impala ram will be used in calculating the body composition of an average bovid.

In order to be able to convert all figures quoted as a percentage of liveweight into a percentage of edible liveweight, the following conversion factor K was derived :

$$K = \frac{100}{(100 - \text{stomach contents as \% of liveweight})} \times \frac{100}{(100 - \% \text{ weight loss in slaughtering})}$$

For impala this is :

$$K = \frac{100}{90,1^*} \times \frac{100}{92,91^\dagger} = 1,195$$

Using data from Van Zyl et al. (1969) for impala rams the total body composition can be derived as follows :

Cold carcass	= 58,84	K = 70,31	() = 70,88	≐	71%
External offal	= 13,8	K = 16,49	($\times \frac{100}{99,19}$) = 16,62	≐	17%
Internal offal	= 10,37	K = 12,39	() = 12,48	≐	12%
Total		<u>99,19</u>			<u>99,98</u>	≐	<u>100%</u>

These figures are used throughout to represent the basic components of an average bovid.

External offal

The external offal of a bovid consists of the skin plus the head, feet and tail, each of which consist of skin, bone and soft tissues. There are no data available for the tissue composition of the external offal so I have estimated the head

* from Ledger (1968)

† from Van Zyl et al. (1969)

and feet to consist of 60% bone and 20% each of skin and soft tissues. The tails of bovids are comparatively small, so they are included with the feet.

$$\begin{aligned} \text{Skin} &= 5,90 \text{ K \%} \quad (\text{van Zyl et al. 1969}) \\ &= 7,05\% \text{ of edible liveweight} \end{aligned}$$

$$\text{Rest of external offal} = 16,62 - 7,05 = 9,57 \cong 10 \%$$

$$\text{Skin of rest of external offal} = 10 \times \frac{20}{100} = 2\%$$

$$\begin{aligned} \text{Similarly soft tissue of rest of} \\ \text{external offal} &= 10 \times \frac{20}{100} = 2\% \end{aligned}$$

$$\begin{aligned} \text{and bone of rest of external offal} &= 10 \times \frac{60}{100} = 6\% \end{aligned}$$

$$\text{Total skin composition} = 7 + 2 = 9\% \text{ of edible liveweight.}$$

Cold carcass

Butterfield (1962) has shown that the tissue composition (muscle, fat, gristle and bone) of the buttock corresponds closely to that of the carcass. Therefore figures for the buttock can be taken to represent the whole carcass.

Huntley (1971) gives the tissue composition of the buttocks of blesbok and kudu. The two results are very similar, so because many more blesbok than kudu were used in the present study the figures for blesbok have been used in the calculations for an average bovid.

$$\% \text{ soft tissue of buttock} = 83,4\%$$

$$\begin{aligned} \text{and \% gristle and bone of} \\ \text{buttock} &= 16,6\% \text{ (Huntley 1971)} \end{aligned}$$

$$\begin{aligned} \text{Soft tissue as a \%} &= 2 \text{ (external offal)} + 12,48 \text{ (internal offal)} \\ \text{of edible liveweight} &+ \frac{(70,88 \times 83,4)}{100} \text{ (cold carcass)} \\ &= 2 + 12,48 + 59,11 = 73,59\% \end{aligned}$$

$$\begin{aligned} \text{Similarly, bone as a \%} &= 6 \text{ (external offal)} + \frac{(70,88 \times 16,6)}{100} \\ \text{of edible liveweight} &= 6 + 11,77 = 17,76 \end{aligned}$$

$$\begin{aligned} \text{Skin as a \% of edible} \\ \text{liveweight} &= 9\% \end{aligned}$$

Tissues as percentages of edible liveweight are ;

Soft tissues	=	73,59	()	=	73,33	≐	73%	
Skin	=	9,0	x	($\frac{100}{100,35}$)	=	8,96	≐	9%
Bone	=	17,76	()	=	17,69	≐	18%	
Total	=	<u>100,35</u>				=	<u>99,98</u>		<u>100%</u>	

At this stage the composition of the body of an average bovid has been calculated in terms of : (i) the cold carcass, external and internal offal, and (ii) soft tissue, skin and bone. What now remains to be calculated, is the distribution of these tissues in the component parts of the body.

Soft Tissue

The total soft tissues of the liveweight can be divided up as follows :

Cold carcass	:	59,11	()	=	80,32	≐	80%	
Internal Offal	:	12,48	x	($\frac{100}{73,59}$)	=	16,96	≐	17%
External Offal	:	<u>2,00</u>				=	<u>2,72</u>	≐	3%	
Total		<u>73,59</u>				=	<u>100,00</u>			

Skin

The distribution of skin over the body has already been calculated as 2 : 7 or 22% to 78% on the external offal to the rest of the body. However in practice, the amount of skin removed by a carnivore was calculated by estimating the area of skin that had been removed as against that of the whole body.

Bone

In order to determine the distribution of bone material in a bovid, I weighed the whole skeleton of a cow (Bos indicus) made available to me by the Transvaal Museum. The bones were all separate and had been cleaned, but they retained a certain amount of fat. How much the relative masses of the bones had changed due to loss of organic matter is not known. The results are presented in Table 2.

Table 2 : Major bones of a cow (*Bos indicus*) and their relative percentages of the total bone mass.

BONE TYPE		PERCENTAGE OF TOTAL MASS	
Cranium and horns		11,8	
Dentaries (2)		5,4	
Cervical vertebrae (7)		4,1	
Thoracic vertebrae (13)		5,9	
Lumbar vertebrae (6)		3,9	
Sacrum		2,5	
Caudal vertebrae (15)		0,7	
Ribs (26)		11,0	
Scapula (2)		4,1	
Pelvis (2)		7,7	
Forelimb	(Humerus (2)	9,3)	17,2
	(Radius & Ulna (2)	5,7)	
	(Metacarpal (2)	2,2)	
Hindlimb	(Femur (2)	9,3)	18,6
	(Tibia (2)	6,6)	
	(Metatarsal (2)	2,7)	
Astragalus (2) and Calcaneum (2)		2,0	
Phalanges (24)		3,0	
Other small bones (48)		<u>2,0</u>	
TOTAL		<u>99,9</u>	

When calculating the mass of bone removed by any carnivore Table 2 was used by assuming that the relative masses of the bones are proportional in all bovids. In this I had to use my discretion because equids and suids have different numbers of certain bone types from the true bovids, and the presence of horns and their size are variable between species and even within species (age and sex differences).

Distribution of soft tissue in the cold carcass

The masses of the soft tissues in the component parts of a cold carcass have been directly correlated to the total mass of each part. Figure 2 illustrates the component parts used in calculations during the study. The percentage composition of the parts are taken directly from Huntley (1971) for blesbok.

Huntley (1971) quoted figures for loin and rump together, so these were separated in proportion similar to that of an eland (von la Chevallerie et al. 1971). This was felt to be justified because the figures for all parts of the carcasses of eland and blesbok are remarkably similar.

Calculating the mass of body tissues removed by scavengers

In Table 3 the total composition of an average bovid (as calculated above) and a giraffe (from Hall - Martin et al. 1977) are illustrated. For the giraffe most of the data were available. Where they were not, the same methods were used as in the average bovid.

There are a number of published methods which can be used to estimate the liveweights of African ungulates without weighing the whole animal (McCulloch and Talbot 1965, Talbot and McCulloch 1965, Sachs 1967, Hall-Martin 1977). However, some of the methods require the slaughtering of the animal while others require a number of external measurements. Excessive handling of carcasses was considered undesirable because it was felt that human scent may influence the scavenger's behaviour. Therefore the estimation of the liveweights of carcasses was only done where a minimum of handling was involved : impala - chest girth (McCulloch and Talbot 1965),

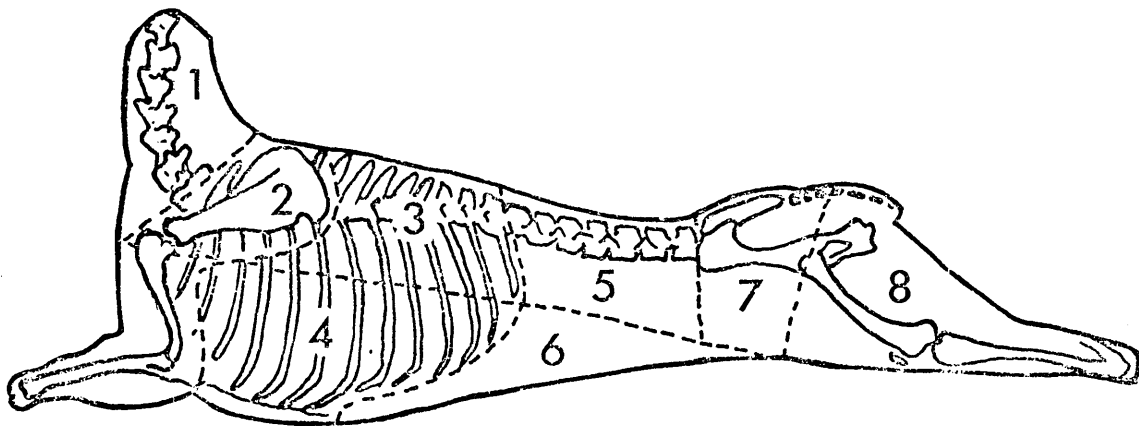


Figure 2 : Standard mutton cuts as described by the South African Meat Board, Pretoria, showing the component parts of carcasses estimated in this study. The "rib" illustrated here combines the standard cuts "rib" and "thick rib". 1 = neck; 2 = shoulder; 3 = rib; 4 = breast; 5 = loin; 6 = flank; 7 = rump; 8 = buttock.

Table 3 : Tissue composition of an average bovid and a male giraffe (*Giraffa camelopardalis*).

AVERAGE BOVID			GIRAFFE		
COMPONENT	% of cold carcass soft tissues	% of all soft tissues	% of edible liveweight	% of all soft tissues	
C O L D C A R C A S S	Neck	13,4	10,7	8,5	10,1
	Shoulder	18,6	14,9	17,9	21,3
	Rib	16,4	13,1	9,0	10,7
	Breast	5,5	4,4	3,0	3,6
	Loin	6,6	5,3	3,6	4,3
	Flank	7,1	5,7	3,9	4,6
	Rump	6,8	5,4	3,7	4,4
	Buttock	25,6	20,5	19,9	23,6
	COLD CARCASS	100,0	80,0	69,5	82,6
	INTERNAL OFFAL		17,0		14,9
	EXTERNAL OFFAL		3,0		2,4
		% of edible liveweight		% of edible liveweight	
	ALL SOFT TISSUES	73		68	
	SKIN	9		13	
	BONE	18		19	

springbok - horn length (Skinner, von la Chevallerie and van Zyl, 1971) and giraffe - shoulder height (Hall-Martin 1977). Otherwise the liveweights of carcasses were calculated by using estimates by the local game ranger or farmer as well as any published data on the liveweights of the bovid concerned (Ledger 1968, von la Chevallerie 1970).

Once the liveweight of a bovid had been calculated this was converted into edible liveweight using the factor K (described above). Using this new weight, the mass of soft tissues, skin and bone were all calculated. The rate of removal of these tissues were then estimated independently : Bone - by the individual bones; skin - by surface area; and soft tissues - by volume and using Fig. 2.

Vulture Behaviour

The scavenging behaviour of vultures at carcasses was recorded in detail from the hides. The main aspects of behaviour that were recorded were the type of food eaten by each species, their positioning around the carcass and aggressive interactions. All observations were made at five minute intervals and recorded on data sheets. Photographs were taken and written observations were made to supplement these data.

Arthropod Decomposition of Carcasses

The analysis of the role of arthropods in the decomposition of large carcasses was done at a very general level. Two main aspects were considered : (i) The succession of arthropods on carcasses at different stages of decomposition. For this specimens were collected and later identified. (ii) The consumption of tissues by arthropods. Here the same methods for estimating the removal of carcass tissues were used as for the other scavengers, with the arthropods as a group being divided into beetles and maggots (blowfly larvae).

Carnivore Damage to Bones

The survival, damage, articulation and fragmentation of all the major bones of 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.

Climate

Whenever a fresh carcass was being observed, certain climatic features were recorded until the soft tissues and skin had been consumed. The most important features recorded were the daily maximum and minimum temperatures. General observations on cloud cover and rainfall were also made.

ANALYSIS OF RESULTS

All the quantified results obtained during the present study and recorded on the data sheets were punched onto computer cards and analysed on the computer using the "Statistical Analysis System" (Barr, Goodnight, Sall, Blair and Chilko 1979).

The statistical tests used on the data are as follows:

1) Chi-squared statistic (χ^2)

$$\chi^2 = \frac{(f_o - f_e)^2}{f_e}$$

Where f_o = observed frequency

f_e = expected (null-hypothetical) frequency

is taken over all the categories

(From Welkowitz, Ewen and Cohen 1971).

2) Correlation coefficient (r)

$$r_{xy} = 1 - \frac{1}{2} \frac{(Z_x - Z_y)^2}{n}$$

Where r_{xy} = symbol for correlation coefficient between x and y.

n = number of pairs

(From Welkowitz, Ewen and Cohen 1971).

3) The t test for two sample means

$$t = \frac{\bar{x}_1 - \bar{x}_2}{S \sqrt{\frac{1}{n_1} + \frac{1}{n_2}}}$$

Where \bar{x}_i = sample mean of the i-th sample; $i = 1, 2$

$S \sqrt{\frac{1}{n_1} + \frac{1}{n_2}}$ = estimated standard error of difference

(From Welkowitz, Ewen and Cohen 1971, Mathews In litt.)

4) The Z test for a proportion

The Z proportion is a test statistic which is used to test the null hypothesis:

$$Z_{p_1 - p_2} = \frac{\frac{x_1}{n_1} - \frac{x_2}{n_2}}{\sqrt{\left(\frac{x_1 + x_2}{n_1 + n_2}\right) \left(1 - \frac{x_1 + x_2}{n_1 + n_2}\right) \left(\frac{1}{n_1} + \frac{1}{n_2}\right)}}$$

$$H_0 : p_1 = p_2$$

$$\text{Where } p_i = \frac{x_i}{n_i}$$

x_i = number of "successes"

n_i = total number of observations for group i

$i = 1, 2$

If H_0 is true, $Z_{p_1 - p_2}$ is approximately distributed as a normal (0 ; 1) random variable. (Du Toit In litt.)

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11 June 1980.

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23 November 1979.

CHAPTER 3 : SCAVENGERS AND THEIR ROLE IN CARCASS DECOMPOSITION

INTRODUCTION

A species scavenges when it feeds on the carcass of an animal not killed by itself or others of its species (Kruuk 1972). Although this definition is widely accepted, it is perhaps the only facet of scavenger behaviour that is clearly defined or understood. Until quite recently very generalised views were held of predators and scavengers. Many naturalists believed that carnivores were almost exclusively one or the other. These beliefs arose from casual observation and were further reinforced by anthropomorphic associations with these life styles; predators being admired while scavengers were despised. Thus it was not acceptable to consider the stately lion as a scavenger or the ill-proportioned and ugly hyaena as a predator.

These views have only recently been seriously challenged, despite the fact that both Brehm (1877) and Johnston (1884, both in Kruuk 1972) mention the predatory behaviour of hyaenas, particularly their ability to take livestock and children. There have subsequently been a number of reports of spotted hyaenas hunting large antelope (Stevenson - Hamilton 1947, Wright 1960, Deane 1962, Pienaar 1963). These were nevertheless still regarded as rare events and it was generally assumed that weak animals were being taken. Eloff (1964) was the first author to describe spotted hyaenas as being predominantly hunting predators, however it was only with Kruuk's (1968, 1972) detailed accounts of these hyaenas hunting in Ngorongoro and Serengeti that they were finally accepted as potential hunters. Similarly lions became accepted as potential scavengers. Kruuk (1972) demonstrated very clearly that these two modes of living are not necessarily exclusive, but that carnivores can switch from one to the other, depending on the local abundance of food and other predators. Furthermore, he showed that in Ngorongoro where there is a very high predator/ungulate ratio, 93% of the carcasses devoured by hyaenas were killed by themselves, whereas 81% of the carcasses devoured by lions were killed by hyaenas.

Kruuk's (1972) study, illustrating the complexity of the whole predator/scavenger system, has been followed by further studies of other large African carnivores (Schaller 1972, Kruuk 1972, Bearder 1977, Mills 1977, Lamprecht 1978). How hunting and scavenging may influence the lifestyles of these species have been considered in wider perspective, nonetheless very little attention has been paid as yet to the concept of a species living exclusively as a scavenger. One notable exception to this being Schaller and Lowther (1969), who considered this aspect in terms of whether early hominids would have been able to live as scavengers. Nobody has as yet clearly defined what the requirements are to make a species an efficient scavenger, the importance of the different scavenger species to carcasses and conversely, the importance of carcasses to these scavengers.

In assigning the roles of predator to the lion and scavenger to the hyaena, naturalists did not take into account what it would mean to these species to live so exclusively. Lions would necessarily leave untouched any carcasses they found, while hyaenas would have to concentrate their entire foraging effort on finding carcasses to feed at. Clearly this is quite impractical. I suggest that the balance between hunting and scavenging lies primarily with opportunity. Any carnivore will scavenge if it is hungry and the opportunity arises. The difference between the hunter and the scavenger being that the hunter is better adapted to kill its prey than to search for carcasses, whereas the scavenger is sufficiently adept at finding carcasses that it need not kill as often, and may even lose the ability to do so. As the availability of carcasses and live prey varies in different areas for different carnivores, so the relative proportions of scavenging and hunting will also change - as shown by Kruuk (1972).

In this chapter the results for the decomposition of carcasses are considered in terms of the roles played by the different scavenger species. These results are discussed in terms of the various physical and behavioural adaptations of these species to this mode of living. Initially the discussion is orientated towards the scavengers' influence on carcasses. Thereafter the importance of

carcasses to the scavengers' existence is considered.

METHODS

Relative scavenging success

The relative success each species had at scavenging was calculated by comparing the amount of carcass tissue consumed by it to the total amount available to that species. A carcass was considered available to a scavenger if the scavenger occurred on the same farm or nature reserve and if it had had at least a week in which to find the carcass. Carcasses were furthermore only considered if there was evidence that particular scavengers had or had not visited them. On the farms, particularly with the feral dog kills, it was often difficult to account for the whole carcass, so these carcasses were excluded from the sample. Similarly the fresh carcasses on Lone Star Ranche were not considered to have been available to lions and spotted hyaenas, because these carnivores were not resident in the study area of the farm and were often hunted. Scavengers were only considered to have eaten from a carcass if they had consumed 1 Kg or more of it.

Total consumption

The basic methods used to determine how much of each carcass was consumed by the various scavengers are described in Chapter 2. When calculating the amount of bone consumed by each carnivore, all bone definitely removed by any one species was said to have been actually eaten by it. This obviously overestimates the bone consumption of all the carnivores. However, as there is no other reliable method and because there were still tremendous differences between the species, this method was regarded as being indicative of the trends and reasonably accurate. When looking for bone remains of a carcass, an area with a radius of approximately 200m was searched. The greatest success was achieved by following spoor and paths made by the carnivores going to and from the carcass.

Individual feeding rates

While observing scavengers from hides, attempts were made to determine the maximum

feeding rates of each scavenger. This was done by recording the number of individuals of a species that were feeding, the time they spent feeding and the amount of food they consumed. This method was quite crude because:(i) the exact amount of food consumed was never known; and (ii) the individuals were never all feeding at the same time for the entire duration of recorded time. Nevertheless, for some species it was still possible to estimate a maximum feeding rate for a group and the individuals of the group. For vultures, the time recorded was from when two or more vultures started feeding, until the moment when the skeleton suddenly appeared to be clean and the skin everted (see Chapter 4).

It was only possible to record a feeding rate for maggots if they were allowed to develop and feed largely undisturbed by the vertebrate scavengers. When this happened, the overall feeding rate was taken as the mass of tissues decomposed from the time of death of the carcass, till its final decomposition. A maximum feeding rate was also calculated by estimating the mass of tissues decomposed from the time that the maggots were fully developed, till there was virtually nothing left of the carcass.

Tissue composition of diet

The scavenging diet of each species was considered from two different aspects : (i) The percentage of specific tissues available that were consumed by the different scavengers. Here a comparison was made between the diets of the major scavengers at lion kills, and at carcasses that were put out or died non-violent deaths; (ii) The diet of each scavenger in terms of the relative amounts of soft tissues, skin and bone consumed.

Organic composition of bone

A number of ashing experiments were performed on bones in order to determine their organic composition and hence their food value to hyaenas. Six cattle femurs were used in the experiment. Two whole bones were crushed manually while the remaining four only had two specific transverse sections crushed - these sections were 1 cm

thick and were taken from the centres of the proximal femur and the shaft. The sections of shaft, having a very low fat content, were milled. However the proximal and distal ends had to be crushed manually. This was done using a heavy steel weight in a steel receptacle.

In the ashing experiment four different samples of bone were used :

- the mixture of the entire bone
- a section of the proximal femur
- a section of the shaft
- the marrow from the section of the shaft.

The experiment was carried out twice. On each occasion four bones were used. The two completely crushed bones were used every time, while two other bones were used for the specific sections of bones. Three sub-samples (approx. 1g) of each sample were ashed, making a total of 24 samples per experiment. Samples were burnt at 600⁰C for over an hour, taking two hours to reach 600⁰C. This was done to prevent the samples from burning too rapidly and smoking excessively. If the samples were too big (5g), this also resulted in excessive smoking.

RESULTS

Species recorded to scavenge carcasses

All the species recorded to scavenge at carcasses observed during the present study are listed in Table 4. A total of 20 vertebrate species were recorded, however only six species (or groups of species) were really effective as scavengers. These were griffon vultures, spotted and brown hyaenas, lions, jackals (black-backed and side-striped Canis adustus) and maggots (five species). These scavengers removed 99% of all the consumed tissues accounted for. The human scavengers were a group of Black railway workers at Tweeputkoppies who, attracted to the carcass by vultures, chased them off and removed the remains of the carcass. I recovered the carcass and replaced it but the vultures did not return.

Table 4 : Species or families of mammals, birds and arthropods recorded to scavenge at carcasses observed in the Transvaal and Zimbabwe, and the total masses of tissues they scavenged.

Scientific Name	Common Name	Min No. Carcasses Scavenged	Min Mass Scavenged kg.
MAMMALS			
<i>Crocuta crocuta</i>	Spotted hyaena	20	1774
<i>Hyaena brunnea</i>	Brown hyaena	13	422
<i>Panthera leo</i>	Lion	3	517
<i>Canis mesomelas</i>	Black-backed jackal	30	427
<i>Canis adustus</i>	Side-striped jackal	1	1
<i>Viverra civetta</i>	Civet	1	23
<i>Panthera pardus</i>	Leopard	1	5
<i>Acinonyx jubatus</i>	Cheetah	1	5
<i>Potamochoerus porcus</i>	Bushpig	1	13
<i>Homo sapiens</i>	Man	1	14
BIRDS			
<i>Gyps coprotheres</i>	Cape vulture	28	3322
<i>Gyps africanus</i>	White-backed vulture	40	
<i>Torgos tracheliotus</i>	Lappet-faced vulture	20	
<i>Trigonoceps occipitalis</i>	White-headed vulture	16	
<i>Necrosyrtes monachus</i>	Hooded vulture	14	
<i>Aquila rapax</i>	Tawny Eagle	6	-
<i>Terathopus ecaudatus</i>	Bateleur	3	-
<i>Milvus aegyptius</i>	Yellow-billed kite	1	-
<i>Leptoptilos crumeniferus</i>	Marabou stork	1	-
<i>Corvus albus</i>	Pied crow	14	-
ARTHROPODS			
<i>Chrysomya albiceps</i>	(Blowflies)	9	799
<i>Chrysomya marginalis</i>		5	
<i>Chrysomya chloropyga</i>		2	
<i>Lucilia cuprina</i>		1	
<i>Calliphora croceipalpis</i>		1	
<i>Dermestidae</i>	Beetles	35	5
<i>Cleridae</i>		27	
<i>Histeridae</i>		14	
<i>Silphidae</i>		10	
<i>Scarabaeidae</i>		6	
<i>Tenebrionidae</i>		6	
<i>Trogidae</i>		4	
<i>Tineidae</i>	Moths	10	-
<i>Isoptera</i>	Termites	2	-
<i>Formicidae</i>	Ants	1	-

Relative scavenging success

The success the different scavengers had at finding and feeding on carcasses is illustrated Fig. 3. In these results no kills were considered as this would have favoured the predator over the scavengers.

Finding carcasses Although they did not necessarily find the carcasses within the first few days, all the main scavengers, except vultures (69%) and lions (23%), found all the carcasses available to them. Spotted hyaenas invariably found a carcass on the first night it was put out in Timbavati, whereas brown hyaenas usually took two to four days to approach it in the Magaliesberg. How much this delay can be attributed to shyness is not known. In the nature reserves jackals always found a carcass on the first night out, however, on the farms they were much shyer and usually waited a day or more before visiting a carcass. If vultures fed at a carcass on the first day, then jackals were not as shy and frequently joined them.

Feeding at carcasses All the major scavengers, except jackals and maggots (blowflies) fed at every carcass they found. While jackals and blowflies visited many more carcasses, they managed to consume 1 kg at only 58% and 30% of them respectively. As griffon vultures and lions did not find all the carcasses available to them, the two hyaena species were the only scavengers which found and fed at every available carcass.

However, vultures still consumed the greatest percentage by mass of the carcasses available to them. These results include all the body tissues (soft tissues, skin and bone) of the carcasses as being available. As vultures only eat the soft tissues of carcasses, their feeding success is most significant. Spotted and brown hyaenas respectively were the next most successful scavengers, with lions, maggots and jackals having the least success. The results for all the scavengers are significantly different from each other (Z proportion, $p < 0,001$).

Total consumption

The feeding success of the scavengers in terms of the relative amounts consumed

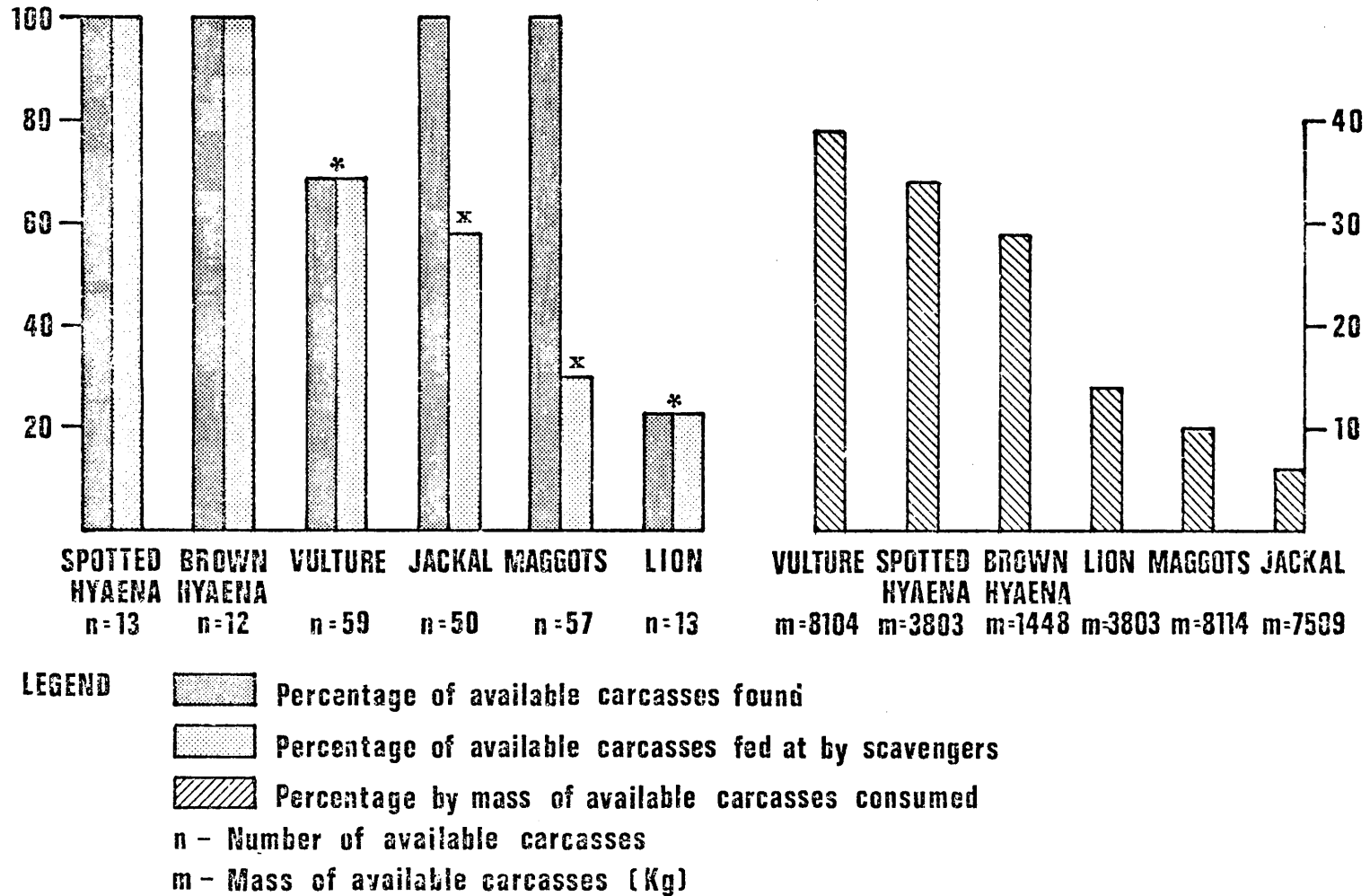


Figure 3 : Percentage success the six major scavenger types had at finding and consuming carcasses available to them. Using the chi-squared statistic, * indicates significant difference ($p < 0,001$) from the maximum success rate, and ^x indicates significant difference ($p < 0,001$) between number of carcasses found and number fed at.

by each, is illustrated in Fig. 4. These results are divided into feeding success on large and small carcasses on nature reserves and farms. On the nature reserves, vultures had significantly less success on the large carcasses than on the small ones. This was because they had to wait for spotted hyaenas to open the large carcasses (primarily giraffe (Giraffa camelopardalis)) further every day, to make new parts accessible to them. On the small carcasses they needed no help and would consume all the soft parts within an hour. Correspondingly, hyaenas had greater success on large than small carcasses. When spotted hyaenas were the first to find a small carcass they consumed it entirely overnight. However, complete carcasses were seldom available so they usually had to finish the remains left by vultures and jackals.

Lions only found three carcasses - two large and one small. The small carcass consisted of skin and bone only, so they ate a little skin and left. The large carcasses presented more opportunity for the lions to scavenge. This was because they contained a large amount of food and they were defended for as long as the lions wished to feed.

Jackals had greater success feeding at small carcasses than at large ones. They did not always arrive while vultures were feeding at small carcasses, but at those that they did, they usually managed to get some meat and often removed most of the skin once the vultures had left. At the large carcasses they had less success because they had to compete with numerous vultures and all the larger scavengers attracted by the size of the carcass. They also found the skin of buffalo (Syncerus caffer) and giraffe very difficult to chew.

On the farms, although the same general pattern still persisted, jackals and maggots had proportionately far greater success than on the nature reserves. This was primarily because the vultures were often shy, so they left more food available to the other scavengers, which although also shy, eventually used to feed. If brown hyaenas found a small carcass they usually finished it within two days (caching some of it), while jackals took three to five days. This meant that

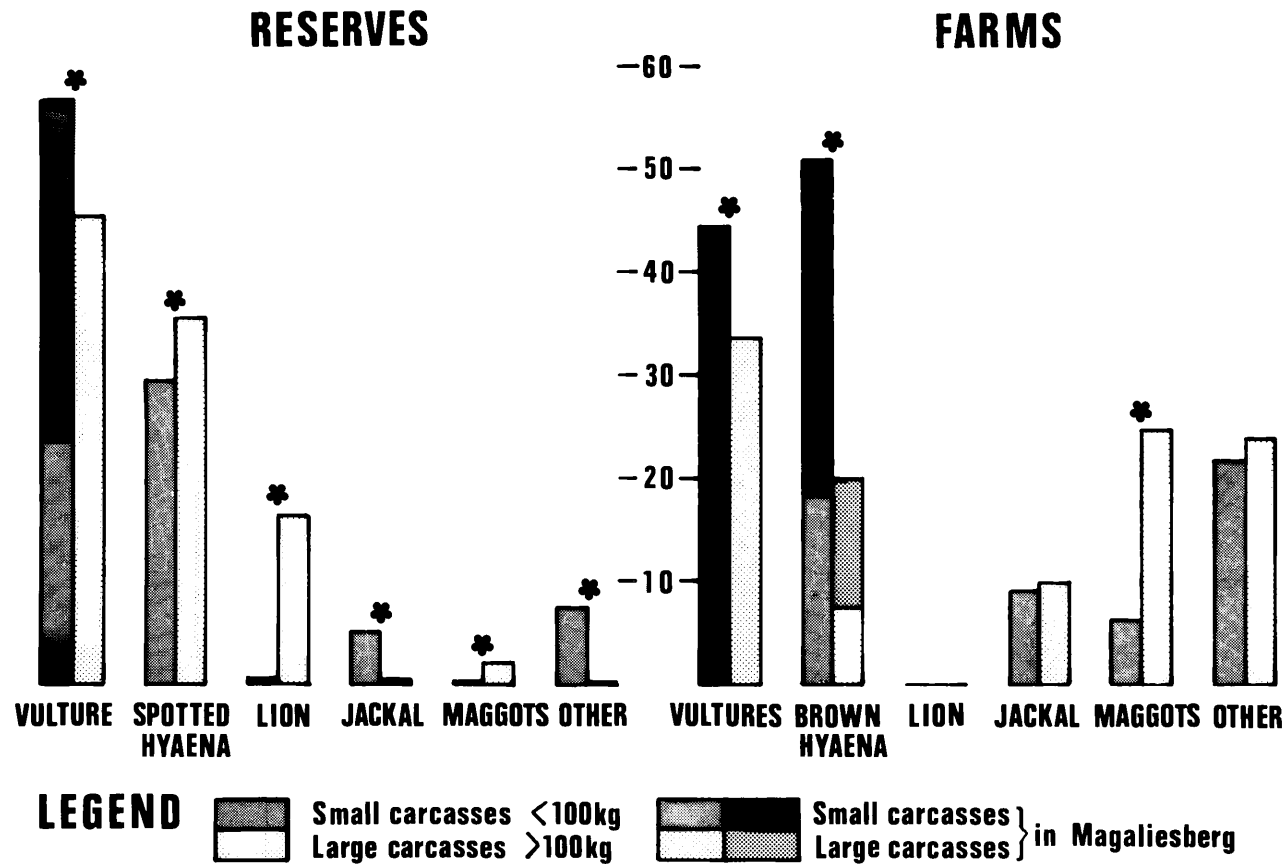


Figure 4: Percentage consumption of carcass tissues, (soft tissues, skin and bone) by different scavengers in the nature reserves and farms of the Transvaal and southern Zimbabwe. "Other" refers to scavengers not listed or where the specific agents were unknown. As the brown hyaena (*Hyaena brunnea*) only occurred in the Magaliesberg and on none of the other farms, its results are divided in two: (i) success on all the farms together; (ii) success in the Magaliesberg. Using the Z proportion, statistical significance is indicated as follows : * $p < 0,001$.

maggots seldom had time to develop and never fed successfully unless these carnivores left the carcass alone. However on large carcasses these carnivores could not eat any faster (unless more jackals arrived), so if vultures did not feed, maggots usually managed to consume most of the soft tissues, provided ambient temperatures were not too low to retard their development.

On the farms a large proportion of the food is under "other". This refers primarily to the scavenger being unknown as opposed to being a different species. This happened because carcasses often took a long time to disappear, so occasionally the entire sequence was not monitored. In addition, the carcasses that were found on the farms could not be watched from hides, and with the passage of time it was often difficult to determine the scavenger. However, probably all the scavengers were involved, so it is suggested that the patterns illustrated are not significantly different from what actually happened.

Individual feeding rates

The maximum rates at which the major scavengers were recorded to feed during the present study, are listed in Table 5. For brown hyaenas the effective rate of removal is given, however, the amount of time actually spent feeding and the mass of food that was cached, are not known.

Tissue composition of diet

The success the different scavengers achieved when consuming the soft tissues, skin and bones of carcasses in the nature reserves is illustrated in Fig. 5. Certain patterns are clearly illustrated in these results. At exclusively scavenged carcasses vultures ate most of the soft tissues, while spotted hyaenas ate some soft tissues, most of the skin and nearly all the bone that was consumed by any scavenger. Lions managed to scavenge very little from these carcasses. At their own kills, lions consumed nearly all the tissues, leaving very little for hyaenas and vultures to scavenge. The exceptions to this were that the lions usually left the thick skin on the neck and shoulders of giraffes and most of the bones of all larger carcasses. These tissues were then scavenged by spotted hyaenas.

Table 5 : Maximum feeding rates of the six major types of scavengers at carcasses observed in the Transvaal and Zimbabwe.

Species	Number	Carcass	Mass (Kg)	Time	Group Kg/min	Individual Kg/min	Total (Kg) /Individual
Griffon Vultures	25	Impala	33	15 min	2,2	0,3	1,3
Spotted Hyaena	1	Impala	18	65 min	-	0,28	18
Brown Hyaena	1	Blesbok	7	Overnight	?	?	7
Lion	16 (6 cubs)	Buffalo	352	12 hr	0,48	0,03	22
Jackal	9	Mule	15	10 hr	0,025	0,003	1,7
Maggots	10 ⁵	Mule	171	3 days	57 Kg/day - max		191
			191	7 days	27 Kg/day - overall		

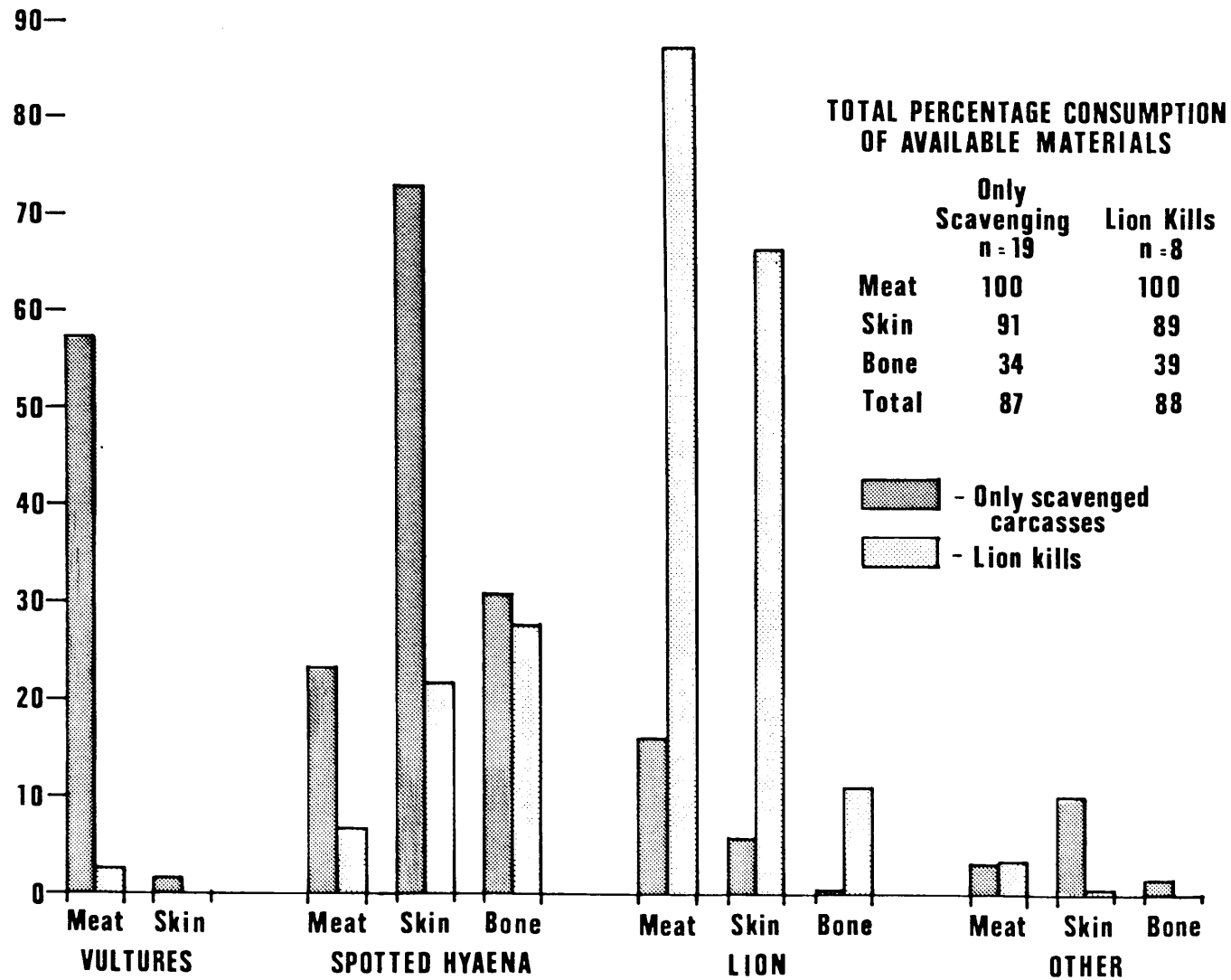


Figure 5 : Percentages of all available tissues - meat (soft tissues), skin and bone - consumed by the major scavengers at lion (*Panthera leo*) kills and exclusively scavenged carcasses in the nature reserves of the Transvaal and southern Zimbabwe.

There is no significant difference ($Z = 0,96$; $df = 1$; $p < 0,2$) between the amount of bone consumed by spotted hyaenas at the exclusively scavenged carcasses and at the lion kills. Otherwise, the results for these two types of carcasses are all significantly different. Jackals and other scavengers played a negligible role on both types of carcasses.

The results for the tissue composition of the diets of the scavengers are presented in Fig. 6. There is no significant difference between the diets of the spotted and brown hyaenas on small carcasses ($\chi^2 = 0,71$; $df = 2$; $p < 0,3$). They were either able to consume entire carcasses on their own, or had to take what was left by vultures and jackals, which was all the bone and some skin. Thus the composition of their diets was similar to the body composition of a carcass, but with some extra skin and double the amount of bone. On large carcasses brown hyaenas could not feed as fast as vultures or maggots (in summer) which therefore consumed most of the meat and skin. The hyaenas still had all the bone available to themselves so they doubled the bone component of their diet.

In contrast, when spotted hyaenas shared buffalo and giraffe carcasses with vultures, they slightly increased the meat component of their diet, because vultures needed the hyaenas to open the carcasses for them. Once again the skin and bones were almost exclusively available to the hyaenas. They consumed all the skin, but because the bones of these ungulates are so large they could only eat 30-40% of them and therefore increased the proportion of skin to bone. At the lion kills, hyaenas ate slightly more skin and bone than on the small carcasses, however these results are not significantly different ($\chi^2 = 3,11$; $df=2$; $p < 0,3$). At these kills, the lions ate most of the meat and skin, however, their inability to eat the thick skin of the neck and shoulders of old giraffe bulls accounted for the proportion of meat in the hyaena's diet. The common factors throughout in the diets of the two hyaena species, are the relatively high proportions of skin and particularly of bone.

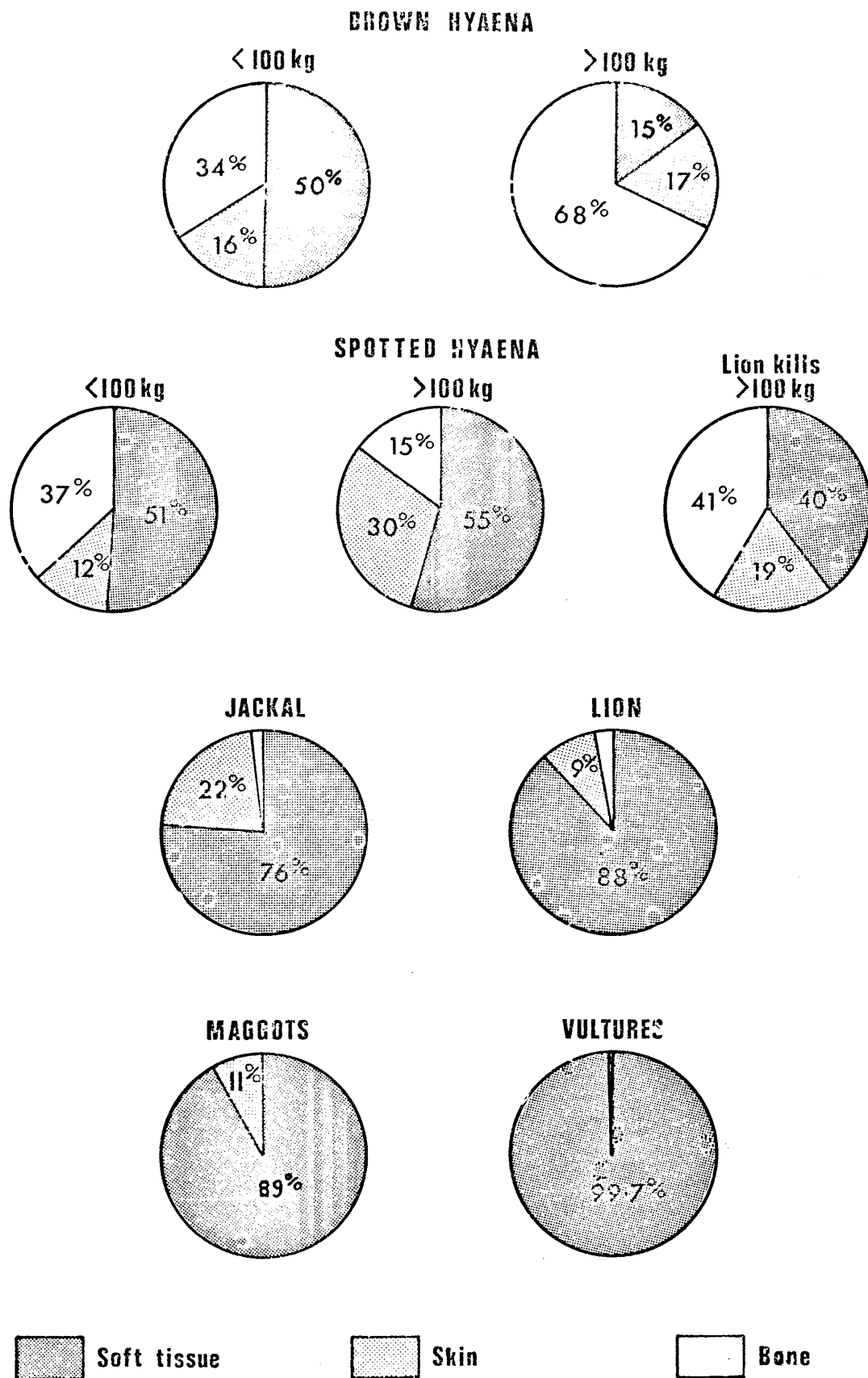


Figure 6 : Tissue composition of the diets of the major scavengers observed in the Transvaal and southern Zimbabwe.

The diets of lions and jackals are noticeably different from the hyaenas', in that they ate virtually no bone. Both species concentrated primarily on soft tissues, so unlike the hyaenas their diets hardly changed at different types of carcasses.

Vultures and maggots ate almost exclusively soft tissues, although if maggots were left undisturbed they also consumed the skin, particularly at the ground interface. The diets of all the above scavengers were significantly different ($p < 0,05$) from each other, except where stated otherwise.

Organic composition of bone

Assuming that the non-ash component of bone is organic, the results for the organic composition are as follows :

Complete bone	55,3	±	1,79%
Proximal femur	52,7	±	0,8%
Shaft	27,1	±	0,6%
Marrow	98,2	±	1,1%

Using the t test for two sample means, the results for the different sections of bones are all significantly different ($p < 0,01$). Although the results for the complete bone mixture are significantly different from those for the proximal femur ($t = 3,85$; $df = 11$; $p < 0,01$), they are within 3% of each other, so the organic composition of the proximal femur can probably be taken as a rough estimate to represent the whole bone.

DISCUSSION

It is apparent from the above results that griffon vultures and hyaenas were very successful as scavengers during this study. What is also noticeable, is that 16 other vertebrates were recorded to scavenge, although the roles they played were, by comparison, negligible. This poses the question: why are there so many scavengers, but with so few of them successful? In order to answer this question, one needs to consider carcasses as a source of food for scavengers and then to determine what adaptations are necessary to make these scavengers successful at

finding and feeding on carcasses.

In the following discussion I have suggested what these requirements are.

They are discussed in terms of the known biology of the main scavengers, and then correlated with the results gained during the study.

Requirements of a scavenger

In order to be a successful scavenger in a competitive situation a species must be pre-adapted to do certain things. Briefly these are :

- | | | |
|---|---|--------------|
| (i) to discover fresh carcasses | } | essential |
| (ii) to utilize fresh carcasses | } | requirements |
| (iii) to maintain possession of carcasses | } | secondary |
| (iv) to utilize old and dried out carcasses | } | requirements |

On consideration these factors are self evident. For a species to make an impact as a scavenger, it has to find a high proportion of available carcasses and to utilize them efficiently. To achieve this the species must maintain possession of the carcasses until it has finished feeding. The feeding success will be further enhanced if it can feed on carcasses not preferred by other scavengers. The ability of scavengers to achieve these four objectives depends on their physiological and morphological adaptations as well as their social organisation. The controlling factors are illustrated in Tables 6, 7 and 8 with the pertinent figures for each scavenger. These figures have been taken directly, or derived from the results of other scientists working in the same regions as myself, or in areas where similar ecological conditions apply. Where suitable figures are not available, I will refer to results from other areas and suggest how they will differ in my study areas. For a suitable comparison of most of the species, Timbavati Private Nature Reserve and/or the Central District of the Kruger National Park have been selected as the main regions. The Magaliesberg and surrounding areas are used for data on the brown hyaena as they are very rare in Timbavati. In the following discussion only those figures which need some explanation will be

mentioned, otherwise the reader is asked to refer to the tables.

Discovering fresh carcasses

Density - The chances of any one carcass being found by a particular scavenger species will to a large degree depend on the local density of that species. The more abundant the scavenger, the greater its chances of finding a carcass. In South Africa there are no density figures for griffon vultures as they are highly mobile and difficult to count. However it is possibly greater than that for spotted hyaenas. The density figures for lions (Smuts 1976) and spotted hyaenas (Smuts 1978) are for the Central District of the Kruger Park. Although Bearder's (1975) figure of $0,5/\text{km}^2$ for hyaenas in Timbavati is higher, he has no definite figures for lions.

There are no available density figures for brown hyaenas. The figure of $0,15/\text{km}^2$ has been adopted from Skinner's (1976) observations just north of the Magaliesberg. This is much greater than Mills' (pers. comm.) estimates for the Kalahari, however the availability of food in the Magaliesberg is probably far greater than in the Kalahari which would account for a higher hyaena density (Skinner pers.comm.). There are also no exact data for jackals, however my personal impression was that they were far more numerous than the other carnivore species.

Daily foraging range - As the daily foraging range of an animal increases, so will its chances of finding a carcass. Griffon vultures should have the greatest success, as an individual may travel 100 km in a few hours and could average over 200 km per active day (Pennycuick 1972). Brown hyaena individuals probably rate top amongst the carnivores. In the Kalahari they averaged 32 km per night during 29 nights of observation (Mills 1978). However their foraging range appears to decrease with the increasing availability of food. Owens and Owens (1978) estimate their foraging range decreases by about 10 km in the wet season in the

M.G.L. Mills. Kalahari Gemsbok National Park, Private Bag X5890, P.O. Gemsbok Park, 8815. March 1980.

J.D. Skinner. Mammal Research Institute, University of Pretoria, Pretoria, 0002. April 1980.

Table 6 : Social and physical characteristics of the main scavengers which determine their success at discovering carcasses in the Transvaal. Values are derived from references listed below.

CHARACTER	GRIFFON VULTURES	SPOTTED HYAENA	BROWN HYAENA	LION	JACKAL	MAGGOTS
Density/Km ² .	?	0,32 ¹	0,15 ²	0,13 ³	1,0 ? ⁴	High ^{4,5}
Daily Range Km	50? - 220 ⁶	10 ⁷	20 ^{4,8,9}	5 ¹⁰	3 ? ⁴	?
Foraging Speed Km/h	47 ⁶	3 - 6 ⁴	3 - 6 ^{8,9}	3 - 4 ¹⁰	3 - 6 ⁴	?
Ave. Group Size	1 ⁶	1,7 ¹¹	1 ⁸	4,0 ¹¹	1,7 ¹¹	?
% Solitary	90 ⁶	59 ¹¹	90 ⁸	28 ¹¹	55 ¹¹	?
Senses	Visibility ⁶	Good ⁷ - 1 ⁰ smell	Good ⁸ - 1 ⁰ smell	Good ¹⁰	Good ⁴	Smell ^{4,5}
Activity Period	Day ^{4,6}	Night ^{4,7}	Night ^{4,8}	1 ⁰ Night ^{4,10}	Night → day ⁴	Day ^{4,5}
Result	Very Good	Good	Good	Very Poor	Good	Very Good

1 - Smuts 1978
2 - Skinner 1976
3 - Smuts 1976

4 - Personal estimate
5 - Smit 1931
6 - Pennycuick 1972

7 - Kruuk 1972
8 - Mills 1978
9 - Owens and Owens 1978

10 Schaller 1972
11 Bearder 1975

Kalahari when there is more game resident in the area. In the Magaliesberg where there is probably both more plant and animal food available to brown hyaenas, their daily foraging range appears to be shorter than in the Kalahari (Skinner pers. comm.). Similarly, lions in the Kalahari appear to have a greater foraging range than those in the Serengeti, where game is more plentiful. Eloff (1973) recorded lions in the Kalahari to travel an average of 16,0 km per night whereas Schaller (1972) recorded a resident pride to average 5,0 km in 11 days. Lions in the Kruger National Park probably follow a similar pattern to those in the Serengeti.

Foraging speed - This is a function of daily range and is included simply to illustrate how fast vultures travel while foraging and the advantage it gives them over carnivores.

Average foraging group size - The advantage a species has at finding carcasses by having a high density is dependent on how much the group splits up while foraging. If the whole social unit forages as one group, it will cover much the same area in one night as would have been covered by a solitary individual. However, the more the group splits up and forages as individuals, the greater the area they will cover, and hence the greater the chances of one of those individuals finding a carcass. The locality of the carcass can then be either actively communicated to the rest of the social unit by means of roaring, whooping or howling or passively, by being back-tracked to the carcass (Mills pers. comm.) or being followed to it the next day (Bearder 1977). These signals can however be picked up by individuals of other species as well.

Percentage solitary - The percentage of foraging individuals that are solitary has an inverse relationship with the average foraging group size and has been included to supplement the group size data where no precise figures are available.

Senses - The senses of smell, sight and hearing obviously help scavengers to locate carcasses. Good eyesight will help vultures to see carcasses on the ground or alternatively to see other vultures descending to a carcass. A keen

sense of smell is probably the most effective in helping carnivores to locate carcasses unaided (Mills 1977, Kruuk 1972) whereas sight and hearing help them to find kills or carcasses already found by other scavengers (Kruuk 1972, Schaller 1972).

Activity period - The methods a species can use in locating carcasses will depend on its period of activity. The use of eyesight will be severely limited at night, and the method of detecting carcasses by the activity of other scavengers will depend on both species being active or at least awake at the same time.

The above factors can be brought together into an index by which one can assess the relative success the different scavengers will have at finding carcasses.

It can be defined as follows :

$$\text{Relative success Rate (R.S.R.)} = \frac{\text{Density} \times \text{Daily Foraging Range} \times \text{Acuity of senses}}{\text{Average Foraging Group Size}}$$

The lion and spotted hyaena have been chosen as examples because they are the only two species for which there are fairly comparable and reliable figures :

$$\text{Lion R.S.R.} = \frac{0,13 \times 5 \times Z}{4} = 0,16 Z \qquad Y > Z$$

$$\text{Spotted Hyaena} = \frac{0,32 \times 10 \times Y}{1,7} = 1,8 Y$$

$$\therefore (\text{Spotted Hyaena R.S.R.}) > 11(\text{Lion R.S.R.})$$

Although no comparative tests have been done, hyaenas are reported to have highly developed senses of smell (Kruuk 1972, Mills 1977) so their "acuity of senses" is probably greater than that of lions. Thus from the index, it is suggested that spotted hyaenas are eleven times more efficient at finding carcasses than lions. This is disregarding the lions' somewhat more diurnal habits, which may reduce the margin slightly. If one considers the factors on the table individually for each species one can see that lions are the only species expected to have poor success at finding carcasses. This is primarily because of their large group size, low daily foraging range and low density.

The rest of the scavengers are apparently highly efficient : vultures because of their tremendous mobility and vision; spotted and brown hyaenas because of their high daily ranges and small foraging group sizes; jackals because of their high density and small group size; and maggots (blowflies) because of their high densities and very good sense of smell.

Utilizing fresh carcasses

A species' success at utilizing a carcass is dependent on its ability to eat as much of the carcass and to share as little of it as possible with other scavengers. The ability to achieve this depends on the following factors :

Average number of individuals feeding - The figures given in Table 7 are the average numbers of individuals of a species expected to feed at an impala carcass. The values for spotted hyaenas and lions are greater than those required to consume a 60 kg bovid. However the figure of four for lions is their average foraging group size (Bearder 1975), while even if only one hyaena found a carcass in Timbavati, usually two or three had joined it by the end of the evening (personal observation).

Maximum number of individuals feeding - These figures have been included simply to illustrate how many scavengers can feed at a large (buffalo, giraffe) carcass in one day. They are regarded as reasonable maxima for the study areas. The maximum number of brown hyaenas that feed at a carcass in the Kalahari is entirely dependent on the size of the resident family unit and the size of the carcass. Up to six brown hyaenas have been recorded to individually visit a wildebeest carcass during a night (Mills pers. comm.).

Individual feeding rate - The faster a scavenger feeds, the greater its chances of devouring its maximum capacity. The figures given in Table 7 are maxima recorded at near optimal conditions.

Individual capacity - The greater the volume of meat a scavenger can consume, the longer the possible period to the next feed, and the less there is for other scavengers. The two figures for griffon vultures are for the white-backed

Table 7 : Social and physical characteristics of the main scavengers which determine their success at utilizing carcasses in the Transvaal. Values from references listed below.

CHARACTER	GRIFFON VULTURES	SPOTTED HYAENA	BROWN HYAENA	LION	JACKAL	MAGGOTS
Average Numbers	50 ¹	3,5 ¹	> 1 ^{2,3}	4 ⁴	2 ¹	30 000 ⁵
Maximum Numbers	300 ^{1,6}	11 ⁷	6 ^{8,12}	16 ¹	9 ¹	93 600 ⁵
Individual Speed Kg/min	0,3 Group = 2,2 ¹	0,32 ⁹	0,1 ¹	0,1 ¹⁰	0,02 ¹	50 kg/day ¹
Individual Capacity Kg	1,2 - 1,5 ¹¹	18 ⁷	7,5 ^{12,13}	30 (♂+♀) ¹⁰	1,5 - 2 ¹	-
Chewing { Meat	Very good	Very good	Very good	Very good	Very good	Very good
Ability { Skin	Poor	Very good	Very good	Good	Fair	Good
{ Bone	-	Very good	Good	Fair	Very poor	-
Result	Very good	Very good	Fair	Good	Poor	Delayed - fair

1 - Personal estimate
2 - Mills 1978
3 - Owens and Owens 1978

4 - Bearder 1975
5 - Hepburn 1943
6 - Kemp and Kemp 1975

7 - Bearder 1977
8 - Skinner 1976
9 - Kruuk 1972

10 - Schaller 1972
11 - Houston 1973
12 - Mills pers. comm.
13 - Skinner pers. comm.

vulture and Ruppell's griffon (Gyps ruppellii) respectively (Houston 1973). As the Cape vulture is almost exactly the same as Ruppell's griffon (Brown and Amadon 1969), this figure is here applied to the Cape vulture and has been confirmed by Mundy (pers. comm.). The figure for lions represents a mean maximum for males and females as the male can eat much more than the female (Schaller 1972, Smuts 1979).

Chewing ability - The chewing or cutting ability of each species will determine the thickness of tissues it can consume. The bone chewing abilities of the different carnivores are discussed in Chapter 6. Suffice to say at this stage that the spotted and then brown hyaenas are the most efficient bone crushers. They are followed by the other carnivores in decreasing order of body size. Not only are lions less efficient at chewing bones than hyaenas, but they are also limited in the thickness of skin they can chew. They are often unable to open the neck of old giraffe bulls (Bearder 1977, personal observation), so the whole neck is left to hyaenas or maggots.

When comparing the feeding ability of these scavengers, one could again multiply each factor - the species with the highest figure being the most efficient scavenger. If time is not a limiting factor the most relevant factors are :

Average Numbers x Individual Capacity

In this respect, lions, vultures and spotted hyaenas are the most efficient feeders. However, in these reserves with the whole spectrum of scavengers, the ability to feed fast is of great importance, so vultures and spotted hyaenas must be considered the most efficient. Both brown hyaenas and jackals are usually limited by low numbers, although jackals can occasionally collect in fairly large numbers at a carcass - Mills (pers. comm.) has seen up to 20 jackals at a large carcass in the Kalahari. They are also limited by having relatively small stomach capacities, so they offer limited competition to the other scavengers. As one

P.J. Mundy, Vulture Study Group, P.O. Box 4190, Johannesburg, 2000.
September 1979.

can see from the figures, maggots can by sheer numbers consume food very rapidly when given the chance. The real limiting factor for maggots is that they take a few days to develop and usually within that time the carcass has been consumed by other scavengers.

Maintaining possession of carcasses

Defence - The most effective way a species can prevent other species from consuming a carcass, is by defending the carcass and not allowing the others access to it. However, a species' success at defending a carcass depends on its status in the hierarchy of scavenger species. Dominance primarily depends on the size of the individuals and then their group number. Thus lions are usually the dominant species, but they may be ousted by spotted hyaenas if there are sufficient of them. In situations where they are quite evenly balanced, motivation will play a prominent role - the hungrier group usually getting the carcass (Kruuk 1972). This is also seen with vultures and jackals, where even two jackals may be kept at bay by the flashing bills of angry vultures. On large carcasses however, they may feed together (Fig. 7).

Activity Period - The activity period of a scavenger directly influences its defence of the carcass. If it can defend the carcass day and night its use of the carcass will be total. Lions usually sleep next to large carcasses by day, occasionally getting up to feed or chase off any intruders (Schaller 1972, personal observation). However, in Timbavati if the carcass was near the boundary of their territory, they usually left it by day and returned that evening (McBride, pers. comm.).

Both hyaena species are almost exclusively nocturnal feeders (Bearder 1977, Mills 1977, personal observation). Although they may both be active in the early morning and evening, whenever spotted hyaenas had visited a carcass throughout the night and into daylight hours, they invariably left by 08h00. Therefore,

C. McBride, Timbavati Private Nature Reserve, Private Bag, Hoedspruit, 1380.
October 1978.

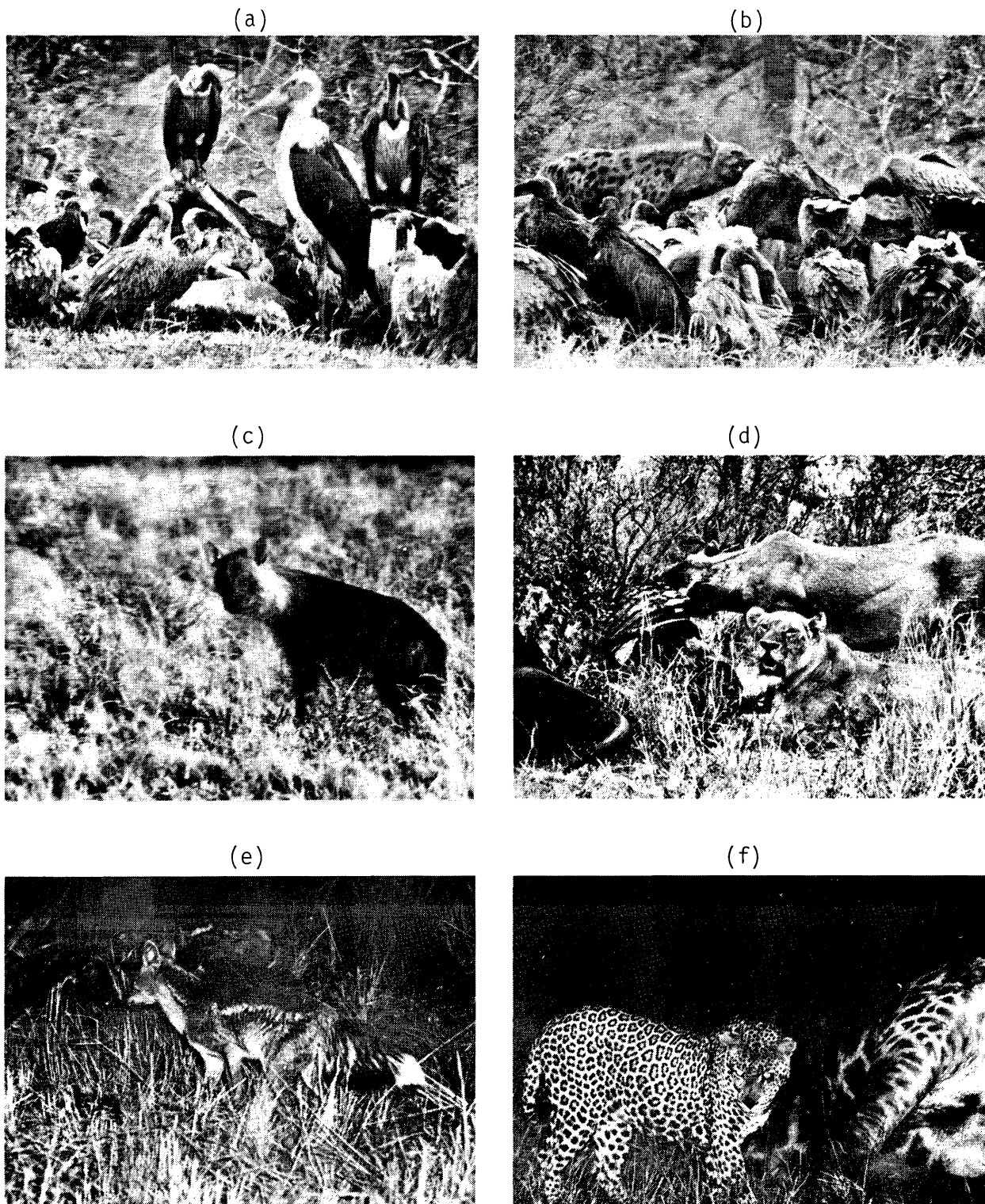


Figure 7 : The major vertebrate species recorded to scavenge at carcasses in the Transvaal and southern Zimbabwe : (a) black-backed jackal (*Canis mesomelas*), griffon vultures (*Gyps* spp.) and a marabou stork (*Leptotilos crumeniferus*) sharing a giraffe (*Giraffa camelopardalis*) carcass (b) spotted hyaena (*Crocuta crocuta*) and griffon vultures at a giraffe carcass at 07h00 (c) solitary brown hyaena (*Hyaena brunnea*) starting to forage at dusk (d) lions (*Panthera leo*) at a buffalo (*Syncerus caffer*) carcass (e) side-striped jackal (*Canis adustus*) at a buffalo carcass (f) leopard (*Panthera pardus*) at a giraffe carcass.

although they could have kept vultures off a large carcass, they had to share it with them as the vultures fed all day while they were gone. This tolerance of vultures sometimes even extended to allowing the vultures to feed at the same time as themselves (Fig. 7).

Caching - Caching is an effective way of storing food that one cannot immediately consume. In this way a scavenger can store food that may otherwise have been lost to other scavengers, and thus prolong its use of the carcass. This is a common behavioural pattern amongst brown hyaenas, particularly with fresh carcasses. They usually detach a whole limb of a small carcass and hide it elsewhere in long grass (Mills 1978, Owens and Owens 1978, personal observation). Skinner and Ilani (1980) and Skinner (pers. comm.) found that in Israel the striped hyaena (H. hyaena) would eat its fill (approximately 7,0 kg), then dismember the carcass and cache the loose parts. In this way an estimated five striped hyaenas (with the assistance of six wolves (Canis lupus)) consumed and removed a donkey (Equus asinus) carcass within three nights on three separate occasions.

In many canids, the caching and retrieving of small food items is a well developed form of behaviour (MacDonald 1976). In this jackals are no exception and regularly cache food, particularly when competing with other scavengers (Lamprecht 1978, Mills pers. comm.).

Spotted hyaenas have occasionally been recorded to store food in water (Kruuk 1972) however, this is probably of very minor importance to the species.

The analysis of the different scavengers' abilities to maintain possession of carcasses can only be done subjectively. Lions are the most efficient because they are the most powerful and usually defend carcasses all day. Spotted hyaenas rate second because they usually give way to lions and do not defend the carcass by day. Brown hyaenas have the same disadvantages (even giving way to spotted hyaenas), but their habit of caching food will increase their utilization of carcasses. Jackals' maintenance of carcasses is poor as the proportion of the

Table 8 : Behavioural and physical characteristics of the main scavengers which determine their success at maintaining possession of fresh carcasses and utilizing old and dried carcasses in the Transvaal.

MAINTAINING POSSESSION OF FRESH CARCASSES						
CHARACTER	GRIFFON VULTURE	SPOTTED HYAENA	BROWN HYAENA	LION	JACKAL	MAGGOTS
Defense - Order	5	2	3	1	4	6
Activity Period	day	night	night	night & day	night & day	-
Cache	-	rare	very common	-	common	-
Result	Very poor	Fair	Fair	Very good	Pocr	-
UTILIZING OLD AND DRIED CARCASSES						
Old Meat	✓	✓	✓	✓	✓	✓
Old Skin	-	✓	✓	-	+	if wet
Old Bone	-	✓	✓	-	-	-
Result	Poor	Very good	Very good	Poor	Fair	Fair

carcass that they can cache is very small (personal observation) and they have limited success in keeping vultures off their carcasses. They may keep vultures off until they have finished feeding, but they never prevented vultures from taking over thereafter.

Utilizing old and dried out carcasses

When an animal is killed or dies a non-violent death, it is not necessarily entirely consumed by the predator or scavengers. Thus old carcasses in various states of decomposition lie in the veld available to any scavenger that wishes to feed on the remains. The ability to utilize this old food will obviously increase a species' success as a scavenger.

Old meat - All carnivores appear to prefer to eat fresh meat, but most, including lions (Bearder 1975, personal observation), will still eat very old meat, probably even if it is infested with maggots. In fact if the maggots are fully developed or pupating they seem to be taken in preference to the carcass, by brown hyaenas (Skinner 1976) and jackals (personal observation). In the Magaliesberg, one brown hyaena ate from a cow that had already been totally decomposed by maggots. At this stage all that remains of the soft tissues is a very fatty residue (Putman 1978 a) which looks like motor car grease. This proved to be too much for the hyaena, which left large blobs of grease as regurgitations.

Old skin - Once the skin of a carcass had dried and gone hard, the only carnivores observed to eat it in the present study were the two hyaena species. Sometimes a fresh carcass is cleaned out by vultures and a dry shell of skin is left encasing the skeleton. If it rains, water can collect in this shell and this is sufficient for blowflies to lay eggs and maggots can develop.

Old bone - Hyaenas were the only carnivores recorded to chew old bones. This they did even to bones that were six months old.

From the above one can see that only hyaenas have any real success at utilizing old carcasses, and this is primarily because of their exceptional ability to eat

old skin and bones.

Summary

In order to predict the final scavenging success of a species, one needs to consider together the four basic requirements listed above. This is because they are interdependent, with the final result being a balance of the individual requirements. A summary of these predictions is illustrated in Fig. 8.

Vultures are rated the best because they are highly efficient at finding carcasses and feeding rapidly - the two most important requirements. Spotted hyaenas come second because although they are good at everything, they are slower to find carcasses. Brown hyaenas are also good scavengers, but are slower feeders than spotted hyaenas. Both hyaena species' success is greatly enhanced by their ability to chew old skin and bones. Lions are poor scavengers simply because they find too few carcasses. Jackals find every carcass, but because they eat so little and so slowly they seldom compete with hyaenas and vultures. In this situation where there are so many efficient scavengers, maggots have little success because they cannot develop in time to compete.

With this background of the relevant physical and behavioural adaptations of these scavengers and how they should effect their scavenging success, it is now pertinent to discuss the results for carcass decomposition and see if they concur with the pattern predicted.

Discussion of results

Discovering fresh carcasses

The predictions for the various species' success at discovering carcasses are basically in accordance with the results achieved (Fig. 3), as lions and vultures were the only main scavengers not to find all the available carcasses. The vultures' limited success is contrary to the above predictions, however, it can be explained by the following two factors : (i) On the farms many carcasses

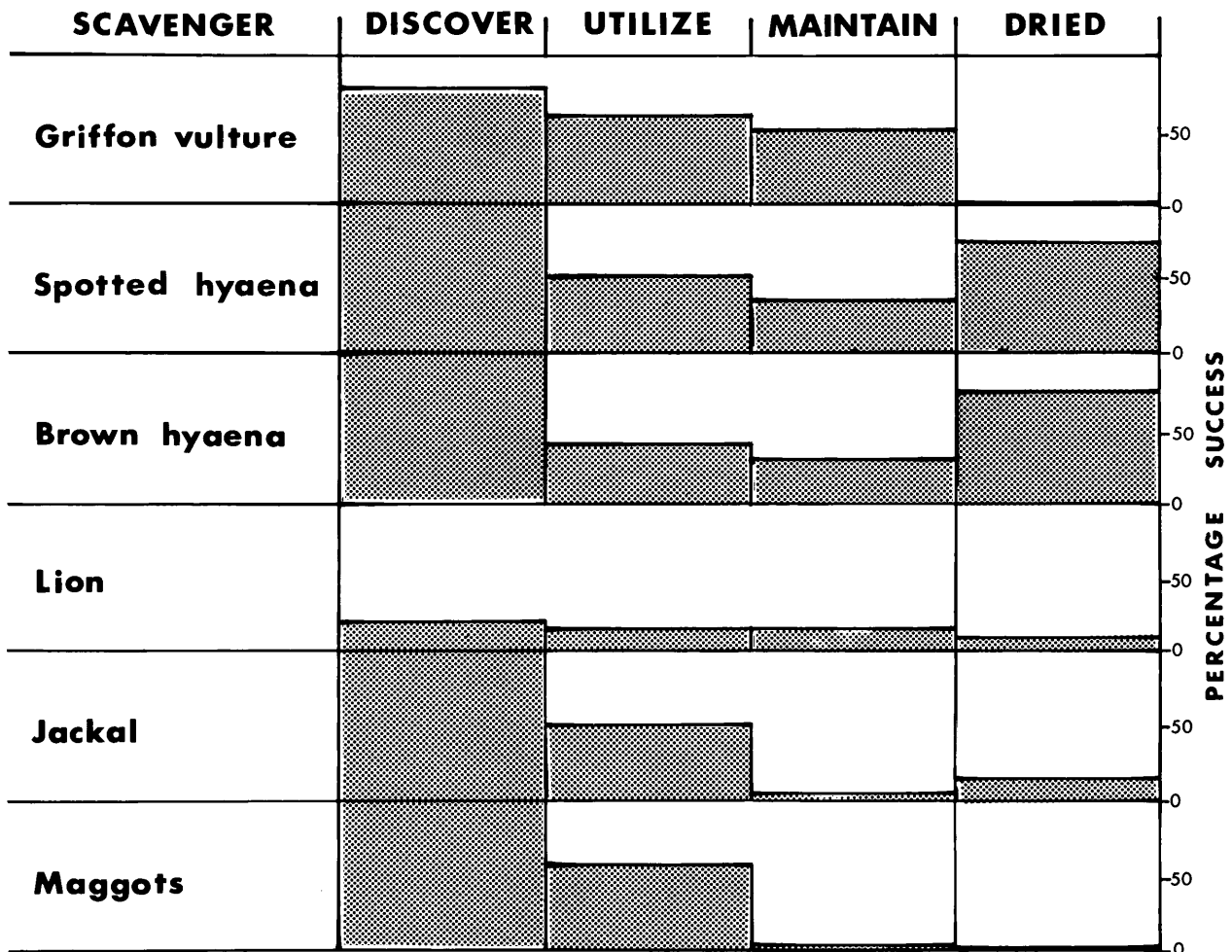


Figure 8 : Diagrammatic summary of the relative abilities of the major scavengers to meet the four basic requirements of scavenging : Discover - ability to find carcasses; Utilize - ability to utilize carcasses found; Maintain - what is actually utilized after loss to other scavengers; Dried - ability to utilize old skin and bones.

were undoubtedly seen by vultures but they were too shy to descend and feed.

(ii) A few small carcasses that were put out in the evening in the reserves were consumed overnight by hyaenas, so they were never really available to the vultures.

The first factor is unnatural and played a major role in limiting vultures' success at carcasses. However, the second factor is simulating the natural situation which will be determined by the hour of the day or night when animals die - those dying early in the evening, being likely to be found by spotted hyaenas. Thus vultures will never be able to find every carcass in the nature reserves, but should be highly successful at discovering those that lie exposed during the day.

Utilizing and maintaining possession of fresh carcasses

Having found a carcass, a species' success at utilizing it is dependant on the balance of how fast it feeds, and how successfully it maintains possession of the carcass. If there are no other vertebrate competitors, a jackal will be able to consume all the soft tissues and skin, provided it does not allow maggots to develop. Thus to maintain the carcass it only needs to "defend" it against maggots. Where there are other vertebrate scavengers, the subordinate species' success will depend on the speed at which it can feed and hence the mass it can consume or store away before the other species arrive, or between their feeding bouts.

Jackals and maggots were the only two scavenger groups which did not consume over 1 kg of tissue from every carcass they visited (Fig. 3). This was because they retain possession of carcasses for only short periods and they are very slow or delayed feeders. Conversely, despite the fact that griffon vultures were usually subordinate to jackals, these vultures consumed both the greatest mass of tissues and the highest percentage of available tissues of all the scavengers on the nature reserves and the farms (Fig. 3 & 4). Their scavenging success is therefore entirely dependant on the speed at which they find carcasses and then, as a group, consume them.

The two hyaena species were the next most successful scavengers in their respective areas in terms of the mass of food and the percentage of available food consumed. The spotted hyaena's feeding efficiency is predicted above to be equal to that of griffon vultures. During this study they did in fact feed very rapidly, however they were limited by two other factors : (i) they were slower to find fresh carcasses than the vultures, so the vultures consumed most of the soft tissues (Fig. 5). (ii) Their retention of the large fresh carcasses that they found was very poor, as they left the carcasses unattended by day so the vultures could feed inside the carcasses and remove most of the soft tissues. The hyaenas then ate most of the skin and the consumable bones.

The major differences between spotted and brown hyaenas became evident at large carcasses. Here, the smaller stomach capacity of the brown hyaena combined with the fact that they usually feed alone became very evident as they were able to do only minor damage to these carcasses, which were largely consumed by vultures and maggots. Although the spotted hyaenas lost a large proportion of the soft tissues to vultures, when they fed in large groups (up to eight) they could consume 100 kg in an evening (personal observation).

The maximum rate at which lions have been recorded to feed is slower than that of spotted hyaenas (Kruuk 1972, Schaller 1972). However, because they are usually the dominant species at a carcass there is no need for them to feed faster in order to improve their scavenging success. The lions were highly successful at scavenging the two large carcasses they found, as well as consuming all their own kills, undisturbed. However, they did not find enough carcasses to be really important scavengers.

Utilizing old and dried out carcasses

All the scavengers will eat old meat if they are really hungry. However, the dried out skin and bones of carcasses provide a food source that is almost exclusively eaten by hyaenas, which therefore greatly increase their impact as scavengers.

The importance of scavenging to scavengers

The above discussion has demonstrated the importance of the different scavengers as scavengers in the Transvaal. However these results do not necessarily imply the inverse. That is, scavenging may not be vitally important to hyaenas, whereas it may play an important role in the life of the jackal. The essential difference in these two concepts, is that now one must consider the success of the individual as opposed to the species. To live as a successful scavenger, each individual of the species will have to be able to find and feed on carcasses on a regular basis throughout the year. This raises the question of the source and availability of carcasses for scavengers.

Kruuk (1967) considered hyaena, lion and other predator kills to be the primary source of food for vultures in the Serengeti. However there is strong evidence to dispute this, either in the Serengeti or elsewhere. It is apparent from Fig. 5 that vultures and hyaenas managed to scavenge very little meat and skin from lion kills. In fact they were only successful at buffalo and giraffe kills because here the lions left somewhat more than they did on smaller carcasses. Thus apart from hyaenas eating the remaining skin and bones, these results suggest that scavengers cannot rely on the remains of lion kills as a food source, and therefore depend on a supply of carcasses from animals that have died non-violent deaths - old age, disease, starvation or accident. Houston (1974a) has reconsidered this question for the Serengeti. He analysed the results of various scientists who had worked on the herbivores and carnivores of the Serengeti. From these he calculated the total annual mortality (in kg) of the herbivores and the total annual consumption of the large carnivores, and estimated that the large carnivores only consume 25% of the herbivores that die annually. This means that the remaining 75% are available to scavengers other than the large carnivores. This figure is probably far higher than in the Kruger Park, because during the huge migrations in the Serengeti, large numbers of herbivores die and carcasses often lie untouched for days, as all the carnivores and scavengers are saturated with food

(Kruuk 1972, Schaller 1972, Houston 1974a). However these migrations are only temporary phenomena, so they alone will not provide carcasses for the annual consumption of vultures. The fact that Houston estimated that less than 10% of the food of vultures comes from predator kills, suggests that there is still sufficient herbivore mortality, other than predation, throughout the year to provide for their needs. Similarly, this should apply to the Kruger National Park.

In Fig. 9 I have created a theoretical model illustrating the success an individual of a species is likely to have as a scavenger, depending on its social organization. This model is primarily considering two factors : (i) the mobility and home range of the potential scavenger (ii) the number and the predictability of carcasses.

On a theoretical basis, there will be a minimum size to a population of antelope which can provide an average of one carcass a week throughout a year. This population will live in an area which will have a limited minimum size. For scavengers to find every carcass successfully, they will have to be able to cover that whole area every week. This of course creates two more requirements : (i) With each scavenger having a maximum area it can effectively search each day, there is a minimum number of vultures which will be able to search the whole area effectively in order to find the carcass. (ii) Once the carcass has been found, the whole system can only continue to run efficiently if every searcher (scavenger) gets enough food to feed itself for a week. If not, some will die, which will reduce the groups' carcass-finding ability. This will decrease their efficiency and they will not be able to exist as pure scavengers.

This is the basic system that griffon vultures employ. Therefore, for them to exist in one area, this region will have to be large enough to support enough game to provide a regular supply of carcasses, sufficient for that population of vultures. A rough calculation of this has in fact been done for the Cape vultures in the south western Cape Province, and the supply of sheep carcasses

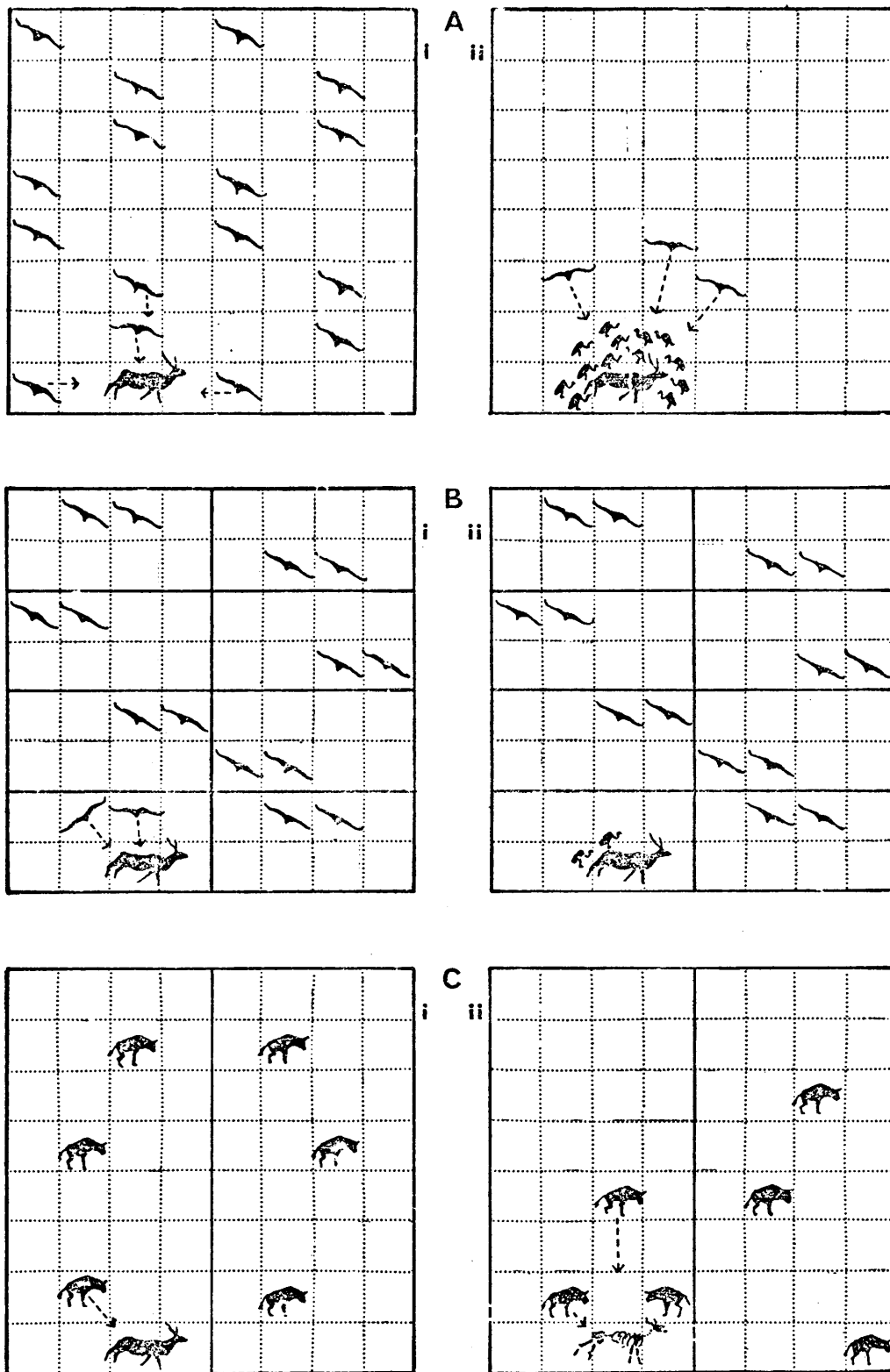


Figure 9 : Diagrammatic representation of the effect of territories, size of home range and population densities on the success of a species at finding carcasses. A : Social organization typical of griffon vultures (*Gyps* spp.) - no foraging territory, density = 1 : 4 unit area, home range = 64 unit area. B : Social organization typical of territorial eagles and vultures, and most carnivores - well defined territories, density = 1 : 4 unit area, home range = 8 unit area = 1/8 A. C : Social organization typical of brown hyaenas (*Hyaena brunnea*) - poorly defined territories, density = 1 : 11 unit area, home range = 32 unit area. (Bold lines represent territorial boundaries).

is apparently more than adequate for their needs (Jarvis, Siegfried and Currie 1974).

If all these requirements are met, one is still presupposing that the vultures have a highly efficient means of communicating the locality of a carcass to each other, and furthermore that they are all allowed access to it. This is in fact so for griffon vultures. The method of communicating the locality of a carcass to each other is passive. A searching vulture has a relatively slow flight and is continually changing its course. Once it sees a carcass it goes into a fast dive straight for the carcass. This change in direction attracts the attention of other vultures, which then follow (Pennycuick 1972). Thus the message is passed on to vultures many kilometres away and soon a large number will congregate at the carcass. Although griffon vultures do compete at carcasses, they do not have a territorial system which would prevent them from all gathering at the one carcass.

Griffon vultures appear to have adapted specifically for this way of life and are probably the only large vertebrates in Africa which can live exclusively as scavengers (Schaller 1972). One of the major physical adaptations of griffon vultures that enables them to search such vast areas effectively, is their use of gliding flight. They use convection thermals to gain altitude and then glide between them, slowly losing height. In this way they can cover large distances rapidly with relatively little energy expenditure (Pennycuick 1972).

There are certain limitations which prevent carnivores from using the same system as the griffon vultures : (i) They do not have the mobility to cover the area required to find carcasses regularly. (ii) Their energy requirements while foraging are much greater. (iii) They are usually further restricted by territorial boundaries, or at any rate have limited home ranges. Thus they are unlikely to have access to sufficient carcasses. Furthermore, the carcasses they do have access to, will often have had most of the soft tissues removed by griffon vultures. This point applies to all territorial species, and

therefore includes territorial vultures (specifically the white-headed vulture) and scavenging eagles.

This argument would then seem to preclude carnivores from being successful scavengers. However, while I agree with the view expressed by Schaller (above), this does not necessarily mean that hyaenas cannot scavenge a fairly high percentage of their diet. Of the two hyaena species in the Transvaal, the brown hyaena is probably the more successful as a scavenger. The very features that make it the less successful scavenger as a species, will actually make it the more successful as individuals. Their lower density and smaller group size, which reduced their food finding and feeding abilities respectively, will, together with their very large home ranges (Mills 1978) increase the amount of food available per carcass per individual (Fig. 4 section C). Where their home ranges are smaller, as in the Magaliesberg (Skinner pers. comm.), this is probably because of a greater availability of food, so they do not need to forage as far to meet their requirements. The smaller size of the brown hyaena (Mills 1977) also decreases their daily requirements. Yet another advantage it has, is its habit of caching food. Although these caches may occasionally be robbed (Mills 1978, Owens and Owens 1978), they undoubtedly increase a scavenger's use of a carcass. Their habit of hiding their cache in long grass (Mills 1978), probably prevents vultures from seeing it and may also decrease the spread of its smell and therefore attract less carnivores.

Both hyaena species have one great advantage over all other scavengers - their ability to chew skin and bones. These are food sources which are often left by other carnivores and vultures at fresh carcasses and which are almost exclusively eaten by hyaenas once old and dry. Thus apart from utilizing carcasses more efficiently, hyaenas can use old skeletons as a sort of supply store with no fear of it being plundered, except of course by the other hyaena species when they occur sympatrically.

In addition to bones being almost exclusively available to hyaenas, they are apparently also a very nutritious food source. Kruuk (1972) states that spotted hyaenas can digest all the organic content of bones - their faeces having the same chemical composition as the inorganic content of bone. If this is true for both hyaenas it means that the entire organic content of a carcass's skeleton is potentially available to them as food.

The results of the bone ashing experiment suggest that the organic content of the proximal femur of a steer (52,7%) is approximately equal to that of the whole femur (55,3%). If one assumes that the balance between spongy and hard bone is fairly constant throughout the skeleton, then one can say that over 50% of a bovid skeleton is organic and therefore digestible by a hyaena.

In Chapter 2, the bone tissues of an average bovid were calculated to comprise 18% of the edible liveweight. As hyaenas can chew all the bones of small and medium-sized bovids (see Chapter 6), this means that over 9% ($18\% \times 50\% = 9,0\%$) of the edible liveweight of all these bovids is potentially available to hyaenas as food in the form of bones. Spotted hyaenas can chew approximately 40% of the bones of a giraffe or a buffalo, so here the edible bone content is about : $40\% \times 18\% \times 50\% = 3,6\%$. In practise it is probably higher than this, as the bones that are chewed are the softer spongy areas which have the higher organic content.

After the hyaenas, lions do the most damage to their herbivore prey, and as they only chew up the bones of small antelope and leave a kudu almost undamaged apart from the ribs, predator kills can be a large source of food for hyaenas, simply from the bones they leave behind. Thus brown hyaenas actually benefit from the presence of lions by eating the remains of their kills (Mills 1978, Owens & Owens 1978), while spotted hyaenas also make extensive use of old carcasses when other food is scarce (Kruuk 1972).

CONCLUSION

In this chapter I have considered two different facets of carcass decomposition: (i) Carcass decomposition itself - what happened to carcasses in different ecological conditions, and which channels (scavengers) their tissues went through. (ii) The scavengers - what factors make species successful scavengers, as a species and as individuals.

Carcass decomposition

The different scavengers involved and their importance in the decomposition of carcasses are well summarised in Fig. 4. Nature reserves and farms are considered ecologically different, simply because of their different scavenger fauna. The main differences were that on the farms the vultures were shyer and there were no spotted hyaenas or lions. Consequently the influence of the two most efficient scavengers, vultures and spotted hyaenas, was reduced and totally removed, respectively. This correspondingly increased the success of jackals and maggots at scavenging. The presence of brown hyaenas in the Magaliesberg created a third situation. They were vitally important in the removal of bones (in contrast to the other two farms where bones lie around for years) and could consume a small carcass within two days. Nevertheless they were basically ineffective on large carcasses, so here again jackals and maggots could take advantage of the shyness of vultures.

Scavengers

Apart from determining the roles played by the major scavengers in the decomposition of carcasses, one of the main aims of this chapter has been to consider the concept of scavenging itself. It is apparent from the above results that a large number of species do scavenge carcasses, however, it is equally apparent that only a few of these species are really important as scavengers.

It is suggested that when a carcass lies in the veld, it can be considered as an energy rich source of food, which is potentially capable of attracting any carnivorous species to it. However, few of these species are adapted to find

carcasses regularly, and having found the carcass, to compete with other scavengers for it. Thus, while large number of species scavenge carcasses occasionally, only a few are of any importance.

Of all the species recorded to scavenge during this study, the cheetah is the most remarkable because it is regarded by many never to scavenge (Schaller' 1972). Similarly the caracal (Felis caracal), also usually regarded as an exclusive predator, has been recorded to scavenge a donkey carcass (Skinner 1979). If my concept of scavenging is correct; viz. any carnivorous species will scavenge if it is hungry and the opportunity presents itself, then these records are to be expected. The reason why they have seldom been recorded, is because the social and feeding behaviour of these species is poorly adapted for scavenging, so they are unlikely to be observed doing so.

The final aspect of scavenging that has been discussed, is the importance of it to particular species. The most essential requirement for an individual to live successfully as a scavenger, is for it to find carcasses regularly throughout the year. In order to achieve this it must be physically adapted to cover large areas of land and have a social organization which allows it to forage in that area unhindered by conspecifics. These requirements immediately preclude strictly territorial species, as their territories are not likely to yield sufficient carcasses on a regular basis.

The griffon vultures, being able to fly over 200 km in a day (Pennycuick 1972), are obviously the best adapted of all the African scavengers. Mammals are more restricted as scavengers, because their average foraging speed is necessarily far slower than that of vultures. Nevertheless, the brown hyaenas' ability to forage long distances and make use of a large home range, combined with its ability to utilize old skin and bones efficiently, make it highly adapted as a mammalian scavenger.

CHAPTER 4 : SCAVENGING BEHAVIOUR OF VULTURES.

INTRODUCTION

The phenomenon of five or six species of vultures feeding together at large carcasses has often been observed in different parts of Africa. Furthermore, at least another ten predatory bird species have been recorded to feed on dead animals (Brown and Amadon 1968, McLachlan and Liversidge 1978) although not necessarily together or at the same carcasses. This variety of avian scavenger species has led to much speculation about their ecological isolation, particularly that of vultures (Chapin 1932, Petrides 1959, Attwell 1963, Kruuk 1967, Houston 1975). Only Kruuk (1967) and Houston (1975) have investigated this phenomenon in any detail. Kruuk divided the six common species of vultures found in East Africa into three different pairs according to the structure of their bills and their related feeding behaviour. He then suggested that each pair of vulture species was separated ecologically from the other pairs, primarily by eating different parts (tissues) of the carcass - the two of griffon vulture species eating soft tissues, the lappet-faced and white-headed vultures eating skin and tendons, and the hooded and Egyptian (Neophron percnopterus) vultures eating small scraps and pecking between bones. The other isolating mechanisms that he suggested may separate the species within each pair, were different nesting requirements, time of arrival at carcasses and interspecific aggression. Houston (1975), while largely confirming Kruuk's conclusions, suggested that the white-headed vulture may be feeding primarily on carcasses not utilized by any other vulture species.

Thus both Kruuk and Houston were assuming that all the common East African vulture species (with the partial exception of the white-headed vulture) feed on the same common food source - large bovid carcasses. Having assumed this, they therefore studied vulture behaviour in the context of how they may avoid competition with each other at this one food source.

The aim of this chapter is to consider the total scavenging behaviour of the common species of African vultures, and in the light of the results obtained during the

present study, to question whether Kruuk (1967) and Houston's (1975) original assumption, regarding their food source, is correct. Thereafter, the roles played by crows, kites, eagles and the marabou stork (Leptoptilos crumeniferus) as scavengers will be discussed, as well as their dependence on this mode of living.

METHODS

Prior to the main study, preliminary observations were made from hides of vultures feeding at five carcasses. Resulting from this preliminary study and using Kruuk (1967) as a guideline, data sheets were compiled to record, at five minute intervals, feeding behaviour, aggressive interactions and the positions of vultures in relation to the carcass. Using these data sheets, a further 17 carcasses at which vultures fed were observed from the time of arrival to the eventual departure of the vultures. A total of 62 h was spent recording in detail the feeding behaviour of some 1408 vultures at these carcasses. More carcasses with vultures were seen, however they could not be watched from hides, so general observations were made from a distance.

Working on the assumption that the main source of food for griffon vultures is ungulate carcasses that have died of causes other than predation (Houston 1974a), an attempt was made to simulate these conditions as closely as possible with the carcasses put out. Most ungulates were shot in the head, but when the skin was torn open on the body surface, the bait was laid out so that the larger hole was on the undersurface. Thus carcasses never had more than a bullet hole on the upper surface. This therefore decreased the vultures' chances of finding carcasses by noticing blood, and more important, once feeding, the hole was small enough to prevent them from using it to gain access to the soft tissues inside. The weight of the carcass prevented vultures from using the hole in contact with the ground until most of the viscera had been removed and after they had torn the carcass open themselves.

At small carcasses (< 100 kg) it was usually possible to record the entire

sequence of behaviour, from the first arrivals to the last departure. At very large carcasses however, vultures and hyaenas took three or more days to finish the carcass. Therefore it was impossible to watch vultures all day and hyaenas all night, so during the day observations were made during every alternate hour. This lowered the number of feeding observations per bird present, however as the analysis of the results is in terms of the relative frequencies of certain behaviours, this should not alter the picture between the species. An occasional exception to this rule was if one of the less common species arrived during an "off" period. Additional records were then taken to increase the number of observations of such species. As the behaviour of all the species was being recorded this should not affect the results much, if anything being a biased in favour of these less common species.

Definitions

Numbers

When recording the feeding behaviour and positions of over 50 birds at a carcass, it is impossible to account for each individual bird at any one time. However, it is possible to see what isolated or individually identifiable birds are doing, as well as estimate a group size and their predominant forms of behaviour. Therefore, to facilitate the recording of all birds at once, code numbers were used to represent a range of numbers, each range having a fixed average value to be used in the final calculations. Between each observation the total number of birds was counted, then the coding checked to see if every bird was accounted for. The coding is given in Table 9.

Positions

All the birds present were recorded in terms of their positions in relation to the carcass. Therefore these figures gave the positions of the birds, as well as the numbers of each species present and hence the time spent at the carcass. The classification is given in Table 10. Although attempts were made to record all this information, in bush country it was however often not possible to see

Table 9 : Code used while recording the numbers of vultures feeding at carcasses in the Transvaal and southern Zimbabwe.

CODE NUMBER	NUMBER OF VULTURES	AVERAGE NUMBER OF VULTURES.
1-4	1-4	1-4
5	5-7	6
6	8-10	9
7	11-14	12,5
8	15-25	20
9	> 25	30

Table 10: Classification of the positions of vultures in relation to the carcass in the Transvaal and southern Zimbabwe.

1	:	<	3	m	from the carcass
2	:	3-10	"	"	"
3	:	10-50	"	"	"
4	:	> 50	"	"	"
5	:	In Trees			

more than 30 m from the carcass. Nevertheless vultures were still counted at this distance, but in the final analysis it was decided that both the accuracy and the relevance of these observations were questionable, so they were discarded.

Behavioural categories

The types of feeding behaviour were based on Kruuk (1967) but with some modifications and additions. They are classified as follows :

- Soft: Feeding on meat and other soft tissues at the carcass
- Skin: Feeding on skin - tearing it or stripping meat off it
- Strip: Stripping meat off nearly clean bones
- Loose: Feeding on large loose pieces of meat (soft tissues)
- Bones: Stripping bits off small loose bones
- Bits: Pecking minute bits off the ground
- Chips: Picking up and swallowing small bones (chips)

This classification differs from Kruuk's primarily in that his one stripping category is divided in two - "strip" and "skin", and the "chips" category has been added. A bird was recorded as behaving in a particular manner if it was actually feeding at the end of the five minute period. If it happened to look up briefly, it was still recorded as feeding. Birds involved in picking up small bits were recorded as such if they were actively searching, although the actual number of "bites" they achieved was far lower than for the other types of behaviour.

Aggressive interactions

As with feeding behaviour, aggressive interactions between individuals at the carcass were only recorded if they occurred on the second at the end of each five minute period. At all interactions between any of the scavengers, the species involved were classified as aggressor or defender, and the result of the interaction was recorded. For these observations the two griffon vultures' records were divided into those for adults and juveniles.

RESULTS

General pattern of feeding behaviour

The order of arrival of the different vulture species will be discussed in more detail later. Suffice it to say at this stage that apart from a bird possibly pecking at one eye, the first species to start feeding in any significant way were griffon vultures. The most dominant birds (one or two) would immediately open the carcass via the anus, soon managing to insert their heads deep inside the carcass. Other birds would peck out the eyes and tongue (if possible), while some would peck ineffectually at the bullet hole and the soft part of the belly. As the meat from the belly, hips and thighs was removed, the skin around the anus was rapidly torn open as far as the belly. At this stage many more vultures could start feeding (approximately eight) and this became a frantic mass of birds feeding, or trying to feed. While this was happening, the loosely attached internal organs could occasionally be pulled free and the waiting vultures would try to grab these pieces of meat or retrieve them from the mouth of the bird in possession. However this seldom happened to birds feeding on muscle inside, because they swallowed as they fed and did not bring out pieces to feed on - for obvious reasons.

Once the frantic feeding all over the carcass began, the skin was rapidly torn and turned inside out, remaining attached to the head and feet. At this stage the skeleton had been stripped of meat and the bared ribs were clearly visible. The transformation from a torn open fleshed carcass to one, virtually stripped of all soft tissues, was extremely rapid, taking two to three minutes. It soon became evident that the feeding behaviour of vultures at these stripped carcasses was quite different from those with flesh on them. They were therefore classified as fleshed and clean carcasses respectively, the latter having less than 10% of the soft tissues left. From a distance it was not possible to say exactly how much flesh was left on these clean carcasses. However they were usually characterized by having the skin pulled off the body and upper limbs,

and with ribs clean and individually exposed. When the skin was not everted, it no longer appeared taut, but lay limp and followed the contours of the skeleton.

The above pattern was typical for griffon vultures feeding on small carcasses. However on larger carcasses the pattern was different. On medium-sized carcasses (100-300 kg) the vultures were eventually able, by climbing right inside the carcass, to devour the soft tissues, once again starting at the anus and slowly tearing it open between the hind legs up to the belly. In this they were occasionally aided by jackals, but their help was not imperative. Once the carcass was clean the sagging skin encased the skeleton, but it was not turned inside out as with small carcasses.

On very large carcasses (> 300 kg), the thick skins prevented vultures from entering even via the anus. They therefore relied on hyaenas to open large carcasses for them, but even when the belly was open, their movements inside the carcass were restricted. They could remove the flesh from the hips, thighs, back and ribs and all the internal organs, however the meat of the neck and upper shoulders remained inaccessible and they required hyaenas to open the carcass further. For this reason it was not feasible to define clean carcasses as having <10% soft tissues left, because although there may have been as much as 30% left, it was not necessarily accessible to the vultures and therefore in terms of feeding behaviour, not there. Therefore the difference between fleshed and clean carcasses was that on the latter there were little or no soft tissues available to vultures. The distinction here was more difficult to make than with small carcasses, as on several regions of the body there may have been flesh available and therefore the change over was less defined. Nevertheless the feeding behaviour at these two categories of carcasses will be seen to be distinctly different.

Order of arrival at carcasses

The different species of birds recorded to arrive first at carcasses at which vultures subsequently fed are listed in Table 11. These results are separated

into those for nature reserves and farms as the scavenger fauna was quite different in these areas. The subsequent order of arrival of species is less easy to define because once any species had found a carcass, many other birds soon followed. Thus within five minutes of the arrival of the first vulture an average of 12,3 (range 2 - 39) had arrived, and within 10 min an average of 20,3 (range 2 - 68) had arrived.

The order of arrival of vultures also depended on the locality used and the size of the carcass. The number of species of scavenging birds was much greater in the nature reserves than on the farms, although crows (Corvus albus) were only recorded on the farms. Very large carcasses lasted for so long (up to three days continuous feeding) that all species of scavengers came and went in no particular order, the only consistent factor being that griffon vultures were continuously present. Nevertheless, the most characteristic pattern for small carcasses in the nature reserves was as follows : The white-headed vulture or one of the scavenging eagles - the bateleur (Terathopius ecaudatus) or the tawny eagle (Aquila rapax) - would arrive first. It was shortly followed by a lappet-faced or white-backed vulture, with the Cape vulture arriving soon after. The above sequence could take anything from five to twenty minutes. Hooded vultures always took over 20 minutes to arrive, by which time other species had already started to leave.

White-headed vultures and the scavenging eagles were usually the first to leave, followed by those griffon vultures which had already fed. Vultures often stayed for some time at the remnants of a carcass, occasionally pecking at it or at scraps on the ground. These last species to leave were usually lappet-faced and hooded vultures as well as a few juvenile griffon vultures.

Numbers of vultures

The numbers of the different species of vultures recorded to feed at carcasses are listed in Table 12. The differences in the species recorded to feed in each area, relate primarily to the species that occur there. However, when

Table 11: Bird species which were recorded to be the first to find a carcass at which vultures subsequently fed in the Transvaal and southern Zimbabwe.

	n	BATELEUR	WHITE-HEADED	TAWNY EAGLE	WHITE-BACKED	CAPE	PIED CROW
Nature Reserves	8	2	2	2	2		
Farms	8			1	3	1	3

Table 12: Average and total numbers of the vulture species recorded to feed at carcasses in different parts of the Transvaal and southern Zimbabwe.

AREA	CARCASS STATUS	n	CAPE	WHITE-BACKED	LAPPET-FACED	WHITE-HEADED	HOODED	TOTAL
Nature Reserves	Fleshed	7	55 (7,9)	307 (43,9)	16 (2,3)	7 (1)	4 (0,6)	389
	Clean	10	57 (5,7)	307 (30,7)	20 (2,0)	6 (0,6)	16 (1,6)	406
Farms I	Fleshed	6	21 (3,5)	305 (50,8)	2 (0,3)			328
	Clean	3	10 (3,3)	77 (25,7)	6 (2)			93
Farms II	Fleshed	5	187 (37,4)	4 (0,8)	2 (0,4)			193
	Clean	3	57 (19)	1 (0,3)				58

Figures in parentheses are the average numbers of each species per carcass. Farms I and Farms II are those farms where the predominant griffon vultures are white-backed and Cape vultures respectively.

Table 13: Results of aggressive interactions between species feeding together as carcasses in the Transvaal and southern Zimbabwe.

SPECIES	RESULT	JACKAL	LAPPET-FACED	CAPE ADULT	CAPE JUV.	W-B ADULT	W-B JUV.
Jackal	Won			2			
	Lost			1			
Lappet-faced	Won				6	1	
	Lost				1		
Cape Adult	Won	1		24	2	5	7
	Lost	2		24		1	
Cape Juvenile	Won		1		1	1	4
	Lost		6	2	1	1	1
White-backed Adult	Won			1	1	6	11
	Lost		1	5	1	6	1
White-backed Juvenile	Won				1	1	26
	Lost			7	4	11	26

comparing the relative numbers of Cape vultures on the white-backed vulture farms I and vice versa, the Cape vultures are seen to be significantly more common in the white-backed vulture areas than the white-backed vultures are in their areas. These results are true for both fleshed ($\chi^2 = 4,9$; $df = 1$; $p < 0,05$) and clean carcasses ($\chi^2 = 4,7$; $df = 1$; $p < 0,05$). In fact at Olifantshoek which has a Cape vulture breeding colony, no white-backed vultures were ever seen, whereas at Vaalboschfontein, which has a white-backed vulture breeding colony, on one occasion six Cape vultures were seen, one of which had been ringed at Olifantshoek (Mundy In litt.).

This pattern of Cape vultures foraging long distances away from their colonies (or roosting sites) is further illustrated in Fig. 10. Here the relative composition of adults to juveniles in the group is compared with the total number of the species and the approximate distance to the nearest roosting site. The figure clearly illustrates that adult birds dominate the group near the roosting sites, while juveniles forage further away and thus are the predominant age group at carcasses long distances away from the colonies. The age group compositions of the three areas are significantly different ($\chi^2 = 108,5$; $df = 2$; $p < 0,001$).

Feeding behaviour

The feeding behaviour of the different vulture species has been divided into a number of categories in order to illustrate their manner of feeding, the food value of their behaviour, the efficiency of their feeding behaviour in terms of their positioning around the carcass and their utilization of time. The different vultures and their characteristic manners of feeding are illustrated in Fig. 11 and 12.

Manner of feeding

The results for the different ways in which vultures and pied crows fed at carcasses are illustrated in Fig. 13. Using the Chi-squared statistic, the results for the two species of griffon vultures and the lappet-faced vulture are

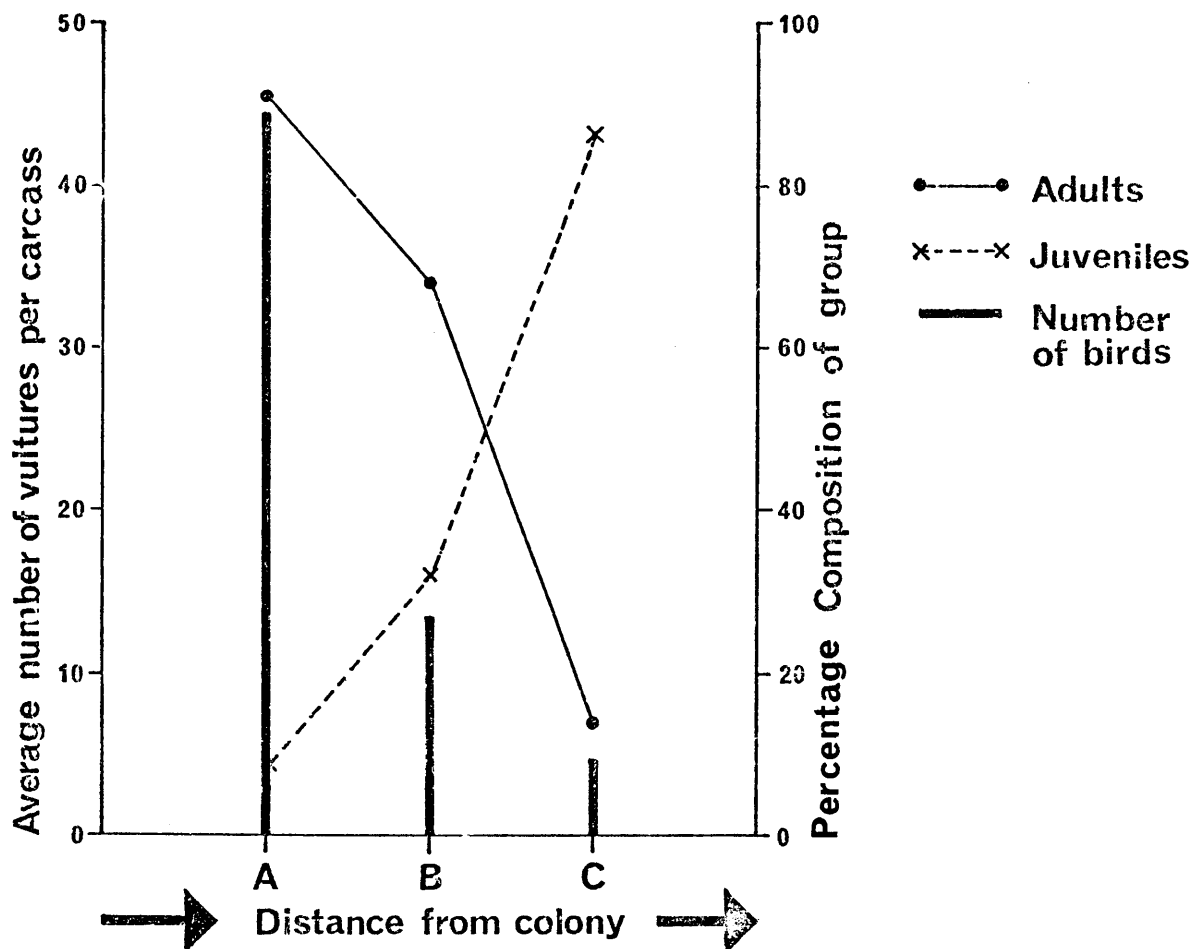


Figure 10 : The effect of distance from the nearest colony or roosting site on the average numbers and adult/juvenile composition of Cape vultures (*Gyps coprotheres*) that visited carcasses in different parts of the Transvaal and southern Zimbabwe : A - Olifantshoek and Tweeputkoppies (<40 km); B - Eastern Transvaal Lowveld - Timbavati, Sabi Sand and Kruger National Park (75-125 km); Vaalboschfontein and Lone Star Ranche (240-350 km).

	Adults	Juveniles	Months	n
A	265(60 - 20)	26(10 - 0)	1,5,6,10,12	6
B	63(13 - 0)	29(10 - 0)	3,8,9,10,11	7
C	4(2 - 0)	24(6 - 0)	3,5,6	6

Figures in parentheses give the ranges of the numbers seen when any species of vulture was recorded to feed. "Months" represent the months of the year during which observations were made.

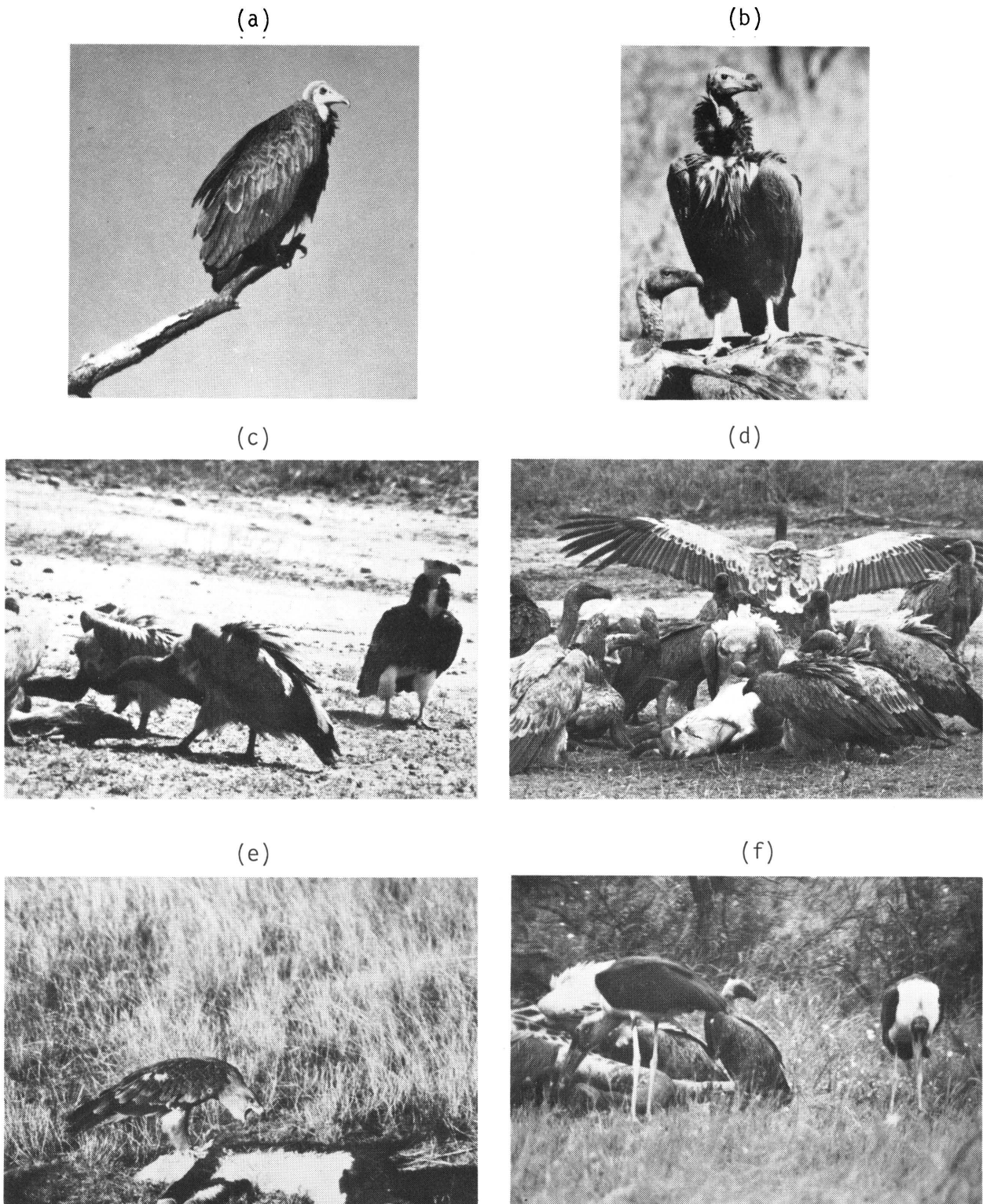


Figure 11 : The major avian species recorded to scavenge at carcasses in the Transvaal and southern Zimbabwe : (a) hooded vulture (Necrosyrtes monachus) - note the narrow bill (b) lappet-faced vulture (Torgos tracheliotus) above - note the heavy bill- and Cape vulture (Gyps coprotheres) (c) white-headed vulture (Trigonoceps occipitalis) (d) Griffon vultures - Cape vulture (left) and white-backed vultures (Gyps africanus), juvenile in foreground. (e) Tawny eagle (Aquila rapax) (f) Marabou storks (Leptotilos crumeniferus) in foreground.

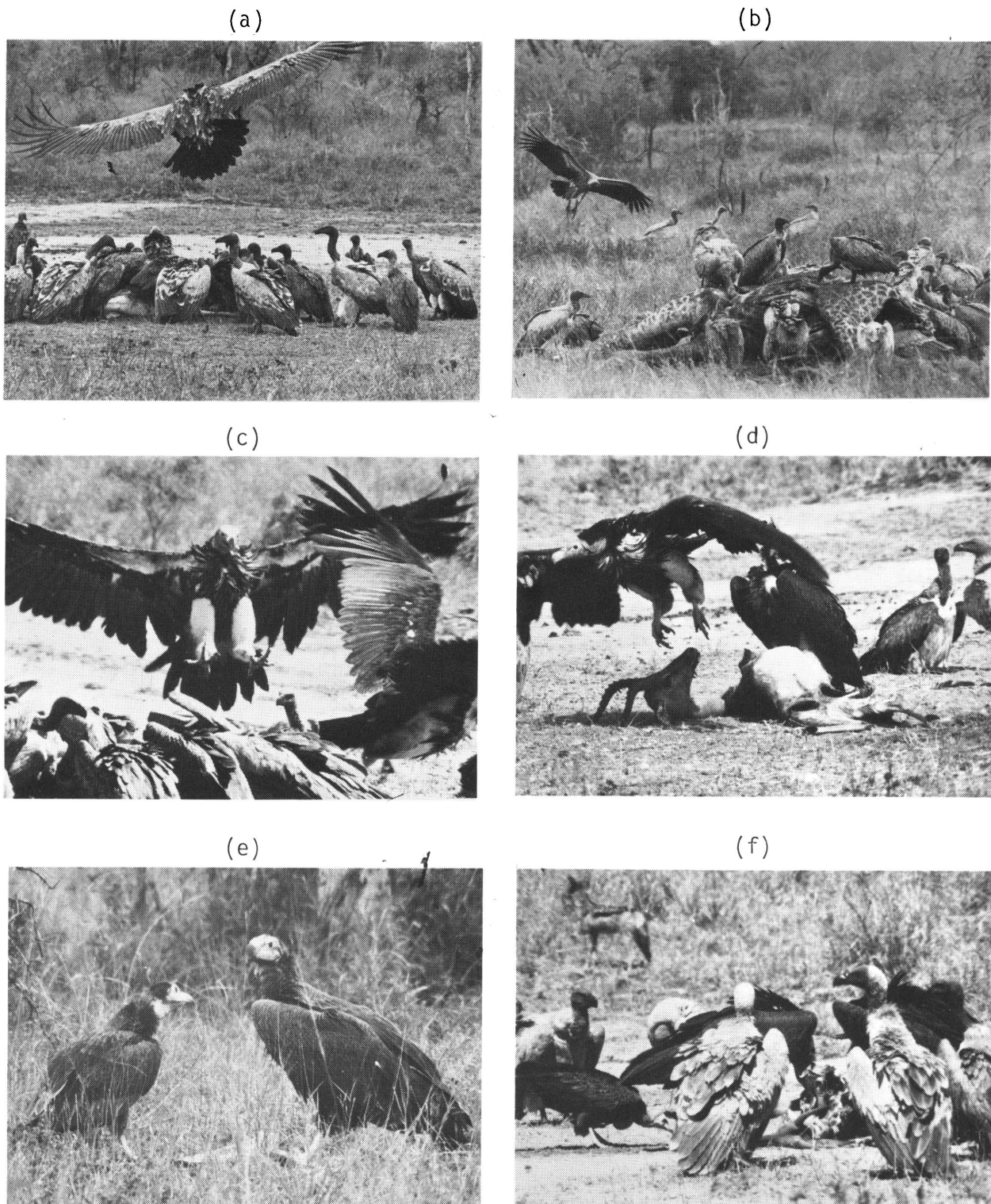


Figure 12 : Typical examples of vulture feeding behaviour : (a) Griffon vultures (*Gyps spp.*) crowding over an impala (*Aepyceros melampus*) carcass (b) Griffon vultures feeding on top of and inside a giraffe (*Giraffa camelopardalis*) carcass (c) lappet-faced vulture (*Torgos tracheliotus*) flying into a feeding group of griffon vultures (d) lappet-faced vulture guarding an impala carcass (e) lappet-faced and white-headed vulture (*Trigonoceps occipitalis*) standing aside and feeding on a loose giraffe scapula (f) lappet-faced vulture tearing at an impala carcass while hooded vulture (*Necrosyrtes monachus*) pecks close by and griffon vultures and a jackal (*Canis mesomelas*) stand aside.

all significantly different ($p < 0,001$). Similarly, within each of these species the differences in feeding behaviour at fleshed and clean carcasses are all significant ($p < 0,001$). When comparing the results for white-headed and hooded vultures and the pied crow, the sample sizes for the different categories of behaviour were always too small to test individually, so these categories were divided into two groups - feeding at the carcass; feeding away from it. Using these two divisions, there were no significant differences ($p < 0,8$) between any of these three species, nor within a species at the two different classes of carcasses. This was because at all times all the three species fed primarily on loose scraps away from the carcass.

Food availability

In Fig. 14 the results of the feeding behaviour illustrated in Fig. 13 are grouped together for all species to demonstrate the major differences between methods of feeding at large and small carcasses when fleshed and when clean. In all cases the griffon vultures represent over 90% of the birds present, so the changing patterns cannot be ascribed to changes in species structure. In order to simplify the figure and emphasise the basic changes in behaviour, the seven types of behaviour have been consolidated into four, essentially in terms of food value. Thus "loose" has been combined with "soft", and "bones", "bits" and "chips" have all been grouped together.

Using the Chi-squared statistic, the differences in feeding behaviour at fleshed and clean carcasses are highly significant ($p < 0,001$) for both large and small carcasses. The biggest difference is the change from mainly "soft" at fleshy carcasses to "strip" at clean ones, which directly relates to the decreased availability of soft tissues at clean carcasses. Most of the differences between large and small carcasses can be explained by the period of transition in the status of a carcass, being longer for large carcasses than small ones. Thus, during this transition on large carcasses, the less dominant birds "stripped" exposed bones while the rest still ate soft tissues, whereas on small carcasses,

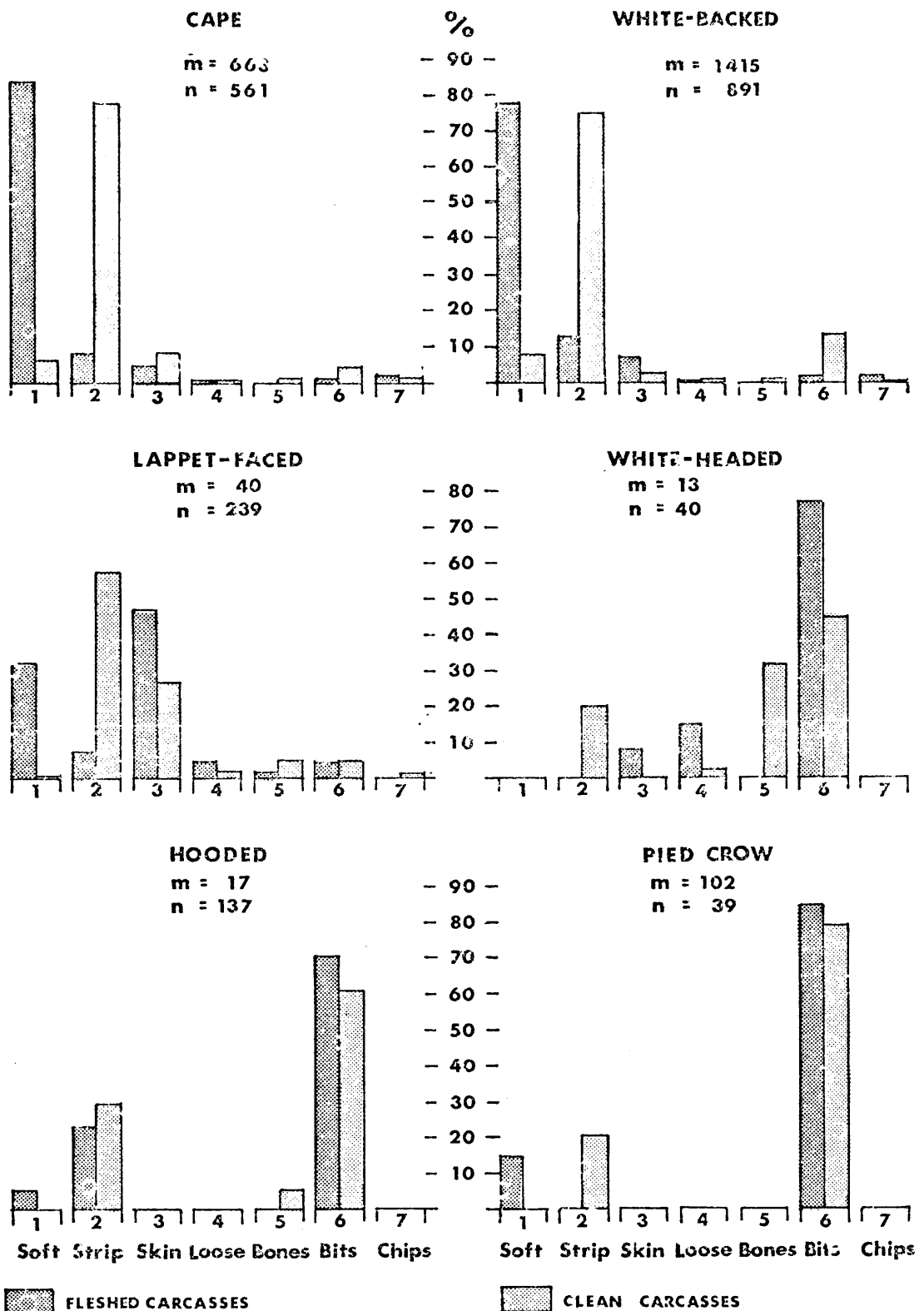


Figure 13 : Feeding behaviour of five vulture species and the pied crow (*Corvus albus*) at carcasses in the two different stages of decomposition in the Transvaal and southern Zimbabwe. m and n = total number of observations per species at fleshed and clean carcasses respectively.

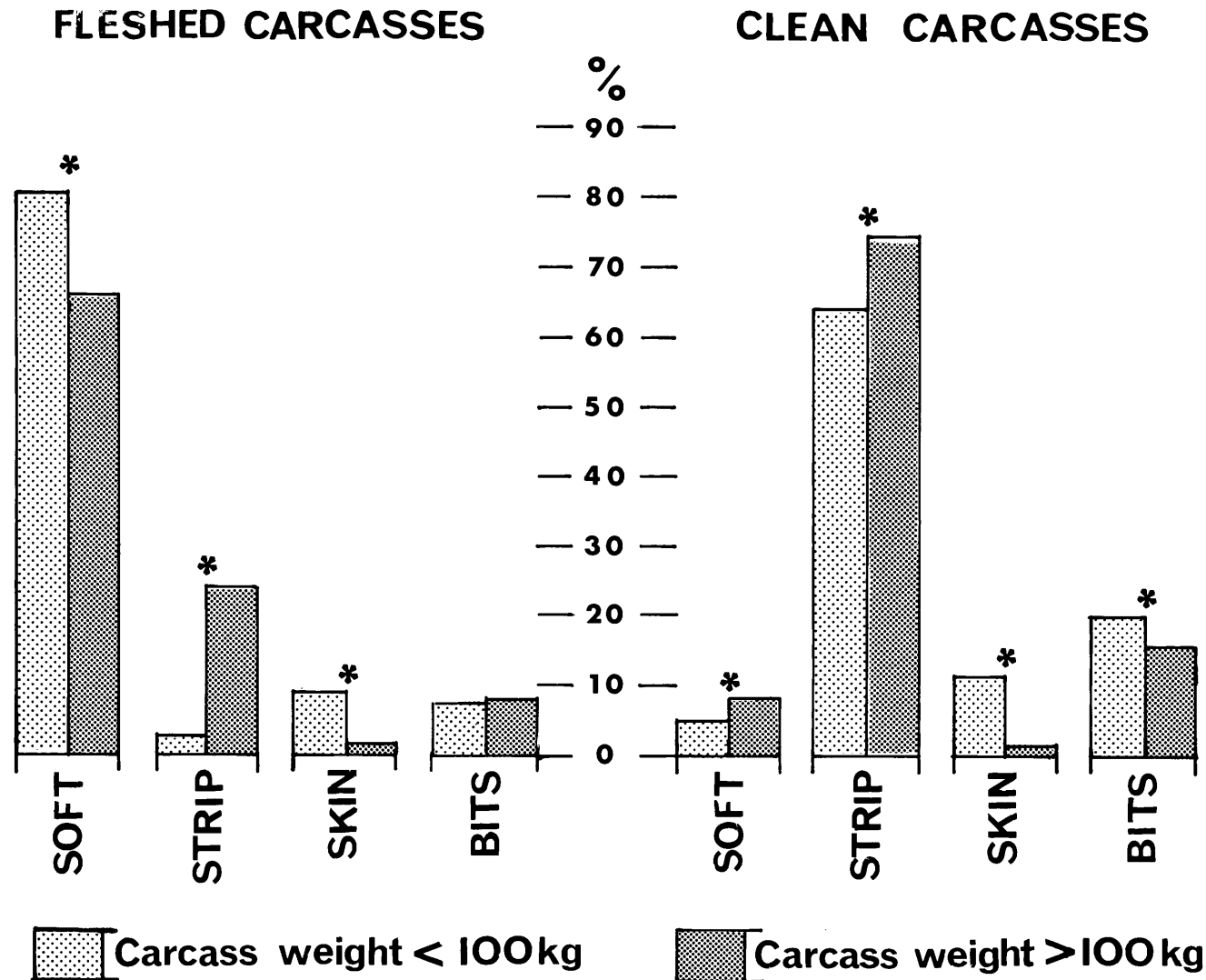


Figure 14 : Total observations of the feeding behaviour of all vultures at large and small carcasses in the two different stages of decomposition in the Transvaal and southern Zimbabwe. Methods of feeding are grouped according to potential food value. Using the chi-squared statistic, statistical significance is indicated as follows: * $p < 0,001$.

nearly all the vultures did one or the other. Whatever the status of a carcass, skin was eaten more on the small carcasses, probably because it was thinner and therefore easier to tear. Feeding on "bits" hardly differed at all on different sized carcasses, but definitely increased at clean carcasses ($\chi^2 = 104, 7; df = 1; p < 0,001$). This need not necessarily reflect an increased availability of bits to eat, but rather a decrease in the preferred food items, with the hungry birds now feeding on bits as a last resort.

Nutritional value of feeding behaviours

In Fig. 15 the different feeding behaviours have been selectively grouped together to illustrate the nutritional benefit to each species. This grouping is the same as in Fig. 14, except here "strip" and "skin" have also been put into one group. This is because their nutritional value is probably much the same, and because no distinction was made between tearing meat off skin and eating the skin itself. One cannot assign definite nutritional values to these three groups, however one can put them in order:

(i) "Soft" must rate the highest as soft tissues are the most plentiful and available food source and therefore can probably be ingested at the greatest rate.

(ii) "Strip" rates second because the food is less plentiful, takes more effort to remove and therefore is probably ingested in smaller quantities at a slower rate.

(iii) "Bits" rates last, because the food is the least abundant and also occurs in the smallest quantities. Therefore more time is spent searching for it and when found, the amount consumed is small.

Using the Chi-squared statistic, the results for the two species of griffon vultures and the lappet-faced vulture are all significantly different ($p < 0,05$) from each other, and within each species at fleshed and clean carcasses. In the cases of the hooded and white-headed vultures, because of the small sample sizes, the analyses of the results are the same as in Fig. 13. There are

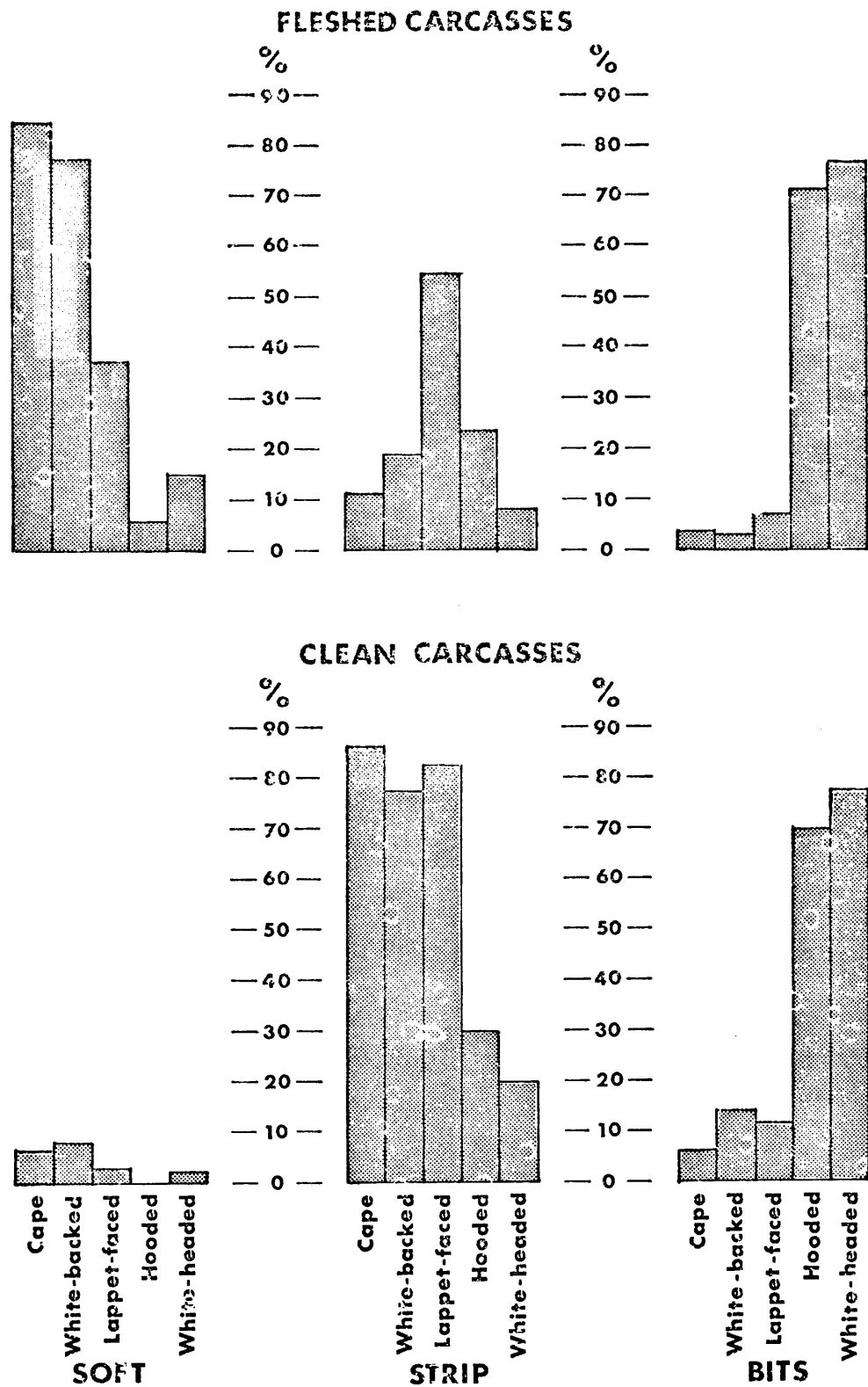


Figure 15 : Feeding behaviour in terms of food value of the five vulture species feeding at carcasses in the two different stages of decomposition in the Transvaal and southern Zimbabwe.

therefore no significant differences ($p < 0,3$) in behaviour. However when these two vultures are tested together against the other species of vultures, the results are always significantly different ($p < 0,001$). Therefore at fleshed carcasses, the griffon vultures were by far the most efficient feeders, followed by the lappet-faced, then the hooded and white-headed vultures together. Probably all vultures feeding at fleshed carcasses gained more food per unit effort of a particular feeding behaviour than at clean ones. This is logical for "soft" and "strip" (unless skin is actually being eaten), and probably also applies to "bits". This is because all birds waiting to feed at the carcass will pick up any reasonable sized bits lying around, leaving only minute bits to be picked up at the end.

At clean carcasses, although there is much less food available, the order of efficiency of the species is much the same. The only difference being that with little or no soft tissues left to eat, the griffon vultures are reduced to the level of the lappet-faced vulture.

Positioning around the carcass

The changing density of vultures around different carcasses has been assumed to reflect both the motivation of these vultures to feed, and the availability of food at the carcass. From watching vultures feeding at carcasses, the following conclusions were drawn in terms of their distances from the carcass :

(i) < 3 m from the carcass:- the motivation of these birds to feed is very high. They are either actively feeding, or feeding is imminent. Species which seldom feed on the carcass itself, still feed close to it to increase their chances of finding scraps.

(ii) 3-10 m from the carcass:- these birds can be divided into three groups, (a) those which have finished feeding but have not departed, (b) those feeding further away from the carcass, and (c) those which still wish to feed, but there is not yet space for them around the carcass. From this, it is suggested that most birds within 10 m of the carcass are intent on feeding from it, those within three metres of it being more successful or dominant to those further away.

(Three metres was subjectively chosen to include those birds feeding at the carcass, as well as those crowding closely around it).

The results for the positioning of vultures around carcasses in the nature reserves are presented in Fig. 16. This figure only illustrates the results for nature reserves, because although those for the farms were essentially the same, not all five species of vultures were present. Similarly, all subsequent figures illustrating competition between the five vulture species are only drawn from the results in the nature reserves. In this and the following figure, the Z proportion is used to test for significant differences in the densities of vultures.

At all carcasses the density of birds was significantly higher ($p < 0,001$) when they were fleshed than when they were clean. This is to be expected considering the amount of available food and hence the chances of feeding successfully. This applied equally to birds within three metres, as within 10 m.

At any one carcass the number of birds within three metres was significantly higher ($p < 0,001$) than that 3 - 10 m away. This was true for all carcasses except small fleshed ones where there were no significant differences ($Z = 1,34; p < 0,1$). This was probably because at these small carcasses the urgency to feed was so great, that even those not able to feed at the carcass, crowded closely around, waiting for an opportunity to do so.

The number of vultures within three metres of the carcass was significantly greater ($p < 0,001$) at large carcasses than small ones. This is to be expected, because there is more food available at large carcasses, more space for vultures to feed in, and the area within three metres of a large carcass is greater than that around a small carcass.

This pattern was reversed when considering the number of birds 3-10 m from the carcass. At large carcasses the numbers were significantly lower ($p < 0,05$), possibly because more birds could stand within three metres and also, with so much food available, there may have been less urgency to feed, so many birds

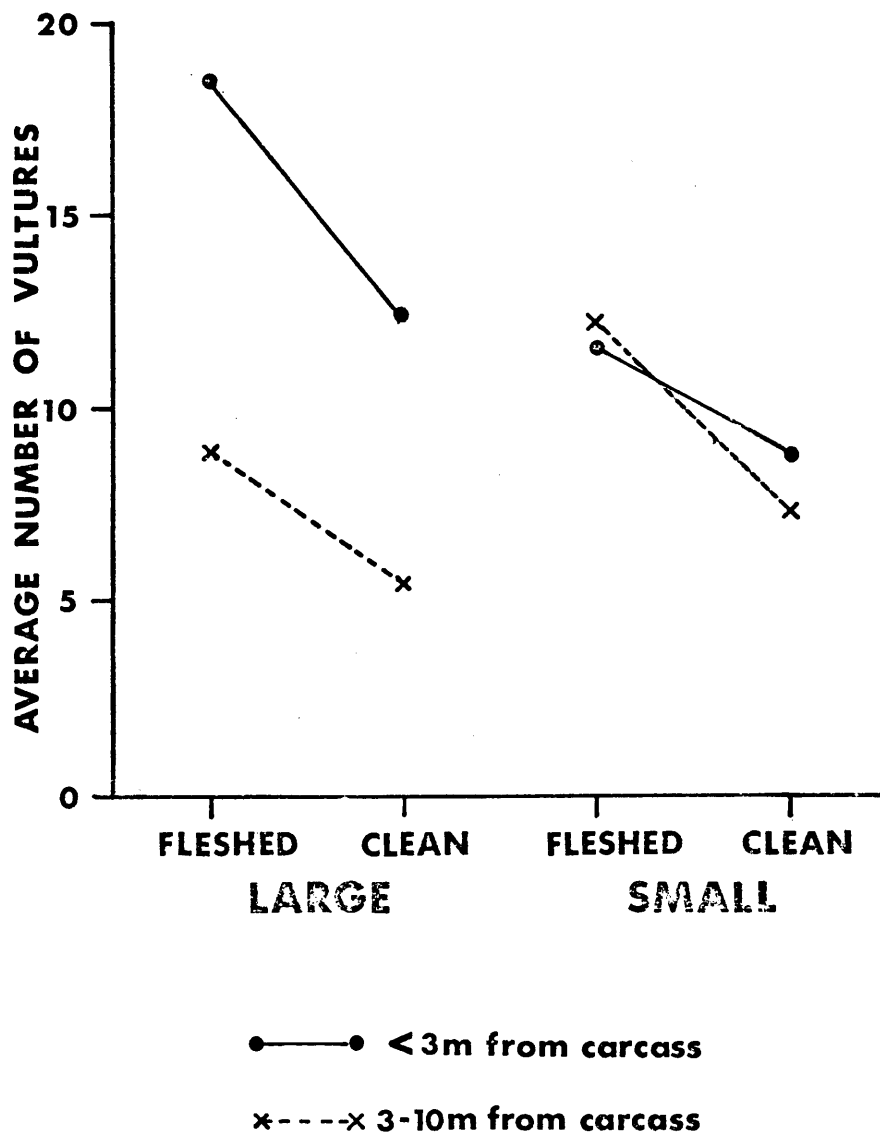


Figure 16 : Relative densities of vultures around large and small carcasses in the two different stages of decomposition, in the nature reserves of the Transvaal and southern Zimbabwe.

waited further away or in the trees.

With reference to Fig. 16, it is apparent that hungry vultures group tightly around a carcass in order to feed, particularly when there are soft tissues available. One can therefore assume that those vultures feeding at or close to the carcass (< 3m), are competing more successfully for this food source than those further away. Working on this assumption, Fig. 17 has been drawn to illustrate the relative abilities of the different vultures to compete for positions around the carcass.

In Fig. 17a one can see that of the two griffon vulture species, Cape vultures competed more successfully as they always had over 50% of their own number within three metres of the carcass. White-backed vultures were also "successful" at large carcasses, however at small fleshed carcasses, where competition for positions was the highest (Fig. 16), they were significantly less successful than the Cape vultures ($Z = 4,5; p < 0,001$).

The differences between these two species are probably more a consequence of their differences in size and total numbers than in their feeding behaviours, which are very similar (Fig. 13). At all carcasses observed during this study there were always more vultures present than were required to consume the carcass. Therefore a number of the smaller griffon vultures were necessarily unsuccessful at every carcass. As the Cape vultures are larger, and their numbers were always much lower than those of the white-backed vultures, they were always successful, while many of the latter species were unsuccessful and lowered the average success rate of the species. Therefore, for comparisons with other vulture species, these two species can essentially be regarded as one, with the Cape vulture representing the larger and more dominant members of the group. This has been done for Fig. 17b and 18.

In Fig. 17b both sizes of carcasses are considered together as the sample sizes were too small to separate them and within each species the results were very similar. At fleshed carcasses the hooded vultures were the most successful at

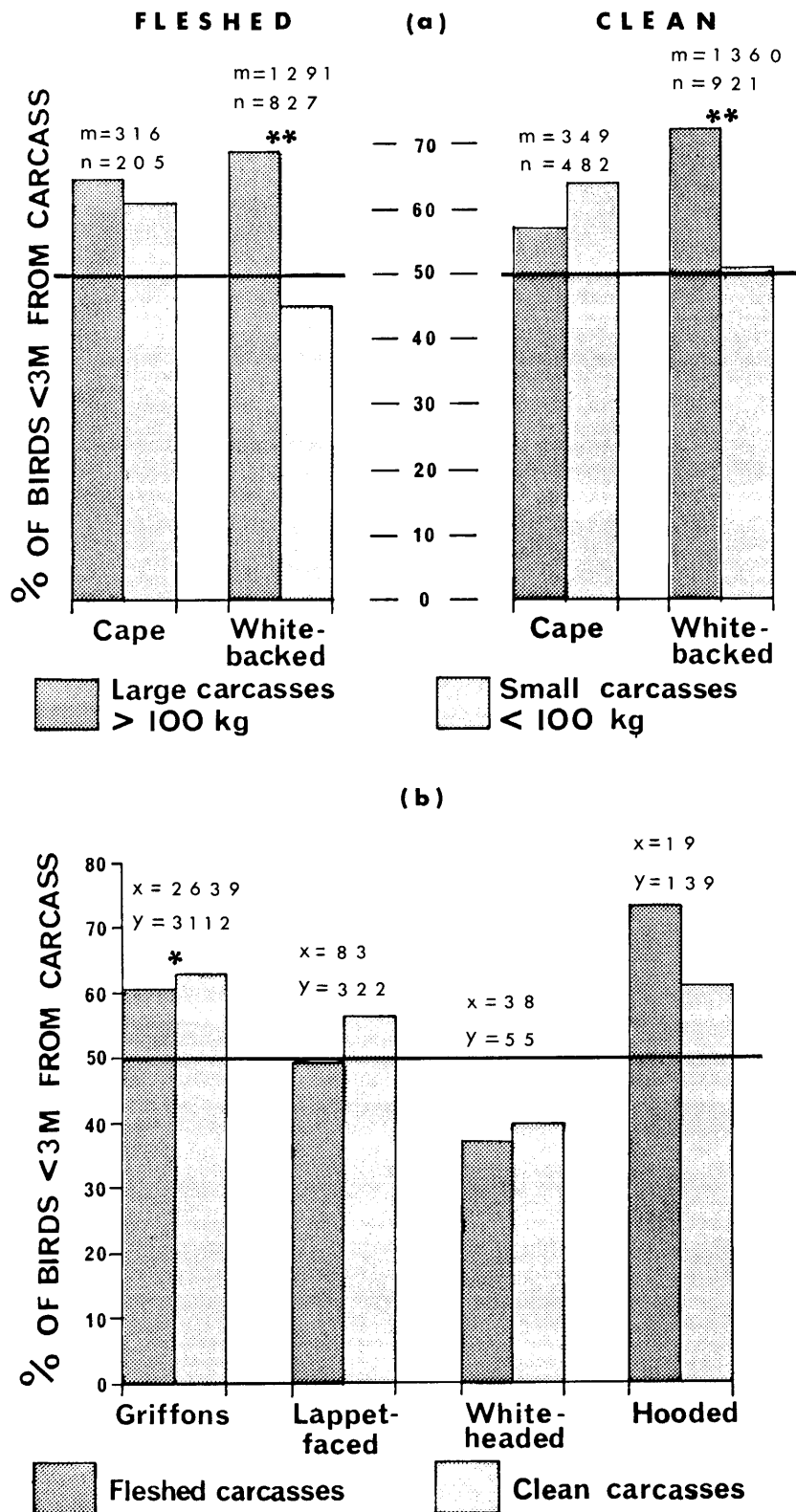


Figure 17 : Percentages of those vultures within 10m of carcasses, that are within three metres of the carcass. Observations are for carcasses in the two different stages of decomposition in the nature reserves of the Transvaal and southern Zimbabwe. m & n and x & y are the number of observations per species at large and small, and fleshed and clean carcasses respectively. Using the Z proportion, statistical significance is indicated as follows : * $p < 0,05$; ** $p < 0,0001$.

remaining close to the carcass, being within three metres of it for over 70% of their observations. They were followed by griffon, lappet-faced and white-headed vultures, the last two having under 50% within three metres of the carcass. At clean carcasses the order of success was the same. These results are all significantly different from each other ($p < 0,05$), except between hooded and griffon vultures at fleshed carcasses, and between the first three species at clean carcasses.

Usage of foraging time

Three different aspects of the foraging efficiency of the five vulture species are illustrated in Fig. 18. The results shown in the top and bottom histograms of this figure cannot be tested for significant differences, because not all species were present at all carcasses, nor were the periods of observation at each carcass the same. Nevertheless the results are still believed to be indicative of the general trends in the feeding efficiency of each species.

In the top histogram (a), the average amount of time spent at the carcass per individual of each species is indicated. At fleshed carcasses the griffon vultures both spent more time than the other three species. However, at clean carcasses the lappet-faced and Cape vultures spent far more time than the others. All the species spent more time at clean carcasses than fleshed ones.

The utilization of the time spent at carcasses by each species is illustrated in the middle histogram (b). These results have been tested for significant differences, by using the Z proportion. This is feasible because they are independent of the variables mentioned above. The results for griffon vultures as a group and the other species independently are all significantly different ($p < 0,001$) from each other, except between lappet-faced and white-headed vultures at fleshed carcasses ($Z = 0,34$; $p < 0,4$).

Hooded vultures made the most efficient usage of their time, as they spent over 85% of their time feeding at both fleshed and clean carcasses. White-backed

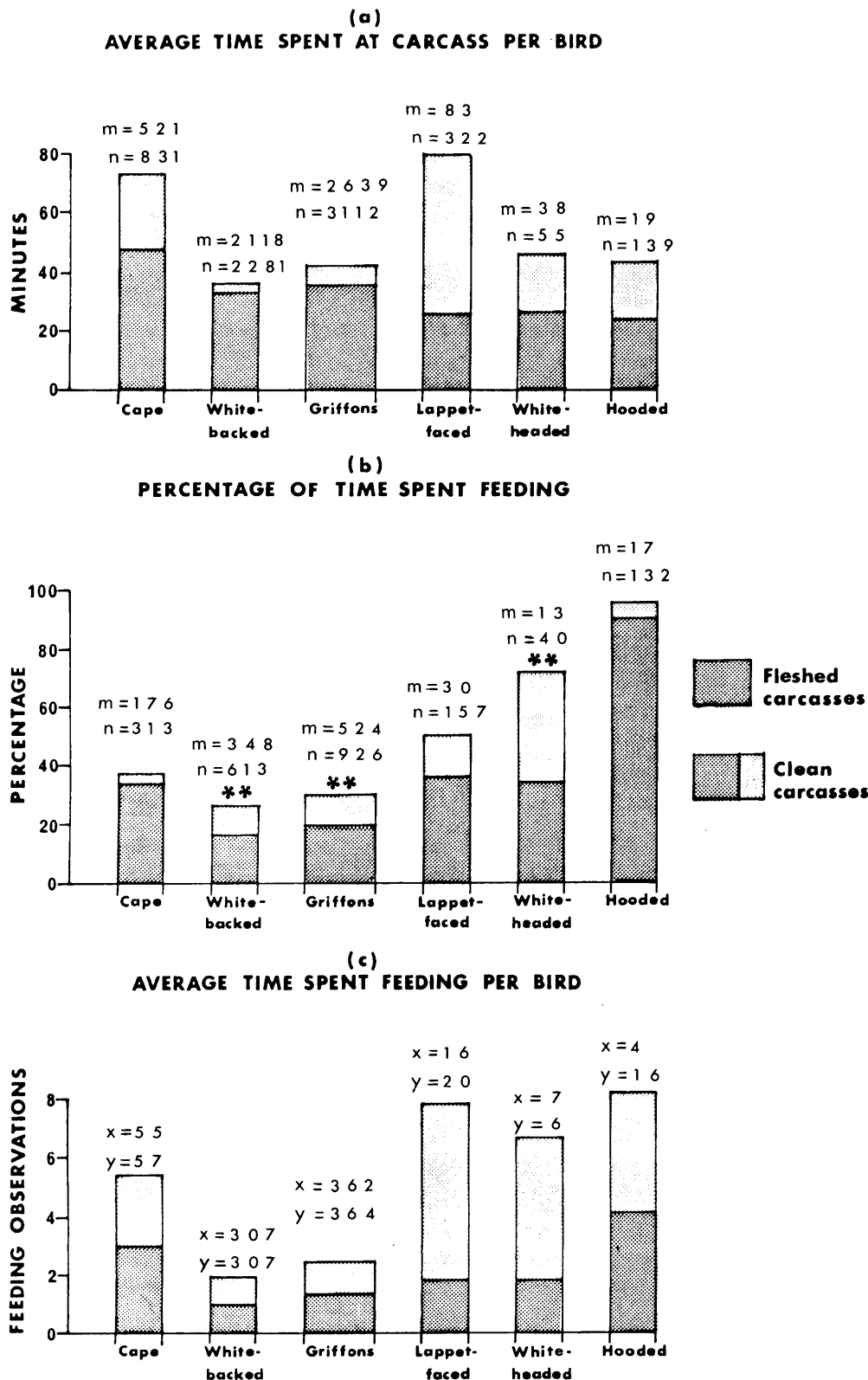


Figure 18: Aspects of the foraging efficiency of the five vulture species at carcasses in the nature reserves of the Transvaal and southern Zimbabwe:- (a) Time spent at carcasses, (b) percentage of time spent feeding, (c) time spent in feeding. m & n and x & y represent the number of observations, and the number of individual vultures, at fleshed and clean carcasses respectively. In (b) using the Z proportion, statistical significance is indicated as follows:-** $p < 0,001$.

vultures were in this respect, always the least efficient species.

The final histogram (c) simply states the average number of feeding observations per individual. Thus while the top two histograms illustrate the trends in foraging strategy of the species, this lower one gives an absolute comparison between the species in terms of the average amount of time each individual vulture spent feeding.

At fleshed carcasses, the hooded vulture achieved the highest average number of feeding observations despite spending the least amount of time at them. It was followed by the Cape vulture, with the others having much less success.

At clean carcasses the lappet-faced, white-headed and hooded vultures all doubled their average number of feeding observations, while the griffon vultures showed much smaller increases.

Aggressive interactions

The results for the recorded interactions between species are listed in Table 13. Because only frequencies were being recorded, the number of observations is low and thus not valid for statistical analysis. Nevertheless, the trends are still very clear, the order of dominance of the species being that given in the table. The only two species where the order of dominance is not indicated by the results in the table are Cape vulture juveniles and white-backed vulture adults, as both species each won one interaction. The Cape vulture juvenile is listed as the dominant bird because in numerous unrecorded observations it was the aggressor and victor. This is illustrated by its success on the farms dominated by white-backed vultures.

There are no results for interactions between white-headed and hooded vultures and the scavenging eagles and kites as these occurrences were too infrequent to be recorded. Nevertheless the order of dominance appeared to be white-headed then hooded vultures, followed by the eagles, the yellow-billed kite (Milvus aegyptius) and the pied crow, although few of these last species were seen to interact with each other. On one occasion a white-headed vulture was seen to

molest a tawny eagle a few metres away from a carcass, however, when the tawny eagle's mate arrived, the pair of them chased the vulture off, even attacking it in mid-air while it was flying off.

DISCUSSION

When a fresh carcass lies in the veld, there are limited masses of the different tissues which are available to be scavenged from it. In a situation where a number of species try to feed on this carcass, they could all be successful if they each prefer to eat entirely different tissues. However, if they all prefer to eat the soft tissues, then a species will only be successful if it manages to consume its requirements before other competitors arrive. Alternatively, if it arrives after the other species, it will still be successful if it can replace them at the carcass before they have consumed the soft tissues entirely.

In the following discussion these different strategies are considered with reference to the common species of Transvaal vultures and the other scavenging birds that were encountered. From this the relative abilities of these species to compete for large bovid carcasses will be evaluated.

Competing species

The species of birds that were recorded to scavenge at carcasses during the present study are listed in Table 4 of the previous chapter. All of these species with the exception of the Cape vulture, are common throughout the savanna regions of Africa south of the Sahara (McLachlan and Liversidge 1978). They are therefore the same species described in similar studies on scavenging birds in East and West Africa and consequently are directly comparable in terms of scavenging behaviour.

There are four species of griffon vulture that live in Africa. Three of these species (the true griffons) have mutually exclusive distributions, look very similar, and have the same breeding and feeding biology (Brown 1970, Mundy and Scott 1979). Thus these true griffons appear to occupy identical niches in their respective parts of Africa and can therefore be directly compared with

each other in terms of behaviour. The true griffon that was encountered by Kruuk (1967) and Houston (1975) in East Africa is Ruppell's griffon. However, because of the similarity of the true griffons this species and the Cape vulture will, in the following discussion, be considered as one species.

The Egyptian vulture is the other vulture that is commonly found in East Africa (Kruuk 1967, Houston 1975) but was not recorded during this study. However, as this species has only been recorded 15 times in the last 35 years in southern Africa (Mundy 1978), it is of little relevance to this discussion.

Order of arrival at Carcasses

When considering the competitive advantages that a species derives by arriving first at a carcass, one needs to determine two points : (i) Which species commonly arrive first at carcasses and how fast can they feed? (ii) How long does it take before large numbers of vultures arrive?

In this study, as in many others (Chapin 1932, Jackson 1938, Kruuk 1967), it was the smaller scavenging birds which were most often the first to find carcasses. These species locate carcasses more readily than the large griffon vultures because they tend to fly lower and thus search the ground better. They can fly lower, either because they can flap fly and soar (kites and crows), have low wing loadings and can soar slower (tawny eagle and white-headed vulture), or in the case of the bateleur, it is almost perfectly adapted to soaring flight and can travel 300 km in a day, flying 60 - 100 m above the ground (Brown and Amadon 1968, Pennycuick 1972).

The above authors therefore ascribe the success of griffon vultures at finding carcasses, not so much to their own ability to see carcasses on the ground, but to their habits of watching the behaviour of these other scavenging birds and following them to carcasses. However the results of the present study and König (1974) both suggest that while griffon vultures do benefit by watching the activities of scavenging birds, they do not necessarily rely on them to find carcasses.

During this study, it was found that an average of over 20 vultures arrived within 10 min of the first vulture finding a carcass. Thus one can conclude that while the smaller scavenging birds and the white-headed vulture are often the first to find carcasses, they probably make little use of this advantage because the other vultures join them at the carcasses very rapidly. Furthermore, none of these smaller birds were ever observed to start feeding immediately on arrival at the carcass.

Thus while individual griffon vultures may be at an advantage if they arrive first at carcasses, the smaller scavengers would appear to derive little benefit from it (unless other vultures do not arrive), and therefore this cannot be considered a viable ecologically isolating mechanism.

The subsequent order of arrival of vultures at carcasses recorded during this study, was similar to that observed by Kruuk (1967). However, unless a species prefers to feed on the remains left by other vultures, their order of arrival after the first species is of little consequence to this argument.

Aggression

The order of dominance of the five common species of Transvaal vultures that was recorded during the present study is the same as that recorded by Kruuk (1967) and Houston (1975) in East Africa. With the partial exception of the lappet-faced vulture, this order is directly proportional to the size of the vulture. The lappet-faced vulture requires mention, because although it is regarded as the largest African bird of prey, it is actually lighter than the true griffon vultures (Brown and Amadon 1968).

Although the order of dominance of vultures is generally quite clear cut, it does have a certain flexibility amongst the larger species, which is influenced by the motivation of individuals in the form of hunger (König 1974). Vultures which have already fed are no longer as aggressive in maintaining their position at the carcass, whereas hungry subordinate birds are prepared to fight for a position. Thus the well fed individual gives way and all get a chance to feed

until the food runs out (personal observation). The lappet-faced vulture is an anomaly in terms of this behaviour. It is undoubtedly the senior vulture species at a carcass, and while it may occasionally arrive at a carcass by flying straight into a mob of feeding birds (Fig. 12), it may also spend considerable time before feeding, standing calmly to one side and behaving as if totally unaware of the carcass (Attwell 1963, personal observation). Later, when it decides to feed, it seldom tolerates the griffons getting too close. However as their hunger spurs them on and they edge closer, the lappet-faced vulture may spend some time going back and forth chasing the hungry throng of griffon vultures off the carcass (Fig. 12), till eventually it gives up and once again stands aloof.

The hooded vulture provides a further anomaly, because although it is apparently at the bottom of the social scale (Kruuk 1967, personal observation), it does not appear to suffer from this inferior status. This is because it seldom elicits aggression from other vultures, and therefore is able to walk amongst them and get quite close to the carcass as it looks for small bits to pick up off the ground (personal observation, Fig. 12).

This tolerance towards hooded vultures, is not only displayed by vultures, but also by most carnivore species. The hooded vulture exploits this relationship and may feed daringly close to a kill while lions are still feeding (Kruuk 1967). Conversely, lappet-faced and white-headed vultures remain at some distance from the carcass if lions are feeding, while the griffon vultures may approach somewhat closer, but still wait for the carnivores to leave before they feed (Kruuk 1967).

Thus here again aggression, like the order of arrival of vultures at carcasses, appears to be of little ecological significance in alleviating competition between the species. Certainly the smaller species have no success in chasing griffon vultures off a carcass, while even the lappet-faced vulture, as the dominant bird, does not appear to use its advantage, and is often crowded off

a carcass by the griffon vultures.

Geographical separation

Houston (1975) has some evidence which suggests that geographical distribution is the main factor which ecologically separates the two species of griffon vultures, and likewise the hooded and Egyptian vultures. The general argument he applies to both pairs, is that one species of each pair (Ruppell's griffon and the Egyptian vulture) breed on cliffs in the highlands and therefore their home ranges are generally limited to being within a day's flying distance of these cliffs. The other species of each pair (white-backed and hooded vultures) nest in trees in the lowland plains and therefore tend to have different foraging areas. In addition Houston has shown that whereas the Egyptian vulture comprises over 75% of observations in areas with less than 40cm annual rainfall, it is almost totally absent where the annual rainfall exceeds 60 cm.

The evidence for the pair of griffon vultures is less conclusive because all of Houston's observations were made in the Serengeti where the white-backed vulture is always the predominant species. He does show that Ruppell's Griffon feeds almost exclusively on carcasses amongst the migrating ungulate herds (seldom occurring more than 30 km away from these herds), but he presents no data for areas where it is the dominant species and where the white-backed vulture is uncommon.

In South Africa the Egyptian vulture is virtually extinct (Mundy 1978), however potential competition between the Cape and white-backed vultures is still very real. Like Ruppell's griffon, the Cape vulture breeds colonially on cliffs, so here again geographical distribution could possibly explain the ecological separation of these species. The results in Table 12 show the numbers of each species seen feeding in areas either dominated by white-backed vultures or by Cape vultures. These results suggest that white-backed vultures are almost totally excluded from the Cape vulture areas, whereas the Cape vultures do manage to feed successfully in the white-backed vulture areas. This is not unexpected because even juvenile Cape vultures are larger and dominant to adult white-backed vultures, so the latter are seldom likely to feed successfully at carcasses near Cape vulture colonies.

The long distance movements of breeding Cape vultures are restricted by the distance

they can travel away from the breeding colonies, feed successfully and return to their nests within a day or two. Juvenile birds have no such limitations and therefore can avoid competing with the larger and more experienced adults by travelling further away from the colonies - hence the higher proportions of juveniles the further away from the colonies (Fig. 10). The areas they move into, are those where there is at least temporarily a fairly abundant food supply, and consequently often a resident population of white-backed vultures. They are successful in feeding amongst the white-backed vultures because of their larger size, but are probably not too detrimental to the white-backed vultures because they only represent a small percentage of the total vulture population. Various adaptations that the Cape and white-backed vultures have for breeding and foraging in their respective habitats are considered in more detail in Chapter 7.

Thus one can suggest that the griffon vultures in southern Africa are ecologically separated by having largely different geographical distributions. However this still leaves four species of vultures (a griffon and the lappet-faced, white-headed and hooded vultures) which commonly feed together at the same carcasses and whose ecological separation is yet to be explained.

Feeding behaviour

While discussing the foraging efficiency of herbivores, Owen-Smith (1980) states that "a submaintenance diet could result either because of the ingestion of poor quality herbage, or because of a too slow rate of intake of otherwise nutritionally adequate material." If one assumes that large bovid carcasses form the basic food supply of the five common South African vulture species, then to meet their metabolic requirements they must all be able to feed efficiently, in terms of both food quality and quantity, at these carcasses. In this next section I aim to consider whether this assumption is potentially valid. This will be achieved, first by considering the feeding behaviour of each species (which can be allied to food quality), and then their feeding rate (food quantity), which can be determined by considering the amount of time spent at carcasses and the efficient utilization of that time.

After describing the three basic methods of feeding behaviour of the six common East African vulture species, Kruuk (1967) then illustrated how well these species skulls and bills were adapted for their various methods of feeding. He showed that lappet-faced and white-headed vultures have broad skulls and bills which enable them to tear at skin and sinews. The griffon vultures bills are proportionately not as broad, and the skulls far narrower as they only need to tear out flesh. The skulls and particularly the bills of the hooded and egyptian vultures are even narrower, and thus well adapted at pecking small pieces off the ground and from between bones.

Because the feeding behaviour of these groups of vultures appeared to be so characteristically different and to correlate so well with their morphology, Kruuk (1967) failed to consider certain biases present in his study. Briefly these are : (i) The fact that he was looking at vultures primarily at hyaena kills. (ii) He assumed that carnivore kills form the basic diet of vultures. (iii) He never considered the status of a kill in terms of how much food was available to vultures. In view of the results of the present study, these biases will be shown to be vitally important in the interpretation of vulture feeding behaviour.

Manner of feeding

It is apparent from Fig. 13 that while the individual methods of feeding of each species were all significantly different, there were distinct similarities and dissimilarities between the various species. At fleshed carcasses, the two griffon vulture species fed almost exclusively on soft tissues, while the white-headed and hooded vultures and the pied crow fed primarily on scraps. In the middle of this range, the lappet-faced vulture had the widest preference of diet, feeding primarily on soft tissues or skin. At clean carcasses, these different patterns still persisted, except that with little soft tissues available the three largest vulture species changed to "stripping" bones instead.

Already from this figure one can see three distinct differences from Kruuk's (1967) results.

(i) He has no record of lappet-faced vultures pulling out soft tissues at all. This may have been because of his own interpretation of his feeding categories, or because of his recording method. He only recorded the most frequently occurring method of feeding for each individual and therefore minimised any variation in behaviour. Thus his records of this species consist almost exclusively of its stripping (tearing) skin or bones. This species, with its massive bill (Fig. 11), is undoubtedly well adapted to tearing skin and during this study was often observed to open a fresh impala carcass by tearing a large hole (approximately 15 x 25 cm) in the skin covering the ribs. However, while it may prefer to feed on the outside of a carcass (as opposed to inserting its head deep inside), it is difficult to imagine why it, or any other vulture species, should not feed on the soft tissues of a carcass if the opportunity arises. In fact Mundy (1976) has recorded hooded vultures in Nigeria (in the absence of other vultures) entirely to consume the soft tissues of carcasses.

(ii) There is no similarity whatsoever between the feeding behaviours of the white-headed vulture recorded during the present study and during Kruuk's (1967) study. Kruuk recorded it to feed in a manner similar to that of the lappet-faced vulture, by either stripping meat off large loose bones or eating large loose pieces of meat. These results are probably entirely dependant on the fact that Kruuk was recording vulture behaviour at spotted hyaena kills. When these hyaenas fed at their kills they usually tore it apart quite extensively, leaving many large bones and "largish pieces of meat lying around the carcass (usually dropped there by a carnivore)" (Kruuk 1967). During the present study, with none of these tissues being so readily available, the white-headed vulture was reduced to feeding primarily on small loose scraps away from the carcass and therefore in a manner similar to that of the hooded-vulture and pied crow. This same argument applies to Houston's (1975)

interpretation of the feeding behaviour of marabou storks at game culling camps, where the carcasses had all been stripped of their skins. This will be discussed in more detail later.

(iii) Fig. 14 clearly demonstrates that the feeding behaviour of vultures is highly dependent on the availability of soft tissues. This is something which is totally neglected by both Kruuk (1967) and Houston (1975) and is very evident in the interpretations of their results. Kruuk emphasises the distinction between the pulling out of soft meat by griffon vultures, and the stripping of skin and bones by lappet-faced vultures. However, Fig. 14 shows that these two methods of feeding are interchangeable, merely depending on the status of the carcass. This fact is emphasised in Fig. 13 and 15.

To summarise, the feeding behaviour of these species can be seen to be related to both their behavioural and physical adaptations. The more dominant birds, lappet-faced and griffon vultures, fed at the carcass, the former, possessing a very powerful bill, ate both meat and skin, while the latter ate almost exclusively meat (soft tissues). The smaller birds, the white-headed and hooded vultures and crows, seldom had access to the carcass, and therefore spent more time feeding on scraps around it.

Nutritional value of feeding behaviours

While Fig. 13 shows the whole range of discernable methods of feeding employed by different vulture species, and Fig. 14 emphasises how this behaviour is often dependent on the status of a carcass, Fig. 15 is the most important in terms of illustrating the competitive success of each species.

If one accepts that the nutritional value of food ingested per unit time during the three basic methods of feeding are as defined above (soft > strip > bits), then one must conclude that in terms of behaviour the griffon vultures were the most successful feeders at carcasses. The next were lappet-faced vultures which in turn were substantially more successful than the hooded and white-headed vultures, which were about equal.

Positioning around the carcass

It has been shown above (Fig. 16) that the number of vultures crowding around a carcass can be directly related to the availability of food at the carcass and the desire of vultures to feed. It has therefore been assumed that there is direct competition between vultures for places around the carcass, those gaining access consequently being the most successful feeders.

It follows from this that the species with the highest proportion of its number within three metres of the carcass, is going to be the most successful in terms of rate of feeding, and if it feeds on bits, also in terms of the size of bits available. From Fig. 17 it is clear that hooded and then griffon vultures (as a group) were the most successful at maintaining positions around the carcass, while the lappet-faced and particularly white-headed vultures were remarkably unsuccessful in this respect.

What is most noticeable in Fig. 17, is that whereas both hooded and white-headed vultures were apparently the least successful in terms of feeding behaviour (Fig. 15), they are now, in terms of positioning around the carcass, at opposite extremes. This confirms the white-headed vultures' general lack of success at scavenging from large carcasses, but suggests that the hooded vulture may thereby be able to compensate for its low quality feeding method.

Usage of foraging time

The final aspect to consider in terms of the feeding efficiency of each species is their utilization of time. For a species to scavenge successfully at a carcass, not only must it feed on food with a high energy content, but it must also feed for the minimum length of time necessary to consume sufficient food for its daily requirements. Therefore the success of a scavenger can be measured by the frequency with which it finds carcasses, and how long it spends feeding at each carcass.

What is most noticeable in Fig. 18 is that here again the hooded vulture

appears to be the most efficient species, spending the highest percentage of time in feeding and achieving the greatest number of feeding observations per individual present at both categories of carcass.

The lappet-faced vulture spent the most time per individual at carcasses, but then spent less than 50% of this time in feeding. This confirms Attwell's (1963) impression, that this species spends considerable time at carcasses standing aloof and doing nothing. Mundy (pers. comm.) has the impression that this species congregates at large carcasses, more for social interactions than for feeding.

If one takes the average number of feeding observations per individual vulture to represent an absolute measure of success in terms of feeding rate, one can make two general conclusions : (i) Hooded vultures were the most successful at both fleshed and clean carcasses. (ii) While lappet-faced and white-headed vultures were the next most successful at clean carcasses, they had essentially the same success rate as griffon vultures at fleshed carcasses.

Final analysis of feeding success

The final analysis of the success each species achieved when feeding at the large carcasses observed during this study, can only be done subjectively. The two most important factors to be evaluated, are the manner of feeding of each species and the average number of feeding observations per individual. These two factors are then also influenced by the status of the carcass whilst feeding and the success the species has at remaining close to the carcass.

Griffon vultures The two griffon vulture species were obviously the most successful species as they fed almost exclusively on soft tissues (when available), were successful at maintaining positions close to the carcass and fed for an average of over seven minutes ($1\frac{1}{2}$ observations) per individual at fleshed carcasses. Although the griffon vultures spent on average less time feeding than the other species, their feeding abilities must be taken into account.

They have highly adapted spoon-like tongues with posteriorly directing tooth-like structures (King, Kieser and Mundy 1977) which enable them to feed on soft tissues very rapidly, consuming 1 kg within three minutes (Mundy In litt., personal observation). In contrast to this tame starved lappet-faced and white-headed vultures take at least 30 min to consume this same amount (Mundy In litt.).

Hooded vultures These vultures fed primarily on small bits around the carcass or by stripping meat off bones on the carcass (20-30%). Thus in comparison to the griffon vultures, their food quality was low, although this deficit is probably alleviated by their small body size (1,5 - 2,1 kg) (Brown and Amadon 1968), which will reduce their daily energy requirements. However their efficiency at remaining close to the carcass, and the fact that they spend more time feeding per individual than any other species, may adequately compensate for the nutritionally poor manner of feeding.

Lappet-faced vulture While these vultures undoubtedly possess the potential to feed successfully at large carcasses, they did not appear to do so during the present study. In all the different aspects of feeding behaviour they were in the middle of the range, neither being particularly successful nor unsuccessful. When one compares these results to those of the griffon vultures and considers how much longer they take to consume 1 kg of meat, then one must conclude that these vultures would seldom have fed successfully. In fact at no carcass during this study was any lappet-faced vulture ever observed to fill its crop.

White-headed vulture As these vultures were in all respects even less successful than lappet-faced vultures, it is highly unlikely that they ever managed to feed successfully at the carcasses observed during this study. The general impression gained of this vulture, was that it would visit a carcass in the hope of feeding. However, after spending some time walking around the periphery of the main group of vultures, and occasionally picking up small

scraps, it would depart having consumed very little.

Social organisation and alternative sources of food

The effect a species' social organisation has on the individual's chances of finding carcasses regularly, has been discussed at length in Chapter 3, and is illustrated in Fig. 9. At this stage of the discussion it is pertinent to consider each species' social organisation and see how well it correlates to the species' ability to scavenge at large bovid carcasses (described above).

Griffon vultures have very large home ranges with no territorial boundaries (Pennycuick 1972, Houston 1975) and can therefore search over huge tracts of countryside thereby increasing their chances of finding carcasses regularly. Conversely, those species with a territorial social system can only forage within the confinement of their own territories, so their chances of finding and utilizing carcasses are greatly reduced. This disadvantage is partially alleviated if the territory is very large, thereby reducing the density of the species and hence competition from conspecifics. Therefore, one can see that the social organisation of griffon vultures is ideally suited to a scavenging way of life and this correlates very well with their highly efficient methods of feeding at a carcass. The social organisation of the hooded vulture is also non-territorial (Houston 1975). However its numbers are very variable, and appear to be inversely proportional to those of griffon vultures. In parts of West Africa and Zambia, where griffon vultures' numbers are low, the hooded vultures are very common (Bannerman 1930, Chapin 1932, Attwell 1963) and capable of consuming the soft tissues of carcasses entirely on their own (Mundy 1976). However in other regions they tend to forage singly, or in pairs (Brown and Amadon 1968), and are seldom seen in numbers over ten (Kruuk 1967), unless there is a plentiful supply of food available. Kemp and Kemp (1975) saw approximately 50 at slaughtered elephant carcasses in the Kruger National Park, while Liversidge (pers. comm.) has seen a group of approximately 15 feeding on insects (in a

R. Liversidge, McGregor Museum, P.O. Box 316, Kimberley, 8300.

manner typical of storks) in a field in the same reserve. In addition to insects, these vultures have also been recorded to supplement their diet by preying on small animals like lizards (Chapin 1932, Attwell 1963, McLachlan and Liversidge 1978). However, it is suggested that in the eastern Transvaal Lowveld they may be able to subsist by feeding exclusively on large carcasses.

The lappet-faced and white-headed vultures are both territorial breeders which patrol limited foraging ranges (Kruuk 1967, Houston 1975, Pennycuick 1976). Thus their social organisation is poorly adapted for scavenging and this is reflected by their numbers at carcasses which rarely exceed eight and two respectively (Pennycuick 1976, personal observation). The lappet-faced vulture appears to have the more flexible social system in terms of territoriality, because in most areas more than two individuals (mated pair) are often seen at carcasses, while in the Namib desert they appear to be quite gregarious, and regularly congregate at waterholes and carcasses, in numbers of up to 40 (Sauer 1973). The more social behaviour of this species in the Namib may correlate with an increase in its scavenging habits, as it appears to have a large foraging range. Nevertheless, it still maintains fixed nesting territories (Clinning 1977).

It is pertinent to note that these two species (particularly the white-headed vulture) were both the least efficient in terms of feeding behaviour at carcasses, and have social organisations which are poorly adapted for scavenging. This would suggest that while they do scavenge large carcasses, they also have alternative sources of food. Anthony and Mundy (In litt.), in their studies on these vultures in Zimbabwe, reached this same conclusion, suggesting that they are both predators and scavengers. Their main lines of evidence concern : (i) items brought back to nestlings (see Plug 1978), (ii) the phlegmatic behaviour of adults at carcasses, and (iii) the dearth of small carcasses in the field (see Herman and Bulger 1979). Both Plug (1978) and Pennycuick (1976) have found a high occurrence of small animal remains (small bovids and carnivores, hares and korhaans) in their nests. Furthermore, of the five common vulture species in

southern Africa, articulating skeletal parts were found only in these two species' nests (Plug 1978).

It is difficult to obtain direct observations of large birds of prey catching their prey in the savanna. There are a number of reports of lappet-faced and white-headed vultures being seen alone at small animal carcasses (Attwell 1963, Kruuk 1967, Houston 1975), however these have usually been assumed to have been scavenged. Brown and Amadon (1968) state that both species definitely do kill both adult and young flamingos in breeding colonies, however most other evidence of kills remains circumstantial (Mackworth-Praed and Grant 1962, Attwell 1963, McLachlan and Liversidge 1978). The white-headed vulture is apparently the more predatory of the two species. Brown (1970) states that it is claimed by "Somalis, who probably know," that the white-headed vulture has the ability to kill dik-dik (Rhynchotragus sp.). Furthermore, Attwell (1963) reports J.B. Shenton as having seen one flying off with a puff adder (Bitis arietans) whose head had been partially eaten, "but it was still writhing when first seen."

Another method of acquiring food that may be used by these two species, is piracy. Both species are large birds, the lappet-faced vulture being the largest bird of prey in Africa (Brown and Amadon 1968). Although he has never seen it happen, Attwell (1963) has suggested that both these vultures could well be successful at pirating eagle kills.

The final food source that has been suggested to be of importance to these two vulture species, are small carcasses that are not detected by the larger griffon vultures (Houston 1975). White-headed vultures are apparently quite adept at finding the remains of eagle and serval (Felis serval) kills (Brown and Amadon 1968). However, small carcasses resulting from non-violent deaths have probably been overestimated as a food source, because animals that die in this way usually seek shelter and become invisible from above (Herman and Bulger 1979). These authors found that in forests sprayed with DDT, dead birds were extremely difficult to find. Similarly, during all the time I have spent in the veld, the only carcasses I have ever found have been a few bovids.

OTHER SCAVENGING BIRDS

The other scavenging birds that were encountered during the present study, were crows, tawny eagles, bateleurs, marabou storks and a yellow-billed kite. These are all species well known for their scavenging habits, however it is doubtful whether any of them are as dependent on scavenging as the griffon or hooded vultures.

Pied crows feed on anything of animal origin (McLachlan and Liversidge 1978) and are well known for their habit of scavenging roadside kills. They are even suggested to have increased their distribution through this scavenging habit (Winterbottom 1975). It is difficult to estimate their scavenging diet, it may however be significant that they were very common in the farming areas, but were never seen in the nature reserves during this study. Whether this was because of the lower numbers of vultures in the farming areas, is not known. At most carcasses two to four birds were seen. However, at one impala in the Magaliesberg I counted at least 20.

The tawny eagle, bateleur and yellow-billed kite are all apparently able to kill for themselves (Steyn 1965, 1973, Brown 1970) but will also scavenge large carcasses and may pirate kills from other birds of prey (Brown and Amadon 1968). At carcasses in the present study their feeding success was considerably less than the white-headed vultures' and it is therefore suggested that they are primarily opportunistic scavengers.

Marabou storks are very well known as scavengers, however, it is suggested that they, like the scavenging eagles, are only opportunistic scavengers. They are very well known for occurring in large numbers at refuse heaps, game culling camps and very large carcasses. These are all situations where large loose scraps of meat may be found, and in these situations they can easily feed on these pieces, or pirate them off vultures (Houston 1975). However, these birds, with their long pointed bills, cannot tear meat from carcasses (Chapin 1932) and therefore would in normal circumstances not be able to feed successfully

when alone.

Houston (1975) states that the marabou pirate most of their food off vultures, taking the pieces they find or tear off, away from them. This of course relies on there being loose pieces to pirate. As has been stated earlier, one would expect that many loose pieces of meat can be found at a game culling camp, but that they would be very rare at normal carcasses. It is pertinent to note that although Houston put out 64 carcasses in the plains, his whole sample for marabou stork behaviour comes from the game culling camp - presumably because he got very few marabous at his carcasses. Of the 47 carcasses seen by Kemp and Kemp (1975), marabous were only seen at two of them. There was one at an impala ram and 250 at some culled elephants. Of 16 carcasses in the nature reserves where vultures were observed feeding during the present study, there were only two marabous at one giraffe carcass. Here they spent most of their time picking up small bits, or dung beetles, attracted to the rumen contents of the giraffe. Seibt and Wickler (1978) have also seen marabous specifically searching for dung beetles in elephant dung. Thus although the marabou is primarily only a summer migrant to South Africa (Kemp 1974), there were numerous carcasses at which they could have fed during the two above mentioned studies.

Marabous can only breed where the adults can catch small vertebrate prey for their young, as they do not get sufficient calcium in their diet from pure meat (Kahl 1966). The ability of the marabou to catch vertebrate prey while breeding and their noticeable absence from carcasses undisturbed by man, suggest that catching a variety of small animals is their true pattern of feeding, while they have also learnt to exploit large, open carcasses and human refuse dumps successfully. As these sources of food are prominent and the storks can accumulate in large numbers at them, scavenging became the most observed feeding behaviour of these birds and therefore they came to be known primarily as scavengers.

CONCLUSION

In the above discussion, numerous aspects of the lifestyles and feeding habits of the five common South African vulture species and other scavenging birds have been considered, in order to try and determine their ecological separation.

Two broad concepts were considered:

(i) The vultures are all feeding successfully at the same large carcasses, being separated by feeding on different parts of the carcass, or at different times.

(ii) The vultures are all feeding at different carcasses, either because of their geographical separation, or because of their different ways of finding / acquiring carcasses. Neither of these concepts is considered to be entirely true, but by applying both, one can probably explain why one often finds five species of vultures and some other scavenging birds all feeding at one carcass.

Griffon vultures are considered to be the primary scavengers of the large bovid carcasses that regularly occur in the veld. They are successful at this because they can find carcasses efficiently, accumulate in large numbers at these carcasses and can usually consume all the soft tissues, before being interfered with by other scavengers (Houston 1974a). The two species of griffon vultures in South Africa appear to be ecologically separated by their different geographical distributions, the breeding populations of the Cape vultures feeding within foraging range of their colonies in the mountains, while the white-backed vultures forage further away on the plains. The mobile juvenile population of Cape vultures may forage in areas with resident white-backed vultures, in which case they are definitely dominant, but are usually present in such low numbers that they do not seriously affect the success of the white-backed vultures.

The hooded vulture, in the parts of Africa where it is the commonest vulture, can feed in very much the same way as the griffon vultures, despite the fact that it is a much smaller bird. However, when they compete with griffon vultures, as in South Africa, their style of feeding must necessarily change. Nevertheless, in these circumstances they still appear to scavenge successfully at large carcasses

They can do this because they are relatively small birds and therefore have lower energy requirements, so can feed successfully, by picking up small bits at carcasses, or picking between the large bones of carcasses and thus reach meat not accessible to other vulture species. Their success in this way is enhanced, because they are very bold birds and are able to feed close to the carcass when either carnivores or griffon vultures are feeding. Furthermore, they waste little time at carcasses, but spend most of their time feeding. These vultures can also supplement their diet with various small live items like lizards and termites.

The lappet-faced and white-headed vultures are in almost every respect inefficient scavengers of large carcasses. Their manner of feeding, positioning around the carcass and utilization of time spent at the carcass, all indicate their inability to scavenge successfully. Likewise, their social organisation may preclude their finding sufficient large carcasses. These factors suggest that lappet-faced and white-headed vultures acquire their food in other ways.

Alternative food items eaten by these two species are suggested to be their own kills of small or juvenile antelope, small carnivores, ground birds and various small reptiles; kills pirated off eagles; and small carcasses hidden in bush and not seen by other vultures. Similarly, I suggest that the other scavenging birds mentioned in this chapter are opportunistic, but not necessarily exclusive, scavengers.

CHAPTER 5:
THE SUCCESSION OF ARTHROPODS AND THEIR ROLE IN
THE DECOMPOSITION OF CARCASSES

INTRODUCTION

During the past 80 years sporadic attention has been given to the succession of arthropod fauna scavenging carcasses. The first major contribution in this field was made by Megnin in 1894 on the fauna of corpses for forensic medicine (Ullyett 1950), and this subject is still being investigated today. The next problem that stimulated interest was that of blowflies causing strike (myiasis) in sheep. Much research was undertaken in South Africa and Australia from 1920 to 1950 on blowflies in order to determine ways of controlling this menace (Smit 1931, Fuller 1934, Hepburn 1943, Waterhouse 1947, Ullyett 1950). Recent studies have been more ecologically orientated, examining the succession of arthropod fauna (Bornemissza 1957, Reed 1958, Payne 1965, Johnson 1975), rates of decay and nutrient cycling (Putman 1977, et seq., Coe 1978). Collins (1970) studied carcass decomposition with an overall ecological perspective. However he was monitoring the decomposition of mice carcasses in a temperate climate, so his results have limited application to the decomposition of ungulate carcasses in the African savannas.

This chapter aims not only to illustrate the basic succession of arthropods feeding on carcasses in the Transvaal, but also to correlate this with what happens when carnivores and vultures feed on these same carcasses. The vertebrate scavengers may remove all the soft tissues and skin from a carcass and therefore only those arthropods which feed on the remaining skin or bone will be present. Thus the differential removal of tissues by vertebrate scavengers emphasises the roles of the arthropods that remain to feed. Finally, the amount of tissues that the arthropods consumed are considered.

METHODS

Although the decomposition of 89 carcasses was recorded in this study, detailed observations on arthropods were made at only 39 of them. As the primary objective of the whole study was to record the roles of all the agents of decomposition of carcasses in the veld, in as natural a situation as possible, the carcasses were only visited when there was no possibility of disturbing any vertebrate scavengers. Therefore recordings on fresh carcasses could not be made every day and older carcasses were visited intermittently with breaks of weeks or months in between.

When observations on arthropods were made, the carcasses were disturbed as little as possible. Samples of all sizes of maggots were collected, fed on remains of the carcass and bred for identification to species level. Pupae were collected wherever they could be found. In the preliminary study it was observed that beetles played a minor role in the decomposition of carcasses and therefore disturbance to carcasses in order to find them was kept to a minimum. Beetles were identified to family level and recorded on a presence or absence basis. Only diurnal observations were made and then only for beetles on or immediately below the carcasses. There was no excavation in the soil beneath carcasses, even though this led to many beetles, especially trogids, being missed. However, because only the presence of families was being recorded the methods were regarded as being adequate. Throughout the decomposition of each carcass estimates were made of the amount and type of food eaten by arthropods, which were divided into beetles and maggots (blowfly larvae).

RESULTS

Stages of decomposition

In the absence of vertebrate scavengers the seral stages of decomposition of carcasses can be allied to the "fresh", "bloat", "decay" and "dry" stages described by Johnson (1975). However, these stages are superficial because this

form of classification is based on outward appearances which are more dependent on environmental factors than the inhabitants of the carcass and the rate of decay (Collins 1970, Putman In litt.). They became quite inappropriate when the vertebrates fed as a carcass may be a few hours old and yet vary from being a complete carcass to a few bones, with or without some skin attached. For the purpose of assigning roles to the arthropod inhabitants and assessing succession, three major groups have been described which are further subdivided into a total of eight stages (Fig. 19) :-

Fresh : This group consists of all carcasses before maggots develop or, if vertebrates have fed on them, before they dry out. It is subdivided into three stages as it is influenced by scavengers : (i) with soft tissues, skin and bone; (ii) with skin and bone; (iii) only bone. Thus (i) corresponds to the "fresh" and "bloat" stages of Johnson (1975), while (ii) and (iii) are new.

Maggots : This group consists of any carcasses on which maggots are feeding and has the same three stages as above. Stage (i) corresponds to the "decay" stage of Johnson. It usually began after 1 - 3 days in summer and after five or more days in winter. Temperatures were never low enough in winter to entirely inhibit maggots from developing. Stages (ii) and (iii) were necessarily older as either maggots would first have to eat all the meat, or it was devoured by vertebrates and the cycle had to start again.

Dry : This group consists only of carcasses with (i) dry skin and bone and (ii) dry bone. The time taken to reach these stages was 2 - 3 weeks. Although the jackals on the farms were occasionally very shy a carcass was always eaten if it was left long enough. So after two weeks all that was found was dry skin and bones, only bones, or nothing at all and no carcass had a chance to mummify as described by Putman (1978a).

Occurrence of arthropods

Blowfly larvae

Because of the competition with vertebrate scavengers, blowfly larvae only developed on 15 of the 89 carcasses. From 12 of these, flies were bred for

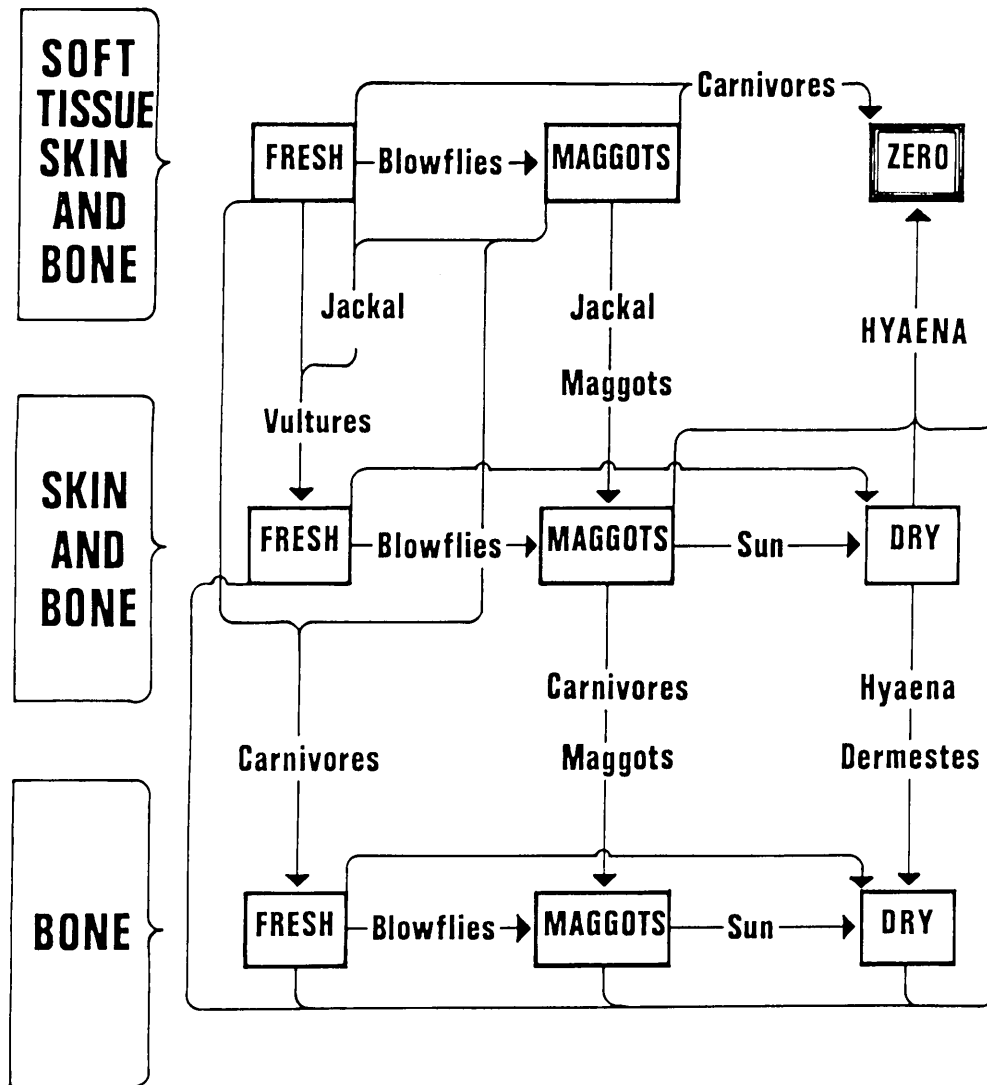


Figure 19 : Flow diagram representing the agents responsible for the possible stages of decomposition carcasses may go through in the Transvaal. "Carnivores" refer to any species of large, African carnivore. Where jackals are indicated specifically, it is because they are small animals doing minor damage. Conversely, hyaenas are powerful bone crushers and the only carnivores that commonly eat dried skin and bones. The divergent fates of carcasses thus depend on their own size and the scavenger(s) concerned.

identification. Five of the six main blowfly species in South Africa were collected (Fig. 20). Only Lucilia sericata, Meigen which is an urban species (Zumpt and Patterson 1952), was not collected. These records are grouped into three classes :

Develop : This class consists of any maggots collected from the still relatively fresh carcass and within two days of their first appearance.

Pupate : This class consists of larvae that had left the carcass or were pupating. Thus they had survived the rigours of interspecific competition.

Bone : This class consists of any larvae (developing or pupating) that had fed on carcasses without any meat; viz. from decomposition stages : Maggots (ii) and (iii). In these cases they were feeding primarily on the brains or the spinal column of the carcass.

The first appearances of blowfly larvae on undisturbed carcasses were recorded and correlated with maximum ($r = -0,54$), minimum ($r = -0,904$) and mean ($r = -0,805$) air temperatures. The linear regression for mean minimum air temperature is plotted in Fig. 21. There is an obvious trend towards decreased emergence time with increasing temperatures, but there are irregularities which may be associated with the seasonal occurrence of different species (Hepburn 1943, Ulliyett 1950) which have different temperature requirements for emergence and oviposition (Fuller 1934, Deornier 1940). In addition, biological activity in carcasses is supposed to correlate better with ground temperature than air temperature (Fuller 1934, Coe 1978, Putman 1978c).

Beetles

Seven families of beetles were collected from 39 carcasses on 51 different occasions. Their occurrence has been recorded in Fig. 22 for the eight stages of decomposition defined above. The records for Dermestidae have been divided in two - for adults and larvae. The records for the three major groups are significantly different ($\chi^2 = 294,75$; $df = 14$; $p < 0,001$), however the interpretation of the figure is best derived by visually comparing the histograms.

SPECIES NAME	CODE	DEVELOP	PUPATE				BONE	SEASON				
			S	A	W	Sp		S	A	W	Sp	
Chrysomya albiceps	a	m,c	m	m	m		m		2	2	3	2
Ch. marginalis	m	a,c	a	a	a		a		3	1	1	1
Ch. chloropyga	c	a,m					p		1		1	
Lucilia cuprina	l										1	
Calliphora croceipalpis	p						c				1	

S - Summer : November to February
A - Autumn : March, April

W - Winter : May to August
Sp - Spring : September, October

Figure 20 : Blowfly species bred from three classes of carcasses in the Transvaal and southern Zimbabwe. When the code letter of a species occurs in a record of another species, it indicates that it was sharing the carcass with that species. A blank record means it was the only species present.

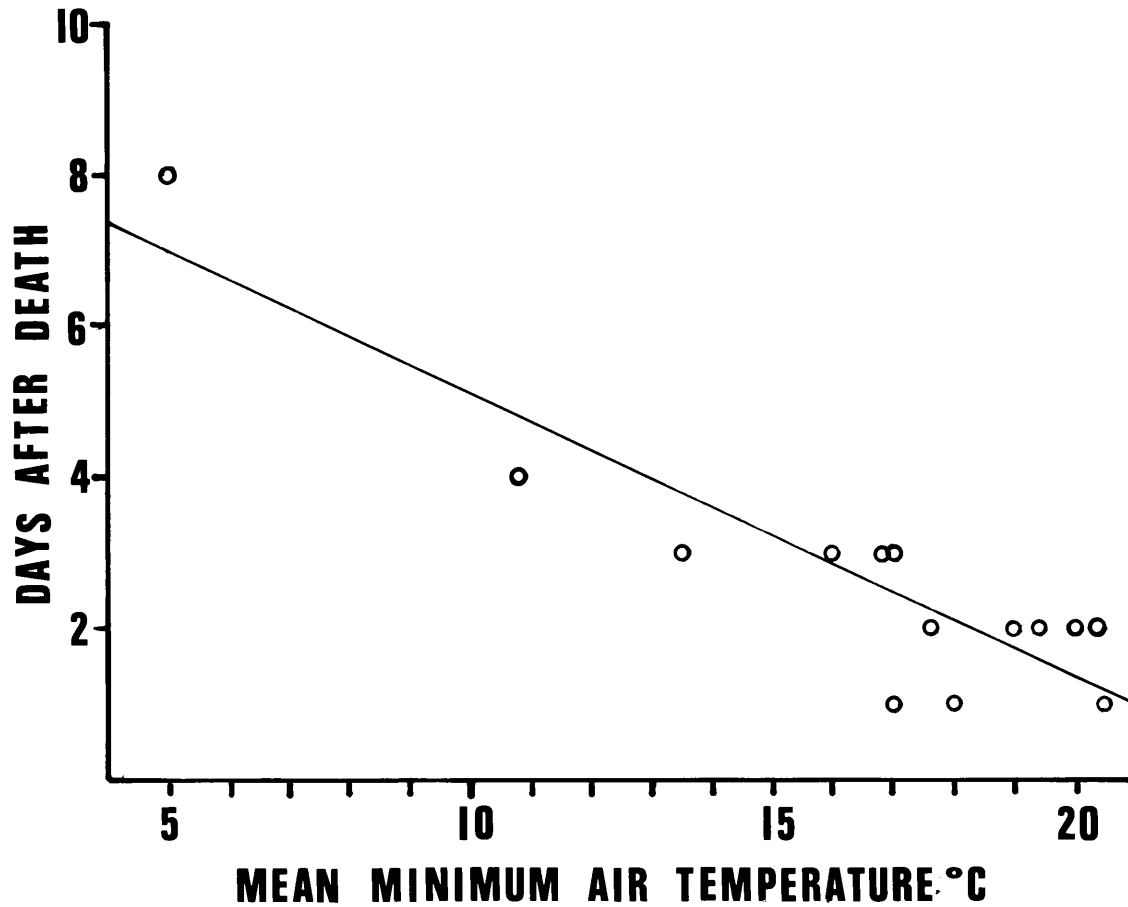
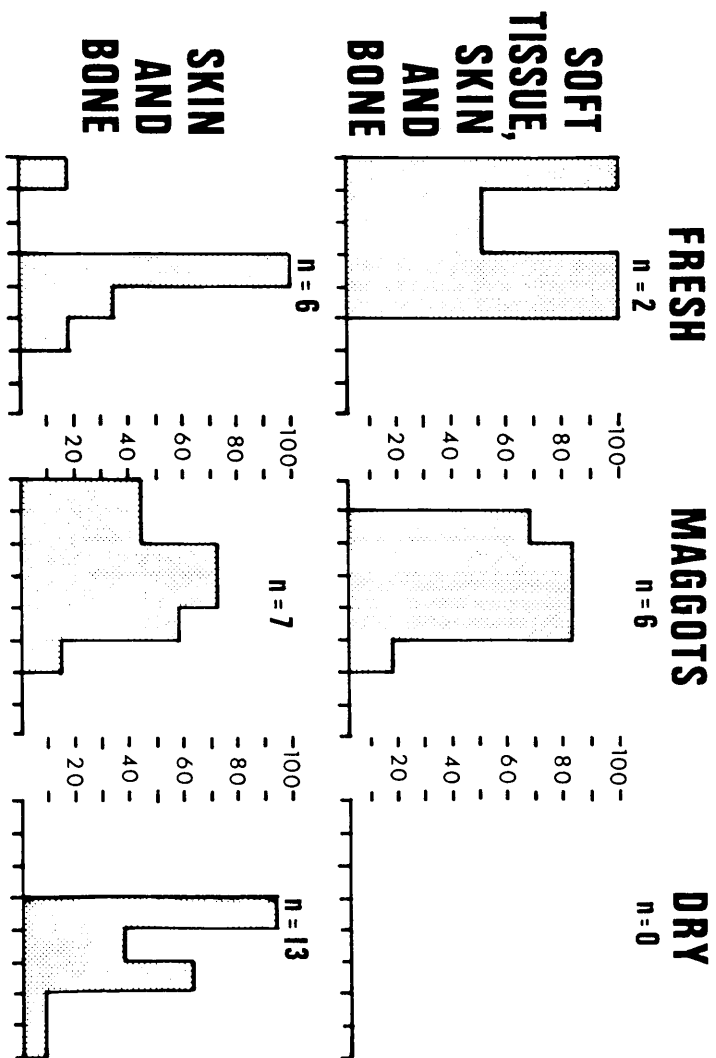


Figure 21 : The rate of development of maggots (first appearance after death of carcass) plotted against the mean of the daily minimum air temperatures. Regression equation is : $y = 8,9 - 0,38x$; $r = 0,904$; $df = 12$; $p = 0,001$.



90c

If one looks at Fig. 19, one can see how the different stages of decomposition illustrated in Fig. 22 may have arisen. It is apparent that the seral stages of decomposition in the absence of vertebrate scavengers (as illustrated by most other authors), can be seen by moving horizontally from left to right. Alternatively, the effect of vertebrate scavengers can be seen moving vertically from top to bottom.

Other Arthropods

Ants only occurred in large numbers on one carcass, and termites on two. In all these cases their nests were nearby. Thus they did not appear to be of any significance to the decomposition of carcasses. Tineid moths were found boring into most of the old horns and hooves that survived.

Consumption

The total calculated amounts of soft tissues and skin consumed by maggots and beetles are given in Table 14. As the effect of arthropods on predated carcasses was negligible, the results given are only for those carcasses that were not killed by predators and were therefore entirely scavenged. The invertebrates, in competition with vertebrate scavengers, only consumed 11% of all the tissues available to them. Those on farms ate a significantly higher proportion than those on nature reserves ($Z = 24,7$; $p < 0,001$). On the farms the arthropods ate significantly more food in the summer months than in winter ($Z = 31,5$; $p < 0,001$). In the nature reserves maggots only managed to develop in one carcass. This was in winter at a large giraffe carcass. Here maggots developed in the neck which had remained largely inaccessible to vultures for a week.

During the present study there were only two carcasses where all the soft tissues were consumed exclusively by invertebrate scavengers. However, on the farms a number of them were consumed primarily by maggots while jackals played a minor role. Illustrations of two such carcasses are given in Fig. 23.

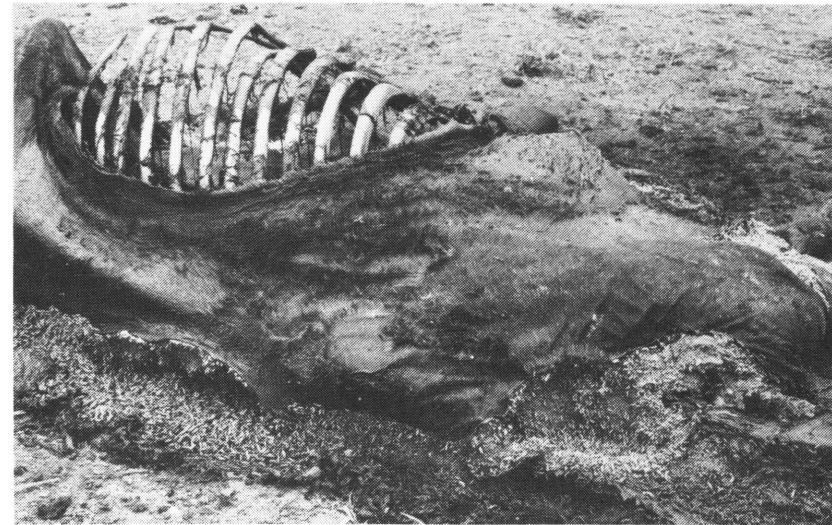
Table 14 : Mass of tissues consumed by arthropods at carcasses placed on farms and nature reserves in the Transvaal and southern Zimbabwe.

	FARMS					NATURE RESERVES				
	Beetles		Maggots		Total available	Beetles		Maggots		Total available
	Kg	%	Kg	%	Kg	Kg	%	Kg	%	Kg
Soft tissues	-	-	677	21	3251	-	-	36	1,2	3067
Skin	5	1,3	56	14	393	-	-	30	6	498
Total Summer	-	-	667	46	1458	-	-	-	-	1023
Total Winter	5	0,2	66	3	2186	-	-	66	2,6	2542
Total	5	0,1	733	20	3644	-	-	66	1,9	3565

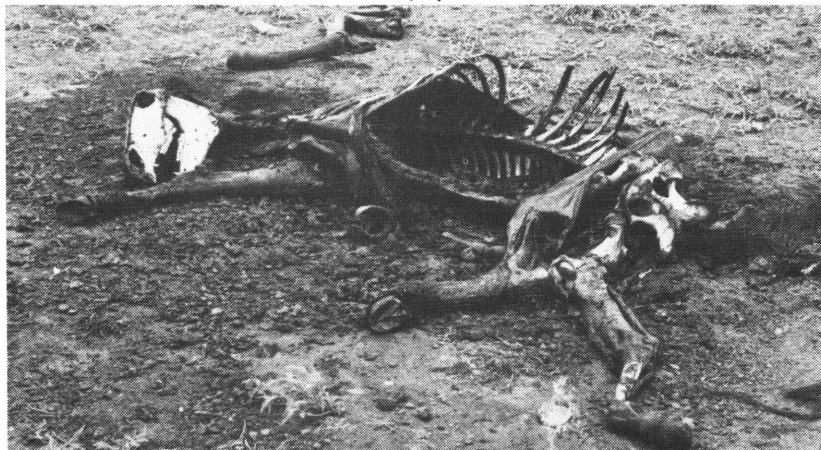
(a)



(b)



(c)



(d)



Figure 23 : Sequence of stages in the decomposition of medium-sized bovids by maggots : (a)(b) and (c) - a mule (Equus sp.) at Tweeputkoppies which was consumed by both maggots and a few jackals (Canis mesomelas). Note the putrefaction fluid (a) and the disintegration of skin at the ground interface (b). A cow (Bos indicus) at Olifantshoek (d) was initially eaten exclusively by maggots. Note the clean bones and the remains of rumen contents and decomposed internal organs.

DISCUSSION

Occurrence of arthropods

In the present study, as in many others (Fuller 1934, Reed 1958, Putman 1978b), the only arthropods that played a major role in the decomposition of carcasses were blowfly larvae. It is therefore worthwhile looking at the factors which influence their occurrence on carcasses in more detail.

Blowflies

Hepburn (1943) stated that previous workers had confused Lucilia cuprina Wied. with L. sericata and that all records of the latter should refer to the former. Ulllyett (1950) subsequently disputed this, questioning the status of L. cuprina as a species. However, Zumpt and Patterson (1952) later stated that the two species are quite distinct and that L. cuprina is a rural species while L. sericata is mainly restricted to the towns. Thus I have assumed that all records of Lucilia in the field refer to Lucilia cuprina.

Ulllyett (1950) carried out a large number of experiments on competition between South African blowfly species using 140 gram pieces of meat. He noted that Lucilia weighed the least, oviposited the earliest, took the shortest time to hatch and grew the most rapidly to mature adult weight. All of these factors are advantageous to a species exploiting temporally limited resources. In almost all these respects Chrysomya marginalis Wied. was the exact opposite, whilst Ch. chloropyga Wied. and Ch. albiceps Wied. were intermediate, each with certain advantages and disadvantages. With the exception of Ch. albiceps (which preys on other larvae), he concluded that, in situations of interspecific competition Lucilia has the greatest competitive advantage, followed by Ch. chloropyga with Ch. marginalis having the least. Ch. albiceps always kills the other species in overcrowded conditions, providing it does not develop long after them. An analogous situation occurs with Ch. rufifacies Macq. in Australia (Fuller 1934), which is apparently very closely related to Ch. albiceps (Smit 1931).

Ulyett (1950) then referred to records by De Vries (unpublished data) of flies bred from carcasses in the northern Karoo (which has cold dry winters), which indicate that the secondary flies (Ch. albiceps and Ch. marginalis) breed on carcasses in summer, while the primary flies (Lucilia and Ch. chloropyga) breed on carcasses in winter, with Ch. chloropyga also extending slightly into the summer period (Fig. 24). Smit's (1931) records from fly traps indicated a somewhat similar trend, with the two populations (primary and secondary flies) only occurring together in spring and autumn when one is declining and the other increasing. Ulyett therefore concluded that the two populations never compete for carcasses as they are either mutually exclusive or occur in such low numbers as to have no effect on each other.

In making these conclusions Ulyett disregarded Hepburn's (1943) results from Onderstepoort in the Transvaal (which has much warmer and wetter winters) because he felt they were too incomplete to draw reliable conclusions from them. However, on analysing Hepburn's data of flies bred from carcasses in the Karoo and in the Transvaal (which lacks data for three months) a different yet very clear pattern emerges (Fig. 25). In the Karoo Lucilia was only the most numerous species during the three coldest months. For the rest of the winter period it was dominated by Ch. chloropyga which was always the dominant primary species in the Transvaal. Furthermore, whereas the primary flies were dominant to secondary flies for seven months in the Karoo, they were only dominant for a maximum of four months in the Transvaal. The opposite extremes of this geographical influence of temperature on the success of blowflies breeding in carcasses can be seen in England where, because of the cold, they only breed in summer and autumn (Putman 1978c) and, in East Africa where only Ch. albiceps and Ch. marginalis (secondary species) were recorded to breed (Coe 1978).

As these results are contrary to what is expected from the results of Ulyett's (1950) laboratory experiments and as results from the present study (Fig. 20) indicate a similar trend to Hepburn's at Onderstepoort, one must conclude that

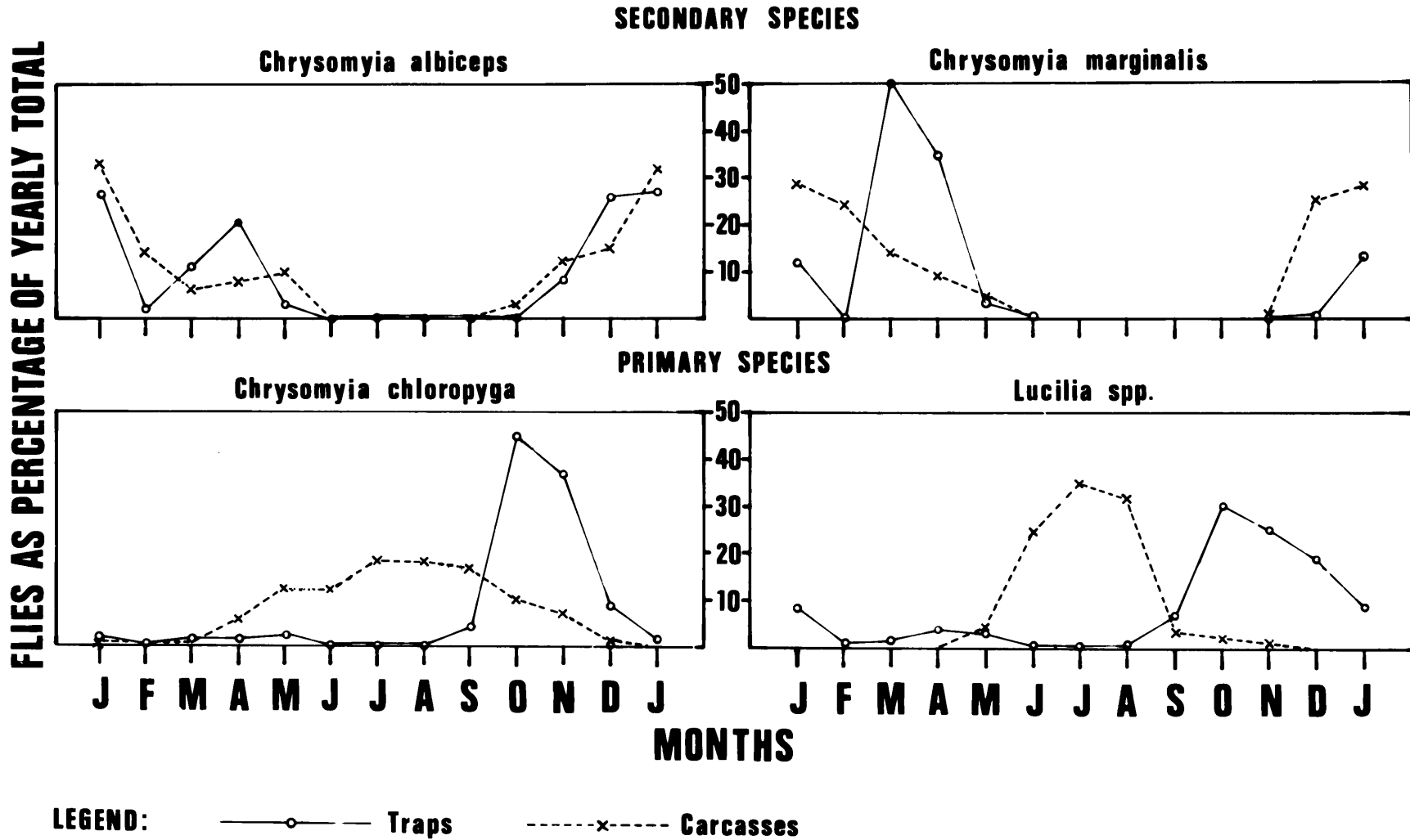


Figure 24 : Seasonal distribution of blowfly populations at Grootfontein (Karoo) as shown by fly-trap captures during the period 1924 to 1926 (Smit 1931), and flies bred from carcasses between 1941 and 1943 (de Vries unpublished data). Populations are expressed as percentage of yearly totals. (After Ulliyett 1950.)

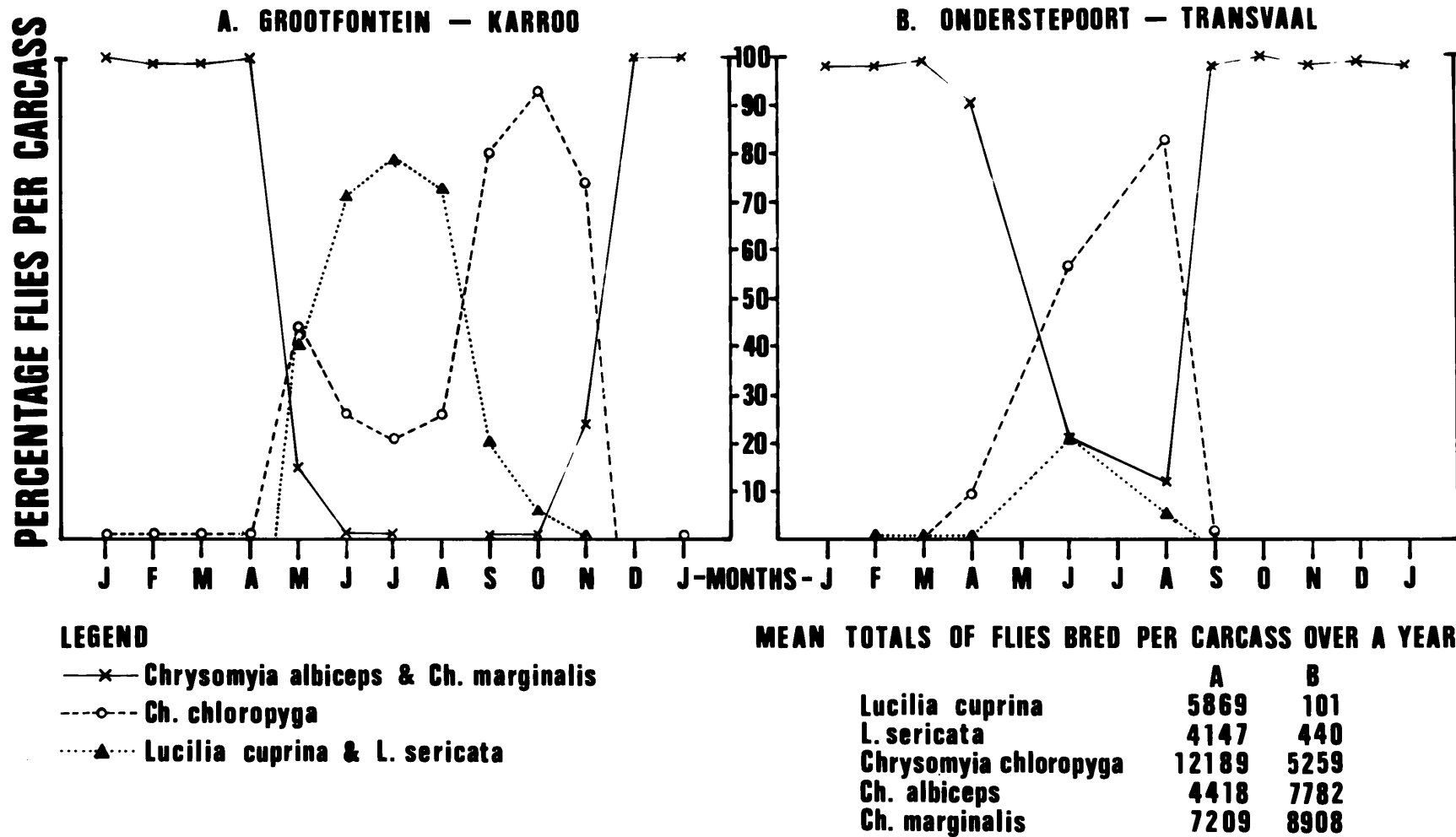


Figure 25 : Seasonal distribution of blowfly populations bred from sheep carcasses at Grootfontein (1941 - 1942) and Onderstepoort (1940 - 1942). Species populations are expressed as mean percentage of total fly population per carcass (From Hepburn 1943.)

there are other factors influencing the success of blowfly species than those accepted by Ulllyett.

Fuller (1934) states that the emergence of flies can be directly related to soil temperature, with each species having a minimum temperature below which no emergence will occur. Similarly Waterhouse (1947) quotes minimum activity and oviposition temperatures for Lucilia, Chrysomya albiceps and Ch. marginalis showing that Lucilia has a better tolerance of low temperatures than the others. Thus one can assume that low temperatures in winter have a greater limiting effect on the success of secondary species in the Karoo than in the Transvaal, which has a warmer climate.

However, the lack of success of primary flies on carcasses in summer is less easy to explain. They obviously do occur at this time (Fig. 24), and it is the main period when they strike sheep in the Karoo (Hepburn 1943, Smit and Du Plessis 1926). So despite all the advantages Lucilia seemingly has and Ch. marginalis lacks in Ulllyett's experiments, other factors must be affecting the success of these flies on carcasses in the field.

In Ulllyett's experiments he exposed small pieces of meat (140 grams). Two noticeable factors here are: (i) the size of the pieces of meat which can only support a low number of larvae and, by virtue of their size, not retain heat generated by larval activity (Waterhouse 1947); (ii) the absence of skin. The skin on decomposing carcasses probably plays an important role in retaining the fluids produced and forming a boundary within which the maggots are generally limited. Although the skin does disintegrate at the soil surface a thick mat of hair still remains. Putman (1977) recorded only a 2% leakage of materials from mice carcasses, but presumably this will increase with the size of the carcass. Thus most of the maggots will have to stay within this casing in order to feed and under these conditions the physical contact of smaller larvae (Lucilia) with vigorous larger larvae (Chrysomya's) may well cause the former to depart (Fuller 1934). The high temperatures associated with larval activity in large carcasses are undesirable to both primary and secondary larvae, but the primary larvae probably have a lower tolerance (Waterhouse 1947).

It is possible that these two factors which were not accounted for in Ulliyett's experiments, may be the ultimate factors enabling secondary fly larvae to exclude primary fly larvae on the same carcasses. In addition, some authors (Fuller 1934, Waterhouse 1947) have stated, in direct contradiction to Ulliyett's results, that secondary fly larvae develop faster than primary ones. If this is so, it would give an even greater advantage to the secondary flies within these two populations. The greater breeding success of Ch. chloropyga over Lucilia in carcasses (Fig. 25) may possibly also be attributed to the factors mentioned above, whilst Mönning and Cilliers (1944) reported that Ch. marginalis larvae are very vigorous and often escape from Ch. albiceps larvae, but do still better when the latter are not present.

If these assumptions are valid, one must question how Lucilia manages to survive at all. A number of authors have suggested that Lucilia primarily breeds in live sheep (strike). Waterhouse (1947) said that L. cuprina was maintained almost exclusively on live sheep in New South Wales, Australia. Mönning and Cilliers (1944) reached the same conclusion for the South-western Cape Province of South Africa. They said that because the area has mild wet winters and warm summers the flies, which need a warm, damp substrate for oviposition, can strike throughout the year. In the Karoo they can only strike in summer as the winters are too cold and dry. This correlates well with Hepburn's (1943) results from traps and carcasses in the Transvaal (where there is a low population of sheep), as Lucilia were scarce even in winter when the secondary species were too low in numbers to compete with them.

A noticeable feature of Fig. 24 is that whereas the numbers of secondary flies at traps resemble those produced from carcasses, these two graphs for the primary flies (particularly Lucilia) are completely different. One may thus conclude that because their numbers at traps are high in summer and they are not breeding on carcasses, they must be breeding on live sheep.

The chances of L. cuprina breeding successfully on live sheep are high because secondary flies only attack some of the struck sheep and these usually only after one generation of primary larvae have matured. In addition, even when the secondary larvae are numerous they have less success in displacing L. cuprina than they have on a carcass (Mackerras 1936, In : Waterhouse 1947). Furthermore, the temperature conditions on live sheep are favourable for L. cuprina, and the larvae and pupae are basically free from predation and parasitism (Waterhouse 1947).

Other factors which may influence the abundance of blowflies are, predation and parasitism of larvae and pupae respectively, availability of oviposition sites and local environmental conditions. Ulyett (1950) in South Africa and Fuller (1934) and Waterhouse (1947) in Australia recorded Mormoniella vitripennis Walk, a pteromalid wasp, as the only parasite found in any numbers and likely to have any affect on the fly populations. Secondary flies, particularly Ch. albiceps and Ch. rufifacies respectively, are the most susceptible as they do not burrow as deeply into the soil as the primary flies do for pupating. Waterhouse (1947) estimated that up to two thirds of the secondary pupae produced from carcasses in summer were parasitised by Mormoniella.

The effect of predation on larvae is considered by Waterhouse (1947) to be far greater than parasitism. Predation is primarily by histerid (Saprinus) and staphylinid (Creophilus) beetles and smooth (primary) larvae are taken in preference to hairy (secondary) larvae. Estimates of the extent of predation vary from negligible (Fuller 1934) to 66% (Putman 1977) to 98% in summer (Waterhouse 1947). Waterhouse did his experiments in sand trays, which may have favoured both the predators and the parasites, and repeated experiments may have encouraged a local increase in their numbers. Whatever the extent of predation and parasitism may be in South Africa, the maggots always occurred in sufficient numbers to consume a carcass completely when not disturbed and later when they emerged, the surrounding trees were covered with thousands of blowflies.

As flies oviposit in the natural orifices of the body or areas of soft skin, the restricted area available may limit the total numbers of eggs laid on any carcass (Putman 1977). If this is so it would favour the primary flies which tend to oviposit earlier than the secondary flies (Ullyett 1950).

Both Smit (1931) and Parrish and Cushing (1938) state that one traps different proportions of blowfly species under different environmental conditions. Thus surface water, relative humidity, density of shade, protection from the wind and density of wooded vegetation all influence the occurrence of flies.

However, the extent to which carcasses occurring in different areas favour the development of any particular species is not known, although Ch. marginalis tends to be more evenly distributed than the others which particularly favour moist and sheltered areas (Smit 1931).

Under field conditions none of these factors seem to particularly influence the success of blowflies on carcasses and probably only reduce the intensity of competition for the food available (Fuller 1934). This is because the numbers of larvae are usually so high that there is insufficient food for all of them and the amount that succumb to various environmental factors may otherwise have died from starvation. Thus although parasitism and lack of oviposition sites may favour primary flies and predation may favour the secondary flies, the dramatic increase in numbers of the secondary flies (Fig. 25) and the corresponding fall off of the primary flies (particularly Lucilia) as soon as the secondary flies emerge after winter, suggest that these factors do little to modify the struggle for supremacy. Rather it is suggested that the effects of direct competition (high physical contact and increase in carcass temperature) are what primarily control the success of species on carcasses.

Calliphora croceipalpis Jaenn. is the fifth blowfly species encountered in the field in South Africa (Zumpt and Patterson 1952). However as it occurs in such low numbers (Hepburn 1943, present study) and oviposits after all the other species (Zumpt and Patterson 1952) it offers very little competition to them.

Beetles

The conditions of this study have helped particularly in elucidating the roles of the beetle species that were encountered. Because of the effect of the vertebrate scavengers the conditions that exist in carcasses can be more precisely defined than in any other study yet done. A range of carcasses from fresh to old has been defined, with or without maggots and with or without soft tissues or skin, with each situation having a different arthropod faunal composition (Fig. 22). Only those beetles actually feeding on the carcass (necrophagous species) or on the inhabitants of the carcass (predatory species) were recorded. The families of beetles will be discussed in their successional order. The Scarabaeidae, sub-family Scarabaeinae, are the wellknown dung beetles of Africa. They were occasionally seen to remove the gut contents of carcasses, but were only recorded when seen eating meat, which they scraped off partly cleaned bones. The other sub-family, the Hybosorinae, were also recorded as feeding on meat. These beetles were only found within the first nine days.

The Histeridae and Silphidae both preyed on maggots and occurred almost exclusively in their presence. Braack (1979) also recorded histerids as the most common predacious beetles in the eastern Transvaal. It is interesting to note that on no occasion during this study were Staphylinidae, usually the most common predacious beetles (Bornemissza 1957, Payne 1958), ever recorded. Putman (1978b) observed a similar anomaly during his study when he never found any histerids on his mice carcasses, but found carabids (and staphylinids) instead. The reasons for these differences of faunal composition can probably be accounted for by zoogeographic, climatic and edaphic factors (Bornemissza 1957).

The most noticeable features of the occurrence of the Dermestidae are that the adults were present at 78% of the carcasses including the freshest ones. This is in contrast to observations made by Fuller (1934), Bornemissza (1957), Reed (1958), Johnson (1975) and others. However, they were still most prevalent (adults and larvae) in their traditional role as described by the above authors - feeding on old dry skin.

The Cleridae, like the Dermestidae, were far more common than recorded by other authors, occurring on 65% of all carcasses. Despite being common on all types of carcasses, their particular niche seemed to be on old bones.

Fuller (1934) states that their larvae eat the fat that exudes from old bones, so it is probable that the adults do the same, particularly as they have very poorly developed mouthparts (Endrödy-Younga pers. comm.).

Whenever the Trogidae were found feeding, it was either on hair, or on the inside of a moist discarded hoof. Coe (1978) also recorded them as feeding on the dried soles of elephant feet. However, other authors (Fuller 1934, Johnson 1975) have recorded them as feeding primarily on old dry skin. Whatever their preferences, the one common factor in their diet appears to be some form of keratinous material. The Tenebrionidae were seldom present but were most common on old dry bones where they may also have been feeding on exuding fat. However this family was seldom found by other workers, so little is known of its feeding habits at carcasses.

Other arthropods

Termites were only recorded on two occasions. Once they removed the lower edges of giraffe hooves and once they removed the hair at the ground interface of a fresh uneaten antelope. On both occasions their nests were within a few metres. On the one occasion that ants were quite numerous at a carcass they were preying on maggots and dragging them to their nest nearby. There is little consistency in the literature concerning the role of ants and termites at carcasses. Many authors (Bornemissza 1957, Cornaby 1974, Johnson 1975, Coe 1978, Braack 1979) found them to be very active at carcasses, while others (Fuller 1934, Putman 1978b) obtained results similar to those found during the present study. As some of these contrasting results were from the same

S. Endrödy-Younga, Transvaal Museum, P.O. Box 413, Pretoria, 0001. May 1979.

geographic regions, it is suggested that these may be temporal variations influenced by the local abundance of food.

Teneid moths are well known in Africa for the damage they do to the horns of antelope trophies. These moths were eventually found in all the horns and many of the larger hooves that survived.

Arthropods in competition with vertebrate scavengers

One of the most noticeable features of this whole study was the minor role played by the arthropods in the decomposition of carcasses (Table 14). As has been suggested in Chapter 3, this was simply a result of maggots not being able to compete successfully with the vertebrate scavengers, particularly griffon vultures and spotted hyaenas. The main reason why maggots cannot compete, is because of their slow rate of development. It has been shown in Fig. 21 that the time taken for the first emergence of maggots, after death, in a carcass is negatively correlated with ambient temperatures. Therefore maggots develop much faster in summer than in winter, and consequently compete more successfully at this time of year.

This pattern was evident on the farms where the vertebrates were often shy and gave the maggots time to develop. Were it not for the vertebrate scavengers being more efficient in the nature reserves, maggots should similarly have greater success in the Lowveld than in the Highveld, which has a colder climate. Their potential to do this was illustrated by them developing within a week in the neck of a giraffe carcass, which was put out in Timbavati in mid-August.

The masses of tissues consumed by maggots were calculated by simply correlating the rapid decline in volume of the carcasses concerned with the immense activity of maggots, and saying that the maggots had consumed all the materials that had been removed. This was considered acceptable because Putman (1977) had calculated that blowflies (Calliphora erythrocephala Meigen) can consume over 80% of available carrion material. As he considers 70% of the body weight to

be available material (Putman In litt.), this means that over 56% of the body weight can be eaten by maggots. This is in accordance with what I estimated.

The only alternative agents under these circumstances are micro-organisms, which Coe (1978) estimated to have consumed 95 - 97% of the soft tissue of elephant carcasses. However, because the roles of other decomposers were hardly effected by the presence or absence of maggots, and as decomposition was very slow and incomplete in the absence of maggots, Putman (1977) suggested that bacterial decomposition was relatively insignificant. It is therefore suggested that decomposition by micro-organisms in the present study was also negligible.

The only beetles that ate any noticeable amount of food were dermestids on old dry skin that had been left by jackals on the farms. Nevertheless, on farms where vultures or jackals do not occur at all, the role of the arthropods will increase to the extent of eventually removing all the available meat and skin.

Although their role is difficult to quantify, the one group of arthropods that are probably very important in the recycling of nutrients on both nature reserves and farms, are the tineid moths. These moths can reduce horn sheaths and hooves of bovid carcasses to hollow masses of larval tubes. When hyaenas eat these parts they are either passed through in the faeces or regurgitated as undigested chips (personal observation). Thus tineid larvae seem to be the only agents that can rapidly recycle the elements tied up in the horns and hooves of antelope.

In this study all carcasses were placed or found in sites accessible to vultures and carnivores. However, many carcasses, particularly smaller ones, may be inaccessible to vertebrate scavengers and the arthropod scavengers in the Transvaal probably play their greatest role in the decomposition of these carcasses.

CHAPTER 6

CARNIVORE DAMAGE TO BONES

AND ITS ARCHAEOLOGICAL IMPLICATIONS

INTRODUCTION

A field of major interest at present is the reconstruction of australopithecine behaviour at various sites in Africa (Wolberg 1970, Read-Martin and Read 1975, Brain 1976a). However, this is no easy task because of the great number of variables involved in the accumulation and subsequent preservation of bones found at these localities. Analysis of these may be directed at establishing the faunal composition or the survival rates of particular bones. The former only really helps to elucidate past environmental conditions and hunting methods (Klein 1977, 1978, Vrba 1974), while 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 (Brain 1976b). However, because definite examples of bones accumulated and damaged by these agents have not and possibly cannot be described, the same bone assemblages are often given quite different interpretations.

Brain (1969a) has shown that the bones of goats fed on by Hottentots and their dogs in the Kuiseb river valley 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 the present study, data on the damage and survival rates of the bones of carcasses that had been consumed by the various carnivores were collected. These data are used here to determine whether Brain's interpretation is correct.

Coe (1978) has suggested that the levels of calcium in the soil and in plants "may well be an important factor on the growth of large mammals." In

his study he was considering the rate of recirculation of the elements contained in elephant bones. During the present study, carcasses ranging in size from 10 - 1200 kg were observed, and therefore the rate of decomposition of a large spectrum of bone sizes was monitored.

The prevalence of osteodystrophy (calcium deficiency) in Cape vulture chicks in cattle ranching areas has been suggested to be an indirect result of the disappearance of large carnivores in these areas (Mundy and Ledger 1976). This is because griffon vulture chicks need bone chips to supplement their diet and their parents are considered to collect these chips by revisiting carcasses that large carnivores have subsequently chewed. Data collected on the bone damage by various carnivores are used here to evaluate each carnivores potential as a supplier of bone chips for griffon vultures.

METHODS

Data on the damage and removal of bones by the various carnivores encountered during the present study were collected at all the carcasses observed. This information was collected between feeding bouts of all the vertebrate scavengers, provided there was no chance of disturbing them. Thus at carcasses where vultures fed, these observations were only made once all the soft tissues had been consumed and vultures were no longer present.

Most of the carcasses observed were revisited at intervals until the end of the study. Thus for the earlier carcasses, data were collected on the decomposition of bones up to 18 months old. However, because of the nature of the present study it was often only possible to make one observation on the status of the bones of a carcass.

A variety of information pertaining to the decomposition of bones was collected at each carcass. The different categories used are defined below :

Definitions of terms

Survival 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.

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

Articulation The percentage articulation for each bone type has been 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 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 (pelvis); 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, as the same bias applies to all carcasses, the few duplications of articulation surfaces between bone types will not affect the relative frequencies between carcasses.

Fragmentation Ratio This gives an average indication of how many pieces each bone was broken into. It was calculated by counting the number of bone pieces that were found and dividing them by the number of bones they came from. It was often difficult to determine the exact origin of long bone chips, in which case the number of original bones was over rather than underestimated. The ratio was expressed as a percentage by multiplying by 100. The relative

fragmentation ratios of whole carcasses were calculated by using only the long bones, the cranium and the ribs as these are the bones which fragment most readily.

RESULTS AND DISCUSSION

The results of the damage caused by carnivores at the end of the initial feeding bouts are recorded in Fig. 26. 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 (cranium) 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 those most susceptible to damage. However, as one of the primary aims of this study was to record any possible differences between carnivore 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 hyaenas (Fig. 27). After a few days the horn sheathes 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

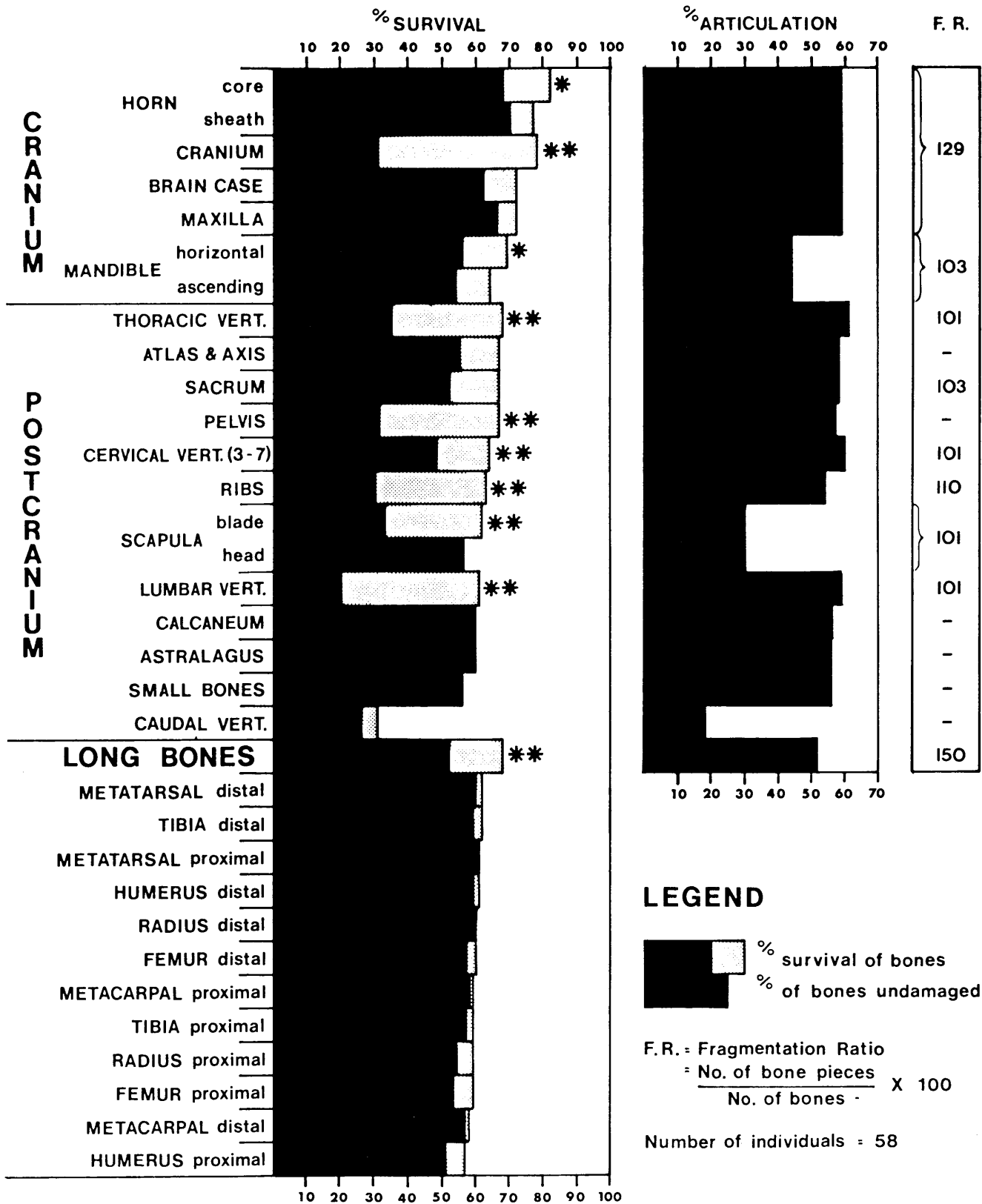


Figure 26: Percentage survival, damage, articulation and fragmentation of parts of bovid skeletons once carnivores had finished feeding in the Transvaal and southern Zimbabwe. Using the Z proportion, statistical significance is indicated as follows: * $p < 0,05$; ** $p < 0,001$.

braincase to remove the brain. Ultimately the back of the brain case remained as a type of cup. Unlike the hyaenas, they left the snout and palate as one unit.

Mandibles: These are fairly thin but very compact bones, 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. 26). 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 (Pelvis): 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. 28). Initial 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. 27). Initially the Hottentots did no damage, but later the blades were extensively damaged.

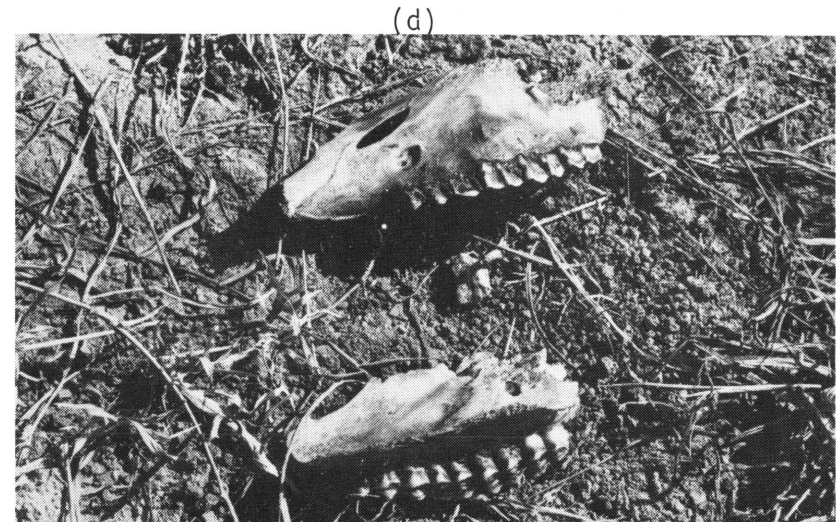
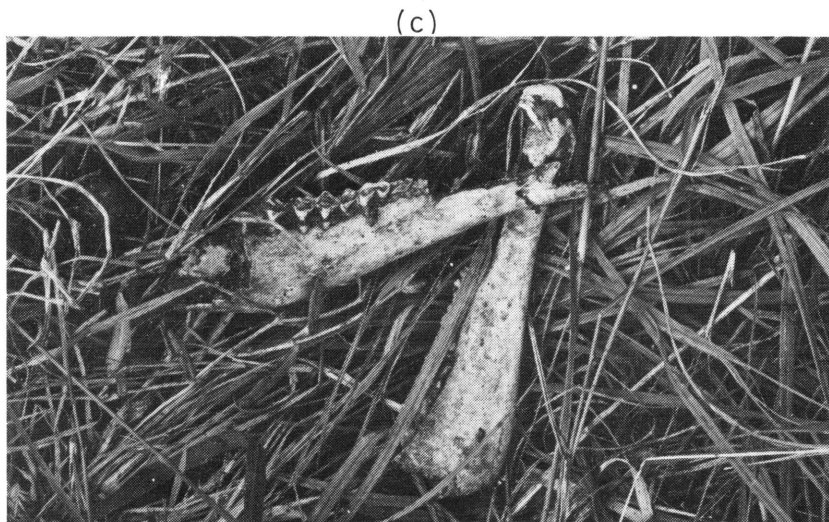
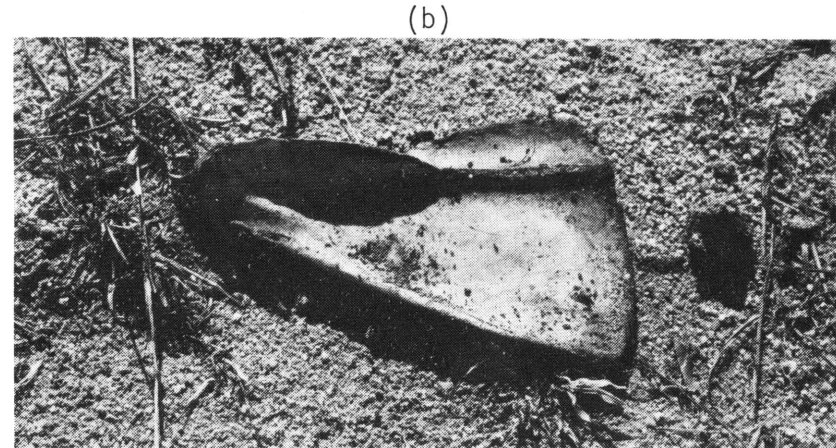
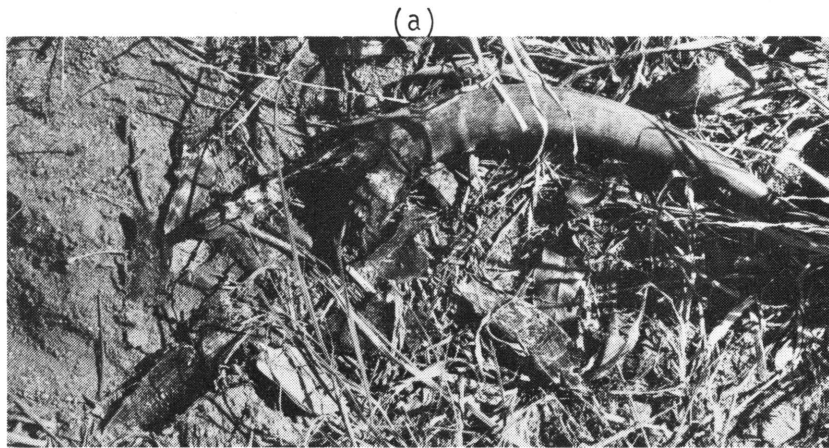
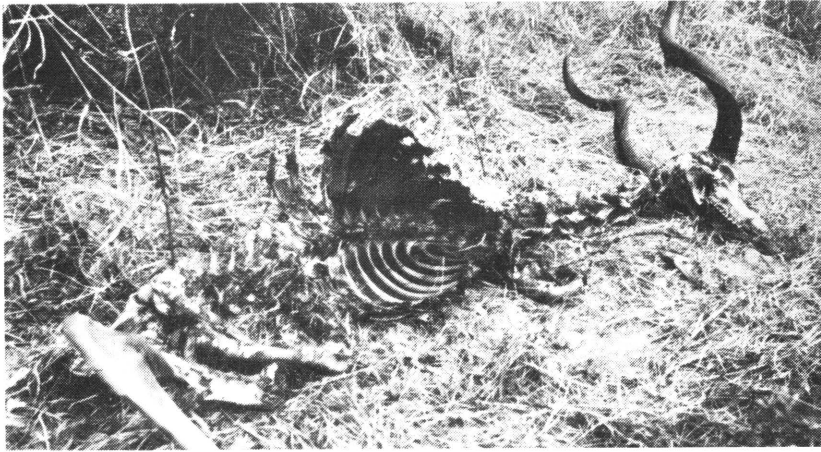
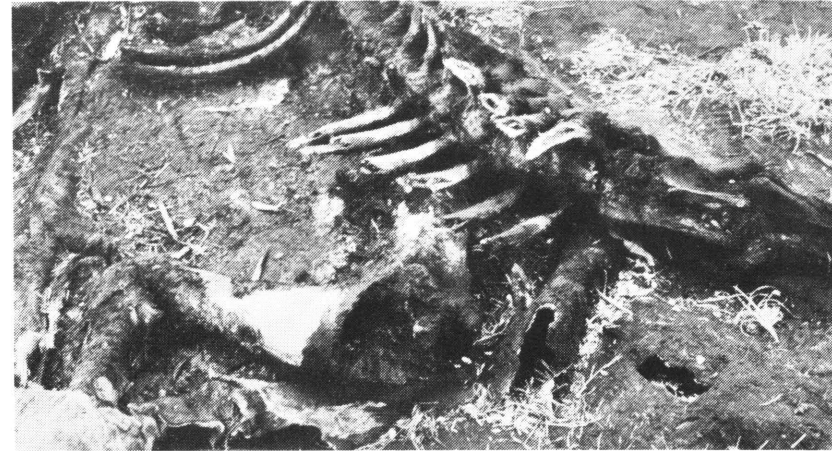


Figure 27 : Remains of an impala (*Aepyceros melampus*) left by spotted hyaenas (*Crocuta crocuta*) immediately after their first feed : (a) Both the horn core and sheath have been chewed. (b) The head of the scapula has been removed. Only the densest portions of the mandibles (c) and maxillae (d) have survived.

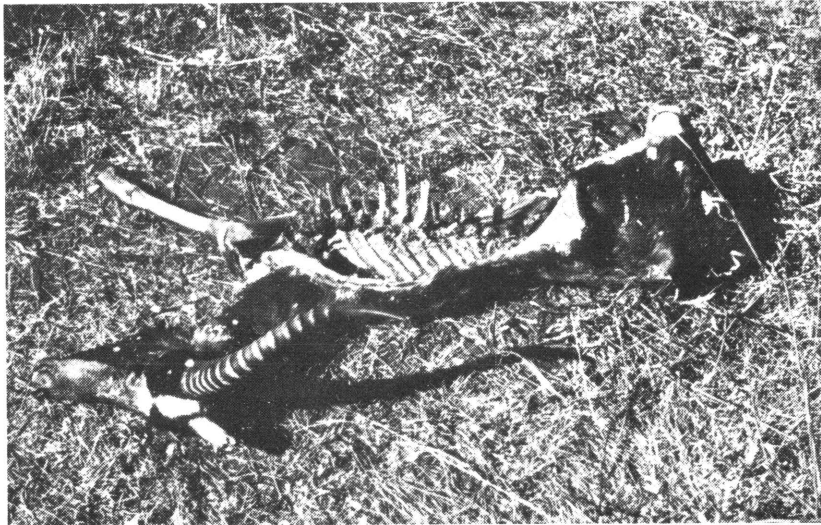
(a)



(b)



(c)



(d)



Figure 28 : Typical examples of bone damage by : (a) lions (*Panthera leo*) to a kudu (*Tragelaphus strepsiceros*) - note the free but intact mandibles; extensive damage to ribs; disappearance of front legs. (b) Spotted hyaenas (*Crocuta crocuta*) to a giraffe (*Giraffa camelopardalis*) - note the entire removal of proximal humerus and severe damage to ribs. (c) Brown hyaenas (*Hyaena brunnea*) to a blesbok (*Damaliscus dorcas*)- note the chewed ribs and horn core. (d) Jackals (*Canis mesomelas*) and vultures to a blesbok - note the lack of damage to ribs.

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 their damage was not recorded.

Long bones: These bones were only very slightly damaged by the carnivores as a whole (Fig. 26). However, distinct differences emerge when one compares hyaenas to the other carnivores (Fig. 29). In this figure the results for spotted and brown hyaenas in the lower two weight classes have been combined while in the upper class the results are only for spotted hyaenas. The rates of survival of long bones chewed by hyaenas are in all cases significantly lower than for the other carnivores ($p < 0,01$). However, there are no significant differences in the rates of survival of long bones chewed by the remaining carnivores, except between lions and jackals in the middle weight class ($Z = 2,5; p < 0,01$).

Thus hyaenas can crush the long bones of small and medium-sized bovids into small chips (Fig. 30), and also do extensive damage to the bones of large bovids (Fig. 28). 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. In Fig. 29 their potential to do this is illustrated by them doing far more damage than either dogs or jackals, although because of small sample sizes this difference was only significant ($Z = 2,4; p < 0,01$) when compared with jackals at medium-sized carcasses.

Obviously lions can also eat the long bones of small bovids, but they do very little damage in the large two weight classes (Fig. 28 and 29). In contrast to this, the Hottentots broke all marrow-containing bones, using two rocks as a hammer and anvil. They then chewed the softer epiphyses, as will be discussed later. Thus the Hottentots broke all the long bones, but left most of the epiphyses with varying degrees of damage.

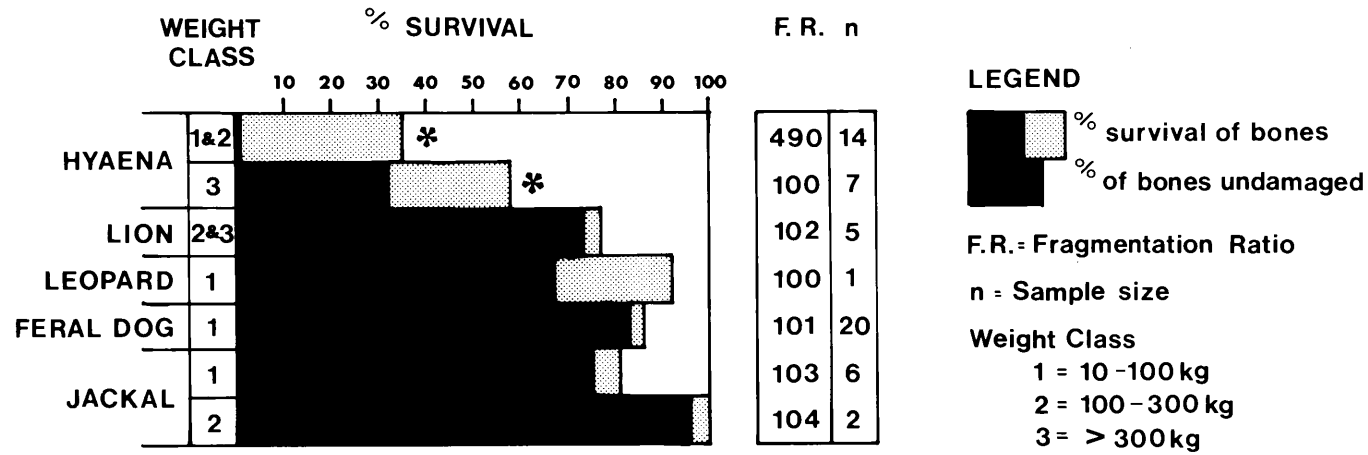


Figure 29: Total percentages survival, damage and fragmentation of bovid long bones when fed on by various carnivores in the Transvaal and southern Zimbabwe. Using the Z proportion, statistical significance is indicated as follows:
 * $p < 0,001$.

Articulation

The most obvious and disproportionate disarticulation of bones occurs with mandibles, scapulae and caudal vertebrae (Fig. 26), their rates of disarticulation being significantly higher (Z proportion, $p < 0,001$) than the remaining bone types. In the case of caudal vertebrae, this is because they have been eaten. However, with the other two 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 as soon as the meat and skin of the face have been eaten they are found detached, although the left and right mandibles 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 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. In fact, mandibles had significantly higher ($Z = 1,98; p < 0,05$) survival rates than the remaining bones excluding caudal vertebrae and scapulae, while in the case of scapulae, there was no significant difference ($Z = 0,47; p < 0,5$). These results reflect these two bones' low potential as food sources, both being hard compact bones.

Like the mandibles, the pelvic girdle was very resistant to separation and often remained intact for many months. However, the hind limbs soon become 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. 28). 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:

- (i) The hind limbs were removed with innominates attached.
- (ii) The feet were separated from the legs at the metapodial/phalangeal joints.
- (iii) The ribs were separated from the thoracic vertebrae, which probably accounts for the greater damage caused to the transverse processes 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. 30). The cranium separated into maxillae and pieces of brain case. The ribs, having a spongy centre, are less likely to chip than long bone shafts and thus were eaten with less 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. 31).

Individual carnivore damage

The cumulative damage to all bone types by the various carnivores is illustrated in Fig. 32. One can see a pattern of decreasing damage caused by hyaenas, lions, leopards, dogs and jackals. Within each bovid weight class, these differences were all significant (Z proportion, $p < 0,05$). However, the corresponding overall survival patterns are remarkably similar, except in that hyaenas consumed or removed over 90% of all bones in the lower two weight classes and were therefore far more effective than any other carnivores. Typical examples of hyaena, lion and jackal damage are shown in Fig. 28.

Individual Bones

The details of individual bone damage are illustrated in Fig. 33. Spotted and

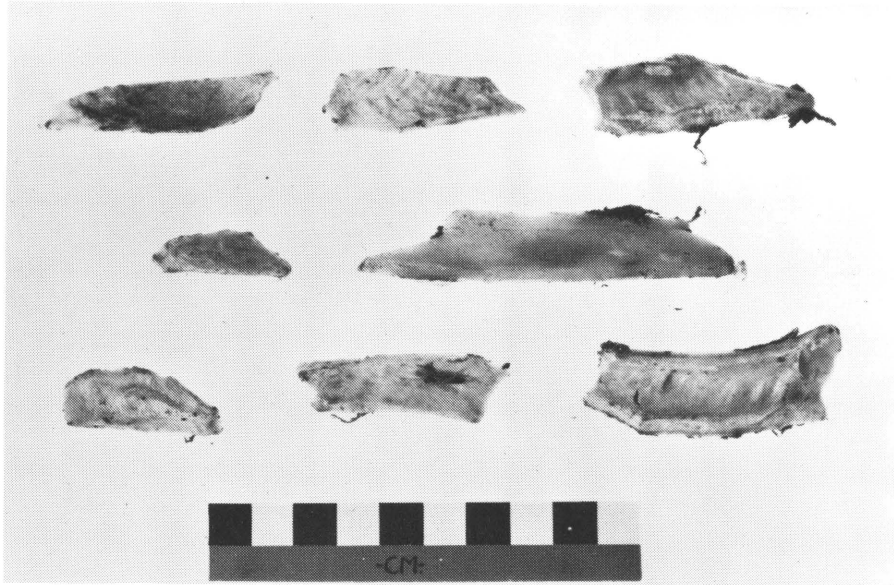
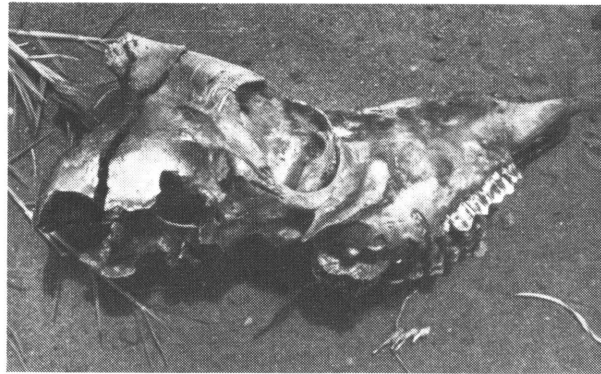
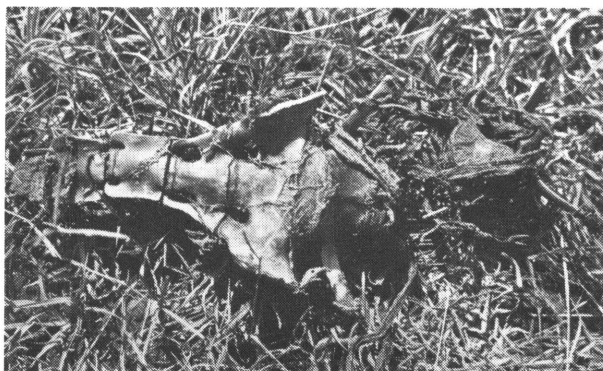


Figure 30 : Typical examples of long bone chips left by a brown hyaena (Hyaena brunnea) after feeding on a blesbok (Damaliscus dorcas).

(a)



(b)



(c)



Figure 31 : Some remains of a blesbok lamb (Damaliscus dorcas) that was fed on by maggots then black-backed jackals (Canis mesomelas), showing how separation can occur within bones that have not yet fused: (a) cranium (b) sacrum (c) distal metapodial.

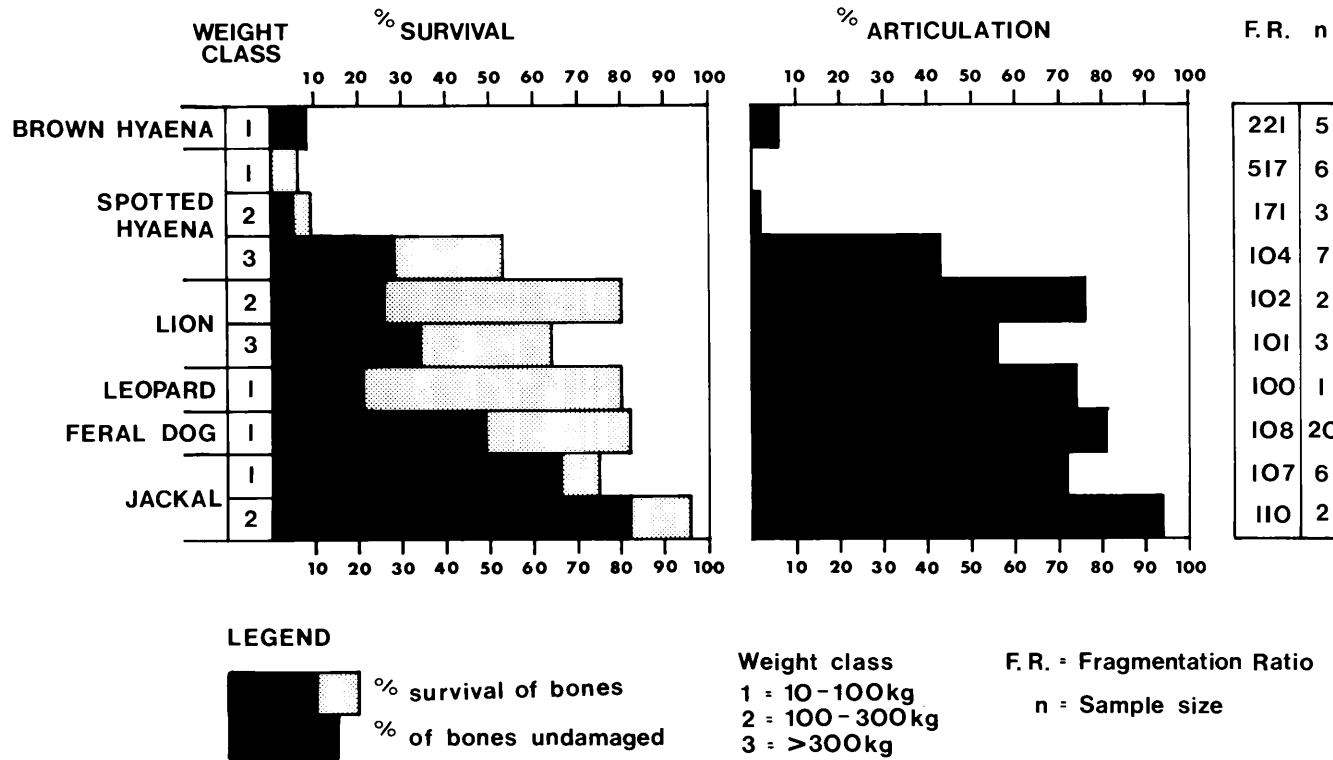


Figure 32: Total percentages survival, damage, articulation and fragmentation of bovid bones when fed on by various carnivores in the Transvaal and southern Zimbabwe.

brown hyaenas are grouped together because they caused similar damage to smaller bovids. Similarly the results for lion damage to medium and large bovids are put together. The leopard is not included in this analysis as there were insufficient data.

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

In the small weight class, it is interesting to note that even when hyaenas fed, the mandibles and scapulae still had relatively high survival rates. In this case the survival of long bones and crania is exaggerated because they consisted almost exclusively of bone chips. Although the survival pattern for dogs and jackals was 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 one can see three distinct patterns (Fig. 34):

- (i) The patterns of damage and survival of all the long bones fed on by the other carnivores were virtually identical. Only the proximal humerus and proximal femur had any noticeable damage.
- (ii) When hyaenas fed on the smaller bovids, there was also no predictable pattern of differential survival of bones. Almost all the bones were completely chewed up and those that survived did so by chance.
- (iii) The predictable pattern of bone survival as described by Brain (1976a) only emerged when hyaenas fed on large bovids.

If one assumes that the specific gravity of the epiphyses of goat bones (Brain 1976a) applies to bovids and equids in general, then with the exception of the

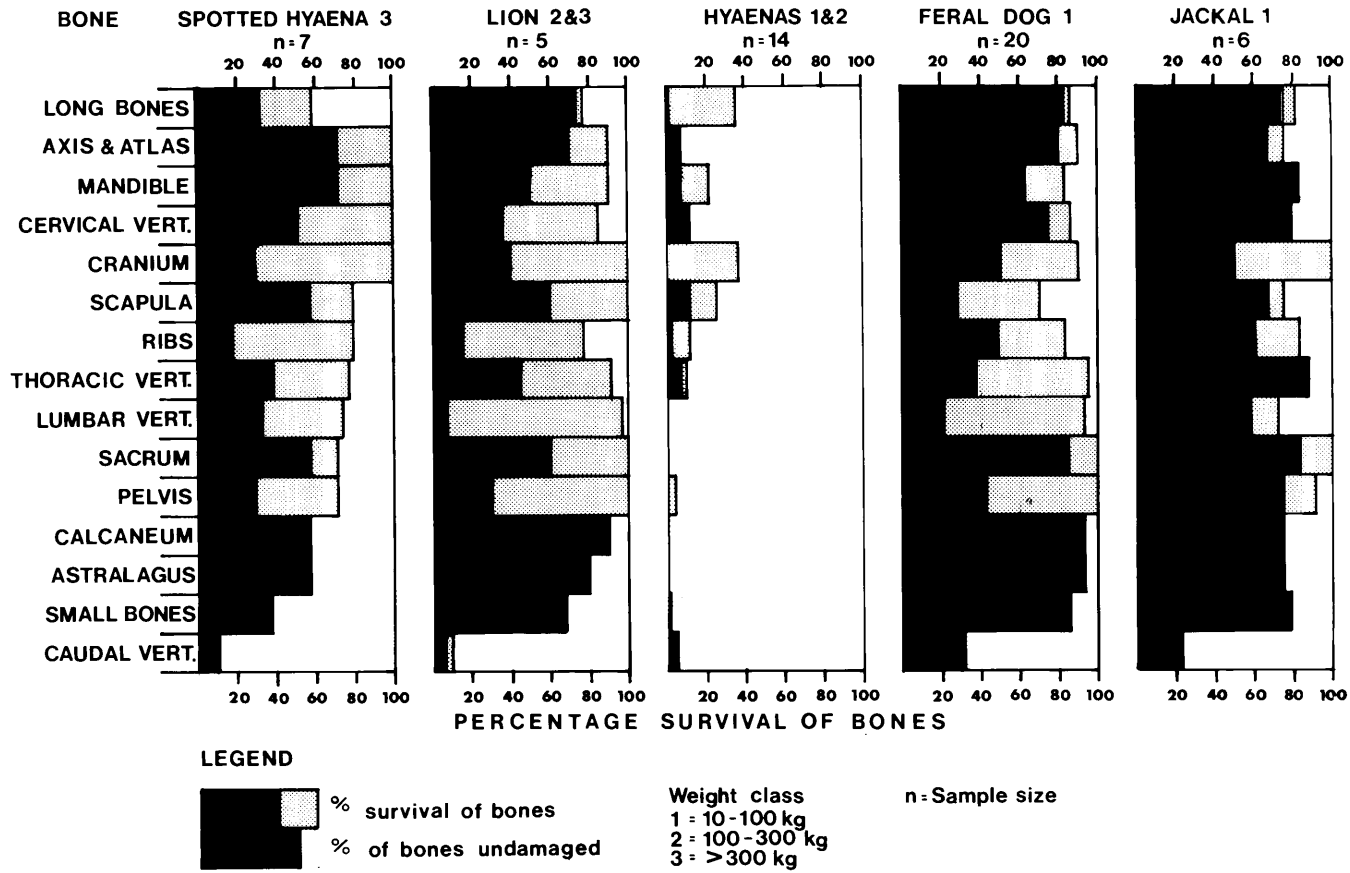


Figure 33: Percentage survival and damage of parts of bovid skeletons when fed on by various carnivores in the Transvaal and southern Zimbabwe.

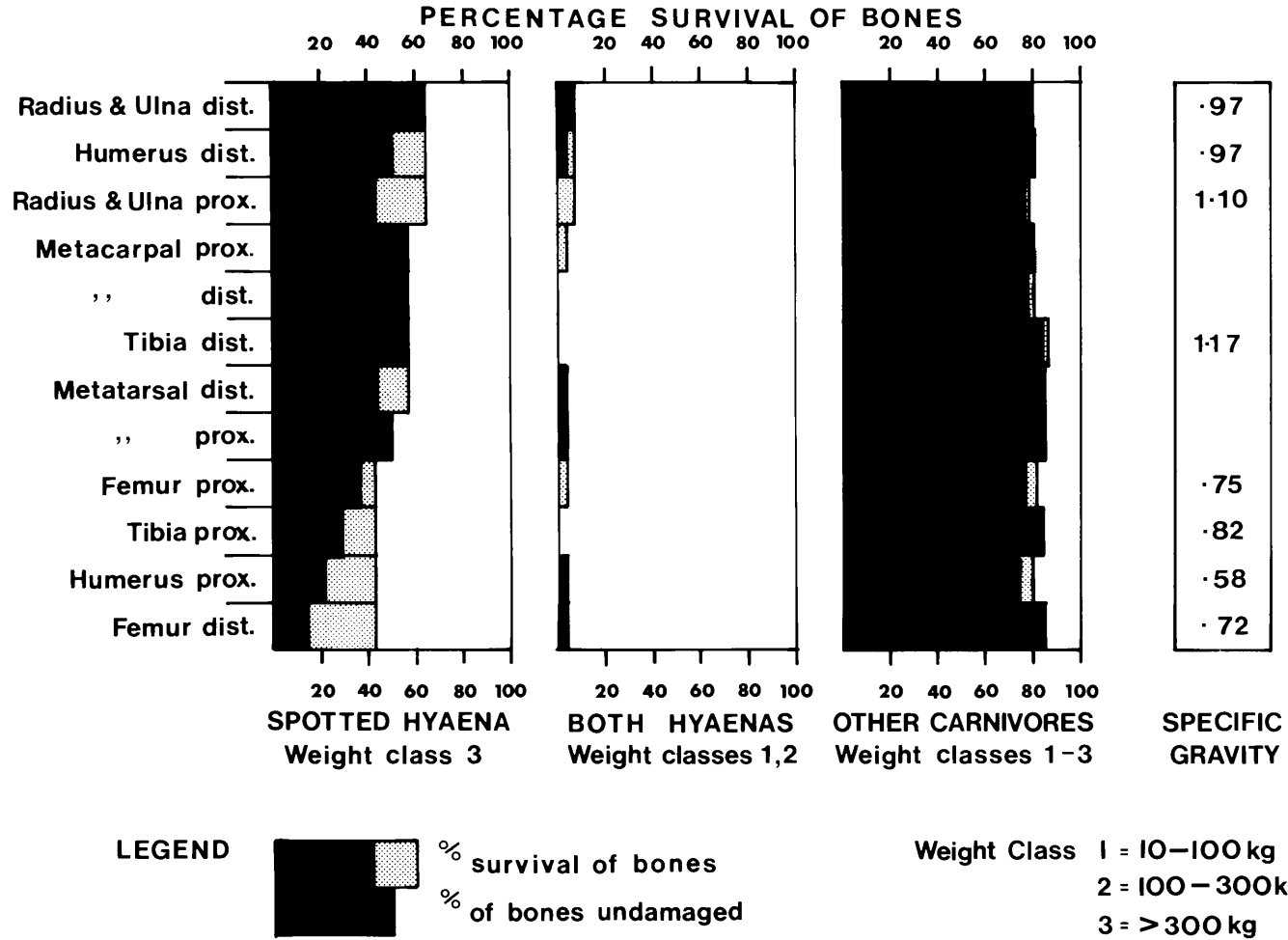


Figure 34: Percentage survival and damage of the individual epiphyses of bovid long bones when fed on by various carnivores in the Transvaal and southern Zimbabwe.

distal tibia, the group with the highest specific gravities have the highest survival rates and those with the lowest specific gravities, the lowest survival rates.

Although the proximal radius and ulna has a very high specific gravity it was often damaged, whereas 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 ultimately likely to have lower survival rates than undamaged ones, the undamaged rate has been plotted against specific gravity (Fig. 35) and the predicted pattern emerges even more clearly ($r = 0,80; df = 6; p < 0,05$). 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. This is 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). In confirmation of this, the four categories of bone damage caused by jackals and vultures to adult and juvenile small bovids are illustrated in Fig. 36. In all four categories the bones of the juveniles had significantly greater damage (Z proportion, $p < 0,001$) and hence less chance of surviving. Typical examples of separation within the bone are shown in Fig. 30.

A final factor which may play a role in the survival of bones is whether maggots (fly larvae) have fed on the carcass before it is eaten by carnivores. Although quantitative data are not available, it was noticed that the bones of carcasses on which maggots had fed, disarticulated much easier and were cleaner than others (see Fig. 23).

Bone survival after six months

In order to more closely approximate to Brain's results of goat bones in the desert, the results of the remains of bones that were in the veld for over six

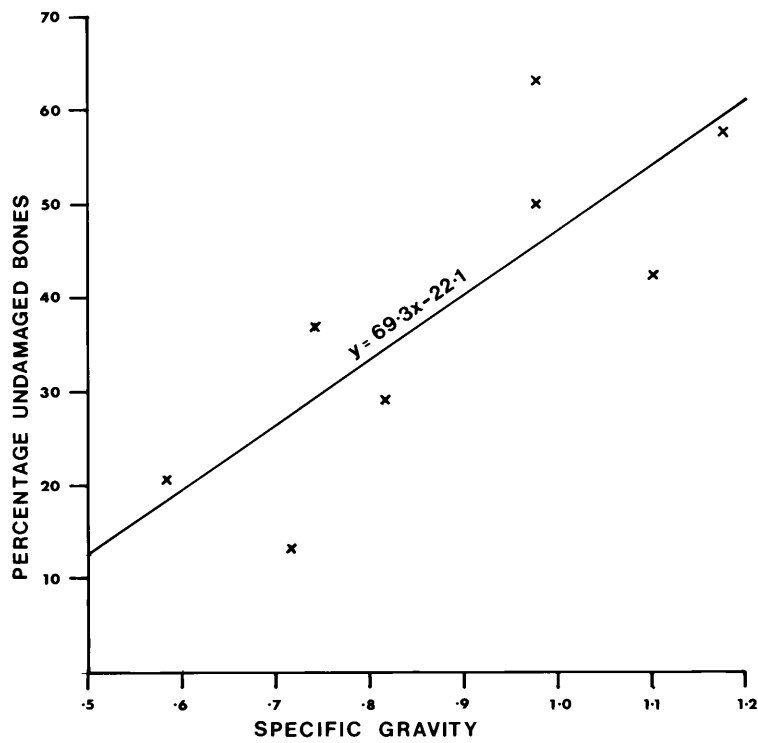


Figure 35: Graphical representation of the relationship between the specific gravity of the epiphyses of large bovid long bones and their rate of damage by spotted hyaenas (Crocuta crocuta) in the Transvaal nature reserves. (Correlation coefficient : $r = 0,798$; $df = 6$; $p < 0,05$).

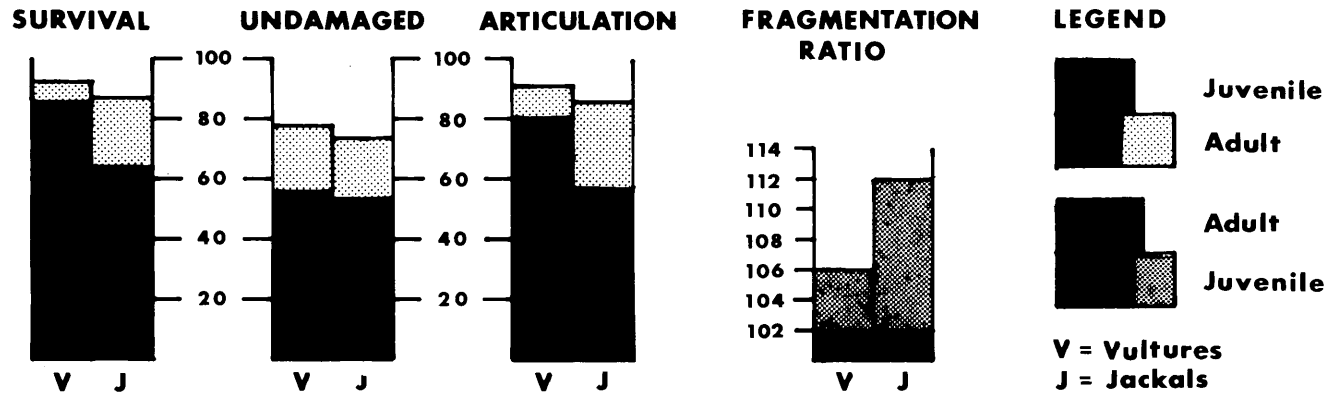


Figure 36: Total percentages survival, damage, articulation and fragmentation of small bovids' bones once black-backed jackals (*Canis mesomelas*) or vultures had finished feeding in the Transvaal and southern Zimbabwe.

months are presented in Fig. 37. These bones were those left on the nature reserves and on the two farms (Olifantshoek and Tweeputkoppies) where, the bush cover is quite thick, the jackals largely undisturbed and there are numerous cattle which may trample the bones. After six months one cannot specifically relate further bone damage to particular carnivores, but rather to the area and its fauna.

In this figure one can see that in areas with hyaenas (Olifantshoek and the nature reserves) nearly all the bones of small and medium-sized bovids were eaten or removed and only the large bovids were well represented. Considering the low 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, the number of undamaged bones and all the articulation ratios were very low.

In Fig. 38 the two extremes of the scale are presented: giraffe bones in the nature reserves and impala bones at Tweeputkoppies. The most noticeable features of this figure are:

- (i) The overall survival rates of the bones in each sample are remarkably similar, considering the small sample sizes and the difficulty experienced in locating these bones in the grass.
- (ii) With the exception of the small bones and ribs which have low survival rates, the survival rates of bones after this period of time are very similar to those of fresh bones.
- (iii) The impala bones were damaged far more than the giraffe bones, despite the fact that jackals do much 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

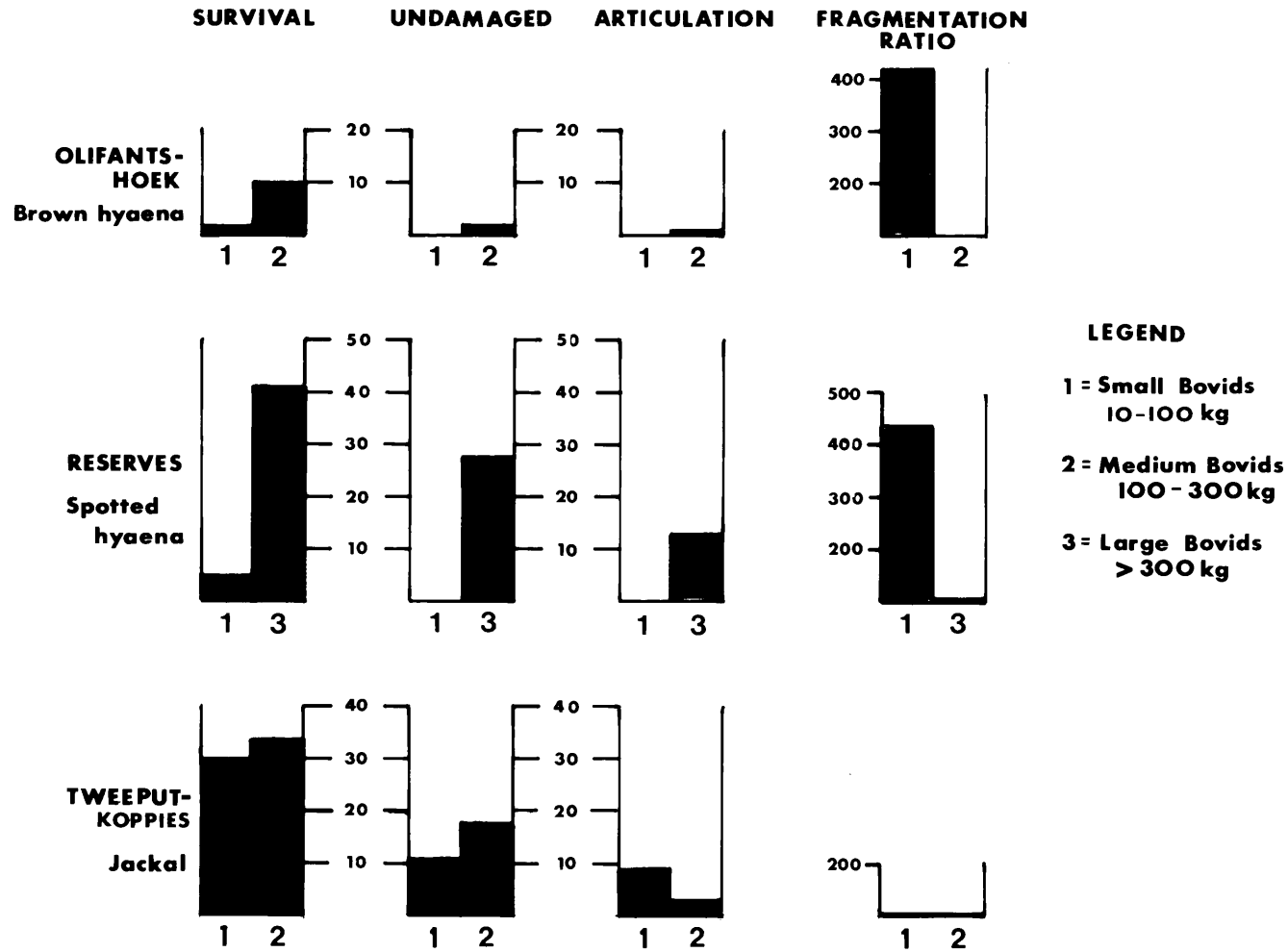


Figure 37: Total percentages survival, damage, articulation and fragmentation of bovid bones six months or more after death, in three different areas of the Transvaal.

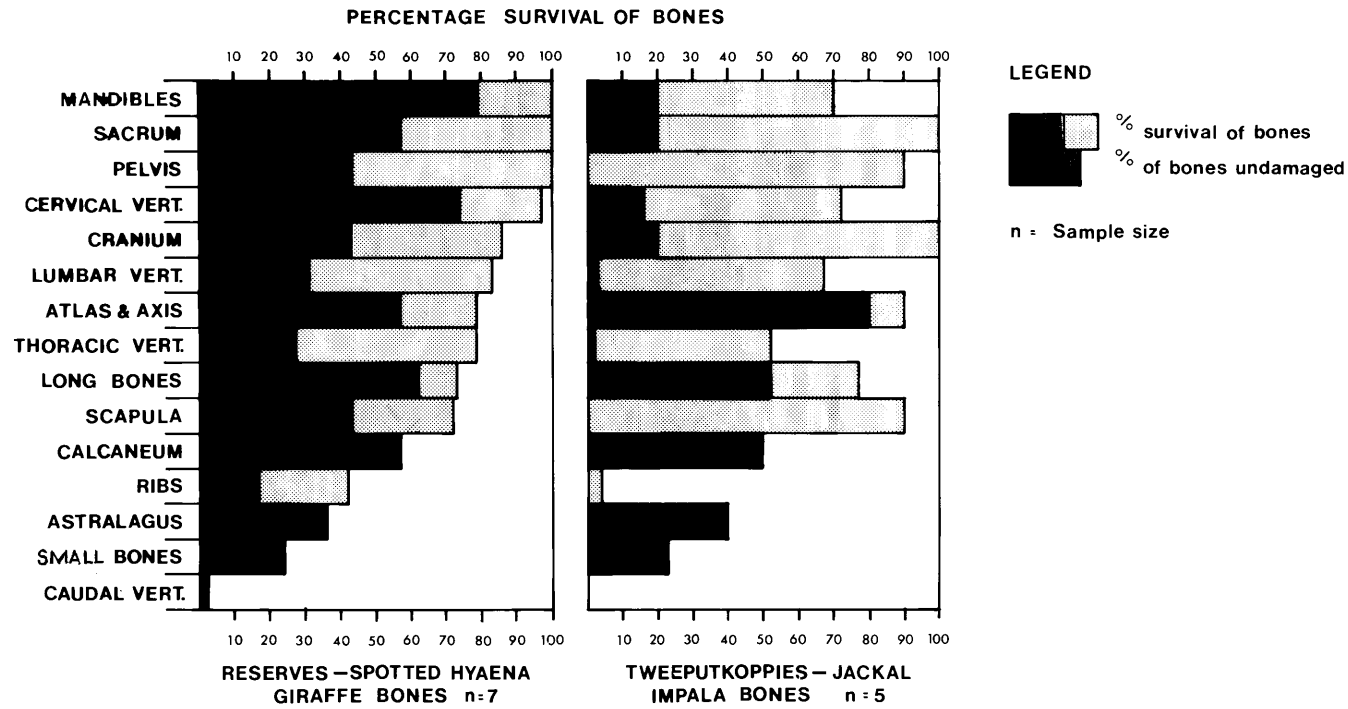


Figure 38: Percentage survival and damage of parts of giraffe (*Giraffa camelopardalis*) skeletons in nature reserves and impala (*Aepyceros melampus*) skeletons on Tweeputkoppies, six months or more after death.

for large animals (~ 12 months) than small ones (\sim six 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. In view of this, the ultimate similarity of the various types of carnivore damage and the fact that one cannot reliably predict beyond this stage, I feel that the grouping of these carcasses (which represent all three weight classes) for comparing carnivore to hominid damage, is justified.

Hominid damage to bones

In Fig. 39 it is apparent that carnivore damage to bones is quite different from that caused by Hottentots in the Kuiseb or the mysterious agents at Makapansgat. 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 accounted for simply by continued weathering and trampling. I feel 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. 33),

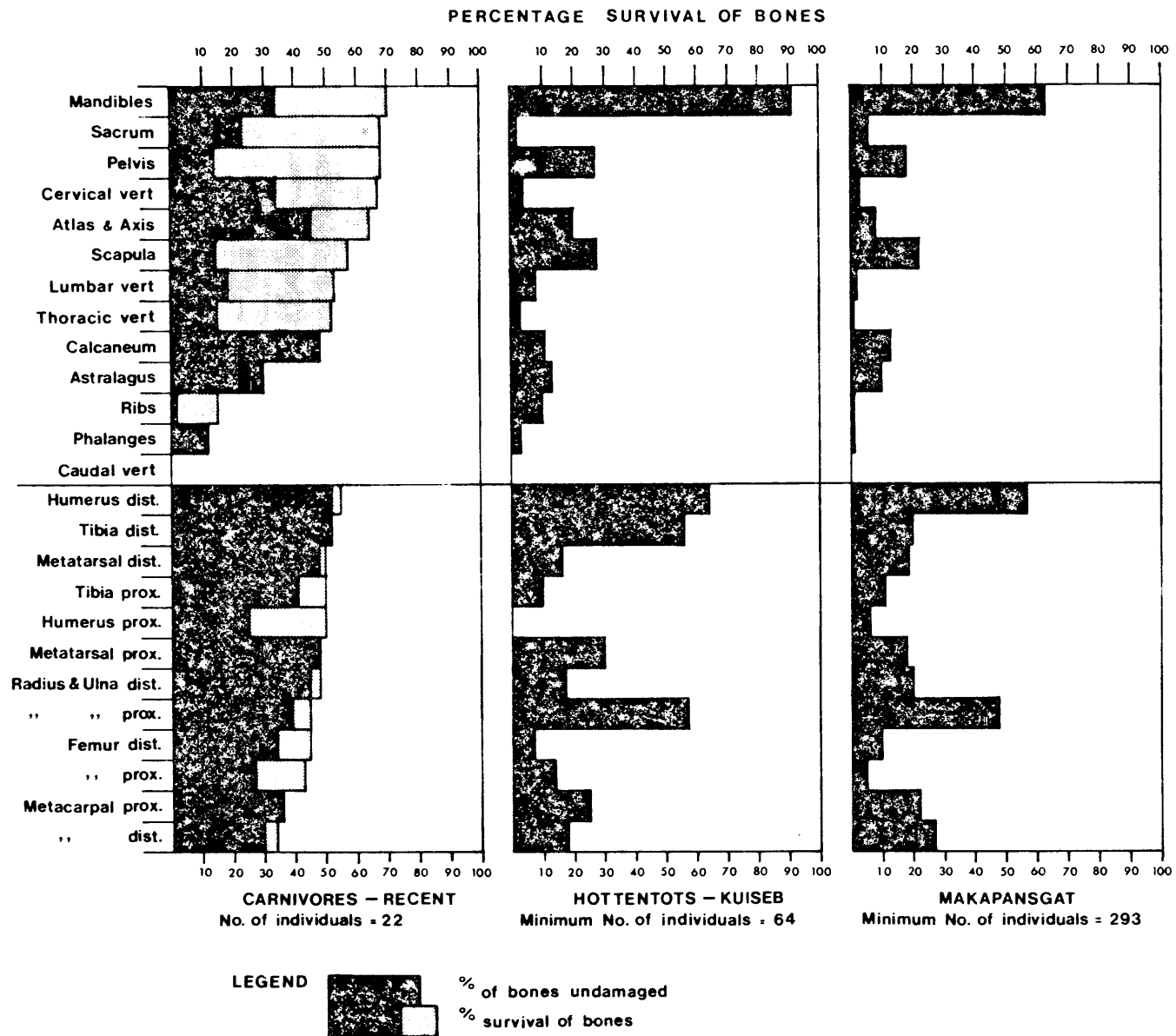


Figure 39: Percentage survival of parts of bovid skeletons at Makapansgat, in the nature reserves and farms of the Transvaal and southern Zimbabwe, and of goat skeletons in the Kuiseb. Data for Kuiseb and Makapansgat derived from Brain 1976a.

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 before. This is because the adjacent shaft is splintered and open to weathering, whereas before it formed a hard impenetrable barrier. Furthermore, the harder end will have far higher chances of surviving than the softer end. This is because the softer end will be chewed more and be more susceptible to trampling and weathering. Thus 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 they were left complete. This argument is supported by the results of three separate archaeological bone accumulations in Germany presented by Read-Martin and Read (1976). These accumulations differ in extent to which the long bones were broken in half. The differences in the survival rates of proximal and distal humeri have a strong positive correlation ($r = 0,955; df = 1; p < 0,1$) to the degree of long bone breakage (Table 15).

Hominid damage If one accepts this argument, one can predict the relative survival rates of the epiphyses of long bones when damaged by particular agents. 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 far 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 the size of a kudu and larger 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.

Hyaena damage The opposite pattern can be expected for hyaenas. The smaller long bones are usually destroyed, so there is no predictable pattern to their

Table 15 : The differential survival and damage of long bones at three northern German levels.

	Hamburgian Stellmoor	Ahrensburgian Stellmoor	Hamburgian Meiendorf
Minimum number individuals	41	650	71
Complete long bones	73	720	0
Loose epiphyses	58	1494	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 between A and B: $r = 0,955$; $df = 1$; $p < 0,1$.			

Data derived from Read-Martin and Read 1975.

survival (Fig. 34). Although the largest bones are seldom broken in half, the epiphyses are gnawed away according to their softness and may even completely disappear (Fig. 28). Thus, one would expect the opposite epiphyses of these bones to show greater differences in survival rates than those of small long bones.

Porcupine damage The analysis of bones collected by porcupines in the Nossob (Brain 1976b), indicates 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. 29 and 34). Because of this one would not expect there to be distinct differences between the patterns of long bone survival for the different weight classes of bovids.

Klein (1975) presents a most convincing argument that the bones at Swartklip I were collected by hyaenas.

The main points are :

- (i) the lack of stone artefacts;
- (ii) a relatively high small-carnivore/ungulate ratio;
- (iii) a fairly low fragmentation rate of bones;
- (iv) a negligible amount of porcupine gnawed bones;
- (v) numerous coprolites of a large carnivore; and
- (vi) numerous long bones with epiphyses gnawed off in typical hyaena fashion.

In Table 16 his results are used to calculate the total survival rates of the epiphyses of bovid long bones of two major weight classes. Darts' (1957) results from Makapansgat, Brain's from the Kuiseb and those from the present study are similarly presented. The two weight classes separate at about 100 kg, with wildebeest (Connochaetes taurinus) and kudu being the smallest species in the larger class. These two weight classes were chosen because in all the samples,

the survival rates of long bones in the upper class were more than double those in the lower class. It was also found that both spotted and brown hyaenas fragmented bones far more in the lower class (Fig. 32 and 37). 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 the figures have simply been doubled where appropriate, to account for left and right sides. Although this will overrepresent some bones, it will probably not seriously effect interpretations, because it is only the relative proportions of bones that are important.

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 ($\chi^2 = 5,45; df = 1; p < 0,05$). This is to be expected as 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 in the larger weight class corresponds to the results obtained during the present study for hyaenas (Fig. 34), 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 ($p < 0,001$). 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

Table 16 : The differential survival rate 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	II	I	II	I	II	χ^2	I	II	I	II	
	No.	% diff	No.	% diff	No.	% diff	No.	% diff	No.	No.	No.	No.
Humerus	proximal	0,58	7	26	33	6	4	0,80	1	6	0	11
			95	27	82,7	82	78		87	2	9	0
Radius & Ulna	proximal	1,10	103	74	279	38	36	3,69	2	9	0	10
			17	29	0,99	42	17		16	2	9	0
Metacarpal	proximal		109	20	129	38	56	0,22	1	8	0	6
			13	3	0,84	11	7		14	0	8	0
Femur	proximal	0,75	11	17	28	12	8	0,05	1	6	0	8
			35	32	0,02	33	48		43	1	6	0
Tibia	proximal	0,82	26	38	64	28	14	5,45	0	6	0	9
			55	12	20,8	30	30		63	0	8	0
Metatarsal	proximal		89	18	107	58	32	0,54	1	7	0	8
			4	16	1,11	1	5		6	1	8	0
<u>Sum of differences x 100</u>			41	22	38	25	33		17	7	0	5
Total no. of bones												
<u>Total no. of bones</u>			4,2	9,6	5,2	4,5	11,5		3	11,3	0	12,2
Minimum no. individuals												
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; S.G. = specific gravity; Difference = $|x_{proximal} - x_{distal}|$;
 % diff. = $\frac{|x_{proximal} - x_{distal}|}{x_{proximal} + x_{distal}} \times 100$; Statistical significance is indicated as follows : $^+p < 0,05$, $^{++}p < 0,001$

Data derived from the following sources:- Makapansgat - Dart 1957; Kuiseb - Brain 1976a; Swartklip I - Klein 1975.

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 17 this problem has been circumvented by first classifying reedbuck as medium, then as small. In both cases the pattern for medium-sized bovids at Swartklip I is opposite to 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 abilities of the agent concerned. For hyaenas (Swartklip I and present study) 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.

Another factor that requires consideration, is that cranial and postcranial bones may have been collected at different rates. The representation of material at Swartklip I suggests that it was all collected at much the same rate, but postcranial material was then selectively chewed. At Makapansgat, the extremely high representation of individuals in the medium-size 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 Fig. 40, where the survival rates of bones at Makapansgat, Stellmoor (high long bone breakage) Meiendorf (little long bone breakage), Swartklip I, and the present results for recent carnivore

Table 17 : The 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 - fresh	Cranial			4 11 ⁺	8 10 ⁺
	Postcranial			2	9
Hyaenas - 6 months	Cranial			1 5 ⁺	9 9 ⁺
	Postcranial			-	9
Carnivores - 6 months	Cranial			6 10 ⁺	12 12 ⁺
	Postcranial			5	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.⁺

Data derived from the following sources:- Makapansgat - Dart 1957; Swartklip I - Klein 1975.

damage are compared. Because of the number of different bones, these results are all statistically significantly different, so the comparison between each site has to be done subjectively.

With the exception of vertebrae and mandibles, which will be discussed later, 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 lone bone breaking habits (Table 15). Typical carnivore damage is at the end of the scale, where the damage is not selective but dependent on the size, hardness and friability of the bones.

The results from Swartklip I appear at first to refute this argument as 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 the present study or those at the two German sites where they were buried in mud (Read-Martin and Read 1976). 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 confirm 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).

In Fig. 41 the survival rates of vertebrae at these sites are illustrated. One can immediately see that the patterns of survival have nothing to do with the agents of accumulation, but correlate quite well with the expected post-depositional damage at each site. I feel that vertebrae should reflect this

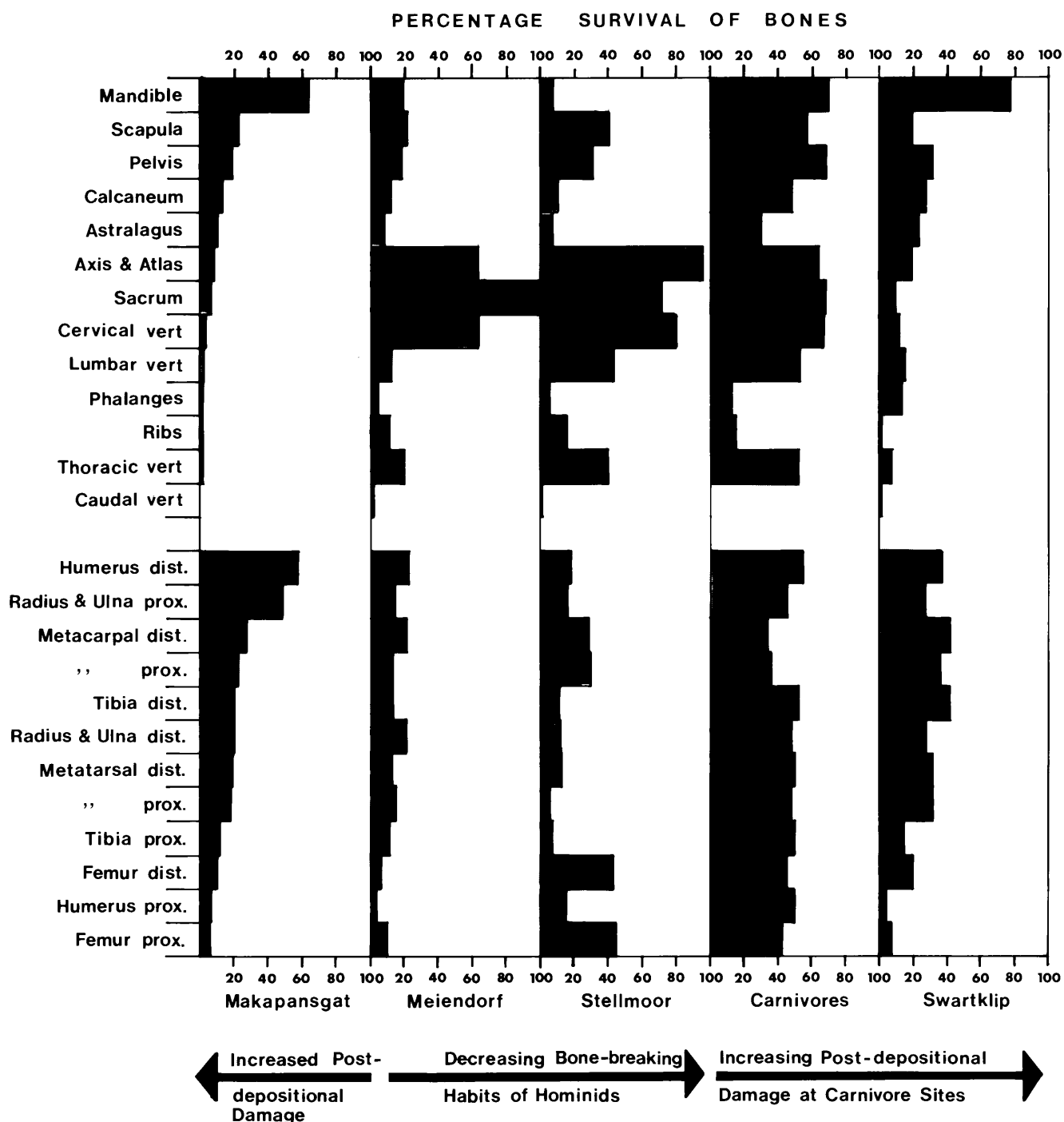


Figure 40: Percentage survival of parts of bovid skeletons from five different bone collections, illustrating how survival depends on both the bone-breaking habits of hominids and on post-depositional damage. Data derived from the following sources:- Makapansgat - Brain 1976a; Meiendorf and Stellmoor - Read-Martin and Read 1975; Swartklip - Klein 1975.

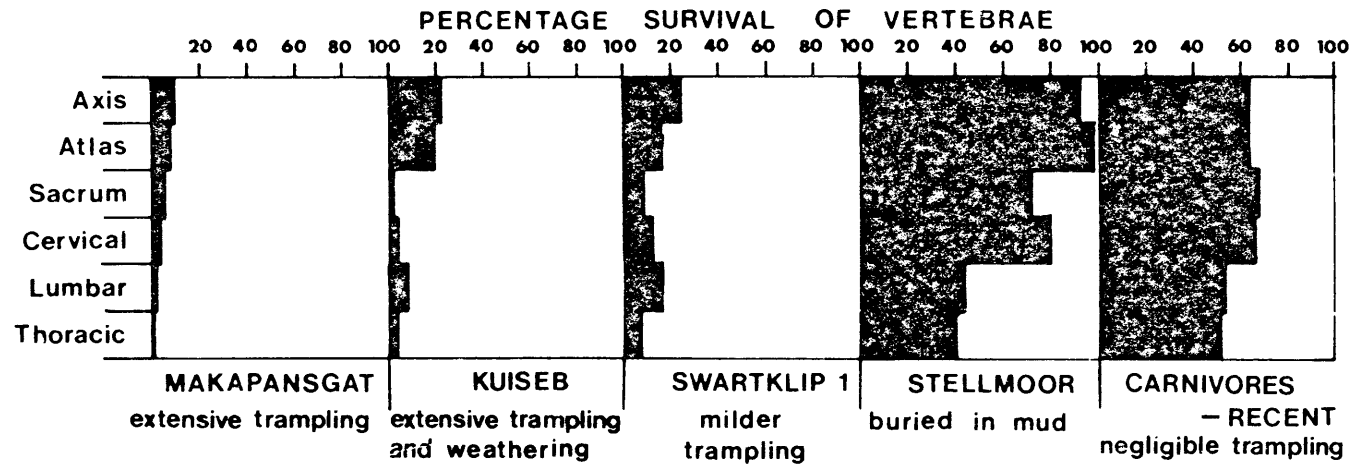


Figure 41: Percentage survival of bovid vertebrae from five different bone collections, illustrating how their survival is dependent on post-depositional damage.

Data derived from the following sources:- Makapansgat and Kuiseb - Brain 1976a; Swartklip I - Klein 1975; Stellmoor - Read-Martin and Read 1975.

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 exerted on them are ultimately likely to collapse and then rapidly disappear. Therefore, if one takes post-depositional damage of vertebrae into account and considers the high and fairly flat survival rate curve of long bones, then 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 Hottentots) have lower survival rates than scapulae at Makapansgat and all the hominid sites, whereas the opposite applies to Swartklip I and the recent carnivore data.

Discussion

There are a great number of variables involved between the initial collecting and the final survival after fossilization of bones. This is true even when there was only one species of bone collector. These variables can be divided into the following three broad categories:

Bone collecting 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 site 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 camp site), Kuiseb (hominids at kill site), Swartklip (hyaenas at camp site) and the present data (carnivores at kill site), it is apparent that it will be very difficult to separate the agents of accumulation in these terms. The only generalization that might be safely 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 hunting methods employed and

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

Initial bone damage 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 which 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.

To use the presence or absence of bone tools also has its inherent problems. First, there is the identification of bones as tools. Second, 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.

Post-depositional damage After bones have been collected, chewed and used as tools they may still have to survive many pressures before they are finally preserved. Bone fragmentation can to a certain extent be related to initial damage by hominids because of their bone breaking habits with stones (Brain 1970). However, really extensive fragmentation seems to result more from slow sedimentation rates associated with continued trampling (Klein 1975, Beaumont 1978).

As has already been suggested above (Fig. 41), 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.

Griffon vultures' utilization of bone chips

In order to evaluate whether griffon vultures depend on carnivores to provide bone chips for them to feed to their nestlings, one first needs to determine whether carnivores do in fact produce bone chips at bovid carcasses and then, whether vultures actually revisit carcasses to pick them up. It is apparent from the present study that carnivores do produce bone chips (Fig. 30) by chewing the bones of bovid carcasses. Similarly, adult griffon vultures have been seen to swallow bones (Mundy and Ledger 1976, personal observation) and judging by the number of bones found at their nests (Plug 1978), they regurgitate them for their chicks.

However, these observations still do not illustrate the dependence that griffon vultures may have on carnivores to produce suitably sized bone chips. This information can be gained by watching carcasses for days after vultures have left them, to see if vultures return to look for bone chips, and by monitoring what bones vultures find and take back to their chicks.

To watch clean carcasses for days after vultures have left can be most time consuming and unrewarding. However during the present study some observations were made which suggest that griffon vultures actively seek out bones at carcasses, and may return to them to find some chips.

At one impala carcass at Tweeputkoppies, vultures started feeding one afternoon then left the partially consumed carcass towards dusk. They continued feeding the next morning and by 10h00 had consumed all the soft tissues and departed. The following morning at 08h00 two Cape vultures were seen to visit the carcass

which had been dragged around by jackals during the night. Both vultures attempted to swallow loose ribs, but with about 6 cm of rib still protruding from their bills they would give up. The two vultures spent an hour searching around the carcass for small bits or bone chips then left, apparently without achieving much success.

At another impala carcass in Timbavati 18 griffon vultures of both species and three lappet-faced vultures were seen to return to a carcass which they had consumed the previous day and which had been partially chewed by hyaenas overnight. However, on this occasion the vultures had fed until late afternoon, so presumably had roosted in the vicinity overnight. Nevertheless, the few vultures (about eight) that did feed were seen to concentrate on looking for and picking up bone chips, as opposed to feeding on the carcass itself.

It is apparent from Fig. 13 in Chapter 4 that griffon vultures do occasionally feed on bone chips at carcasses. These observations are not only from the two situations described above, but also from some carcasses at Vaalboschfontein. On this farm the owner regularly put out crushed bones near the hide he constructed. Vultures feeding at carcasses often used to swallow these chips, particularly after they had finished feeding.

What was most remarkable however, was the behaviour displayed by white-backed vultures at this site when there were no carcasses available. For a period of about a month, mainly in May 1978, these vultures used to congregate at the hide every morning prior to taking off and foraging over the countryside (Lindbergh pers. comm.). On two consecutive mornings the activities of this group of vultures were observed.

It soon became apparent from the behaviour of these vultures that it was the start of their breeding season. Numerous attempts to mate were observed, while other vultures were seen to collect twigs and bone fragments (Fig. 42). There appeared

F.M. Lindbergh, Vaalboschfontein Estates, Private Bag X101, Wolmaranstad, 2630.
May 1978.

(a)



(b)



Figure 42 : Behaviour of white-backed vultures (Gyps africanus) that were attracted to small piles of artificially distributed bone fragments at Vaalboschfontein in May 1978 : (a) Two adults mating (b) Vultures picking up bone fragments or playing with sticks.

to be some division in the age groups performing these different behaviours. Only adults were seen to mate; both adults and juveniles picked up bone chips; and only juveniles picked up twigs. Mundy (*In litt.*) states that all age groups "from the nestlings onwards have a nest-repair syndrome when they play with sticks."

Whatever interpretation one may put on this behaviour, it would appear safe to conclude that these vultures were involved in various breeding activities. Furthermore, as the hide (which they ignored) and the bone fragments were the only exceptional features of this site, they therefore appeared to congregate there primarily in order to pick up bone fragments.

All the above observations suggest that griffon vultures do make some special effort to collect bone fragments. The numerous bones collected by Mundy (Plug 1978) at their nests further suggest these fragments are collected primarily to feed to their chicks. What now remains to be established are the sources of these fragments. That carnivores feeding at bovid carcasses can produce bone chips is a well accepted fact (Mundy and Ledger 1976, Mills 1977). However nobody has as yet clearly stated exactly which carnivores may or may not be responsible.

It would appear from the present study that only the two hyaena species are likely to be of any real significance in this respect. It is very clear from the fragmentation ratios given in Fig. 29 and 32 for long bones and whole carcasses respectively, that the two hyaena species were the only carnivores which could make an appreciable contribution in breaking up bones. None of the other species ever had fragmentation ratios of over 110.

Obviously lions and occasionally leopards at small kills will chew the bones extensively and make numerous chips from the long bones. However these kills are unlikely to be found by griffon vultures, while at the one clean impala carcass that lions visited, they did no damage to the bones at all.

If vultures are to get bone chips by revisiting carcasses, then the only carnivores that are likely to be important, are those that chew the bones of the unfleshed carcasses. Jackals have been suggested (Mundy and Piper 1979) to fulfil this role in cattle ranching areas however, the evidence of the present study suggests quite the contrary (Fig. 29 and 32). On no occasion during this study, were jackals ever suspected of chewing long bones in half. The only damage they ever did was to gnaw the softer epiphyses, while occasionally in young bovids the developing epiphyses would separate from the shaft (Fig. 31).

There are apparently inherent differences in the bone collecting behaviour displayed by Cape and white-backed vultures (Plug 1978). Furthermore, Plug does not state the nesting sites of Cape vultures sampled, so one does not know the carnivore fauna involved. Therefore, because the results for bone types collected by white-backed vultures in "cattle ranching" and "wild areas" (nature reserves) were more divergent than the corresponding results for Cape vultures, the data obtained for the former will be used in the following discussion.

In the nature reserves the white-backed vultures collected mainly long bone flakes (47%), numerous cranial fragments and a mixture of other less common items. However in ranching areas these vultures collected very few long bone flakes or cranial fragments, but collected mainly small bones such as phalanges. These results are entirely logical in terms of the results illustrated in Fig. 26 and 37.

At freshly consumed carcasses, long bones and crania are fragmented far more than any other bones and therefore are the most available and suitable for selection by vultures. Because the methods of recording data for survival and articulation are different, these results are not directly comparable. Nevertheless, it is still apparent in Fig. 26 that with the exception of scapulae and mandibles the disarticulation of bones was low and closely followed the survival rate. In particular this applied to the small bones in the limbs. These were

either eaten off by a large carnivore, or they remained attached to the limb for a considerable time before they became disarticulated.

This question of bone fragmentation and disarticulation is further illustrated in Fig. 37. In this figure, one can see the effect that weathering, trampling and further chewing by carnivores had on bones after they had lain in the veld for over six months. After this time, most of the bones of all sizes of bovids had disarticulated. However, despite the high degree to which the bones had been damaged and disarticulated, at Tweeputkoppies, where jackals were the only carnivores present, the bones had been negligibly fragmented. These results suggest that in ranching areas where there are no hyaenas present, vultures should eventually be able to find small disarticulated bones (particularly phalanges), but will have difficulty finding fragments of larger bones.

As bone fragments were very rare and whole small bones were common in the nests of white-backed vultures in ranching areas, it is suggested these vultures seldom collected bones from fresh carcasses, but had to collect small disarticulated bones from carcasses that had weathered in the open for many months.

The pattern of bones collected by Cape vultures is said to be less variable for cattle ranching and nature reserve areas, with the pattern being inbetween the two extremes of the white-backed vulture (Plug 1978). However, as I know of no area in Southern Africa where Cape vultures nest in a total wilderness area (where spotted hyaenas are common), I do not think the two extremes have been adequately sampled. Furthermore, the brown hyaena probably occurs (Skinner 1976), although in low numbers, within the ranges of all the Cape vultures sampled (Botswana and Transvaal (Plug 1978)), and therefore could account for the long bone fragments found in their nests.

Recycling of bone

From the fairly crude methods employed during the present study, it is not possible to say exactly how long the bones of particular sized carcasses will last in the veld. Nevertheless, one can still make a few general conclusions.

The results of the present study suggest the smaller a bovid is, the less chance its bones will have of surviving, and hence the faster they are likely to be recycled. This is both because of the propensity of hyaenas to chew their bones and leave very little behind, and because of their susceptibility to damage by trampling (Fig. 38). The bones of impala at Tweeputkoppies after six months or more, had survived just as well as those of the donkey and mules (Fig. 37). However, judging by the extent of damage suffered by the smaller bones, they will ultimately disappear faster than the larger bones. This differential survival of bones has been confirmed by Behrensmeyer, Western and Boaz (1979), who found that the bones of small animals have disproportionately low survival rates relative to their numbers in the living community.

This trend is clearly demonstrated in Fig. 37, where the bones with the highest survival rates were those of the largest bovids in nature reserves despite the fact that they were extensively chewed by hyaenas. Coe (1978) found the same with elephant carcasses in Tsavo. He has suggested that the bones of these carcasses will take at least 20 years to decompose completely.

It is difficult to say how long it will take before the calcium in the faeces of a hyaena can be absorbed by plants and thus effectively re-enter the nutrient cycle. Nevertheless, this time must be shorter than if the original bones were left to weather in open. Therefore, it is suggested that hyaenas play a vital role in speeding up the recycling time of nutrients stored up in the bones of carcasses. In the case of small and medium sized carcasses their effect can almost be 100%, however on large carcasses they can only chew up to 40% of the bones by mass, so the rest will need to weather over an extended period of time.

CONCLUSIONS

Archaeological implications of bone damage

It is apparent from the preceding discussion that there are many factors involved in the accumulation, deposition and fossilization of bones in caves. Therefore many contrasting interpretations have been made of the same collections. In particular, numerous papers have been written about the collection at Makapansgat. Many have drawn definite conclusions, while Wolberg (1970) and Read-Martin and Read (1975) have concentrated on evaluating all the evidence available, to show how each variable factor may be interpreted. The aim of the present study is simply to give interpretations relating 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, have hands with which they can manipulate and selectively separate or break bones. It is this selective removal and destruction of bones which I think may ultimately distinguish hominid and carnivore damage from each other.

It has been shown in Table 15 that the hominids at the three German levels broke long bones to different extents. This probably reflects the degree to which they utilized bones as food. Similarly, one would expect all hominids who have a food shortage (as in the Kuiseb) to extract as many nutrients as possible from the bones of the animals which they find or kill. This would obviously also apply to any meat-eating australopithecines.

Although the slaughtering and subsequent bone-breaking habits will differ between various hominid communities, the most likely and distinctive bones to break, will

be the marrow-containing long bones. They will therefore provide the most reliable evidence in comparisons between carnivore and hominid damage.

Apart from typical damage associated with hyaenas, porcupines or humans, one can look at the survival rates of opposite epiphyses and, on a relative basis between different weight classes, see whether they fit the expected patterns for hyaena or hominid damage. A notable feature of this method is that it incorporates not only the method of feeding of the main accumulating agents, but also the fact that this pattern should remain unaltered by subsequent post-depositional damage.

In view of the high fragmentation rate, the low occurrence of porcupine gnawed bones (Maquire, Pemberton and Collett 1980), the similarity of the Makapansgat and Kuiseb bone collections, and the representation by cranial and postcranial bone material and the survival pattern of long bone epiphyses being those expected for hominid damage, it is suggested that australopithecines were the primary bone accumulators at Makapansgat.

Carnivores as sources of bone fragments for griffon vultures

It has been suggested (Mundy and Ledger 1976) that griffon vultures rely extensively on large carnivores to provide bone fragments for them to feed to their chicks. The results of the present study show that the only carnivores which do extensive damage to the bones of carcasses lying in the veld, are the two hyaena species.

The results of bones collected from white-backed vulture nests in nature reserve and cattle ranching areas (Plug 1978) correlate directly with the carnivore fauna expected in each area. In the nature reserves, which should have spotted hyaenas, numerous long bone and cranial fragments were found in the nests. These bones are the ones most readily fragmented by hyaenas. In ranching areas however, these fragments were rare. Most of the bones collected were smaller complete bones which would have to be disarticulated before vultures could swallow them.

As jackals are common throughout the ranching areas in South Africa, it is apparent that they are of little or no use in breaking up the bones of carcasses for vultures.

The dependence of Cape vultures for suitable bone fragments at carcasses has been confirmed by the effect vulture restaurants (supplied with whole carcasses and bone fragments) have had on the local populations. Vulture restaurants have only been going for the past few years in the Magaliesberg (Mundy pers. comm.) and already there is a marked decline in the incidence of osteodystrophy in Cape vulture chicks (Plug 1979).

Recycling of bone

It is a direct consequence of hyaenas being the only important bone crushers in Africa, that they should be the most important vertebrates involved in the recycling of the nutrients tied up in bones. In terms of recycling time, it is difficult to give an absolute measure of the affect of hyaenas. However one can say that their influence on small and medium sized carcass can be almost immediate and nearly total. Therefore, as probably 90% of the annual mortality (by mass) of large herbivores in the Serengeti occurs within these two weight classes (Houston 1974a), hyaenas can be seen to be vitally important in terms of the total available supply of calcium in an ecosystem.

CHAPTER 7 : CONCLUSION

INTRODUCTION

The present study has been concerned with all the facets of the natural removal of carcasses in southern Africa with the rate of decomposition of carcasses under different ecological and environmental conditions being of prime concern. In order to give meaning to the interpretation of these results it was necessary to consider all the scavengers involved and their various adaptations to the roles they perform. This was considered in terms of both the importance of each scavenger species to carcasses and the importance of carcasses to each scavenger species. Finally, the results obtained on carnivore damage to bones were used in the interpretation of some fossil and recent bone accumulations.

The aims of this chapter are threefold. First, it is to discuss carcass decomposition as a whole, by considering the sources of carcasses and, in terms of the prevailing ecological conditions, to give general predictions on the fate of carcasses. Second, it is to consider the major scavenger species and their evolution in terms of the scavenging lifestyle. Third, it is to discuss certain ecological implications of the study in terms of nutrient cycling and the spreading of disease.

CARCASS DECOMPOSITION

Sources of carcasses

It is a general fact of life, on both game reserves and livestock farms, that the animals living in these areas eventually die. In the game reserve this is a well known and an accepted phenomenon. However despite this, the exact proportions and reasons for this mortality are largely unknown and probably misunderstood. Carnivore kills are well known and frequently observed phenomena, and this has generally led to an over-estimation of the importance of carnivores as agents of mortality. Furthermore it has also led to the belief that those species which exist primarily as scavengers, make their living from

the remains of carnivore kills.

Houston (1974a) has shown that the total annual consumption of all the large carnivores in the Serengeti accounts for only 25% of the annual mortality of the large herbivores, therefore leaving 75% to be consumed by non-mammalian scavengers. The Serengeti is characterised by having temporary, large scale migrations of ungulates, during which many of these ungulates die (Kruuk 1972, Schaller 1972, Houston 1974a). Therefore these migrations may create an added mortality factor which is not as evident in other game reserves in Africa. Nevertheless, it is still suggested that the mortality of ungulates in the game reserves, due to disease, starvation and old age, vastly exceeds that due to carnivore predation.

In the ranching areas of South Africa, natural mortality of domestic livestock is a factor recognised by the farmers themselves, while the non-farming public generally do not fully realise its proportions. Jarvis et al. (1974) have calculated, from information given to them by local farmers in the Potberg district of the Cape Province, that every year 0,7 adult sheep die undetected by man in each km². This figure for the natural mortality of livestock (which will include some predation by jackal and caracal) is very high. In fact, Jarvis et al. (1974) calculated it to be 50 to 60 times greater than the minimum requirements of the resident population of about 111 Cape vultures.

From these results it will be appreciated that there is a large food supply for scavengers in both the nature reserves and livestock farming areas in South Africa. In the ranching areas of the Transvaal, better methods of farming and greater vigilance by the farmers are decreasing both the mortality rates of livestock, and the number of ungulates that are left to die in the veld (Ball pers. comm.). These factors do necessarily decrease the potential food supply of vultures. However, judging from the figures for Potberg (Jarvis et al. 1974), certain livestock farming areas should be able to support vultures for many years to come.

D.C. Ball, Wegkruip, P.O. Box 12, Bandelierkop. 0800. January 1977.

Pathways of decomposition

In order to predict the manner of decomposition of a carcass in a given area, one needs first to consider two factors : (i) the potential supply of carcasses, and (ii) the scavenger fauna that occurs in that area. As has been suggested in Chapter 4, in the case of griffon vultures, their presence is entirely dependent on there being a sufficiently large population of game (or livestock) to provide carcasses on a regular basis throughout the year. The presence or absence of the other scavengers however, appears to be more dependent on human activities and the threat that the scavengers may pose towards livestock.

In the Transvaal, lions and spotted hyaenas are almost exclusively limited to the main conservation areas, which are the Kruger National Park and the adjacent private nature reserves in the eastern Lowveld (Von Richter 1972). Similarly, these were the only areas in which all five species of vulture were seen. Therefore, the patterns of carcass decomposition described for the nature reserve areas will, in the Transvaal, only apply to these conservation areas of the eastern Lowveld.

Over the rest of the Transvaal a number of situations are possible and will be determined by the species of scavengers that occur in each area. One can distinguish four potential situations. Areas inhabited by: (i) brown hyaenas, vultures and jackals (ii) vultures and jackals (iii) only jackals (iv) no large vertebrate scavengers. During the present study, all four situations were to some extent experienced, because when certain scavengers were too shy to visit a carcass, the result was the same as if they did not occur there.

If one were to try and predict the rate of decomposition of a number of carcasses in any one given area over an extended period of time, then one must know which scavengers exist in the area, but also realise that only a certain percentage of the carcasses will be visited by each species. Olifantshoek can be taken as a fairly typical situation of where brown hyaenas, griffon vultures and

jackals all occur together. It is apparent from Skinner (1976) and my own personal observations, that the brown hyaena is widely distributed throughout the Transvaal, occurring in most regions where farming methods are extensive and the vegetation or surrounding hills provide adequate cover. As griffon vultures have similar prerequisites (certainly livestock farming is required), their distribution in the Transvaal probably correlates fairly well with that of the brown hyaena.

It is apparent from the present study that griffon vultures do occur where brown hyaenas are absent, as at Vaalboschfontein and Tweeputkoppies. However, on both these farms brown hyaenas have been seen within the past five years, so the present situation is not necessarily typical. One may also find areas, eg. around Bronkhorstspruit in the eastern Transvaal Highveld, where brown hyaenas are resident (personal observation) but griffon vultures are absent (Kemp pers. comm.). Thus it is clear that the situation is variable and while both groups appear to have similar habitat requirements and do occur together in many areas of the Transvaal, this is not necessarily always the case.

Black-backed jackals are very adaptable carnivores and appear to live in most regions of the Transvaal that are not heavily populated (personal observation). Thus they have wider distributions in the Transvaal than either brown hyaenas or griffon vultures, and can be expected to scavenge at most carcasses outside the urban areas.

It is only in ranching areas that one is likely to encounter carcasses in the veld. Because these areas provide suitable habitat for jackals, most of these carcasses are likely to be scavenged by them. There are obviously exceptions to this, and these apply where jackals have to a large extent been shot out by the farmers, or the occasions where they are suspicious of carcasses and leave them alone. It is under these circumstances, or where the carcass is too big for jackals to consume rapidly, that maggots will play a major role in the decomposition process.

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EVOLUTION AND LIFESTYLES OF THE MAJOR SCAVENGERS

Ewer (1973) states that the answer to the question "What do the Carnivora eat?" is very simple - "What they can get." She continues to say that "the highly successful carnivore is the one that combines sufficient specialisation to make it an effective predator on its chosen type of prey with flexibility enough to permit it to utilise a variety of foods in relation to changing seasons or varied habitats."

These statements provide the main clues to the question of predation versus scavenging and the evolution of scavengers. In the case of lions and the other incidental scavengers recorded during the present study, they scavenged at the carcasses simply because the food happened to be available. However, for reasons explained in Chapter 3, they are poorly adapted to depend on scavenging as a way of life. When considering the more characteristic scavengers, viz. hyaenas, jackals and vultures, it is worthwhile to consider their evolution and present day lifestyles in more detail.

Hyaenas

The present day hyaenas have, like the Felidae, highly specialised dentitions. Both groups possess slicing carnassial teeth, however the hyaenas are further characterised by having heavy, conical, hammer-like premolars. It is these teeth, combined with very powerful jaw and neck muscles, that make it possible for the hyaenas to dismember carcasses and crush bones more readily than any other carnivores (Ewer 1973).

It has been suggested by Ewer (1973) that the evolution of the hyaenas can be correlated directly to the dominance of the sabre-tooth cats amongst the carnivores, during the Oligocene and Pliocene. The sabre-tooth cats had extremely long upper canines and the most developed carnassials of any carnivore, so their dentition was adapted exclusively for two purposes : to kill their prey and to slice meat from the kill. This extreme specialisation by these cats meant that they would have to leave most of the bones of their kills and possibly other

tissues as well. These remains could provide a rich food source for any scavenger adept at crushing bones.

The first aberrant form of hyaenid is recorded from the early Miocene, a time when the sabre-tooth cats were already in existence. Ewer (1973) suggests that the hyaenas may originally have been rather civet-like, having an all-purpose dentition. They then started to exploit this extra food source provided by the sabre-tooth cats and gradually developed their typical hyaena dentition. The genus Ictitherium provides a likely intermediate between the two extremes, as it shows the development of both the carnassial shear and the thickening of the crushing premolars, but still retains more teeth (two molars) and is less specialised than the present day hyaenas.

The hyaenas radiated considerably and were present in great variety during the early Pleistocene. However with the decline of sabre-tooth cats, the hyaena species also became greatly reduced in numbers, with only three species remaining today.

Ewer does not suggest that the hyaenas developed exclusively as scavengers, but she does state that "scavenging provided a food source sufficiently important to confer decisive selective advantage on the acquisition of such special adaptations". With the decline of the sabre-tooth cats and the corresponding decline in readily available carrion, the hyaenas had to revert to a more omnivorous diet, or become more predacious. In both directions there was competition from other carnivores. The canids were partially omnivorous while the felids were highly predacious. Consequently most of the species of hyaenas became extinct.

The hyaena species existing today appear to have been successful at establishing themselves in these two different niches, while still retaining their scavenging abilities. The brown hyaena (Mills 1977) and the striped hyaena (Hyaena hyaena) (Kruuk 1976) have mutually exclusive distributions and appear to feed in very much the same manner. This consists of feeding on a variety of different sized

animals and plants, but still heavily relying on scavenging old remains of carcasses lying in the veld (Mills and Mills 1978).

The spotted hyaena has been shown by Kruuk (1972) to be a highly efficient predator on the plains in East Africa, while also remaining an effective scavenger. Similarly, Mills (pers. comm.) estimates that in the Kalahari Gemsbok National Park in South Africa the spotted hyaena catches 80% of the food it eats. This area, like the Serengeti, is characterized by the openness of its vegetation. It has been suggested by a number of naturalists, that spotted hyaenas are only successful as predators in this type of habitat, and where they occur in bushy vegetation, as in the eastern Transvaal Lowveld, they exist primarily as scavengers.

I cannot agree with this opinion, for two basic reasons: (i) The problems of a mammalian scavenger finding sufficient food has been explained at length in Chapter 3. Furthermore, the spotted hyaena has a social organization atypical of an exclusive scavenger. (ii) The spotted hyaena has often been described as being a highly efficient cursorial predator, which chases its prey at medium speeds over long distances. I do not see why this method of hunting should be any less successful in a wooded habitat than in open country. Presumably the vegetation should hinder the prey equally as much as the predator, so in view of the fact that the wild dog and the cheetah (which is less robust and chases at far higher speeds) are both successful at cursorial hunting in this habitat, the spotted hyaena should similarly be an efficient predator in the eastern Lowveld nature reserves.

Jackals

The canids are distinct from the felids in terms of dentition, in that their carnassials are less developed and they have retained their molars, thereby enabling them to chew vegetable matter as well as meat (Ewer 1973).

The black-backed jackal is a typical example of a carnivore that will eat anything that is available. Hirst (1969) recorded them to be efficient

predators of impala lambs in Timbavati, while Grafton (1965) and Bothma (1971) who studied the stomach contents of carcasses collected in the Transvaal, recorded them to feed primarily on carrion, sheep, small mammals and birds, insects and fruits. Both authors found carrion and sheep, in terms of volume, to be the most important items. However, the sampling method was probably heavily biased in favour of these items, as most of the stomachs were those of problem animals collected on sheep farms. Similarly Bester (pers. comm.) has found that over 90% of the stomachs of problem Cape foxes (Vulpes chama) shot in the Orange Free State, contain remains of sheep lambs. This is a deviation from the norm, as this species usually feeds primarily on rodents and insects (Smithers 1971).

The bias created by this sampling method in the case of the Cape fox probably also applies to the samples analysed by Grafton (1965) and Bothma (1971). If so, this suggests that small mammals and birds, insects and fruits are more important in the diet of the jackals in the Transvaal than suggested by the above authors. This would correlate very well with data collected by Wyman (1967) and Lamprecht (1978) in the Serengeti. Both authors found the above items of food to be the major sources for black-backed jackals in this region. Wyman (1967) suggests that jackals obtained only 3% of their food by scavenging and while Lamprecht (1978) thinks this may be a slight underestimation, he confirms "that in the Serengeti jackals live mainly on self-caught invertebrate and vertebrate food."

The conclusion one draws from this is that jackals like lions, scavenge opportunistically at carcasses, although they do not depend on scavenging as a food source. The reason why jackals are so frequently seen at carcasses is a result of their usually high density, but does not necessarily mean that any one jackal often gets an opportunity to scavenge.

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May 1980.

Vultures

There are no fossil data available on the evolution of vultures, so the discussion in this section will consider the relative flying abilities and foraging and breeding strategies of these birds in relation to their scavenging lifestyles.

Pennycuick (1972) spent many hours in the Serengeti following soaring vultures in a motorised glider and recording their flying abilities and habits. These he found to correlate very well with their different scavenging habits.

One of the main factors which determines a bird's ability and method of soaring is its wing loading, which is a ratio between the mass of the bird and its wing area. The higher the wing loading, the faster the bird can glide, but it also has less lift and a poorer ability to sustain flapping flight. A bird with a low wing loading can therefore use weaker thermals but cannot glide as fast (Pennycuick 1972). Of the African vultures the Cape vulture and Rüppell's griffon have the highest wing loading (89,5) and are followed by the white-backed (76,5), lappet-faced (63), white-headed (54), and hooded vultures (45) respectively (Brown and Amadon 1968, Pennycuick 1972).

The griffon vultures were the only vultures that Pennycuick often found making long distance flights. Of the two species, the Rüppell's griffon has an appreciably higher wing loading and this has been correlated to its greater need for long distance flight. Pennycuick (1972) has suggested that this vulture, which breeds on cliffs and feeds amongst game migrations many kilometres away, needs to be able to fly faster (in order to be able to find food and return to its nest) than the white-backed vulture, which breeds on the plains where the game occurs.

Houston (1975) has suggested that these two species have adapted to two basically different habitats. The smaller white-backed vulture, having a lower wing loading and being able to flap fly for about 2 km, has adapted to a lowland or flat

savanna habitat. It breeds in trees and feeds locally on resident or migratory game, but never has to fly exceptionally far to find food. Because of its ability to flap fly it is still reasonably mobile in poor weather conditions.

Houston (1975) suggests that Rüppell's griffon has adapted to a more highland habitat. By breeding on cliffs it is able to utilize slope lift and can therefore dispense with the ability for continuous flapping flight and develop a larger body size. This increases its wing loading, and also enables it to consume more at each meal and withstand longer periods of starvation.

Kemp (pers. comm.) has expanded on these ideas, by emphasizing the importance of food finding in the evolution of these vultures. He suggests that the white-backed vulture has the strategy of breeding in wooded savanna where game populations tend to be resident and sedentary. They breed throughout the area, forming loose nesting aggregations and appear to find carcasses by having a network of vultures covering the whole region. When a vulture finds a carcass it descends to feed and thereby communicates the message to others within range of vision.

Kemp believes that the true griffon vultures evolved in more open habitats where game migrations are more common than in the woodlands. Because migrations are mobile, the vultures needed to develop an efficient method of keeping in contact with them. They achieved this by developing a social system of breeding colonially on cliffs, and using the colony as an "information - centre". Ward and Zahavi (1973) state that colonial breeding in birds evolved "primarily for the efficient exploitation of unevenly - distributed food sources by serving as 'information-centres'". Game migrations are an ideal example of "unevenly - distributed food sources", and in the case of griffon vultures the message of a bird feeding successfully is easily conveyed by the fullness of its crop.

Houston (1975) found that the two species of griffon vultures did in fact use these two different foraging strategies. White-backed vultures were seen at carcasses throughout the Serengeti; while Ruppells' griffons fed almost exclusively at carcasses amongst the migratory ungulate herds.

In South Africa, large scale ungulate migrations are something of the past, so while the Cape vulture still breeds on cliffs, it has otherwise had to adopt the foraging strategy of the white-backed vulture. It is this decline of the regular food supply afforded by game migrations, that Kemp (pers. comm.) and Houston (1974b) suggest may be primarily responsible for the declining population of this species.

It has been suggested in Chapter 4 that lappet-faced and white-headed vultures do not depend on scavenging at large ungulate carcasses for their primary food source. This is borne out by their flying and breeding habits. Pennycuick (1972) found that although lappet-faced vultures patrolled in search of food in much the same way as griffon vultures, they were different in that they flew more often in pairs and did not conserve height, which is a prerequisite for cross-country flying. Furthermore, they were often seen to have mid-air clashes which suggest that pairs or small groups of vultures were defending their foraging territories.

Pennycuick (1972) seldom encountered white-headed vultures in the air, but has found that like lappet-faced vultures, they are solitary breeders which probably defend their foraging territories (Pennycuick 1976). As has been suggested in Chapter 3, a species with a limited foraging range is unlikely to be a successful scavenger.

Another major difference between the above two species and the griffon vultures, is that the former pair both fledge their young when there are no game migrations present, whereas the latter do so when the migrations are active and therefore plenty of carrion is available (Houston 1976, Pennycuick 1976). Various

explanations for this have been put forward. I will not go into any of them, however it is pertinent to note that the two groups of vultures are using entirely different breeding strategies, which suggests that they are also using different sources of food.

The hooded vulture is a solitary breeder, and having the lowest wing loading, is also the slowest flier amongst the vultures (Pennycuick 1972). Nevertheless, Pennycuick found it to show more similarities in flight to the griffon vultures than to lappet-faced vultures. One of the main features here was that they did occasionally engage in cross-country flight. He recorded one hooded vulture to fly 25 km in 28 minutes as it made excellent use of a thermal street. Thus, although the hooded vulture is atypical of a scavenging vulture in a number of respects, it still appears to possess the ability to search for and feed at large carcasses (see Chapter 4) in a successful manner.

NUTRIENT CYCLING AND DISEASE

The scope of the present study has been too large to be able to consider in any detail the ecological aspects of nutrient cycling from carcasses and their potential role in the distribution of diseases. It is pertinent at this stage to make a few general conclusions in terms of the study, and suggest lines of further research.

It has been shown in Chapters 3 and 6 that the decomposition of carcasses can be quite accurately predicted if one knows the size of the carcasses and which scavengers will be involved. When one considers an ecosystem as a whole however, one needs to know the relative numbers of predators and ungulates, as well as the overall size structure of the ungulate population, in terms of the numbers in each different weight class. These factors are important in determining the food supply of scavengers and hence how quickly they are likely to consume carcasses, as well as the extent to which hyaenas will chew bones - the greater the proportion of large ungulates, the longer it will take for bones to be recycled.

Coe (In litt.) states that in some semi-arid regions of Africa the levels of calcium in the soil are notoriously low, while large amounts are immobilised in large mammals. This being so, one can see that the rate at which hyaenas recycle the calcium and other minerals tied up in dead skeletal remains of large mammals, can potentially be very important in general ecological terms.

The subject of diseases being spread from carcasses lying in the veld is something that is highly complex and requires extensive research before one can reach any meaningful conclusions. One can consider this topic from two different aspects: (i) the spreading of a disease from a carcass which had died as a result of that disease; (ii) carcasses as a food source for potential vectors of disease.

When considering the spread of disease from an infected carcass, one first needs to know a number of details of the infecting organisms. All the organisms have been inhabiting a living mammal which has a fairly constant internal environment. When the mammal dies a number of changes take place. These are primarily temperature and pH changes, but once the organism is exposed to the air it may also suffer from desiccation and ultra-violet irradiation. Thus in order to know whether the disease organism will even remain viable, one needs to know all its tolerance limits as well as conditions of temperature and pH in carcasses (Howell pers. comm.).

At this stage it is pertinent briefly to consider the potential role of griffon vultures in spreading diseases. Houston and Cooper (1975) found that the fluids in the stomach of white-backed vultures were extremely acid, being as low as pH 1. This probably enables them to kill all pathogenic organisms apart from those that have already formed highly resistant spores. Mundy and Brand (1978) collected 261 swabs from the bills and feet of the five common species

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of vulture in southern Africa. These swabs were tested for anthrax (Bacillus anthracis) without a single positive result. While these results do not suggest that vultures cannot transmit diseases, they do show that they are likely to be far less important in this respect than is often suspected.

The second way in which carcasses can promote the spreading of diseases, is by providing a food source for potential vectors. The most obvious examples here are blowflies, which are the cause of myiasis in sheep. Any carcasses which are available for blowflies to breed in, are therefore helping in maintaining the blowfly population and consequently their potential to strike sheep.

Furthermore, blowflies are characterized by their habits of visiting carcasses and faeces, so presumably can pick up diseases from the sources and transmit them elsewhere.

The present study has emphasized the importance of interrelationships and interdependence between species in the African savannas. In studying just one facet of the ecology of ecosystems - carcass removal - it has been necessary to consider various aspects of the biology of a large number of vertebrate and invertebrate species. In particular, the roles played by the different scavengers in the decomposition of carcasses and hence in maintaining the nutrient cycle, are stressed. The importance of the roles performed by griffon vultures and hyaenas are emphasized by comparing carcass decomposition in nature reserve and farming areas. The dominant part they play as scavengers in the nature reserves is, in their absence, reduced on the farms and consequently jackals and maggots have much greater opportunities to scavenge.

SUMMARY

Carcasses of large ungulates form an integral component of African savanna ecosystems. However, while there is a considerable amount of data available on the various live African ungulates, very little is known about their role as carcasses. Carcass decomposition is considered in terms of the rate of removal of tissues of different-sized carcasses, in different areas during the various seasons. The scavenger species are considered in terms of their efficiency as scavengers, and the importance of the scavenging lifestyle to themselves as individuals. Three main groups of scavengers are discussed - carnivores, vultures and arthropods.

The study was carried out over three years on three farms above the escarpment, and three Lowveld nature reserves in the Transvaal and one game ranch in southern Zimbabwe. These sites differed mainly in two respects : (i) the scavenger fauna and (ii) the climate. In the nature reserves and the game ranch all the common species of southern African carnivores and vultures were present, while on the farms only griffon vultures (Gyps spp.) and black-backed jackals (Canis mesomelas) were common throughout. Brown hyaenas (Hyaena brunnea) also occurred on one farm in the Magaliesberg.

Carcasses of ungulates were placed at particular sites and observed from hides. Any carcasses incidentally found were also observed, making a total sample of 89. Data were collected of the scavenging behaviour of all the vertebrate scavengers at five minute intervals. Between the feeding bouts of scavengers, estimates were made of the soft tissues and skin that remained, while bone survival and damage were recorded in detail. The scavenging beetles were collected and identified to family level, while the maggots that developed, were collected and bred for identification at species level.

In the nature reserves small carcasses were generally consumed within a day. Usually vultures consumed all the soft tissues within an hour of finding it

and spotted hyaenas (Crocuta crocuta) removed the remaining skin and bones overnight. On very large carcasses, vultures fed by day and hyaenas by night, taking three to four days to consume the soft tissues. Subsequent feeding by hyaenas on the remaining skin and bones extended over a week or more, depending on the availability of other sources of food.

On the farms, there were no spotted hyaenas and vultures were often shy, so the carcasses took much longer to be consumed. Here black-backed jackals and maggots, which could not compete in the nature reserves, became far more important as scavengers.

The adaptations of scavengers are analysed in terms of their social organization and physical abilities. Social organization is important as it influences their success at finding carcasses. The greater the home range and the more solitary the foraging habits, the greater their chances of finding a carcass. The ability to feed quickly, defend a carcass and, in the case of hyaenas, to chew dry skin and bones all contribute to scavenging success. Of the carnivores, only the two hyaena species scavenged successfully. Lions (Panthera leo) found too few carcasses, and jackals were too small and usually too few in number to compete. A number of other species were recorded to scavenge opportunistically.

The scavenging behaviour of five species of vultures has been analysed. The two griffon vultures, the Cape (Gyps coprotheres) and white-backed vultures (Gyps africanus) are the most successful because they feed very rapidly on the soft tissues of carcasses. The hooded vulture (Necrosyrtes monachus) is a much smaller species and feeds on small scraps around the carcass and between large bones. It is considered to scavenge successfully because it feeds very close to the carcass and spends most of its time at the carcass in feeding. The lappet-faced (Torgos tracheliotus) and white-headed vultures (Trigonoceps occipitalis) are considered to scavenge unsuccessfully at large carcasses. This is because they

are slow feeders, seldom feed on soft tissues, and spend the greater percentage of their time standing away from the carcass and not feeding. It is suggested that they utilize alternative sources of food.

Eight different stages in the decomposition of carcasses are described. These stages relate to the amount of tissue left by vertebrate scavengers on the one hand, and decay as determined by the effects of maggots, the weather and time on the other. The occurrence of the arthropod fauna is related to these stages of decomposition. Because of the variance in tissue composition of the carcasses, the preferences of the main beetle families are well illustrated.

Factors influencing the success of blowflies breeding on carcasses are discussed. Secondary fly larvae are suggested as having greater interspecific competitive abilities than the primary larvae, except during winter when the activity of secondary larvae was limited.

Arthropods consumed only 11% of the soft tissues and skin of all the carcasses put out, the rest being eaten by vertebrate scavengers. Maggots were the most important arthropods involved. The only other important arthropods were Dermestes beetles, which ate dried out skin, and tineid moths, which ate old horn sheaths and hooves. Micro-organisms are considered to have consumed negligible amounts of tissues.

The rates of survival, damage, disarticulation and fragmentation of the bones of all the bovids observed have been presented and evaluated. These results were predictable considering the size, density, shape and mode of attachment of the bones. The hyaenas have disproportionately high abilities to crush bones, particularly the long limb bones. The bones all had fairly uniform survival rates except the smaller bones 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 bovids' bones were far more susceptible to damage by trampling, than those of larger bovids. Certain differences between carnivore and hominid damage to bones are indicated. 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 inside. One can thus predict a different pattern of survival of long bone epiphyses, caused by hominids, from that caused by carnivores (especially hyaenas).

Griffon vultures collect bone fragments from old carcasses to feed to their chicks. These habits are discussed. The presence of hyaenas in nature reserves, means that in these areas there is an ample supply of bone fragments. However, where hyaenas are absent, small bones only became available to vultures after they have been weathered and finally disarticulated.

The unique ability of hyaenas to chew and digest bones is discussed in terms of their potential in the recycling of nutrients, particularly calcium, in the ecosystem.

The evolution of the main vertebrate scavengers is discussed in terms of their involvement in this life style. In the case of the carnivores the discussion is primarily orientated towards the development of their dentition and methods of hunting. As there is little fossil evidence on vultures, their evolution is discussed in terms of their long distance flying abilities, breeding strategies and social organization.

The results of the present study clearly illustrate the importance of griffon vultures and hyaenas as scavengers. Their abilities to consume the soft tissues of carcasses rapidly, make them important both from ecological and hygienic points of view. They can rapidly recycle the nutrients stored in carcasses, destroy pathogenic organisms living in carcasses, as well as remove a potential food source for blowflies. For these reasons, the conservation of vultures and

hyaenas, particularly griffon vultures and brown hyaenas in farming areas, is to be encouraged.

OPSOMMING

Karkasse van die groot hoefdiere vorm 'n integrale deel van savanne ekosisteme in Afrika. Terwyl heelwat bekend is aangaande die soogdiere van Afrika is min bekend oor hul rol nadat hulle gevrek het. Karkasontbinding word oorweeg in terme van die tempo van verwydering van weefsel van karkasse van verskillende groottes, in verskillende gebiede gedurende die onderskeie seisoene. Die spesies van aasdiere word oorweeg in terme van hul doeltreffendheid as aasdiere en die belangrikheid van hierdie leefwyse vir die individue. Drie groepe aasdiere word bespreek - roofdiere, aasvoëls en arthropoda.

Die studie is oor 'n tydperk van drie jaar op drie plase bokant die eskarpement en op drie laeveldse natuurreservate in die Transvaal en 'n wildplaas in die suide van Zimbabwe uitgevoer. Hierdie studiegebiede het veral ten opsigte van twee kenmerke van mekaar verskil: (i) die aasdier fauna en (ii) die klimaat. Die meer algemene Suid-Afrikaanse karnivoor en aasvoëlsoorte was teenwoordig in die natuurreservate en op die wildplaas terwyl "griffon" aasvoëls (Gyps spp.) en rooijakkalse (Canis mesomelas) regdeur voorgekom het. Bruin hienas (Hyaena brunnea) het ook op een plaas in die Magaliesberg voorgekom.

Karkasse van hoefdiere is op spesifieke lokaliteite geplaas en vanuit skerms waargeneem. Karkasse wat toevallig gevind is is ook gebruik vir waarnemings wat die totale steekproef op 89 te staan gebring het. Inligting aangaande die aasgedrag van al die verbraat aasdiersoorte is op vyf-minuut intervalle versamel. Tussen die voedingstydperke van aasdiere is skattings gemaak van die hoeveelheid sagte weefsel en vel gemaak. Die oorlewing van bene sowel as die skade wat aan bene gedoen is is in detail aangeteken. Aasende kewers is

versamel en tot op familie-vlak geïdentifiseer, terwyl inseklarwes in gevangenis toegelaat is om tot die volwasse stadium te ontwikkel vir identifikasie tot op spesiesvlak.

In die natuurreservate is klein karkasse in die algemeen verbruik binne 'n tydperk van een dag. Aasvoëls het gewoonlik al die sagte weefsel binne 'n uur nadat hulle die karkas gevind het verwyder en gevlekte hiënas (Crocuta crocuta) het die oorblywende vel en bene gedurende die nag verwyder. In die geval van baie groot karkasse het aasvoëls gedurende die dag en hiënas gedurende die nag gevreet en het dit drie tot vier nagte gedoen voordat al die sagte weefsel verbruik is. Daaropvolgende voeding deur hiënas op die oorblywende vel en bene het afhangende van die beskikbaarheid van ander voedselbronne 'n week of meer geduur.

Op die plase waar geen hienas voorgekom het nie en waar aasvoëls dikwels sku was, is karkasse oor 'n baie langer tydperk verbruik. Hier het rooijakkalse en inseklarwes wat nie in die natuurreservate kon kompeteer nie 'n meer belangrike rol gespeel.

Die aanpassings van aasdiere is geanaliseer in terme van hulle sosiale organisasies en fisiese vermoëns. Sosiale organisasie is belangrik omdat dit die sukses waarmee karkasse gevind word beïnvloed. Hoe groter die tuisgebied en die solitêre aasgewoontes, hoe groter is die kans om 'n karkas te vind. Die vermoë om vinnig te voed, om die karkas te verdedig en, in die geval van hiënas, om droeë vel en bene te kou dra by tot die mate van sukses. Van al die karnivore is dit slegs die twee hiëna-soorte wat suksesvol aas. Leeus (Panthera leo) het te min karkasse gevind, en jakkalse was te klein en gewoonlik te min in getalle om te kan kompeteer. Ander spesies is waargeneem om opportunisties te aas.

Die aasgedrag van vyf aasvoëlsoorte is geanaliseer. Die krans-aasvoël (Gyps

coprotheres) en die witrug-aasvoël (Gyps africanus) was weens hul vermoë om vinnig op die sagte weefsel van karkasse te voed die mees suksesvolste. Die monnik-aasvoël (Necrosyrtes monachus) is 'n baie klein aasvoëlsoort en voed op klein stukkies oorblyfsels rondom die karkas en tussen die bene. Hulle word beskou as 'n suksesvolle aasdiersoort omdat hulle baie na aan die karkas voed en omdat hulle die meeste van hulle tyd by die karkas spandeer aan voeding. Die swart aasvoël (Torgos tracheliotus) en die witkop-aasvoël (Trigonoceps occipitalis) word by groot karkasse beskou as onsuksesvolle aasdiersoorte. Dit word toegeskryf aan die feit dat hulle stadig voed, dat hulle selde op sagte weefsel voed en dat hulle 'n groot persentasie van hulle tyd op 'n afstand weg van die karkas spandeer. Dit word voorgestel dat hulle alternatiewe voedselbronne verbruik.

Agt onderskeie stadiums in die ontbinding van karkasse word beskryf. Hierdie stadia verwys eerstens na die hoeveelheid weefsel wat nie deur vertebrat aasdiersoorte verbruik is nie, en tweedens ontbinding soos bepaal word deur die invloed van inseklarwes, die weersomstandighede en die verloop van tyd. Die voorkoms van die arthropodsoorte het 'n verwantskap met hierdie stadia van ontbinding. Weens die variasie in die weefselamestelling van karkasse kan die voorkeur van die belangrikste kewer families goed geïllustreer word.

Faktore van belang in die teel sukses van brommers op karkasse word bespreek. Dit word voorgestel dat sekondêre vliegklarwes 'n groter vermoë tot interspesifieke kompetisie het as primêre larwes, behalwe gedurende die winter wanneer sekondêre larwes se aktiwiteite beperk was.

Arthropoda het slegs 11% van die sagte weefsel en vel van alle karkasse wat uitgeplaas is verbruik, terwyl die res verbruik is deur verbrat aasdiersoorte. Vliegklarwes was die mees belangrike arthropoda. Die enigste ander belangrike arthropoda was Dermestes kewers wat uitgedroogde vel verbruik het en tineid motte wat ou horings en hoewe gevreet het. Weglaatbare hoeveelhede van die

weefsels is deur mikro-organismes verbruik.

Die oorlewingstempo, skade, disartikulasie en verbrokkeling van bene van al die waargenome beesagtiges is geëvalueer. Hierdie resultate was voorspelbaar wanneer die grootte, digtheid, vorm en wyse van verbinding van bene in ag geneem word. Die hiënas het 'n besondere vermoë om bene te verbreek, veral die lang ledemaat bene. Met die uitsondering van kleiner bene wat maklik gevreet of verwyder kan word het bene in die algemeen 'n eenvormige oorlewingstempo. Mandibels en scapulae het 'n besondere lae artikulatie tempo gehad en lang bene, craniums en ribbe het die hoogste fragmentasie tempo gehad. Klein beesagtige diere se bene was meer vatbaar vir beskadiging deur vertrapping as die van groter beesagtiges. Sekere verskille tussen karnivoor en menslike skade aan bene word aangetoon. Hierdie verwys hoofsaaklik na menslikes wat hul hande gebruik het om bene selektief te verwyder en te beskadig, veral die lang bene wat gebreek is om beenmurg te bekom. 'n Verskil in die oorlewingspatroon van die epiphyse van langbene verbruik deur menslikes en karnivore (veral hiënas) kan dus voorspel word.

Die gedrag van "griffon" aasvoëls gedurende die versameling van beenfragmente om aan hulle kuikens te voed, word bespreek. Die teenwoordigheid van hiënas in natuurreservate gee daartoe aanleiding dat genoeg beenfragmente in hierdie gebiede beskikbaar is. In gebiede waar hiënas egter afwesig is is beentjies slegs beskikbaar vir aasvoëls na 'n tydperk van verwerking en uiteindelijke disartikulasie.

Die unieke vermoë van hiënas om bene te kou en verteer word bespreek in terme van die moontlike hersirkulering van nutriente, veral kalsium, in die ekosisteem.

Die evolusie van die belangrikste aasdiersoorte word bespreek in terme van hul deelname in hierdie lewenswyse. In die geval van die karnivore is die bespreking hoofsaaklik georiënteer ten opsigte van die ontwikkeling van hul gebit en hul jagmetodes. Omdat fossiele bewyse nie beskikbaar is vir aasvoëls nie, word hul evolusie in terme van hul vermoë om lang afstande te vlieg, hul teelstrategie en

en sosiale organisasie bespreek.

Die resultate verkry gedurende die studie het die belangrikheid van "griffon" aasvoëls en hiënas as aasdiere duidelik geïllustreer. Hulle vermoë om sagte weefsels vinnig te verbruik gee daartoe aanleiding dat hulle vanuit 'n ekologiese sowel as 'n higiëniese standpunt belangrik is. Hulle kan voedingstowwe wat in karkasse is vinnig hersirkuleer, patogeniese organismes vinnig vernietig, en ook potensiele voedselbronne van brommers verwyder. Weens hierdie redes word die bewaring van aasvoëls en hiënas, veral "griffon" aasvoëls en bruin hiënas, in landbou gebiede aangemoedig.

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										21	MAX)
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										24	VEGETATION
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										30	MAGGOTS
										31	FLIES
										32	BETLES
										33	ANTS
										34	SMELL
										35	BLACK (L-F)
										36	VULTURE
										37	CAPE
										38	ADULT
										39	CAPE
										40	JUV
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										43	Species
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										45	Sex
										76	NUMBER of
										77	Carcass
										78	Period
										79	Sheet No

TIME	No of Vultures	FEEDING	POSITION	INTERACTIONS	RESULTS	Others	Carcass Numbers	Period Number	Sheet No.
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