

Food choice and diet of the bearded vulture *Gypaetus barbatus* in southern Africa

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When offered a selection of food items, bearded vultures *Gypaetus barbatus* in southern Africa chose bones in preference to meat or to feeding from a fleshed carcass. Once a carcass had been stripped of soft tissue by *Gyps* vultures, bearded vultures disarticulated sections or individual bones (depending on the size of the dead animal) in the order: limbs, ribs, vertebrae, skull. Their overall diet was estimated as 70% bone with marrow, 25% meat and 5% skin. This diet is about 15% higher in energy than an equivalent mass of meat. Of 683 identified prey items from five sources of data, over 80% consisted of domestic livestock; about 60% of this was sheep and goats. Even birds nesting within conservation areas derived more than half of their food from domestic stock which they found by foraging over adjacent commercial and subsistence farming areas. Bearded vultures obtain all their food by scavenging, and reports of attacks on live animals and even humans are rejected.

Tydens die verskaffing van voedselitems aan baardaasvoëls *Gypaetus barbatus* in suider Afrika, is daar bevind dat die voëls voorkeur gee aan bene bo vleis, of verkies om aan 'n karkas te vreet waarvan die vleis verwyder is. Nadat *Gyps* aasvoëls die sagte weefsel van 'n karkas gestroop het, het die baardaasvoëls artikulerende dele of enkel bene van 'n karkas verwyder (afhangende van die grootte van die dooie dier) in die volgorde: ledemate, ribbes, werwels, skedel. Daar is beraam dat hulle algemene normale dieet bestaan uit 70% bene met murg, 25% vleis and 5% vel. Hierdie dieet verskaf 15% meer energie as 'n ooreenstemmende massa vleis. Van 683 geïdentifiseerde prooi-items, versamel vanaf vyf verskillende waarnemingspunte, was 80% afkomstig van vee, waarvan 60% skaap en mak bok reste was. Selfs voëls wat hulle neste in bewaringsgebiede gehad het, het meer as die helfte van hulle voedsel verkry van vee wat hulle buite die reservate gevind het in onliggende kommersiële en selfversorgende landbougebiede. Baardaasvoëls verkry al hulle voedsel deur te aas. Berigte dat hierdie voëls lewendige diere en selfs mense aanval, word verwerp.

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While it is generally accepted that the bearded vulture *Gypaetus barbatus* feeds mainly on carrion (Glutz von Blotzheim, Bauer & Bezzel 1971; Cramp & Simmons 1980; Brown, Urban & Newman 1982; Steyn 1982), little quantitative information exists on its diet apart from that gleaned from incidental records. The most detailed information previously available was that obtained from two nests in Spain where, of 53 identified items, 86% consisted of bones from large animals but wood pigeons *Columba palumbus* and redlegged partridges *Alectoris rufa* were also recorded (Suetens & van Groenendael 1973). Fifty birds collected in Ethiopia all had bones in their stomachs (Cramp & Simmons 1980). The diet of the bearded vulture in southern Africa has not previously been studied. In this paper we investigate the diet of this large (5.2–6.3 kg), solitary-nesting mountain specialist as broadly as possible to determine the nature of its food and the species involved which make up this food.

Methods

On six occasions different food items were set out at a feeding site in the Giant's Castle Game Reserve (Figure 1), and the choice of bearded vultures and other bird species was recorded. The following food was made available: (a) fresh carcasses (four horses and two cows) slit along the belly and with the meat from one hindlimb

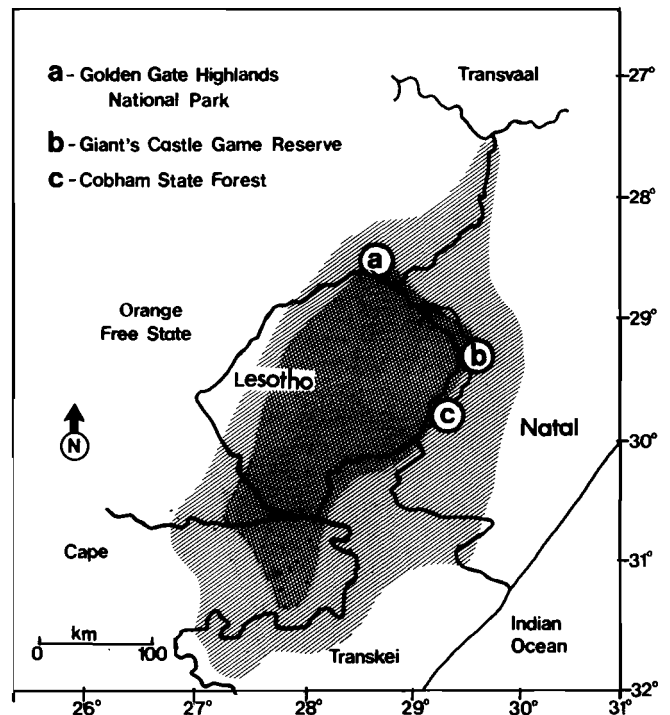


Figure 1 Foraging (hatched) and breeding (cross-hatched) ranges of the bearded vulture in southern Africa and place names mentioned in the text.

removed; (b) this same meat, cut into pieces about 15 cm long and 6 cm in diameter; (c) sections of the lower limb bones of pigs sawn into sections about 5 cm by 8 cm including the marrow and bits of attached meat. Some of these bones (obtained each week) were sun-dried, providing a regular range of ages from fresh to five weeks old. Some bones were placed in a sealed plastic bag for two weeks, the contents becoming partly liquid and rotten. These different items were spread over the feeding area of about 30 × 30 m in equal numbers and evenly distributed about the carcass. The experiment ran until particular items had been so preferentially consumed that the birds were no longer offered an equal choice of foods.

Observations were also made at four carcasses (two sheep and two antelopes) away from the feeding site (all discovered by the descent of Cape vultures *Gyps coprotheres*) and the parts of the carcasses which were selected by bearded vultures were determined.

The natural food of bearded vultures was determined from five different sources: (a) information provided by farmers via a questionnaire survey on what they had seen bearded vultures eating on their farms, (b) our direct observations of birds feeding on 'natural' prey (i.e. not provided at one of the feeding stations, but including domestic livestock), as well as birds carrying food, (c) food brought to nests to feed nestlings, (d) prey remains

collected at bone-dropping sites (ossuaries) and (e) prey remains collected below nest sites. All collected prey remains are housed in the Transvaal Museum, and were analysed according to procedures suggested by Brain (1974), Voigt & Plug (1981) and Voigt (1983).

Results

When offered a selection of foods, bearded vultures chose bones in preference to meat, and paid very little attention to the carcasses (Table 1). On only four occasions did bearded vultures depart with meat. These were all during the breeding season when the birds were known to have nestlings and the meat was probably destined for the nestlings. Bearded vultures selected the older dried bones significantly more often (χ^2 test, $p < 0,05$) than more fresh bones, 66% of those eaten being three weeks old or more. The rotten bones aged in plastic were avoided. This can be contrasted to the behaviour of other species: Cape vultures ate mainly from the carcasses, although when approaching a carcass, pieces encountered *en route*, particularly lumps of meat, were consumed. Cape vultures had difficulty in swallowing all but the smallest pieces of bone, because of their narrow gape. Cape vultures temporarily evicted from a place at the carcass would pounce on nearby meat before returning to the fight. Black eagles *Aquila verreauxii*, jackal buzzards *Buteo rufofuscus*, lanner

Table 1 The food choice of scavenging birds attracted to carrion in the Giant's Castle Game Reserve

Species	No. birds	Number of records of food choice									Totals
		Carcass	Meat	Bones							
				fresh	1 week	2 weeks	3 weeks	4 weeks	5 weeks	plastic	
Bearded vulture	15	1	4	7	6	9	13	16	14	0	70
Cape vulture	134	134	27	7	8	0	1	0	0	2	179
Black eagle	14	1	12	5	1	0	0	0	0	0	19
Jackal buzzard	9	0	7	4	0	1	0	0	0	0	12
Lanner falcon	5	0	1	5	0	0	0	0	0	0	6
Whitenecked raven	18	17	14	19	6	1	2	5	0	3	67
Black crow	11	0	8	9	0	0	0	0	0	0	17

Table 2 The sequence of removal by bearded vultures of parts from four carcasses in the Giant's Castle area, after the Cape vultures had completed their feeding

Order of removal	Carcasses			
	Sheep (adult)	Sheep (subadult)	Red hartebeest (adult)	Mountain Reedbuck (adult)
1	left humerus to hoof	left scapula to hoof	left metacarpals to hoof	left femur to hoof
2	left femur to hoof	right humerus to hoof	left radius/ulna	left radius/ulna
3	right tibia/fibula	ribcage	left tibia/fibula to hoof	left carpals to hoof
4	left scapula	skull	rib	left humerus
5	rib		rib	caudal vertebrae
6	right femur		rib	right humerus
7	cervical vertebrae		thoracic vertebrae	rib
8	rib		rib	
9	caudal vertebrae			

Table 3 The number of farmers who reported sightings of bearded vultures on their farms, who saw the birds feeding, and the frequency with which feeding was seen

Province	Number of sightings	% feeding	Frequency of sightings (%)								Totals
			Once or twice	Seldom	Occasionally	Often	When stock is lost	Mainly summer	Winter & Lambing season		
Natal	216	39	41	20	20	9	7	3	1	0	101
Orange Free State	59	27	31	31	6	6	13	0	0	13	100
Cape	90	51	22	17	22	29	10	0	0	0	100
Totals	365	40	34	20	19	15	8	2	1	2	101

falcons *Falco biarmicus* and black crows *Corvus capensis* selected fresh meat and fresh bones (although all but the lanner falcons would eat dried meat from three-week-old bones when fresh meat was not available). Whitenecked ravens *Corvus albicollis* were less selective than the other species. Although favouring fresher food, they often flew off with whatever was nearest at hand.

Being carrion feeders, bearded vultures are bound to be largely opportunistic in obtaining food. At a carcass, however, a certain amount of selection can take place, particularly in the sequence in which different parts of the carcass are eaten. Four further carcasses, an adult and a subadult sheep, a mountain reedbeek *Redunca fulvorufula* and a red hartebeest *Alcelaphus buselaphus*, cleaned of most soft tissue by Cape vultures, were monitored for food selection. Although some picking at attached flesh did take place, the bearded vultures preferred to remove sections of the carcass and fly off with these. Observations were over a period of two to three days per carcass; blackbacked jackals *Canis mesomelas* often removed parts of the carcasses at night. It is apparent (Table 2) that limbs were the first choice of bearded vultures, being removed whole where possible. From smaller carcasses such as the subadult sheep, a forelimb from scapula to hoof inclusive was carried off, while from larger carcasses, e.g. adult sheep, the humerus to hoof was taken. In the case of the still larger red hartebeest, the limbs were disarticulated into a number of sections before being removed. Ribs and vertebrae were the next to be removed, and in one case, the skull was also taken. Although detailed observations were not made after three days, bearded vultures revisited the sites of the carcasses for at least two weeks after the animals' deaths.

Of 367 farmers who reported the presence of bearded vultures on their farms, only 40% actually saw the birds feeding and few recorded this on more than one or two occasions (Table 3). By contrast, 73% of the farmers reported regular observations of Cape vultures feeding (Brown & Piper 1988). Farmers in the north-eastern Cape Province reported the most frequent sightings of bearded vultures feeding. These farms are in the mountains, in some cases nest sites were on the farms (Brown in press b), whereas in the provinces of Natal and the Orange Free State most farms are some way

Table 4 The food preference of bearded vultures as recorded by farmers for birds seen on their farms

Food	Number of food items reported				
	Natal	O.F.S	Cape	Totals	%
Unspecified					
carrion	16	1	10	27	15
Left-overs from carcass after Cape vultures have eaten	2	2	2	6	3
Bones	6	1	3	10	6
Dead cattle	16	2	2	20	11
Dead sheep (adult)	35	6	18	59	33
Dead lambs	18	2	4	24	14
Sheep afterbirth	1	1	1	3	2
Small stock, particularly limbs	1	0	2	3	2
Lambs killed by bearded vultures	3	0	1	4	2
Goat kids killed by bearded vultures	0	2	0	2	1
Antelope carcass	1	0	0	1	1
Black wildebeest carcass	0	1	0	1	1
Rock hyrax	2	0	6	8	5
Hares	0	1	2	3	2
Road kill	0	0	1	1	1
Small mammals	0	2	0	2	1
Birds	0	1	2	3	2
Totals	101	22	54	177	102

from the mountains and birds visit these areas only to forage. Table 4 lists the food items reported by farmers from the three provinces covered by the questionnaire survey. Although no farmer actually observed a bearded vulture make a kill, 5% claimed that they take young lambs and goat kids. A further 9% of their food could conceivably have been obtained by predation, i.e. hyraxes, hares, birds and small mammals, and whilst birds would appear perfectly capable of predatory

behaviour, no farmer actually saw a kill take place. As would be expected from commercial farmlands, most of the food items consisted of domestic animals (89%), with sheep and lambs predominating.

Our observations on the food of the bearded vulture away from the nest were made mainly in Giant's Castle Game Reserve and the Lesotho highlands with only incidental sightings from adjacent regions (Table 5). In areas outside the game reserve all food items identified (with the exception of a mountain reedruck) were of domestic animals, mainly sheep and lambs. In Giant's Castle Game Reserve 68% of the identified food was of non-domestic animals, mainly small antelopes.

Of 65 food items seen brought to four nests by bearded vultures (Table 6), domestic stock predominated (94%). Limbs, sections of limbs and long-bones were well represented (62%). Lumps of meat formed 12% of all food items brought to the nest, 73% of these being brought within the first three weeks of the nestling having hatched.

A total of 1034 bones, and bone fragments were

Table 5 Food items recorded for bearded vultures away from the nest

Food	Number of food items					Totals	%
	Lesotho high-lands	Giant's Castle Reserve	KwaZulu Natal farms	N.E. Cape farms	Totals		
Horse carcass	2	0	0	0	2	1	
Cattle carcass	3	0	1	0	4	2	
Sheep carcass	8	0	4	1	13	6	
Lamb carcass	5	0	1	0	6	3	
Sheep afterbirth	2	0	0	0	2	1	
Sheep limb	17	7	7	1	32	15	
Sheep skull	1	0	0	0	1	0	
Eland carcass	0	3	0	0	3	1	
Black wildebeest carcass	0	1	0	0	1	0	
Red hartebeest carcass	0	1	0	0	1	0	
Mountain reedruck carcass	0	3	1	0	4	2	
Mountain reedruck lamb	0	1	0	0	1	0	
Grey rhebok carcass	0	2	0	0	2	1	
Small antelope limb	0	4	0	0	4	2	
Small ungulate scapula	2	2	1	0	5	2	
Bones — long	26	29	7	2	64	30	
Ribs	3	5	1	0	9	4	
Vertebrae	3	3	0	0	6	3	
Red meat	7	4	0	0	11	5	
Dog carcass	1	0	0	0	1	0	
Unidentified	19	14	9	0	42	19	
Totals	99	79	32	4	214		

Table 6 Food brought by bearded vultures to their nests

Nature of food	Number of food items					Total	%
	Nest 1	Nest 2	Nest 3	Nest 4	Total		
Horse hoof and tarsals	1	0	0	0	1	2	
Cattle hoof and tarsals / carpals	0	0	1	0	1	2	
Sheep forelimb	7	1	2	1	11	17	
Sheep hindlimb	2	0	1	0	3	5	
Sheep hoof and tarsals / carpals	2	0	2	0	4	6	
Sheep head	1	0	0	0	1	2	
Unidentified sheep piece	1	0	0	0	1	2	
Goat hindlimb	2	0	0	0	2	3	
Smallstock hindlimb	3	2	0	0	5	8	
Small ungulate ribcage	1	0	0	0	1	2	
Small ungulate longbone	10	1	2	1	14	21	
Dog carcass	1	0	0	0	1	2	
Hare	0	0	1	0	1	2	
Lumps of meat	7	1	0	0	8	12	
Unidentified	7	1	1	2	11	17	
Totals	45	6	10	4	65	104	

Table 7 Bones and bone fragments collected from bearded vulture nesting sites and ossuaries

Skeletal parts	Nesting sites		Ossuaries	
	No.	%	No.	%
Bovid teeth and tooth rows	8	1,7	39	3,8
Bovid skeletal parts	198	43,0	64	6,2
Other identified remains	50	10,9	18	1,7
Enamel fragments	0	0,0	6	0,6
Skull fragments	22	4,8	34	3,3
Vertebral fragments	53	11,5	2	0,2
Sternum fragments	4	0,9	0	0,0
Rib fragments	56	12,2	3	0,3
Bone flakes	42	9,1	732	70,8
Miscellaneous fragments, skin	27	5,8	136	13,2
Total	460		1034	

collected from 12 ossuaries and 460 bones were retrieved from underneath eight nest sites, well distributed throughout the species range in southern Africa (Table 7). A number of bones from the ossuaries had tissue adhering, and there was tissue on most of the bones collected beneath the nests. Evidence of digestion or regurgitation was found on only 10 items, but scratch and peck marks were common, particularly on bones from the nest sites. Carnivore and rodent damage was

present on only two bones, both from the Giant's Castle Game Reserve.

A few bones from both ossuaries and nest sites showed burn or scorch marks. While some of these could have been collected by the birds after veld fires (game deaths owing to uncontrolled fires are fairly common in the Drakensberg), many of the bones collected at ossuaries were scorched when those areas were burned subsequent to the bone-dropping. No non-faunal remains were found at either nest sites or ossuaries. The collection from ossuaries consisted mainly of bone flakes and unidentifiable fragments, whereas the collection from the nesting sites consisted mostly of identifiable pieces.

Domestic animals were present in almost all the samples, forming at least 67% of the bones collected at ossuaries (Table 8) and 65% of those from nest sites (Table 9). The few wild animals represented were mainly found at sites within Drakensberg conservation areas. Ageing of animals was based on patterns of tooth wear. Sheep/goat, wild bovids and hyrax teeth were present from nesting sites and ossuaries. Although equid remains were quite common, teeth were virtually absent from the sample. Cattle teeth were present only in the ossuary collection. Teeth from the ossuaries were mainly those of adult to old animals, but the nesting sites yielded teeth of young animals, particularly in the sheep/goat group. Post-cranial remains from juveniles were also more common from the nesting sites than from the ossuaries (11,2% and 0,3% respectively). All bone fragments were measured along the longest axis and are plotted in 10-mm categories (Figure 2). It is evident that the fragments from nest sites are generally larger than

Table 8 The identifiable prey remains collected from ossuaries of bearded vultures

Species	Ossuaries									Total	%	
	1	2	3	4	5	6	7	8	9			
Horse		8								2	10	6,3
Donkey										2	2	1,3
Equid	1				2						3	1,9
Cattle	3	1				1	2				7	4,4
Probably cattle	22	8		1	1		1	1	12		46	29,1
Sheep	1	1									2	1,3
Goat	1									1	2	1,3
Sheep/goat	17	2	1		2	7	4		1		34	21,5
Grey rhebok	2										2	1,3
Oribi		3									3	1,3
Small antelope		1		1							2	1,3
Sheep / goat size	15	1		2				1	8		27	17,1
Bovid		3				3					6	3,8
Baboon		1									1	0,6
Rock hyrax	1								5		6	3,8
Genet					1						1	0,6
Hare	2										2	1,3
Rodent						1					1	0,6
Large bird	1										1	0,6
Total	66	29	1	4	6	12	7	2	31		158	

Table 9 Prey remains collected from below the nests of bearded vultures

Species	Nest sites							Total	%	
	1	2	3	4	5	6	7			
Horse	2							2	0,7	
Donkey	2							2	0,7	
Equid		2		4				21	10,2	
Cattle			3	9				21	12,5	
Probably cattle	12			2	1			15	5,7	
Sheep			35	3	1			16	55	20,7
Goat	1			1		1		3	1,1	
Sheep/goat	1	2	14	15	3			35	13,2	
Grey rhebok					1	6		7	2,6	
Common duiker					1			1	0,4	
Small antelope					3		1	4	1,5	
Sheep / goat size			4	3	1	18		26	9,8	
Non-domestic bovid	8			6	4	14		32	12,1	
Bovid							4	4	1,5	
Rock hyrax	5		3	1	5			14	5,3	
Hare				1		1	1	3	1,1	
Medium-large bird					1	1		2	0,7	
Total	31	4	59	45	21	41	64	265		

those found at ossuaries.

The composite picture of food eaten by bearded vultures as determined from identifiable items from the five sources of data is shown in Figure 3. It is evident that in southern Africa, bearded vultures are dependent on domestic livestock throughout their range, particularly on sheep and cattle, which they obtain probably solely as carrion. Non-domestic bovids constitute on average only 12% of the bearded vulture's diet in this region, and probably considerably less in some parts. Non-domestic animals from other groups, e.g. small mammals, birds, genets, contributed 7% in number, but certainly less in biomass to the bearded vulture's diet.

Skeletal remains retrieved at nests and ossuaries are shown in Table 10. The high percentage of skulls, vertebrae, ribs and sterna from these sites are in contrast to the observed selection of limbs at carcasses and the high percentage of limbs and long-bones seen carried and consumed by the birds.

Discussion

It is difficult to obtain an accurate idea of the diets of raptors that do not regularly produce pellets of indigestible portions of food. Many studies are based on prey remains collected at nests (e.g. Boshoff & Palmer 1980; Plug 1978; Steyn 1964, 1965, 1973), but it is unlikely that these remains accurately reflect the prey spectrum of the species in question. The extent of the bias varies from species to species, and would be greatest in those birds that use their nests only during the breeding season, in those species in which the diets of the nestlings and parents differ and in those species that feed predominantly on soft material (usually carried in the crop) with most of the 'hard remains' found at nests

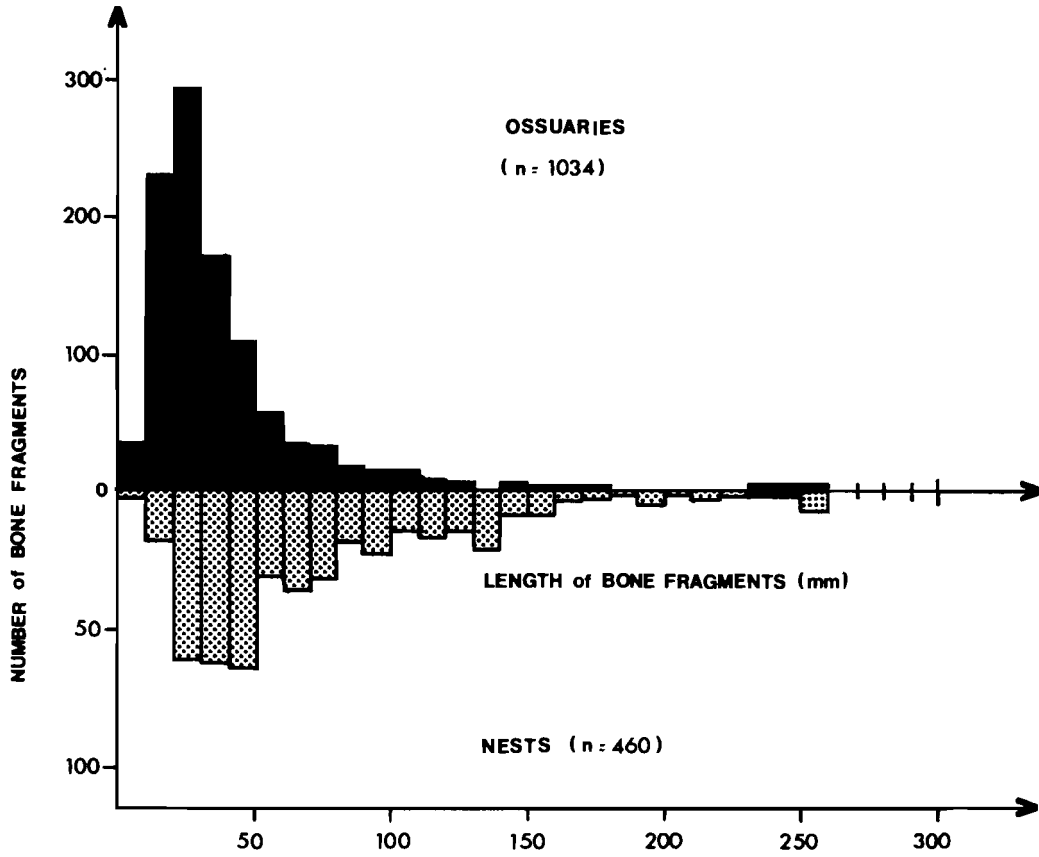


Figure 2 Lengths of bone and bone fragments (measured along the longest axis) collected from bearded vulture nests and ossuaries in southern Africa.

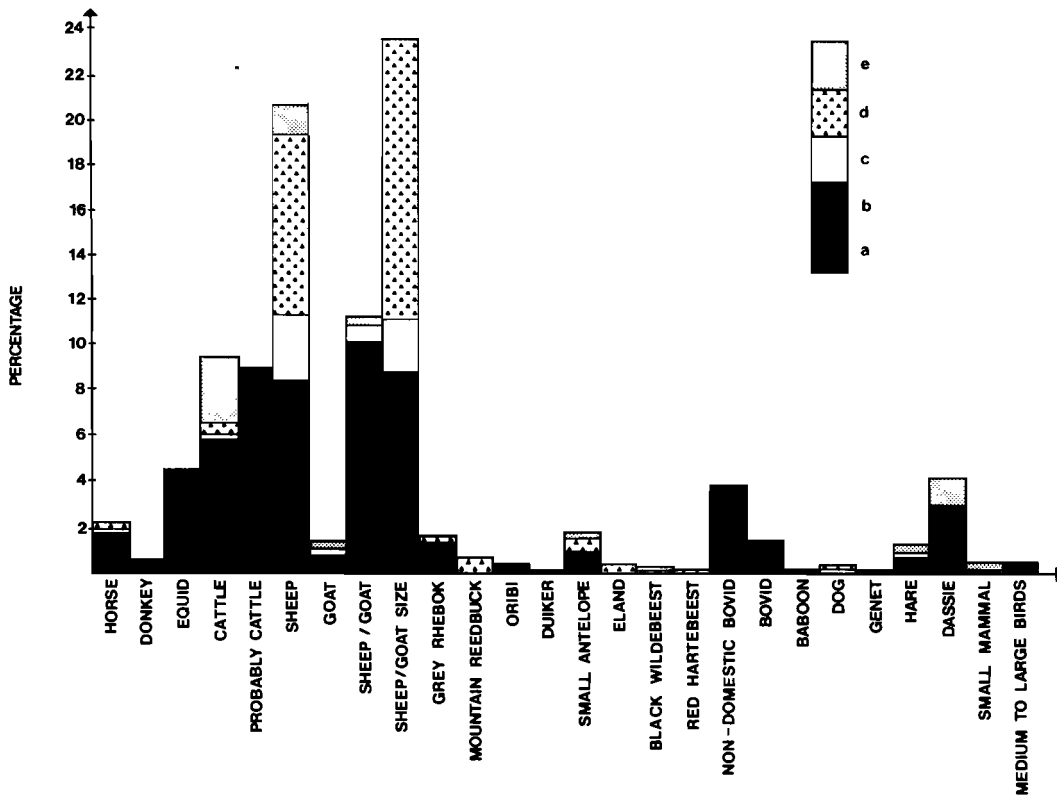


Figure 3 The diet of the bearded vulture in southern Africa, determined from 683 identifiable prey items (a) collected at nests, (b) collected at ossuaries, (c) seen brought to the nest by parent birds, (d) seen being carried and eaten away from the nest, and (e) reported by farmers via a questionnaire survey.

Table 10 Summary of skeletal remains of food items from bearded vulture ossuaries and nesting/roosting sites

Skeletal parts	Ossuaries		Nests	
	No.	%	No.	%
Skull	79	7,6	89	19,3
Axis	1	0,1	1	0,2
Vertebra	2	0,2	53	11,5
Scapula	7	0,7	27	5,9
Humerus	11	1,1	10	2,2
Radius	4	0,4	6	1,3
Ulna	3	0,3	8	1,7
Rib and sternum	3	0,3	60	13,0
Pelvis	1	0,1	12	2,6
Femur	10	1,0	8	1,7
Tibia	3	0,3	20	4,3
Metapodial	13	1,2	32	7,0
Astragalus	1	0,1	5	1,1
Calcaneum	1	0,1	6	1,3
Patella	0	0,0	1	0,2
Sesmoid	3	0,3	3	0,7
Naviculo-cuboid	2	0,2	4	0,9
Carpal / tarsal	1	0,1	1	0,2
Phalanx 1	9	0,9	13	2,9
Phalanx 2	5	0,5	14	3,0
Terminal phalanx	7	0,7	18	3,9
Bone flakes	732	70,8	42	9,1
Miscellaneous fragments	136	13,2	27	4,8
Total	1034		460	

representing discarded items.

The bearded vulture uses its nest throughout the year, but food is brought to the nest only once the first nestling hatches (Brown in press a). Although nearby ledges used for roosting may also be used for feeding, very few prey remains were found under these sites compared to under nests. The nest site collections would therefore reflect the diet destined mainly for the nestling, covering the period from mid-August to the end of December. During this study an effort was made to obtain as wide a coverage as possible of the food eaten by bearded vultures. Nevertheless, items such as soft tissue and small food items will have been under-represented because these are swallowed whole and no evidence remains. In addition, samples from different sources i.e. nests, ossuaries, farmlands, etc. are not of equal size, so that, while Tables 4–9 have been kept separate, the composite picture in Figure 3 is intended to show only general trends. It is nevertheless obvious that bearded vultures are highly dependent on domestic stock for food. Even birds nesting in conservation areas, e.g. Giant's Castle Game Reserve, Golden Gate Highlands National Park and Cobham Forestry Reserve, were largely dependent on domestic stock from adjacent regions; 55% of bones collected below four nests ($n = 121$) in these conservation areas were from domestic stock. This is not surprising, as the home range

size of the bearded vulture is many times the size of the largest conservation area in the Drakensberg (Brown 1988). This means that these reserves can neither adequately contain a single pair of bearded vultures nor provide sufficient food throughout the year to support a viable population. Bearded vultures are therefore reliant on the adjacent farming communities of Natal and KwaZulu, and on the Basotho stockmen of Lesotho for their long-term survival.

Tooth remains found at ossuaries indicated that the bones of mainly adult and old mammals were brought for breaking, and these were mostly larger animals (e.g. horses and cattle). This is to be expected as the bones of adult larger animals would be too large to swallow whole and would need to be broken. In addition, larger bones contain less energy per net weight and bearded vultures are inclined to scoop out the marrow and reject much of the calcified material. Smaller bones, which are nevertheless too large to swallow whole, are often broken into two or three pieces and these are then swallowed in their entirety, leaving no more than a few unidentifiable flakes of bone behind. Cattle and horse bones made up only 12% of the food that bearded vultures brought to their nests, whereas sheep and goats accounted for 84%. Conversely, of the items collected below nests, 50% were cattle, horse and donkey bones and 48% were sheep and goat bones. Much evidence of young animals in the diet of bearded vultures was obtained from below nests.

Bearded vultures have a nestling in the nest from September to January. This coincides with both the period of spring lambing and the period of highest game and domestic-stock mortality (Brown 1988). Young animals are most vulnerable, particularly if their parents are in poor condition, and it would be expected that these would form a substantial part of the diet of scavengers during this period. While smaller bones and soft parts are usually fed to the young nestlings, they soon take larger bones. Bones too large for the nestlings are eaten by the parents (Brown in press a). Bones of medium and small ungulates found below nests have therefore probably fallen out or been knocked out accidentally. Birds never deliberately cleaned out old bones or other food, and never flew from their nest with food remains. Bones of larger animals that could not be swallowed by adult birds would therefore accumulate and eventually fall out of the nest, which probably accounts for the high percentage of larger bones found below nests.

While the ability of a bird as large as the bearded vulture to live mainly off bone may seem incredible (Newman 1969) this study supports the more recent literature (e.g. Hiraldo, Delibes & Calderon 1979; Cramp & Simmons 1980; Steyn 1982) which states that bones are by far the most important component of their diet. Hiraldo *et al.* (1979) give figures of bones accounting for over 90% of stomach contents and over 80% of all food brought to the nest. In this study birds actively selected bones in preference to lumps of meat and to feeding from a carcass. Of the identifiable food items seen carried by bearded vultures away from the

nest ($n = 136$), 89% (by number) were bones, 8% lumps of meat and the rest were whole or large sections of small carcasses. Of the identifiable items brought to nests ($n = 53$), 81% were bones, 15% meat and 4% carcasses of smaller animals. We estimate that the overall diet of the bearded vulture normally comprises about 70% bone (with its associated marrow), 25% muscle and 5% skin, giving a ratio of 14:5:1. Using figures for the energy contents of these various components of 6,7; 5,8 and 11,7 kJ/g, respectively (see Brown 1988), 100 g of food eaten by bearded vultures contains about 674 kJ of energy whereas the same mass of muscle provides about 586 kJ. The diet of the bearded vulture is therefore 15% higher in energy than an equivalent mass of meat, and it is not surprising that bearded vultures are able to survive mainly on bones, with older, dried-out ones providing a particularly concentrated source of energy.

During this study, bearded vultures were never seen to capture live prey and no incident led to the speculation that this was probable. Although rock hyrax *Procavia capensis*, skulls made up over 4% of all prey remains found at nests and ossuaries, this does not automatically mean that the animals were killed by bearded vultures. Black eagles are common residents throughout the range of the bearded vulture in southern Africa (Brown in press b), and these eagles feed almost exclusively on the rock hyrax (Gargett 1971; Steyn 1982). During the breeding season rock hyraxes are often brought to the nests of black eagles already beheaded (Rowe 1947; Gargett 1971, 1972). In addition, while the skull may be picked clean of external musculature, black eagles cannot get at the brains, and the skull usually falls off the nest or feeding perch and may then be picked up by bearded vultures which would be able to feed on the brains by dropping the skull to crack it open. While a number of records exist confirming that whole rock hyrax carcasses were carried by bearded vultures (and even reputedly dropped) (Newman 1969; farmers questionnaires in this study), these animals could well have been picked up dead. Two observations support this: (a) bearded vultures were never seen hunting in a manner which would be effective for capturing a hyrax, and (b) when bearded vultures flew over a group of sunning hyraxes the hyraxes paid little attention to the bird, whereas, when a black eagle appeared the group scattered for shelter, some emerging cautiously to screech at the eagle. Other instances of predator avoidance have been seen, in which mountain reedbeek and grey rhebok *Pelea capreolus* with small young took off in haste down steep hillsides to gain the protection of patches of woody vegetation at the approach of a pair of black eagles. These antelopes paid no attention to bearded vultures passing low overhead. This is even more apparent in the case of domestic smallstock. During lambing in the highlands of Lesotho the presence of a black eagle caused sheep to huddle in small groups, protecting their lambs. Bearded vultures, by contrast, would fly in and land between the sheep and walk to within 1 m of animals with lambs to feed on the afterbirths, causing no concern whatsoever. A similar situation has been reported by Rudebeck (1956) for domestic goats in Lesotho, and by

Kelham (1909) for goats and *Ibex* in the Himalayas.

The record of a rodent at an ossuary in Giant's Castle Game Reserve is probably not attributable to bearded vultures, as such food would have been swallowed whole. Two farmers reported small mammals in the diet of bearded vultures, but did not see them being caught; live white mice in a bal-chatri trap evoked no interest in the birds. A bearded vulture was seen bringing rodents to its nest in the Cobham State Forestry Reserve (W. Small pers. comm.). While it is possible that bearded vultures capture these animals alive, it is more likely that they scavenged them, as these observations coincided with the burning season in the Drakensberg when rodent mortality is high (Rowe-Rowe & Lowry 1982). In Spain dead rats were also brought to a nest (Ferguson-Lees 1960) and these were obviously scavenged as they were dried out on delivery. Prey records of species such as wood pigeons and partridge recorded by Suetens & von Groenendael (1973) at nests in Spain were considered by the authors as 'most probably collected as dead birds, as there are many under the snow on passes, where the Lammergeiers (sic.) are frequently seen hunting on the fringe of the receding snow'.

The report by a few farmers that bearded vultures kill young smallstock are highly unlikely. Less than 5% of farmers who reported the birds on their farms held this view, whereas 28% thought that Cape vultures attacked young and calving livestock (Brown & Piper 1988). The impression that scavengers are responsible for predation is sometimes gained when a farmer arrives at a dead animal to find a large bird of prey present and feeding. For example, at seven lamb and sheep carcasses that were reported by farmers to have been killed by black eagles in the southern Drakensberg areas of Natal, six had clear evidence of domestic dog, blackbacked jackal or caracal *Felis caracal* predation before the arrival of the eagles, and at only one carcass could no other evidence of predation or disease be found (CJB, pers. obs.). The behaviour of small domestic stock in the presence of bearded vultures suggests that these birds do not attack live animals.

Reports of attacks on other animals and even humans, particularly when near the edge of a precipice, are not uncommon, but mainly from old literature (e.g. Bree 1875; von Czynk 1890), although these have been quoted widely in modern writings. The most recent reports of this behaviour are by Meinertzhagen (1959) who, in highly emotive terms, refers to the despicable character of the bearded vulture, 'a bird of unashamed cowardice, ready to take advantage of any animal in distress'. He recounts how, when in difficulty on a moving scree slope a bearded vulture sailed close by him until, by throwing stones, he was able to drive it away. Such stories of attacks on healthy animals, and particularly man, should be regarded as highly unlikely. Bearded vultures in flight are very confiding and inquisitive and they will glide about a person at remarkably close quarters. Their blood red scleral eye-ring gives them an appearance of ferocity, but despite being given every opportunity on many occasions to dislodge the senior author and his colleagues

while sitting on the edge of the Drakensberg escarpment, never once did a bird give the impression that it might attack, even when observers were descending by rope to inspect their nests.

Bearded vultures were also seen sailing closely past klipspringers *Oreotragus oreotragus* grazing on narrow ledges high above vertical cliffs. The birds showed no interest in the antelopes and they made no attempt to move to more protected sites. Bearded vultures may be attracted by the sound of falling rocks. On two occasions when accidental rock slides were started in mountain passes, which echoed over some considerable distance, bearded vultures appeared within minutes to circle overhead. This may be coincidence or inquisitiveness, or it may be a response to a sound that may well indicate the death of one or more animals.

Bearded vultures are specialist scavengers, capable of feeding from a large carcass but also able to find small food items. This study provides no evidence to support the statement that 'in South Africa at least it (the bearded vulture) is a more active predator than is generally realized' (Newman 1969). If the bearded vulture does kill any prey, it must do so very rarely indeed.

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