

An analysis of bones and other materials collected by Cape Vultures at the Kransberg and Blouberg colonies, Limpopo Province, South Africa

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We compared bones and non-faunal items collected by Cape Vultures at the Blouberg and Kransberg colonies. Bones from the base of the nesting cliffs were on average longer than those from the crops and stomachs of birds. Bones from the Blouberg cliff base were on average shorter than those from the Kransberg. A larger proportion of bones from smaller animals was the reason for this. The smaller size of the crop material was due to a greater proportion of fragmented bone. Fragmentation made bones less identifiable to species. The proportion of fragmented material and the particular skeletal elements discovered at the two sites were very similar and did not influence this size difference. Material from these colonies was, for the most part, smaller than bones collected from other Cape and Whitebacked Vulture colonies in Zimbabwe, Botswana and South Africa. Higher proportions of bones from smaller animals and smaller skeletal elements collected were the reasons for the smaller average size.

In wildlife reserves, *Gyps* vultures compete with large mammalian carnivores and other scavenging birds for food, including bone. Where these competitors are absent or rare (i.e. farming areas), *Gyps* vultures eat more bone. Small bones (i.e. carpals, tarsals, phalanges, etc.), quickly eaten by spotted hyenas in game reserves, are collected in large numbers by *Gyps* vultures in farming areas, where competition is reduced. As a food, bone is almost as good nutritionally and energetically as meat. Where meat is scarce (e.g. farming areas), *Gyps* vultures collect more bone as an alternative food source.

In areas of high human density, vultures eat more human-made material. Substitution or confusion of one item for another (e.g. human-made items for bone/food) will occur more regularly as the replacement item becomes more prevalent in the environment. Most of the non-faunal pieces did not resemble bone and were probably not confused for that item. Glass was the most common human-made substance found in vulture crops and stomachs, and rocks the most common overall. Grass and sticks were collected from nestling crops and stomachs but rarely from adults. When food is scarce, vulture nestlings feed on non-food items, particularly nesting material. The increase in collection and eating of bone and non-food items is a result of the shift in *Gyps* vulture's diet where meat is scarce and alternative foods are sought.

Introduction

Dobbs and Benson (1984a, 1984b) suggested that: 1) skeletal abnormalities in the wings of nestling Cape Vultures, *Gyps coprotheres*, in southern African farming areas are due to various causes, but particularly traumatic injury and 2) non-faunal items are eaten by vultures in response to food deprivation. These hypotheses are in response to Mundy and Ledger's (1976) suggestion that skeletal abnormalities result from an insufficient calcium intake in nestling vultures, due to a paucity of bone fragments because large mammalian carnivores (particularly spotted hyenas, *Crocuta crocuta*, that would normally fragment bones) have disappeared in farming areas. Those authors propose that Cape Vulture nestlings eat human-made items because bone fragments are absent.

Mundy and Ledger's hypothesis is quoted in the popular media (e.g. Steyn 1982, Anonymous 1986, Butchart 1988, Viviers 1992) and scientific literature as one cause of the Cape Vultures' decline (e.g. Newton 1979, Boshoff and Vernon 1980, Tarboton and Allan 1984, Maclean 1993),

though no critical analyses of the type of skeletal anomalies have been conducted nor alternative causes considered. Here we discuss Cape Vulture collecting patterns in relation to these hypotheses. The specifics of Cape Vulture skeletal abnormalities will be addressed elsewhere (Benson and Dobbs in prep.).

Gyps vultures swallow bone fragments and regurgitate them at the nest when feeding their young (Grubh 1973, Kemp and Kemp 1975, König 1975, Mundy and Ledger 1976, Richardson *et al.* 1986, PCB pers. obs.). Cape Vultures were first recorded to collect human-made items in the 1950s in the Magaliesberg Mountains of South Africa (Paterson 1952), and subsequently elsewhere (Jarvis *et al.* 1974, Boshoff and Currie 1981, Robertson 1983, Dobbs and Benson 1984a, HA Scott pers. comm.). Some researchers (e.g. Mundy and Ledger 1976, Richardson *et al.* 1986) consider the Cape Vultures' behaviour of collecting ceramic, glass and plastic fragments as evidence of an inadequate supply of bone fragments in farming areas.

As part of a long-term study of Cape Vulture biology in the former Transvaal Province (now Gauteng, Limpopo, Northwest and Mpumalanga Provinces), South Africa, we collected bones, human-made items and other materials from the base of the Kransberg and Blouberg nesting cliffs, from the crops and stomachs of dead adults and nestlings discovered there, and from several Kransberg nests.

In this paper we: 1) evaluate the patterns of collection of bone and non-faunal items by Cape Vultures at the Kransberg and Blouberg colonies, 2) compare our results with studies of *Gyps* vultures and other species elsewhere, 3) in light of these findings and a review of other studies of *Gyps* vulture, large mammalian carnivore and ungulate interactions, examine the previous hypotheses presented to explain Cape Vulture collecting patterns and 4) consider other possible explanations for the patterns observed.

Study areas and methods

The Kransberg and Blouberg Cape Vulture colonies in South Africa's Limpopo Province are the largest Cape Vulture breeding sites, with over 900 and 800 pairs recorded nesting there respectively (Benson *et al.* 1990). Farming of domestic stock and indigenous ungulates is the main land-use in both areas. Both colonies are located in the savanna biome (Rutherford and Westfall 1994). Few large mammalian carnivores remain in either area (Rautenbach 1982, Smithers 1983).

The Kransberg (24°28'S, 27°36'E) is 20km north-east of the mining community of Thabazimbi, on the south-western edge of the Waterberg mountains, in the south-western Limpopo Province. The 200m high nesting cliff is the southern boundary of the Marakele National Park, a developing conservation area. Private cattle, *Bos taurus*, grazing is more common than wild ungulate farming in the area. The colony is 60km from Botswana, where communal grazing of goats (*Capra hircus*), sheep (*Ovis aries*) and cattle is the predominant land-use (communal area). Communal grazing also occurs in the former South African homeland, Bophuthatswana, about 65km south-west of Kransberg.

The Blouberg (23°02'S, 29°03'E) is an isolated mountain, 100km north of Polokwane (Pietersburg) and 217km north-north-east of the Kransberg in the Limpopo Province. The nesting cliff is 250m high. The western half of this colony is in the former South African homeland of Lebowa, the eastern in the Blouberg Nature Reserve administered by Limpopo Province Directorate of Environmental and Nature Conservation. Private farming of cattle and game species is the main land-use outside Lebowa, with more emphasis on indigenous ungulates than at Thabazimbi. Communal grazing occurs in Lebowa. The Blouberg is approximately 50km from communal grazing areas in Botswana and from the Tuli Block, a private wildlife reserve where some large carnivores (e.g. spotted hyaenas and lions, *Panthera leo*) still remain.

While searching for vulture carcasses, at the base of the Kransberg and Blouberg breeding cliffs, we collected human-made items and bones that had fallen from vulture nests. The Kransberg assemblage was collected from 1981 to 1988, the Blouberg sample from 1984 to 1986. We collected all materials from crops and stomachs of carcasses

(henceforth referred to collectively as 'crop' samples). We collected bones from a few nests in 1981, but discontinued this practice to avoid disturbing breeding birds.

Bones, human-made items, rocks and botanical materials were measured and categorised according to Brain (1974) and Voigt (1983). Bones were identified to order, genera or species when possible, otherwise to size class, age class, domestic or wild or unidentifiable fragment (Tables 1 and 2). We noted carnivore and porcupine damage and weathering. Human-made items were grouped by material (e.g. plastic, metal, glass) and colours (Table 3). We classified rocks by colour and type. The botanical material was grouped into sticks, grass/sedges, leaves and seeds.

Items were weighed to 0.1g and the longest dimension measured to the nearest millimetre. Statistical analyses were conducted on length rather than weights, as bone weights change depending on their treatment (e.g. boiled and scrubbed — Mundy and Ledger, 1976, length measured from photographs of bones — Richardson *et al.* 1986). We compared our mammal bones with similar material from other researchers' work. For statistical analysis we followed the method of Richardson (1980) and Richardson *et al.* (1986), grouping ungulate carcasses as <100kg (classes Bov I, Bov II — Brain 1974) and >100kg (classes Bov III, Bov IV). Richardson (1980, p 105) indicates: 'hyaenas consumed or removed over 90% of all bones in the lower two weight classes'. Bones of ungulates <100kg, are therefore not regularly available to vultures in areas where hyaenas are present. We have identified specific bones, but when referring to related groups have used the categories of Richardson *et al.* (1986). We also include a ribs category, but have excluded hoof sheaths, in small bones, as they are not bony material. Plug (1978) defines 'long bone flakes' (LBF) as fragments of the most dense (cortical) bone of the skeleton, mostly of the long limb bones. These have a relatively high calcium content and may be of particular importance to vultures. We have considered these bones separately from other whole and fragmented long bones. We have conducted statistical analyses on mammal bones only. Hard parts of birds, reptiles and invertebrates represent a small portion of the samples (Tables 1 and 2) and their exclusion from statistical analyses does not effect our conclusions.

Sampling problems

There are inherent problems when sampling materials collected by vultures. The bones of greatest interest are eaten and completely digested and are therefore unavailable to the researcher. Collection of those remaining is biased by the researchers' ability to discover them. Items from the crop are a once-off sample constrained by the birds' age, state of hunger and what was in the nest at the time. What is available in the nest is limited by not only what the parents brought, but also what is knocked off the nest ledge, or ground into the nesting material. Both of these losses also occur in tree-nesting species (e.g. Whitebacked Vulture (*Gyps africanus*), Lappetfaced Vulture (*Torgos tracheliotus*) — PCB pers. obs.) and unless a nest is dismantled, many smaller items go unnoticed. We avoided disturbing nesting birds so our nest samples are limited.

Once bones reach the cliff base, the state of the vegeta-

Table 1: Identifiable bone fragments and faunal hard parts collected from cliff bases, nests and crops/stomachs of dead birds found at the Blouberg and Kransberg Cape Vulture nesting colonies

Species	Blouberg cliff		Blouberg crops		Kransberg cliff		Kransberg crops		Kransberg nests	
	No.	%	No.	%	No.	%	No.	%	No.	%
<i>Panthera pardus</i>	1	0.1	0	—	0	—	0	—	0	—
<i>Canis mesomelas</i>	1	0.1	0	—	0	—	0	—	0	—
Viverridae — Herpestinae	1	0.1	0	—	0	—	0	—	0	—
Carnivore sp. — small	0	—	0	—	0	—	1	0.5	0	—
<i>Equus caballus</i>	6	0.6	0	—	4	0.4	0	—	0	—
<i>Equus asinus</i>	79	7.9	0	—	26	2.4	0	—	0	—
<i>Equus burchelli</i>	9	0.9	0	—	15	1.4	0	—	0	—
<i>Equus sp.</i>	25	2.5	1	11.1	22	2.0	0	—	1	5.6
<i>Sus scrofa</i>	2	0.2	0	—	9	0.8	0	—	0	—
<i>Phacochoerus aethiopicus</i>	4	0.4	0	—	0	—	0	—	0	—
Suidae sp. indet.	2	0.2	0	—	5	0.5	0	—	0	—
<i>Giraffa camelopardalis</i>	1	0.1	0	—	2	0.2	0	—	0	—
<i>Chonnochaetes taurinus</i>	17	1.7	0	—	0	—	0	—	0	—
<i>Alcelaphus buselaphus</i>	5	0.5	0	—	0	—	0	—	0	—
Alcelaphinae sp. indet.	1	0.1	0	—	1	0.1	0	—	0	—
<i>Sylvicapra grimmia</i>	1	0.1	0	—	0	—	0	—	0	—
<i>Raphicerus campestris</i>	2	0.2	0	—	0	—	0	—	0	—
<i>Aepyceros melampus</i>	58	5.8	0	—	34	3.1	5	2.6	0	—
<i>Hippotragus niger</i>	2	0.2	0	—	0	—	0	—	0	—
<i>Hippotragus sp.</i>	2	0.2	0	—	0	—	0	—	0	—
<i>Syncerus caffer</i>	5	0.5	0	—	0	—	0	—	0	—
<i>Tragelaphus strepsiceros</i>	7	0.7	0	—	16	1.4	0	—	0	—
<i>Taurotragus oryx</i>	3	0.3	0	—	1	0.1	0	—	0	—
<i>Bos taurus</i>	342	34.2	0	—	567	51.3	10	5.1	10	55.6
<i>Capra hircus</i>	0	—	0	—	3	0.3	0	—	1	5.6
<i>Ovis aries</i>	0	—	0	—	1	0.1	0	—	0	—
<i>Ovis/Capra</i>	6	0.6	0	—	9	0.8	9	4.6	0	—
Bovidae gen. et sp. indet. (Bov I)	4	0.4	1	11.1	1	0.1	0	—	0	—
Bovidae gen. et sp. indet. (Bov II indet.)	71	7.1	1	11.1	73	6.6	28	14.4	4	22.2
Bovidae gen. et sp. indet. (Bov II non-domestic)	8	0.8	0	—	7	0.6	1	0.5	0	—
Bovidae gen. et sp. indet. (Bov III indet.)	200	20.0	2	22.2	255	23.1	48	24.6	2	11.1
Bovidae gen. et sp. indet. (Bov III non-domestic)	34	3.4	0	—	15	1.4	0	—	0	—
Bovidae gen. et sp. indet. (Bov II/Bov III indet.)	0	—	0	—	0	—	9	4.6	0	—
Bovidae gen. et sp. indet. (Bov ? indet.)	65	6.5	4	44.4	10	0.9	56	28.7	0	—
Bovidae/Equidae gen. et sp. indet. (Bov III/Equid)	7	0.7	0	—	20	1.8	0	—	0	—
<i>Hystrix africaeaustralis</i>	0	—	0	—	1	0.1	0	—	0	—
<i>Struthio camelus</i>	2	0.2	0	—	2	0.2	0	—	0	—
<i>Gyps coprotheres</i>	0	—	0	—	0	—	11	5.6	0	—
<i>Aves sp.</i>	0	—	0	—	0	—	16	8.2	0	—
<i>Varanus sp.</i>	2	0.2	0	—	1	0.1	0	—	0	—
Tortoise	3	0.3	0	—	0	—	0	—	0	—
<i>Clarias gariepinus</i>	0	—	0	—	1	0.1	0	—	0	—
<i>Achatina sp.</i>	13	1.3	0	—	0	—	0	—	0	—
<i>Aspatharia sp.</i>	9	0.9	0	—	4	0.4	0	—	0	—
Unionidae	1	0.1	0	—	0	—	0	—	0	—
<i>Coleoptera sp.</i>	0	—	0	—	0	—	1	0.5	0	—
Total	1 001	100.1	9	99.9	1 105	100.3	195	99.9	18	100.1

tion and the substrate affect their condition and the likelihood of finding them. Deep grass and boulders inhibit visibility and items can fall great distances from the cliff base, increasing the area to be searched. Again, small items are most easily overlooked. Porcupines, *Hystrix africaeaustralis*, gnaw some bones and may carry off or destroy others completely. Cold to hot and dry to sodden conditions at the cliff base affect decomposition of organic materials. It is impossible to determine if bone-weathering occurred at the cliff base or before being collected by the bird. If left long enough, all bones will disintegrate.

Inorganic materials (e.g. rock, glass, porcelain) decompose more slowly than organic materials. Their proportion in the samples is probably not representative of the ratio of such items ingested by vultures. Many pieces of white quartz similar to those found in vulture crops occur at the Kransberg cliff base; however, no stones or sticks are included in the cliff base or nest samples, because it is impossible to recognise if vultures consumed these items. No other large, bone-accumulating raptors (e.g. Bearded Vulture, *Gypaetus barbatus*) that could account for the materials discovered nest on the study cliffs. We recognise

Table 2: Summary of mammalian skeletal and other parts from the cliffbases, crops of dead birds found there and some nests at the Blouberg and Kransberg Cape Vulture colonies

Part	Blouberg cliff		Kransberg cliff		Kransberg nests		Blouberg/Kransberg crops	
	no.	%	no.	%	no.	%	no.	%
Skull	17	1.8	25	2.3	0	—	12	11.8
Mandible	5	0.5	8	0.7	0	—	1	1.0
Teeth	102	10.5	119	11.0	0	—	3	2.9
Hyoid	3	0.3	3	0.3	2	11.8	3	2.9
Vertebrae	78	8.0	86	7.9	1	5.9	2	2.0
Rib	113	11.6	140	12.9	6	35.3	27	26.5
Sternum	1	0.1	2	0.2	0	—	0	—
Scapula	1	0.1	5	0.5	0	—	0	—
Humerus	5	0.5	5	0.5	1	5.9	1	1.0
Radius	3	0.3	2	0.2	0	—	2	2.0
Ulna	5	0.5	2	0.2	0	—	1	1.0
Pelvis	3	0.3	8	0.7	1	5.9	1	1.0
Femur	11	1.1	4	0.4	0	—	1	1.0
Tibia	20	2.1	18	1.7	0	—	0	—
Patella	7	0.7	4	0.4	0	—	0	—
Carpals	156	16.1	134	12.4	3	17.6	2	2.0
Metacarpals	9	0.9	6	0.6	0	—	0	—
Tarsals	44	4.5	42	3.9	0	—	2	2.0
Metatarsals	13	1.3	17	1.6	0	—	1	1.0
Phalanx 1	132	13.6	125	11.5	1	5.9	0	—
Phalanx 2	93	9.6	174	16.1	1	5.9	4	3.9
Phalanx 3	29	3.0	42	3.9	1	5.9	0	—
Long bone flakes (LBF)	70	7.2	64	5.9	0	—	1	1.0
Unidentifiable fragments	50	5.2	49	4.5	0	—	38	37.3
Sub-total mammal bones	970		1 084		17		102	
Horn/h hoof sheath	0		11		1		75	
Cartilage	1		0		0		6	
Skin	1		2		1		0	
Facia	0		0		0		3	
Ear	0		1		0		0	
Meat	1		0		0		0	
Feather	0		0		0		19	
Bird bone	0		1		0		7	
Egg shell (bird)	2		1		0		0	
Reptile bone	2		1		0		0	
Carapace (tortoise)	2		0		0		0	
Plastron (tortoise)	1		0		0		0	
Fish bone	0		1		0		0	
Shell fragments (invertebrate)	23		4		0		0	
Carapace (insect)	0		0		0		1	
Excreta	0		0		0		1	
Sub-total miscellaneous parts	33		22		2		112	
Total	1 003		1 106		19		214	

the problems of conducting statistical analyses on these types of data (see James and McCulloch 1985). Our assumption is that all researchers examining this type of material deal with the same problems and their data are therefore comparable. We have used well-known standard statistical tests (Sokal and Rohlf 1981), for analyses of these data.

Results

Bone fragments — cliff samples

Mammal bones (Tables 1 and 2) from the Kransberg cliff base ($\bar{x} = 57.3\text{mm}$, $s^2 = 1\,174.1$, $n = 1\,084$) are statistically longer than those from Blouberg ($\bar{x} = 49.5\text{mm}$, $s^2 = 742.6$, n

$= 970$) (Mann-Whitney $Z = 5.73$, $P < 0.0000$). In the composition of skeletal parts, the samples are similar (Table 2). Small bones make up almost half of both samples and together with ribs and teeth, represent over 70% of both sets. Whole, fragmented and flaked long bones bring the total to over 80% of the samples, and with unidentifiable fragments almost 90% of the bones are accounted for. The proportion of fragmented long bones is identical in both samples (89.5%). The overall proportion of fragmented bones in the samples (Blouberg = 52.5%, Kransberg = 50.6%) is not statistically different ($\chi^2 = 0.614$, $P = 0.433$).

Of identifiable material, the Blouberg sample contained 27.1% wild ungulate bones, the Kransberg sample 13.0% (Table 1). The proportions are statistically different ($\chi^2 =$

Table 3: Colour and number of human-made items and rocks collected from the cliff-bases and crops/stomachs of dead birds found at the Kransberg and Blouberg Cape Vulture colonies

Type	Colour	Kransberg Cliff		Blouberg Cliff		Kransberg/Blouberg Crops	
		No.	%	No.	%	No.	%
Glass	Untinted	310	39.0	59	26.6	63	17.7
	White	214		46		60	
	Blue	64		9		2	
	Brown	3		3		1	
	Green	13		0		0	
	Red	15		1		0	
Porcelain/earthenware	Red	1		0		0	
	White	427	53.7	136	63.1	20	5.6
	Blue	409		134		20	
	Brown	10		1		0	
	Green	2		0		0	
	Red	1		0		0	
	Yellow	2		1		0	
	Multi-coloured	1		0		0	
Metal	Multi-coloured	2		0		0	
	White	20	2.5	6	2.7	3	0.8
	Brass	7		2		0	
	Copper	1		0		0	
Plastic	Silver	0		0		1	
	Untinted	12		3		2	
	White	31	3.9	21	9.5	17	4.8
	Black	0		4		0	
	Blue	23		14		3	
	Brown	1		0		0	
	Green	3		0		1	
	Red	1		0		3	
Asbestos	Yellow	0		1		0	
	Grey	2		2		6	
Cement	Grey	4	0.5	0	-	0	-
	White	4		0		0	
Wood	White	1	0.1	0	-	0	-
	Brown	1		0		0	
Rock	Yellow	2	0.3	0	-	0	-
	Untinted	1		0		0	
	White	-	-	-	-	253	71.1
	Black	-	-	-	-	1	
	Brown	-	-	-	-	110	
	Green	-	-	-	-	7	
	Grey	-	-	-	-	11	
	Red	-	-	-	-	6	
	Tan	-	-	-	-	22	
	Yellow	-	-	-	-	60	
Total		795		222		356	

40.74, $P < 0.0000$). The number of species at the Blouberg was greater with 20 mammals (17 ungulates) versus 13 mammal species (12 ungulate) identified in the Kransberg cliff sample (Table 1). Cattle bones, the most abundant in both, were more prevalent in the Kransberg than the Blouberg sample.

The proportion of bones from animals $< 100\text{kg}$ is greater in the Blouberg (18.4%) than the Kransberg (14.8%) cliff sample ($\chi^2 = 4.31$, $P = 0.038$). Cliff base samples (Table 1) were not statistically different in the proportion of unidenti-

able ungulate fragments ($\chi^2 = 2.08$, $P = 0.149$).

Long bone flakes (LBF) on average were longer than other bones from the nesting cliff bases (Blouberg LBF $\bar{x} = 51.6\text{mm}$, $s^2 = 417.3$; non-flakes $\bar{x} = 49.4\text{mm}$, $s^2 = 768.0$; Mann-Whitney $Z = 2.23$, $P = 0.026$. Kransberg LBF $\bar{x} = 58.9\text{mm}$, $s^2 = 524.4$; non-flakes $\bar{x} = 57.2\text{mm}$, $s^2 = 1215.2$; Mann-Whitney $Z = 2.19$, $P = 0.029$). LBF from the colonies were not statistically different (Mann-Whitney $Z = 1.718$, $P = 0.086$). A single LBF was found in the crop samples. It was longer than average for those fragments.

Few of the bones in the cliff samples were from very old (Blouberg = 3.0%, Kransberg = 4.8%) or very young animals (Blouberg = 5.7%, Kransberg = 3.2%). Even fewer showed definite carnivore damage (Blouberg = 0.7%, Kransberg = 0.6%). Only two bones from the Kransberg cliff sample and none from the Blouberg sample were visibly weathered. Nineteen of the Kransberg and none of the Blouberg cliff bones showed porcupine damage. A small number showed signs of digestion (Blouberg = 4.9%, Kransberg = 5.6%).

Bone fragments — crop samples

The average lengths of bones from Kransberg (\bar{x} = 44.2mm, s^2 = 1 680.5, n = 67) and Blouberg (\bar{x} = 27.9mm, s^2 = 77.0, n = 8) nestling crops were not significantly different (Mann-Whitney Z = 0.240, P = 0.810). The length of those combined samples was not statistically different from Kransberg adult crop bones (adults \bar{x} = 52.7mm, s^2 = 2 198.2, n = 27; nestlings \bar{x} = 42.5mm, s^2 = 1 531.8, n = 75; Mann-Whitney Z = 1.005, P = 0.315). We found no bones in Blouberg adult/sub-adult crops.

Of the bones from the crops, 96.1% were fragmented. They were statistically smaller than the corresponding cliff samples (Blouberg Mann-Whitney Z = 3.17, P = 0.0015; Kransberg \bar{x} = 47.1mm, s^2 = 1 816.1, n = 94, Mann-Whitney Z = 4.89, P < 0.0000).

Long bone fragments and flakes represent 5.9%, small bones and teeth 11.8% and ribs and fragments 26.5% of the crop sample (Table 2). By comparison, small bones and teeth make up over half of the cliff base material and ribs are about half as common as in the crop samples. Unidentifiable

bone fragments make up 37.3% of the crop contents but 5.2% and 4.5% respectively of the Blouberg and Kransberg cliff samples. Skull fragments were the third most common bone (11.8%) from the crops. Though the crop samples are small, the proportions of specific bones are very different from the cliff. Hoof/horn sheaths represented 67.0% of non-bone faunal material and 35.0% of all faunal items from the crops. The average length of hoof/horn sheaths was less but not statistically different from the crop bones (\bar{x} = 32.9mm, s^2 = 238.0, n = 75; Mann-Whitney Z = 0.387, P = 0.698). They were the most common non-bone faunal items in the Kransberg cliff base sample (Table 2).

A statistically larger proportion (χ^2 = 157.3, P = 0.0000) of all ungulate fragments from crops (85.2%) were unidentifiable to domestic or wild origin (Table 2) than those from the cliffs (Blouberg = 38.1%, Kransberg = 35.1%). This is consistent with the high proportion of fragmented bone and the small fragment size from crops as they become less recognisable when broken into smaller pieces. None of the bones from the crop samples showed weathering or porcupine damage.

Bone fragments — nest samples

We collected only 19 items from nests at the Kransberg (Table 1 and Figure 2). Of the 17 bones, six were small bones and six rib fragments (Table 2). The nest items were statistically larger than both cliff base and crop material (\bar{x} = 83.7mm, s^2 = 2 751.3; cliff Mann-Whitney Z = 3.25, P = 0.0012; crop Mann-Whitney Z = 3.647, P = 0.0003). Eleven (64.7%) of the 17 bones were fragmented; 12 were of Bovid

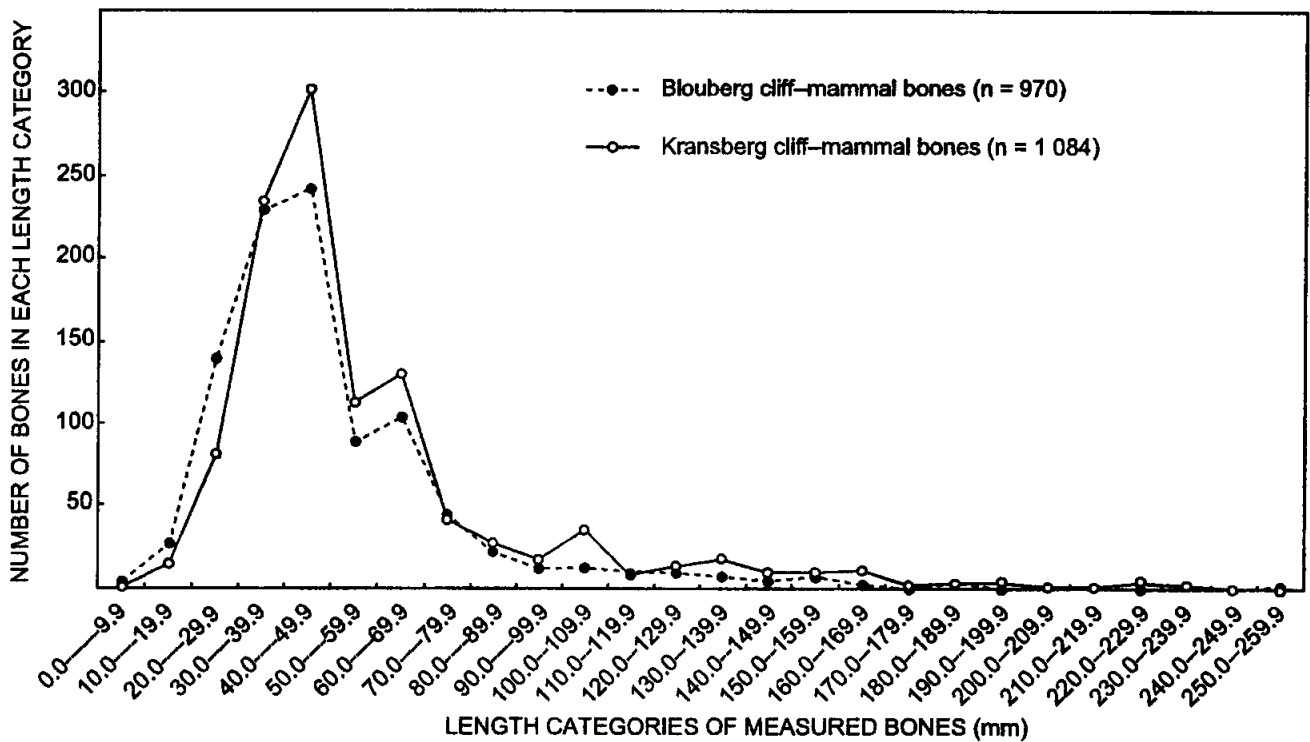


Figure 1: Lengths and number of mammal bones collected from the cliffbases at the Blouberg and Kransberg Cape Vulture colonies

III/Equid size, mainly cow; four bones were Bovid II size and one was an indeterminate bovid. One Bovid III hoof sheath was identified.

Human-made items — cliff and crop samples

Human-made items (Table 3 and Figure 3) from the two cliffs were significantly different in length (Kransberg \bar{x} = 34.7mm, s^2 = 314.2, n = 795; Blouberg \bar{x} = 30.1mm, s^2 = 402.1, n = 222; Mann-Whitney Z = 5.98, P < 0.0000). Items from crop samples (Figure 3) were markedly fewer in number, and more similar in size, than those from the cliff samples (Kransberg \bar{x} = 26.5mm, s^2 = 140.8, n = 91; Blouberg \bar{x} = 31.5mm, s^2 = 76.6, n = 12; Mann-Whitney Z = 1.94, P = 0.052). There was no significant difference in the size of human-made items from the crops of adults (\bar{x} = 23.0mm, s^2 = 151.7, n = 20) and nestlings (\bar{x} = 27.5mm, s^2 = 109.3, n = 83); (Mann-Whitney Z = 1.398, P = 0.162). The Blouberg cliff and crop samples were more similar to each other than were the Kransberg samples (Kransberg Mann-Whitney Z = 5.71, P < 0.0000; Blouberg Mann-Whitney Z = 1.36, P = 0.174). The small crop samples, particularly from Blouberg, may account for the difference.

Over 90% of human-made items from cliff bases and 82.5% from the crop samples were white or untinted (glass) (Table 3). The white to untinted proportions were not significantly different between cliffs (χ^2 = 2.47, P = 0.116), nor between crops (χ^2 = 0.44, P = 0.507). The ratio of untinted to white human-made fragments in the combined cliff and combined crop samples are reversed and statistically very different (χ^2 = 61.51, P < 0.0000).

Rocks — crop samples

The size of rocks from the adult and nestling crops of the Kransberg birds was not significantly different (adults \bar{x} = 17.9mm, s^2 = 102.5, n = 33; nestlings \bar{x} = 20.5mm, s^2 = 105.8, n = 191; Mann-Whitney Z = 1.533, P = 0.125). The Blouberg adult and nestling crop samples were significantly different (adults \bar{x} = 25.2mm, s^2 = 96.2, n = 9; nestlings \bar{x} = 15.4mm, s^2 = 37.0, n = 20; Mann-Whitney Z = 3.144, P = 0.0017). That the samples are small and the nestling stones from only three small birds may account for the difference (Figure 4).

Of the crop stones, 43.5% are white. We classified a single stone untinted, but such rocks are rare. Of the remainder, red was most common (Table 3). The nesting cliffs are reddish quartzite. This probably accounts for the high proportions of white and red rocks in the crop samples. The majority of the crop stones (71.9%) were quartz or quartzite, suggesting that they probably originated from the quartzite cliffs themselves. Only a single stone (calcrete), from the Kransberg sample, was considered as a potential calcium source for the vultures.

Plant material — crop samples

Plant material from birds' crops (Figure 4) consisted mainly of sedges/grasses, seeds, sticks and a few larger leaves. Most seeds were *Acacia* spp. and, along with the grasses, had an uncharacteristic yellow colour, appearing to come from ungulate stomach contents. The sedges, larger leaves and sticks probably came from the nest and/or its surround-

ings. Sticks were much larger than other items. There were no sticks in adult/sub-adult crops. We excluded sedges and grasses from statistical analyses.

The plant items (seeds, sticks, leaves) from Kransberg nestling (\bar{x} = 23.3mm, s^2 = 1 076.0, n = 239) and adult crops (\bar{x} = 6.8mm, s^2 = 163.5, n = 54) were statistically very different (Mann-Whitney Z = 4.602, P = 0.0000). No plant material occurred in Blouberg adult/sub-adult crops. The Blouberg (\bar{x} = 39.0mm, s^2 = 1 447.6, n = 10) and Kransberg nestling samples were not different statistically (Mann-Whitney Z = 1.329, P = 0.184).

The lengths of sticks eaten by nestlings at the two colonies were not statistically different (Mann-Whitney Z = 0.400, P = 0.689, Kransberg \bar{x} = 71.5mm, s^2 = 960.1, n = 59; Blouberg \bar{x} = 72.8mm, s^2 = 400.7, n = 5) nor were the other items (seeds and leaves) (Mann-Whitney Z = 0.303, P = 0.762; Kransberg \bar{x} = 7.5mm, s^2 = 101.3, n = 180; Blouberg \bar{x} = 5.2mm, s^2 = 0.2, n = 5). The lengths of combined stick (\bar{x} = 71.6mm) and non-stick samples (\bar{x} = 7.43mm) were, however, very different (Mann-Whitney Z = 12.414, P = 0).

Discussion

Blouberg and Kransberg Cape Vulture bone collections

The Blouberg and Kransberg cliff base faunal samples (Table 2) are similar, with high proportions of small bones (i.e. carpals, tarsals etc.) and comparable proportions of fragmented long and other bones. More small ungulate bones (Table 1) account for the Blouberg sample's smaller average length. Long bone flakes (LBF) were more common in the Blouberg sample. LBF in both samples were on average larger than other bones and much more common in the cliff base material than in the crops, suggesting they were rejected, rather than preferred items. Wild ungulate farming and wildlife reserves (e.g. Blouberg, Langjan, Tuli Block) are more common near the Blouberg, explaining the greater number of species represented in that sample and larger proportion of wild animal bones.

Extensive cattle farming near Thabazimbi accounts for the higher proportion of those bones in the Kransberg sample than in the Blouberg sample where game farming is more prevalent. In communal areas, where goats and sheep are more common, the local people eat livestock that die of natural causes, if found before scavengers consume them (Blumenshine 1986, PCB pers. obs.), accounting for the relative lack of those bones in the Blouberg sample. Donkeys, *Equus asinus*, a common form of transport in the communal areas, are not eaten by the local people. Donkey bones were three times more prevalent in the Blouberg sample (Table 1).

Though scarce in the Blouberg samples, horn/h hoof sheaths were the most common non-bone faunal material from the Kransberg cliff and crop samples. Hoof sheaths were probably eaten with small bones intact as they are firmly attached and removed with great difficulty. Hoof and horn sheaths are made of keratin, which is resistant to digestive acids (Thibault *et al.* 1993, Robert and Vigne 2002), accounting for their large numbers in the sample.

The largest portion of crop items was unidentifiable bone fragments (Table 2). The smaller size and higher proportion

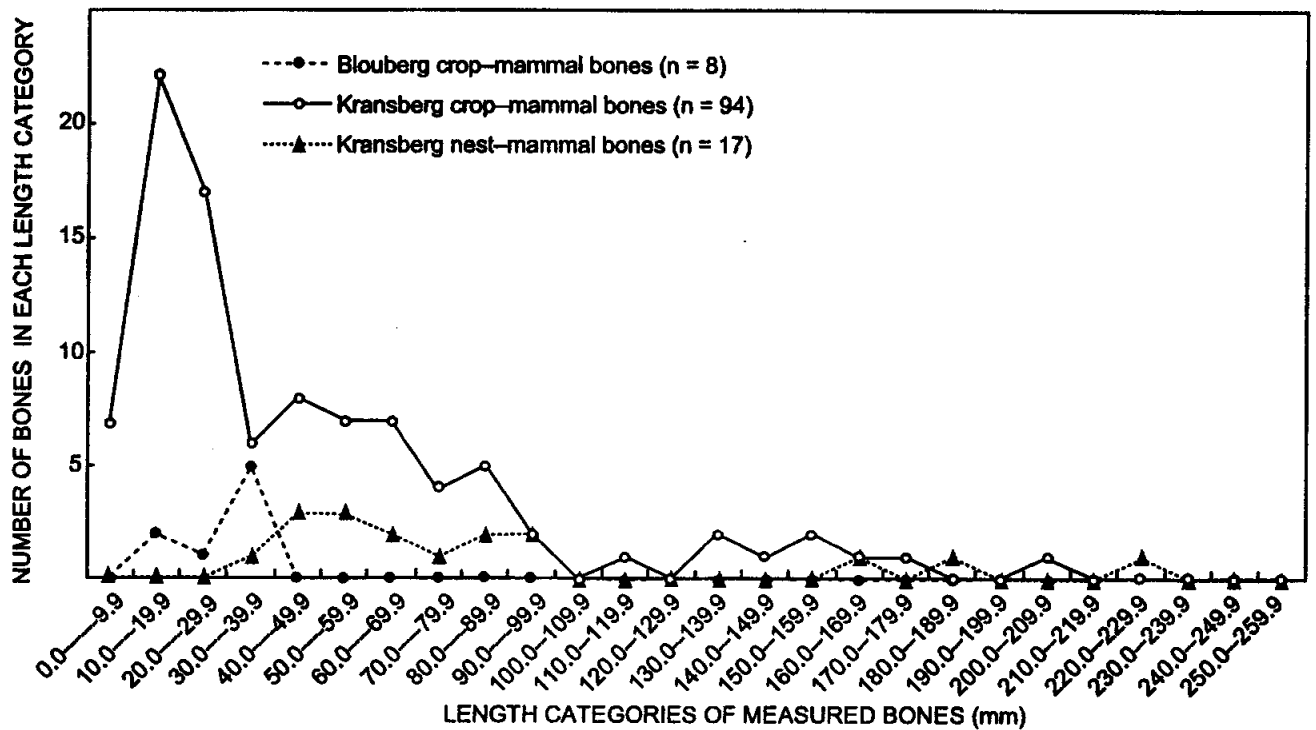


Figure 2: Lengths and number of mammal bones from the crops of birds found at the Blouberg and crops and nests at the Kransberg Cape Vulture colonies

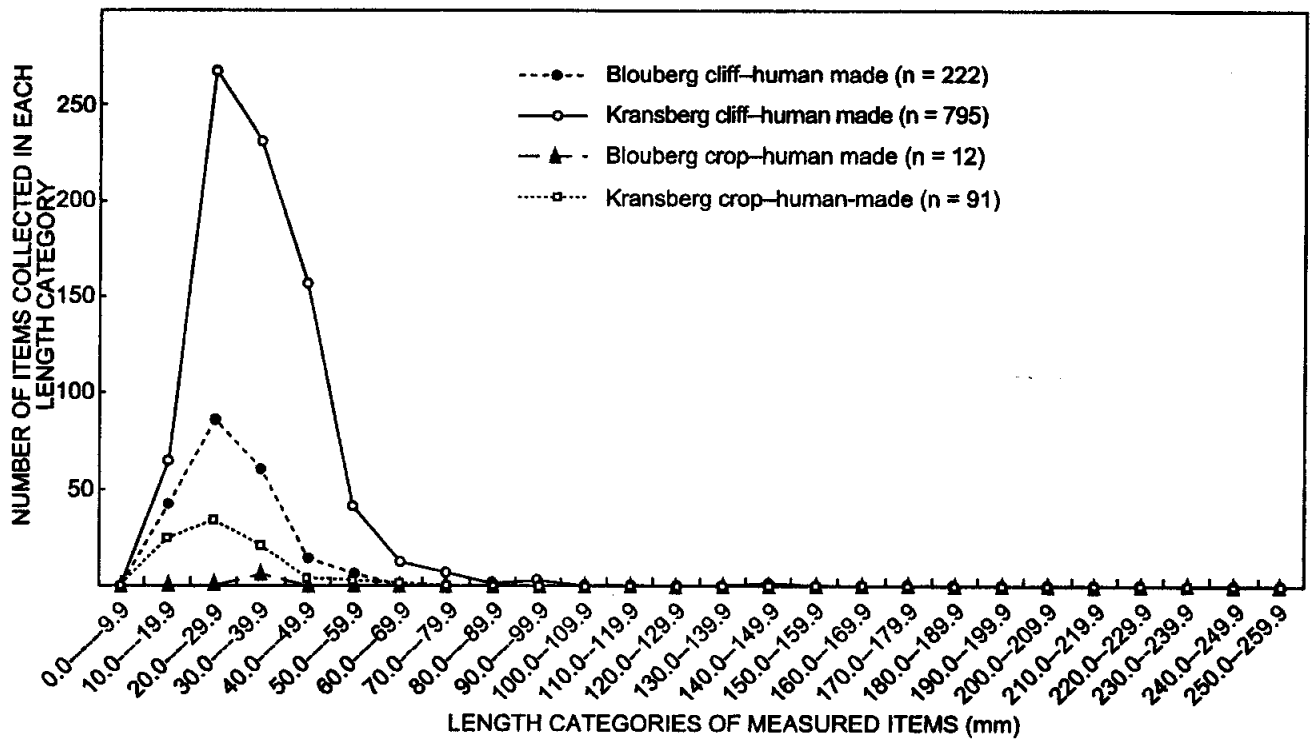


Figure 3: Number and lengths of human-made items collected from the cliffbases of the Blouberg and Kransberg Cape Vulture colonies and crops of dead birds found there

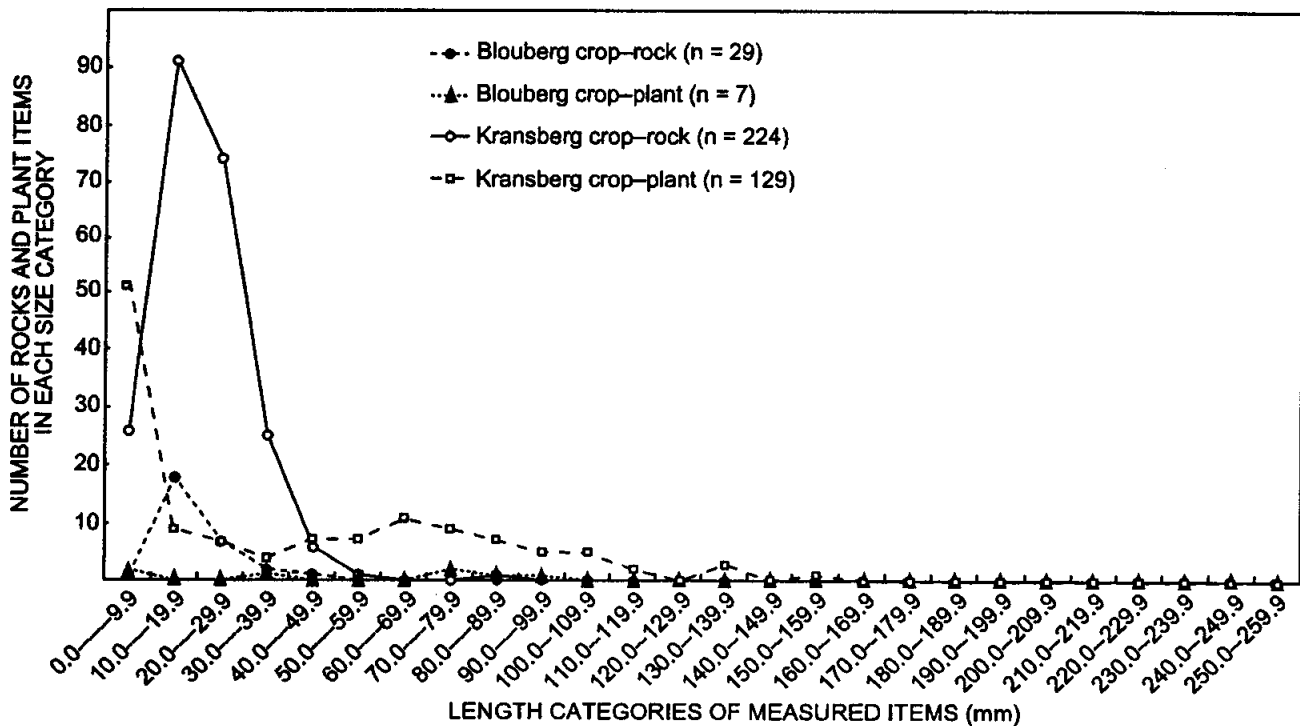


Figure 4: Lengths and number of rocks and plant items found in the crops of dead birds found at the Blouberg and Kransberg Cape Vulture colonies

of fragmented bone from the crops of birds indicates nestlings choose smaller pieces from the bones brought to the nest. Bones from Bearded Vulture, *Gypaetus barbatus*, nests were also smaller than bones from the cliff base (Brown and Plug 1990). This cliff and crop disparity makes us question the validity of using only large cliff base samples to assess what bones nestlings eat. A selection process occurs and some cliff base items are certainly rejected material. Our nest sample is small, but its intermediate proportion of fragmented bone supports this view, though its greater average length does not. The sample may be too small, the nest material may represent a range of bones prior to selection by the nestling, or it may be a biased sample, because larger items are more visible or smaller items more easily eaten or ground into the nesting material. It is interesting that the average length of our nest material is similar to Mundy's (1982) Magaliesberg/Botswana Cape Vulture samples. He collected more nest material than we did, probably accounting for those samples' greater average length.

Mammal bones from the Blouberg cliff base are statistically smaller than those Mundy (1982) collected from Whitebacked Vulture nests in Rhodesian (Zimbabwean) nature reserves ($t = 5.37$, $P < 0.0001$), the collection with the smallest average length of any *Gyps* vultures he studied. There is no statistical difference between the Kransberg cliff sample and the Zimbabwean sample ($t = 0.817$, $P > 0.25$) or his Manutsa (Limpopo Province, South Africa) 'wild area' Cape Vulture sample ($t = 0.86$, $P > 0.20$). The Kransberg sample is significantly smaller than his 'farming area' samples of the Magaliesberg/Botswana Cape

Vulture colonies ($t = 10.04$, $P < 0.000$) and Kimberley (Dronfield) Whitebacked Vultures ($t = 2.18$, $P < 0.05$). The Blouberg and Kransberg birds collected large numbers of small bones, accounting for differences between our and Mundy's (1982) collections (0.9–26.8%).

As with Richardson *et al.*'s (1986) material, the majority of our cliff sample bones are less than 90mm (Figure 1). The Blouberg and Kransberg overall fragmentation rates are between their lowest rates (Dronfield and Magaliesberg) and the long bone fragmentation rates within the upper range of their Cape Vulture material. Richardson *et al.*'s (1986) Dronfield sample, with the smallest average length, had a lower proportion of small bones (30%+) but a much higher proportion of bones from smaller ungulates (92%) than our cliff base samples.

Richardson *et al.* (1986) collected more material from Cape Vulture nests than we did. They combined cliff base, nest and crop samples, most coming from cliff bases. Their proportions of fragmented bone are intermediate between our cliff base and crop samples. We believe the cliff base material masks the influence of the crop and nest samples. The similarity of the proportions of fragmented bones to our cliff base samples supports this view.

Bone collecting — the birds' size difference

Natural differences in *Gyps* vultures' size, distribution, foraging behaviour, habitat use and inter/intraspecific interactions affect their use of food/bone resources. A bird's size affects the spectrum of items it can collect and eat, varying with species and age. The Whitebacked Vulture's stomach length

(16cm — Houston and Cooper 1975), suggests Mundy's (1982) estimated maximum length (140mm) of bones consumable by the larger Cape Vulture is conservative. From vulture carcasses, we collected some partially digested bones, longer than the stomach. Most bones analysed by Mundy and others (Richardson *et al.* 1986) were well within the usable range for Whitebacked and Cape Vultures, but for bone length, Richardson *et al.*'s (1986) Whitebacked Vulture samples were more similar to each other, as were their Cape Vulture samples, suggesting each species selects different size bones whether in wild or farming areas.

Bone size — small vs broken

Mundy and Ledger (1976) proposed that vultures are dependent on large mammalian carnivores to provide 'suitable bone pieces' (i.e. long bone flakes (LBF)). At Dronfield, where sheep and springbok are farmed extensively and large carnivores are rare or absent, Whitebacked Vultures collected smaller bones than in Zimbabwean reserves, where large carnivores are more abundant (Plug 1978, Richardson *et al.* 1986). Dronfield and Zimbabwean samples had respectively: 1) the lowest and highest proportions of fragmented bones, 2) highest and second highest proportions of small ungulate bones and 3) smallest and second smallest average lengths. Though Mundy (1982) found proportionally more carnivore-produced LBF in bones collected by Whitebacked Vultures in Zimbabwean wildlife reserves than elsewhere, the majority of that sample were not LBF, did not show carnivore damage and were on average smaller than the LBF.

The particular bone collected also affects average length. From impala, *Aepyceros melampus*, carcasses, partially consumed by spotted hyaenas, over 70% of the larger bones survived, while 'few of the ribs and smaller bones remained' (Richardson *et al.* 1986, p 29). The remaining bones were statistically larger and of a different type than those collected by *Gyps* vultures. Vultures most commonly collected small bones (i.e. carpals, phalanges tarsals, etc.) and ribs at Dronfield (Plug 1978, Richardson *et al.* 1986), from carcasses untouched by mammalian carnivores, suggesting hyaenas compete for rather than provide *Gyps* vultures with bones. As we found, Mundy's (1982) and Richardson *et al.*'s (1986) data indicate that the size of the animal of origin, and the particular bone collected, are more important than fragmentation in determining the bone size used by vultures. Large mammalian carnivores are relatively unimportant in that determination, although that was not those authors' conclusion.

Large carnivore–ungulate–vulture interactions in different environments

The abundance of LBF will vary with large carnivore densities. Large carnivore densities vary with the prey population size and its sedentary or migratory nature (Kruuk 1972, Schaller 1972). In east and southern Africa, in well watered areas, both natural and human-created (e.g. Ngorongoro Crater and Kruger National Park), ungulate numbers are higher and more sedentary, large carnivore densities higher and predation pressures greater than in drier habitats (e.g. Serengeti and Kgalagadi Trans-frontier Park) dependent on

seasonal rains (Plenaar 1970, Kruuk 1972, Smuts 1976, 1978, Mills 1984, 1990). In dryer areas, resident ungulate populations are smaller. There, migratory ungulates provide a temporary flush of food for mammalian carnivores, but as grazing conditions deteriorate these animals move on and the territorial predators' numbers are again limited by the smaller resident herds. Predation has more influence on resident ungulates than on migratory herds, which die more regularly by non-violent means (Kruuk 1972, Schaller 1972, Smuts 1976, 1979, Bearder 1977, Mills 1984, 1990).

Large ungulate herds moved over southern Africa in nomadic or migratory patterns, influenced by pasture condition and water availability (Cronwright-Schreiner 1925, Sidney 1965, Du Plessis 1969, Liversidge 1978, Smithers 1983, Owen-Smith and Cumming 1993). The Serengeti is a good model for southern African conditions prior to the Europeans' arrival (Houston 1974, 1975, 1983). There, where at least two-thirds of migratory ungulates die non-violently, Whitebacked and Rüppell's Vultures, *Gyps rueppellii*, feed primarily on carcasses that die from causes other than predation (Schaller 1972, Houston 1974, 1975, 1983). The vultures' ability to forage over great distances within a single day accords an advantage over the less mobile, territorial mammalian scavengers (Kruuk 1972, Pennycuik 1972, Schaller 1972, Houston 1974, 1983). 'Their advantage is that they find carcasses that the mammalian scavengers often never reach at all' (Houston 1983, p 143). Mammalian carnivores failed to find 84% of carcasses ($n = 64$) Houston (1974) watched from arrival of the first vultures until all available food was consumed. Only 27% of carcasses ($n = 870$), where Houston (1983) observed vultures feeding, were predator kills. Less than 5% of the food available to Serengeti vultures is from animals killed by predators. Disease, starvation and accidental death are greater limiting factors than predation on Africa's migratory herds (Talbot and Talbot 1963, Hirst 1969, Kruuk 1972, Schaller 1972, Bearder 1977, Mills 1990, De Vos 1994, PCB pers. obs.). We believe southern African *Gyps* vultures are no more dependent on carnivores for food than those of east Africa.

Habitat partitioning

Closely related raptors reduce competition by using separate food supplies, or the same resource discretely (Lack 1946). Southern Africa's Whitebacked and Cape Vultures' relationship is similar to the Serengeti vultures, the smaller bird occupying the low altitude savanna, the larger the highlands (Houston 1975, 1983, Maclean 1993). Whitebacked Vultures exploit a wider range of food sources because they can successfully forage under energetically more expensive conditions (e.g. overcast days) than larger *Gyps* vultures (Pennycuik 1972, Houston 1975). Serengeti *Gyps* species are not equally dependent on migratory ungulates, foraging differentially over migratory herds and sedentary ungulates, resident in woodlands (Houston, 1975, 1983). Whitebacked Vultures use non-migratory ungulates more than Rüppell's Vultures. Large mammalian carnivores depend most on these sedentary ungulates and the potential for their interaction with Whitebacked Vultures is greater than for the larger *Gyps* vultures (Kruuk 1972, Schaller 1972, Houston 1983). Under pristine conditions, habitat partitioning will account for

foraging behaviour differences, species encountered and bones available, and Whitebacked Vultures, feeding on resident ungulates, will collect more carnivore-produced bone fragments than the larger *Gyps* vultures. If both use migratory ungulates, the proportions should be more similar.

However, fencing, artificial water points and culling can change an ungulate population from migratory/nomadic to sedentary and large carnivore numbers can increase (Pienaar 1970, Smuts 1976, 1978, Whyte and Joubert 1988, P Funston pers. comm.). Under such conditions, vulture-large carnivore interactions at carcasses will increase and *Gyps* vultures will encounter greater numbers of carnivore-produced bone fragments. It is unlikely ungulate-carnivore-vulture interactions were ever identical in the xeric Kalahari thornveld of Dronfield and the *Brachystegia boehmii* woodland of Zimbabwe's Chizarira Wildlife Reserve, studied by others (e.g. Mundy 1982, Richardson *et al.* 1986), where natural water supplies are 'well distributed throughout the Reserve' (Thomson 1975, p 11) and extensive management activities occur (Sherry 1975, Anthony 1976, Guy 1981). We believe Richardson *et al.*'s (1986) Dronfield sample (i.e. low bone fragmentation rate, high numbers of small bones and bones from small animals) more closely resembles what *Gyps* vultures would collect under pristine conditions feeding on migratory ungulates that die non-violently in the drier highveld, bushveld, Karoo and Kalahari thornveld of southern Africa.

Competition for bone

When vultures and large mammalian carnivores do interact, their behaviour makes the predators a poor provider of food for the birds. Lions and hyaenas compete for food with vultures (Kruuk 1967, 1972, Schaller 1972). Lions steal from vultures (Kruuk 1972) and guard their kills aggressively, even killing intruding birds (Schaller 1972). Leopards, *Panthera pardus*, drag carcasses into trees, making it difficult for vultures to use them (Kruuk and Turner 1967, Hirst 1969, Pienaar 1969, Schaller 1972, Bearder 1977). Cheetah, *Acinonyx jubatus*, may leave some food (Schaller 1968), and vultures do follow wild dogs, *Lycan pictus*, (MGL Mills pers. comm.), but both animals are rare and provide little for the birds.

At best, hyaenas are an erratic bone source, providing little food for vultures because they: 1) often rapidly consume an entire carcass, including the bones, 2) carry off pieces of large carcasses to avoid losing them to lions, scattering any possible remains, 3) hunt/feed mainly at night, when vultures are inactive and unable to observe them, 4) steal carcasses from vultures, and 5) defend their kills from vultures by snapping at or grabbing them (Hirst 1969, Pienaar 1969, Kruuk 1972, Schaller 1972, Houston 1974, Bearder 1977, Skinner *et al.* 1986, Mills 1990, H Kruuk *in litt.*, PCB pers. obs.). In the Serengeti and Ngorongoro Crater, Kruuk (1972) found little bone remained in areas of high spotted hyaena density but in low-density areas whole skeletons remained untouched. A similar situation exists in South Africa's lowveld (Bearder 1977) and where hyaenas are present; skeletons of small/medium-sized ungulates may disappear completely (Richardson 1980).

Other birds also compete for bone. Brown and Plug

(1990) found both predatory raptors and corvids fed on bone placed out to determine scavenging birds' carrion preferences. Lappetfaced and Whiteheaded Vultures, *Trigonoceps occipitalis*, in wildlife reserves, collect high proportions of small bones and bones from smaller animals (Pennycuik 1976, Plug 1978, Mundy 1982). Both birds have a wide gape similar to the bone-eating Bearded Vulture, facilitating the swallowing of large items, and Lappetfaced Vultures collect whole articulating limb sets, removing small bones from the veld (Kruuk 1967, Pennycuik 1976, König 1983, Brown 1988, Brown and Plug 1990, Houston and Copsey 1994). Both species often dominate *Gyps* vultures at carcasses (Petrides 1959, Attwell 1963, Kruuk 1967, Richardson 1984).

Richardson *et al.* (1986, p 41) state: 'in wildlife reserves bones are unlikely to be in short supply, and certainly not so as to produce the intraspecific competition among the vultures that occurs over meat'. Though intraspecific competition for bone may not exist in nature reserves, we believe interspecific competition induces the lower rate and different type of bone collected by *Gyps* vultures there. Richardson *et al.* (1986) found both *Gyps* species collected more bones in ranching than in wild areas, and Mundy *et al.* (1992) indicate, when collecting bone fragments, adult Cape Vultures 'greatly exceed' the minimum rate necessary for normal skeletal development of nestlings. Mundy and Ledger (1976) suggest Cape Vultures take small bones, ribs and teeth in farming areas because large carnivores are not present to break up other bones, but the selection of these items probably represents reduced competition where Lappetfaced Vultures, Whiteheaded Vultures and spotted hyaenas are absent or rare.

Bone as food

Food limits the number of birds and breeding success at some Cape Vulture colonies (Benson *et al.* 1990, Benson 1998, 2000, Vernon 1999). Barton and Houston (1993, p 363) state: 'For generalist feeders and those species feeding on a spatially and temporally unpredictable food supply efficient digestion of a wide range of food types including poor quality foods would be adaptive'. Bone-eating birds gain more than just calcium. Bone is high in energy and protein and if used as food is almost as good as meat (Brown and Plug 1990, Barton and Houston 1994).

'Collagen is the most abundant protein in metazoan animals. This is due largely to its occurrence as the principal constituent of bones' (Miller 1984, p 455). The Bearded Vulture's predominantly bone diet contains 15% more energy than the equivalent mass of meat (Brown and Plug 1990), and even with a lower digestive efficiency, is almost as valuable energetically (Barton and Houston 1994). Though limited by the size of fragments it can consume (Brown and Plug 1990), a *Gyps* vulture's digestive system is suited to bone eating. Raptor small intestine length influences digestive efficiency, independent of body size (Barton and Houston 1993). Soaring scavengers and those catching slow-moving prey have longer intestines and digest more efficiently than fast-flying raptors. The similar-sized Bearded and Whitebacked Vultures have comparable small intestine length (Whitebacked Vulture average = 190cm, n = 3,

Houston and Cooper 1975; Bearded Vulture 184cm and 185cm, $n = 2$, Houston and Copsey 1994). Raptor digestive efficiency normally ranges from 75–85% (Duke *et al.* 1975, Castro *et al.* 1989, Barton and Houston 1993). Rüppell's Vultures fed meat had a higher digestive efficiency ($91.3 \pm 2.7\%$, $n = 7$), similar to spotted hyaenas ($90.2 \pm 0.83\%$, $n = 7$, Houston 1988).

Low stomach pH accounts for bone corrosion in raptors (Duke *et al.* 1975, Houston and Copsey 1994). Whitebacked Vulture stomach pH is 1, similar to other Falconiformes (Houston and Cooper 1975). *Gyps* vultures do eat bone and are probably quite efficient at it. Similar more extreme shifts of diet occur in Black Vultures, *Coragyps atratus*, and Turkey Vultures, *Cathartes aura*, that feed on coconut and palm nuts where carrion is scarce (Haverschmidt 1947, Crafts 1968, Elias and Valencia 1982). The vultures' ability to use bone can easily be tested with captive feeding trials.

We suggest vultures collect more alternative foods (e.g. bone) when meat is limited. Bone-eating has its greatest benefit at times and in environments where other protein and energy sources are scarce. That southern African *Gyps* vultures collect bone at higher rates in farming areas than in wildlife reserves (Richardson *et al.* 1986) supports this view. In the Serengeti, where food is relatively abundant, Houston (1973) did not observe *Gyps* vultures eating bone. It must have occurred, but perhaps less than in southern Africa.

Non-faunal items

The contrast of light-coloured bone fragments, rocks and human-made items against dark ground or nesting material will enhance their collection by birds. California Condors, *Gymnogyps californianus* (Koford 1953), and Wrynecks, *Jynx torquilla* (Terhivuo 1983), favour white objects in their collecting, and many of the articles on stone-eating reviewed by Baker (1956) report preference for white rocks. Rocks were the most common objects in vulture crops at Blouberg and Kransberg. The low proportion of white rocks in the sample, when white quartz is common on and around the nesting cliff and the selection of other non-white materials, makes us question the view that birds choose white items because there is a paucity of suitable bone (e.g. Mundy and Ledger 1976, Mundy 1982). Most southern African vulture species have been observed eating stones, or stones have been recovered from their nests (i.e. Cape Vulture, Whitebacked Vulture, Lappetfaced Vulture, Hooded Vulture (*Necrosyrtes monachus*) — Plug 1978, Mundy 1982, Dobbs and Benson 1984a, PCB pers. obs.). Many of these stones do not resemble bone.

Visibility of white ceramic fragments partially accounts for the high proportion collected by Kransberg and Blouberg vultures, but white ceramic is more common and probably broken and discarded more regularly. The proportions of various colours of ceramic and rocks collected make us believe this is true. Based on availability alone, one might expect more glass than ceramic in the samples. The transparency of untinted, clear glass makes it difficult to see when collecting at the cliff base, researcher insensitivity probably accounting for its lower representation in those samples. Its greater abundance in birds' crops supports this view. The small size of china and glass fragments is partially a result

of the size of the original items (Plug 1978) and the brittleness of the material.

The frequency of confusion of one item for another will change with the relative abundance of each in the environment. Richardson *et al.* (1986) found more human-made items in vulture nests in areas with high human densities, their incidence declining in areas with lower human numbers. Wrynecks collected more litter near human settlements (Terhivuo 1983). The type of gizzard stones of Southern Skuas, *Catharacta skua*, at Macquarie Island, changed to pumice, washed onto the island's shores, subsequent to a submarine volcanic eruption near the South Sandwich Islands (Simpson 1965). Pumice in the Skua diet did not represent a decrease in abundance of other stones, but an increase in the volcanic material present. Buttons found in Southern Bald Ibis, *Geronticus calvus*, nests and below the nesting cliffs fit the 'search image' for beetles, and were accidentally substituted for the insect, one of the birds' main food items (Milstein 1973, 1974, Kopij 2001).

Eating of non-food items is documented in many extant and extinct orders and attributed to many reasons (Baker 1956, Miller 1962, Raath 1974, Taylor 1993). Birds are the group most regularly observed feeding on non-food items (Siegfried and Grindley 1967, Brooke and Grobler 1973, Milstein 1973, 1974, Rothstein 1973, Fox 1976, Dolensek and Bruning 1978, Below 1979, Albuquerque 1982, Terhivuo 1983, Billet 1984, Ryan 1986). Baker (1956) discusses six reasons why animals eat stones: 1) ballast, 2) accidental, 3) swallowed with food attached, 4) already in the food swallowed, 5) gastric 'chewing gum', to prevent atrophy of stomach muscles during fasting, and 6) trituration of food. Stones may be a calcium source in areas with calcareous rocks (Mendelssohn and Leshem 1983). Falconers feed their birds stones (rangle) to scour out loose fatty material from the crop and stomach (Latham 1615, Blaine 1936, Cade 1982). Substance coated stones eaten and regurgitated by wild falcons (Fox 1976, Albuquerque 1982) and those used by Southern Skuas (Simpson 1965), lending credence to the falconers' practice. Birds feeding on a wide range of foods use grit for trituration (Gionfriddo and Best 1996) and coyotes, *Canis latrans*, use plant material as filler when hungry. Stone-eating by birds and reptiles may serve the same purpose (Miller 1962).

Boredom in captive raptors can lead to feeding on cage litter (Halliwell *et al.* 1973). When feeding was delayed, young captive Cape Vultures began eating plastic and wood in their enclosure (PCB and JCD pers. obs.). When inclement weather prevented Kransberg adult vultures from foraging for two to three days their young ate nesting material, resulting in impacted crops (Dobbs and Benson 1984a). Eating of nest material occurs at other colonies (Mundy and Ledger 1976, Mundy 1982). Extreme hunger may cause young vultures to feed on nesting material, but slight hunger may be necessary to provide the impetus for nestlings to feed on bone chips. A captive European Griffon Vulture, *Gyps fulvus*, nestling refused to eat bone fragments after consuming meat (Heinroth and Heinroth 1926) and the same was true for our captive Cape Vulture nestlings. Collecting of large amounts of bone and non-food items are not mutually exclusive behaviours. Nests at the

Colleywobbles Cape Vulture colony contained more bones and human-made items than other colonies surveyed by Mundy (1983).

Explaining the collection of non-food items by vultures as the result of a lack of suitable bone fragments, due to a decline in large mammalian carnivores, is simplistic. That vultures confuse porcelain chips for bone fragments is probable. The high proportion of non-food items collected, not resembling bone, suggests the birds are seeking something else. We believe it is food generally, and high bone-collecting rates by vultures in farming areas represents an increased use of an alternative food source when meat is limited. The collection of human-made items is part of this shift, albeit misguided, rather than merely bone substitution.

Conclusions

The size of the animal of origin, the particular skeletal element collected and its fragmentation are the factors affecting the size of bones collected by the Kransberg and Blouberg Cape Vultures. The Blouberg vultures collected more bones from smaller ungulates, accounting for that collection's smaller average length. The higher proportion of fragmented bones in the samples from adult/sub-adult and nestling crops explains their smaller average lengths, compared to the cliff base collections.

Higher proportions of bones from smaller animals and smaller skeletal elements in our collections account for their smaller average lengths, compared to material collected elsewhere. Differences in other researchers' collections showed a similar pattern. These factors, rather than the fragmentation rate, are more important in determining the size of bones vultures collect. Carnivore-produced long bone flakes were, on average, longer than the other bones vultures collected, indicating vultures are not dependent on mammalian carnivores for suitably-sized bone fragments. Large mammalian carnivores and other raptors, particularly large vulture species, compete with *Gyps* vultures for food/bone. Where these competitors are absent or rare, *Gyps* vultures have greater access to smaller bones and bones from smaller ungulates. Because less food is available in farming areas, vultures collect more bone as an alternate food source, which is energetically and nutritionally almost as valuable as meat. The collection of non-faunal items is probably part of this shift in food types, where meat is scarce; however, other factors probably also influence the use of these materials (e.g. trituration, rangle).

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References

- Albuquerque JLB 1982. Observations on the use of rangle by the Peregrine Falcon (*Falco peregrinus tundrius*) wintering in southern Brazil. *Raptor Research* 16: 91–92
- Anonymous 1986. Bonecrushers lend support to young vultures. *New Scientist* 112(1534): 30
- Anthony AJ 1976. The Breeding Biology of the Lappet-faced Vulture *Torgos tracheliotus* (Forster) in the Gonarezhou National Park Rhodesia. Certificate of Field Ecology thesis, University of Rhodesia, southern Rhodesia
- Attwell RIG 1963. Some observations on feeding habits, behaviour and inter-relationships of Northern Rhodesian vultures. *Ostrich* 34: 235–247
- Baker AA 1956. The swallowing of stones by animals. *Victoria Naturalist* 73: 82–95
- Barton NWH and Houston DC 1993. A comparison of digestive efficiency in birds of prey. *Ibis* 135: 363–371
- Barton NWH and Houston DC 1994. Morphological adaptation of the digestive tract in relation to feeding ecology of raptors. *Journal of Zoology, London* 232: 133–150
- Bearder SK 1977. Feeding habits of spotted hyaenas in a woodland habitat. *East African Wildlife Journal* 15: 263–280
- Below TH 1979. First reports of pellet ejection in 11 species. *Wilson Bulletin* 91: 626–628
- Benson PC 1998. Status of vultures in the Northern Province, South Africa. In: Boshoff AF, Anderson MD and Borello WD (eds) *Vultures in the 21st Century: Proceedings of a Workshop on Vulture Research and Conservation in Southern Africa*. pp 21–29. Vulture Study Group, Johannesburg
- Benson PC 2000. Causes of Cape Vulture mortality at the Kransberg colony: a 17 year update. In: Chancellor RD and Meyburg B-U (eds) *Raptors at Risk*. pp 77–86. World Working Group on Birds of Prey and Owls. Hancock House, Blaine, Washington, USA
- Benson PC, Tarboton WR, Allan DG and Dobbs JC 1990. The breeding status of the Cape Vulture in the Transvaal during 1980–1985. *Ostrich* 61: 134–142
- Billet R 1984. Ostrich feedlotting. *Farmers Weekly* 74028: 7–9
- Blaine G 1936. *Falconry*. Neville Spearman, London
- Blumenshine RJ 1986. Early Hominid Scavenging Opportunities. *BAR International Series* 283, Oxford
- Boshoff AF and Currie MH 1981. Notes on the Cape Vulture colony at Potberg, Bredasdorp. *Ostrich* 52: 1–8
- Boshoff AF and Vernon CJ 1980. The past and present distribution and status of the Cape Vulture in the Cape Province. *Ostrich* 51: 230–250
- Brain CK 1974. Some suggested procedures in the analysis of bone accumulations from southern African Quaternary sites. *Annals of the Transvaal Museum* 29: 1–8
- Brooke RK and Grobler JH 1973. Notes on the foraging, food and

- relationships of *Corvus albus* (Aves: Corvidae). *Arnoldia* 6(10): 1–13
- Brown CJ 1988. A Study of the Bearded Vulture *Gypaetus barbatus* in Southern Africa. PhD thesis, University of Natal, Pietermaritzburg, South Africa
- Brown CJ and Plug I 1990. Food choice and diet of the Bearded Vulture *Gypaetus barbatus* in southern Africa. *South African Journal of Zoology* 25: 169–177
- Butchart D 1988. Give a bird a bone. *African Wildlife* 42: 316–322
- Cade TJ 1982. *The Falcons of the World*. Collins, London
- Castro G, Stoyan N and Myers JP 1989. Assimilation efficiency in birds: a function of taxon or food type? *Comparative Biochemical Physiology* 92A: 271–278
- Crafts RC Jr. 1968. Turkey Vultures found to feed on coconut. *Wilson Bulletin* 80: 327–328
- Cronwright-Schreiner SC 1925. *The Migratory Springbuck of South Africa*. T Fisher Unwin Ltd, London
- De Vos V 1994. Anthrax. In: Coetzer JAW, Thomson GR and Tustin RC (eds) *Infectious Diseases of Livestock with Special Reference to Southern Africa*, Vol. 2. pp 1262–1289. Oxford University Press, Cape Town
- Dobbs JC and Benson PC 1984a. Behavioural and metabolic responses to food deprivation in the Cape Vulture. In: Mendelsohn JM and Sapsford CW (eds) *Proceedings of the 2nd Symposium on African Predatory Birds*. pp 211–214. Natal Bird Club, Durban
- Dobbs JC and Benson PC 1984b. Calcium requirements and bone abnormalities in the Cape Vulture. In: Mendelsohn JM and Sapsford CW (eds) *Proceedings of the 2nd Symposium on African Predatory Birds*. pp 219–228. Natal Bird Club, Durban
- Dolensek E and Bruning D 1978. Ratites (Struthioniformes, Rheiformes and Casuariiformes). In: Fowler ME (ed) *Zoo and Wild Animal Medicine*. pp 165–180. WB Saunders Co., Philadelphia
- Duke GE, Jegers AA, Loff G and Evanson OA 1975. Gastric digestion in some raptors. *Comparative Biochemical Physiology* 50A: 649–656
- Du Plessis SF 1969. The Past and Present Geographical Distribution of the Perissodactyla and Artiodactyla in Southern Africa. MSc thesis, University of Pretoria, Pretoria, South Africa
- Elias DJ and Valencia D 1982. Unusual feeding behavior by a population of Black Vultures. *Wilson Bulletin* 94: 214
- Fox N 1976. Rangle. *Raptor Research* 10(2): 61–64
- Gionfriddo JP and Best LB 1996. Grit-use patterns in North American birds: the influence of diet, body size, and gender. *Wilson Bulletin* 108: 685–696
- Grubb RB 1973. Calcium intake in vultures of the genus *Gyps*. *Journal of the Bombay Natural History Society* 70: 199–200
- Guy PR 1981. Changes in biomass and productivity of woodlands in the Sengwa Wildlife Research Area, Zimbabwe. *Journal of Applied Ecology* 18: 507–519
- Halliwell WH, Graham DL and Ward FP 1973. Nutritional diseases in birds of prey. *Journal of Zoo Animal Medicine* 4(3): 18–20
- Haverschmidt F 1947. The Black Vulture and the Caracara as vegetarians. *Condor* 49: 210
- Heinroth O and Heinroth M 1926. *Die Vogel Mitteleuropas II*. Hugo Bermühler Verlag, Berlin
- Hirst SM 1969. Predation as a regulating factor of wild ungulate populations in a Transvaal lowveld nature reserve. *Zoologica Africa* 4: 199–230
- Houston DC 1973. *The Ecology of Serengeti Vultures*. PhD thesis, Oxford University, United Kingdom.
- Houston DC 1974. The role of griffon vultures *Gyps africanus* and *Gyps rueppellii* as scavengers. *Journal of the Zoological Society, London* 172: 35–46
- Houston DC 1975. Ecological isolation of African scavenging birds. *Ardea* 63: 55–64
- Houston DC 1983. The adaptive radiation of the griffon vultures. In: Wilbur SR and Jackson JA (eds) *Vulture Biology and Management*. pp 135–152. University of California Press, Berkeley
- Houston DC 1988. Digestive efficiency and hunting behaviour in cats, dogs and vultures. *Journal of the Zoological Society, London*, 216: 603–605
- Houston DC and Cooper JE 1975. The digestive tract of the Whiteback Griffon Vulture and its role in disease transmission among wild ungulates. *Journal of Wildlife Disease* 11: 306–313
- Houston DC and Copsay JA 1994. Bone digestion and intestinal morphology of the Bearded Vulture. *Journal of Raptor Research* 28: 73–78.
- James FC and McCulloch CE 1985. Data analysis and the design of experiments in ornithology. In: Johnston RF (ed) *Current Ornithology* 2. pp 1–63. Plenum Press, New York
- Jarvis MJF, Siegfried WR and Currie MH 1974. Conservation of the Cape Vulture in the Cape Province. *Journal of the Southern African Wildlife Management Association* 4: 29–34
- Kemp AC and Kemp MI 1975. Observations on the White-backed Vulture *Gyps africanus* in the Kruger National Park, with notes on other avian scavengers. *Koedoe* 18: 51–68
- Koford CB 1953. *The California Condor*. Dover Publications, Inc., New York
- König C 1975. Buitres del género *Gyps* comiendo trozos de huesos. *Ardeola* 21: 219–220
- König C 1983. Interspecific and intraspecific competition for food among old world vultures. In: Wilbur SR and Jackson JA (eds) *Vulture Biology and Management*. pp 153–171. University of California Press, Berkeley
- Kopij G 2001. Feeding ecology of the Southern Bald Ibis, *Geronticus calvus*, in the Free State, South Africa. *Ostrich* 72: 193–198
- Kruuk H 1967. Competition for food between vultures in East Africa. *Ardea* 55: 171–193
- Kruuk H 1972. *The Spotted Hyena*. University of Chicago Press, Chicago
- Kruuk H and Turner M 1967. Comparative notes on predation by lion, leopard, cheetah and wild dog in the Serengeti area, East Africa. *Mammalia* 31: 1–27
- Lack D 1946. Competition for food by birds of prey. *Journal of Animal Ecology* 15: 123–129
- Latham S 1615. *Latham's falconry: or, the faulcons lure, and cure: in two books*. Roger Jackson, London
- Liversidge R 1978. It was all exaggeration. *African Wildlife* 32(3): 26–27
- Maclean GL 1993. *Roberts' Birds of Southern Africa* (6th edn). John Voelcker Bird Book Fund, Cape Town
- Mendelsohn H and Leshem Y 1983. Observations on reproduction and growth of old world vultures. In: Wilbur SR and Jackson JA (eds) *Vulture Biology and Management*. pp 214–241. University of California Press, Berkeley
- Miller A 1984. Collagen: the organic matrix of bone. *Philosophical Transactions of the Royal Society of London B* 304: 455–477
- Miller L 1962. "Stomach stones". *Zoonoos* 35: 10–13
- Mills MGL 1984. The comparative behavioural ecology of the brown hyaena *Hyaena brunnea* and the spotted hyaena *Crocuta crocuta* in the southern Kalahari. *Koedoe* 27(supplement): 237–247
- Mills MGL 1990. *Kalahari Hyenas: Comparative Behavioral Ecology of Two Species*. Chapman Hall, London
- Milstein P leS 1973. Buttons and Bald Ibises. *Bokmakierie* 25(3): 57–60
- Milstein P leS 1974. More Bald Ibis buttons. *Bokmakierie* 26(4): 88
- Mundy P, Butchart D, Ledger J and Piper S 1992. *The Vultures of Africa*. Acorn Books cc, Randburg