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OBSERVATIONS ON THE WHITE-BACKED VULTURE *GYPS AFRICANUS* IN THE KRUGER NATIONAL PARK, WITH NOTES ON OTHER AVIAN SCAVENGERS

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Abstract – Observations on the breeding biology of vultures in the central Kruger National Park, Republic of South Africa, were made over two consecutive seasons. The breeding success of the White-backed Vulture *Gyps africanus* appeared to be lower than in the Serengeti National Park, Tanzania. Its incubation period was about 8 weeks and its nestling period about 4,5 months. The relative abundance of vultures species recorded at food, is similar to results from other areas of Africa. Some resightings of marked birds indicate that vultures roam at least over the whole of the Kruger National Park.

Introduction

Studies on the Old World vultures are few, despite their being conspicuous and common scavengers. Aspects of the feeding behaviour have been observed (Attwell 1963; Houston 1972; Kemp 1969; Kruuk 1967; Petrides 1959), the flight activities have been studied (Pennycuick 1972) and some observations on breeding have been made (Houston 1972; Ledger and Mundy 1973; Sharma 1970; van Someren 1956).

Observations on scavenging birds were made during 1967 and 1968 in the area round Satara (23°24′S; 31°47′E) in the central Kruger National Park (K. N. P.) Republic of South Africa. The White-backed Vulture *Gyps africanus,* by far the commonest vulture, the Lappet-faced Vulture *Torgos tracheliotus* and the White-headed Vulture *Trigonoceps occipitalis* breed in the area. The Hooded Vulture *Necrosyrtes monachus* and the Cape Vulture *Gyps coprotheres* occur in the area throughout the year but do not breed there. Other avian scavengers in the area are the Bataleur *Terathopius ecaudatus* and the Tawny Eagle *Aquila rapax* which are breeding residents, and the Marabou Stork *Leptoptilos crumeniferus* which is a wet season visitor.

Study area

The topography of the K. N. P. has been well described (Pienaar 1963; 1966; 1968). The study area around Satara (Fig. 1) is a very shallow basin grooved by watercourses draining east to pass through the Lebombo Hills at the Nwanedzi Gorge. The only relief is provided by the north-south line of the Lebombo Hills along the eastern boundary and sandstone outcrops down the western third of the area. The altitude rises from 200 m a.s.l. at Nwanedzi to 450 m a.s.l. in the west. The Timbavati river, which forms the northwestern corner of the area drains to the northeast. The savanna vegetation of the study area was divided into four main types:

(1) Parkland tree savanna, dominated by *Acacia nigrescens* and *Sclerocarya caffra* trees, in the eastern two thirds;

(2) Dense tree savanna, dominated by *Acacia delagoensis* trees, along the immediate west of the sandstone divide;

(3) Mixed tree and bush savanna, with large *Acacia nigrescens* trees and bushes mainly of *Combretum* species, in the western one third;

(4) Riparian woodland, with a variety of trees most of which, in contrast to the other vegetation types, are non-deciduous, along the main watercourses.

There are no natural permanent surface waters in the area – even the largest waterholes dry up during drought – but artificial watering points are scattered throughout the area. The annual rainfall averaged 570 mm during the study period, and is largely confined to the hot season from October to April, with a cool dry season intervening.

Breeding Biology

During the 1967 breeding season all vulture nests seen in the central K. N. P. were recorded, and a few visited regularly to determine details of the nesting cycle. During the 1968 season as many nests as possible were found within the limits of the Satara study area (Fig. 1), by travelling all the roads within the area as often as possible, but visits to individual nests were less frequent than in 1967. Most of the nests in 1967 were within the 1968 study area. The majority of nests were of the White-backed Vulture but some observations were made on other avian scavengers breeding in the area.

Nest site

One hundred and six nests of the White-backed Vulture were examined. All were built on the canopy of trees except for four which were subcanopy in large forks. North (1944) reported that of 250 nests, 70 per cent were on top of the trees and 30 per cent in a solid fork below the canopy. Each tree contained one nest, except for one where there were two nests active at the same time, one subcanopy. The latter two nests were about 5 m above one another, and apart from the droppings from the top nest falling on the occupants of the lower, no interactions were

observed between the pairs during two full-day watches. In Tanzania Houston (1972) very occasionally found two nests in one tree, and North (1944) in Kenya "often" found two nests per tree, and once six nests in a tree. Lowe (1929) reports several instances of more than one nest per tree. Salvan (1968) found a Lappet-faced Vulture and Ruppell's Vulture *Gyps ruppellii* (possibly mis-identified for a White-backed Vulture since the former is normally a cliff nesting species) nesting in the same tree in Tchad.

Table 1

The main aspects of White-backed Vulture nest sites in the central Kruger National Park

Tree species	Vegetation type surrounding nest (see text)				Totals
	1	*2*	*3*	*4*	
Acacia nigrescens	21	5	3	2	31 (29%)
Acacia robusta		1		20	21 (19%)
Acacia delagoensis			16	1	17 (16%)
Acacia xanthophloea				1	1 ((1%)
Ficus sycomorus				12	12 (12%)
Diospyros mespiliformes		1		8	9 (8%)
Lonchocarpus capassa	1			8	9 (8%)
Sclerocarya caffra	2	1			3 (3%)
Combretum imberbe				1	1 (1%)
Schotia brachypetala				1	1 (1%)
Pseudocadia zambesiaca				1	1 (1%)
Dead tree				1	1 (%)
TOTALS	24 (23%)	8 (7%)	19 (18%)	56 (52%)	106 (100%)
Number associated with Buffalo Weaver nests	14 (58%)	4 (50%)	4 (21%)	8 (17%)	30 (28%)

The heights of nests above the ground depends mainly on the heights of trees chosen, and were estimated to range from 10 m – 25 metre. The main aspects of the nest sites are shown in Table 1. Sixty three per cent of the nests were in thorny *Acacia* trees, the species used being that most common within the vegetation type. A further 28 per cent were in the three non-thorny tree species most common in the riparian woodland *(Ficus sycomorus, Diospyros mespiliformis* and *Lonchocarpus capassa). Acacia delagoensis* and riparian woodlands are the preferred habitats in terms of the number of nests found in relation to the area of habitat available (Fig. 1).

The highest proportion of nests found with those of the Buffalo Weaver *Bubalornis albirostris* are found in the parkland tree savanna and mixed tree and bush savanna habitats. The vulture's nest was sometimes on the weaver's nests, or with the weaver's nests surrounding it (Fig. 2). At a few nests, *Ploceus* weavers built their nests around that of the vulture (Fig. 3). Salvan (1968) found Ruppell's Vulture (possibly misidentified for White-backed Vulture) and Lappet-faced Vulture nesting on the nests of Buffalo Weaver, and the starlings *Spreo pulcher* and *Lamprocolius chalybeus* in Tchad.

During the same period six nests of the Lappet-faced Vulture and four of the White-headed Vulture were found, all on the canopy but none in riparian vegetation. Tawny Eagles are the only other scavengers in the area that nest on top of the canopy. A single Hooded Vulture nest was

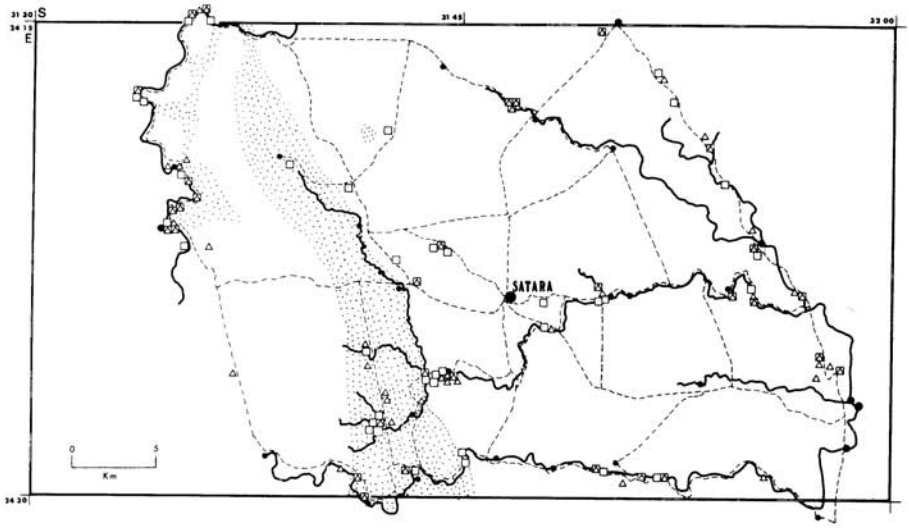


Fig. 1. Map of the Satara study area in the central Kruger National Park showing the position of White-backed Vulture nests in 1967 (triangles) and 1968 (squares). Water points (solid circle) and the roads regularly travelled (broken lines) marked. Riparian vegetation (heavy black lines) and *Acacia delagoensis* woodland (stippled) distribution are given to indicate the relative areas of each vegetation type.

Fig. 2. View from below of a White-backed Vulture nest (arrowed) surrounded by Buffalo Weaver nests.

found 36 km eastnortheast of the Satara study area (Kemp 1969) and the nearest colony of the cliff-nesting Cape Vulture is at Mariepskop, about 100 km west of the study area.

Nest structure

Thirty nests of the White-backed Vulture were examined. They ranged in diameter from 45 cm to 1 m, and in depth from 15 cm – 90 centimetre. They were constructed of sticks of a maximum diameter of 3 cm, and were surmounted by a shallow cup of 18 cm – 20 cm diameter. The cup was lined except in two nests, but often the lining was very

scanty. Eleven nests were lined with grass, two with green sprigs and 15 with a mixture of grass and sprigs. The sprigs were of tree or bush species in the immediate vicinity of the nest (sometimes of the same species as the nest tree):

Fig. 3. A White-backed Vulture on the nest at the beginning of summer, surrounded by Buffalo Weaver and *Ploceus* weaver nests.

Table 2

Records of interchange of vulture nests in the central Kruger National Park from 1967 to 1973

Original occupant recorded (? builder)	Subsequent occupant			
	Gyps africanus	*Torgos tracheliotus*	*Aquila rapax*	*Ephippiorhynchus senegalensis**
Gyps africanus			1	1
Torgos tracheliotus	1			
Trigonoceps occipitalis	3			
*Sagittarius serpentarius**		1		
*Hieraaëtus spilogaster**	1			
Aquila rapax	1			
*Aquila wahlbergi**	2			
*Polemaetus bellicosus**	1			

* *Ephippiorhynchus senegalensis* Saddlebilled Stork; *Sagittarius serpentarius* Secretary Bird; *Hieraaëtus spilogaster* African Hawk-eagle; *Aquila wahlbergi* Wahlberg's Eagle; *Polemaetus bellicosus* Martial Eagle.

Lonchocarpus capassa, Sclerocarya birrea, Euclea divinorum, Combretum apiculatum, Diospyros mespiliformis and *Combretum imberbe* being recorded. One nest contained pieces of creeper as lining, and another a sprig of *Solanum* species. All nests had fragments of bone in the cup or on the rim.

In several cases the nest may not have been constructed by the vultures themselves. Five nests were built on top of Buffalo Weaver nests and one on top of an epiphyte, and these nests required little construction. There was also interchange of nests among raptors in the area (Table 2) and it is therefore difficult to determine which species undertook the initial construction. The use of Wahlberg's Eagle nests by the White-backed Vulture may explain the four instances of subcanopy nesting by this species. An Augur Buzzard *Buteo rufofuscus* has also been recorded as taking over the nest of a White-backed Vulture (van Someren 1956).

Nesting density

All nests found in the Satara study area during 1967 and 1968 are shown in Fig. 1. Sixty four active nests of the White-backed Vulture were found in the area in 1967, and 68 with more intensive searching in 1968. There is a tendency for nests to be clumped in the vicinity of some watering points, especially where these are close to suitable riparian woodland. In 1968, 51 of the 1967 nest sites could be found again and 34 (67 per cent) were used again. Only one of these sites was known to have been unsuccessful in the previous year, which compares well with a 72 per cent re-use of successful nest sites recorded in Tanzania (Houston 1972). At nine of the sites the nest was still present but was not used, at seven of the sites the nest had fallen down, and one site was taken over by a Tawny Eagle.

Two active Lappet-faced Vulture nests were found in the area in 1967 and one in 1968, all in different sites.

Two active nests of the White-headed Vulture were found in the area in 1967 and three in 1968, one site being used both years.

Nesting cycle

Laying dates of White-backed Vultures were determined, or estimated by knowing the incubation period and estimating the age of young chicks, after studying the development of one. Laying dates at 11 nests in 1967 were calculated at 14, 26, 27, 28, 31 May and 3, 3, 6, 13, 20, 30 June; and for eight nests in 1968 at 21, 21, 25, 27 May and 2, 3, 11, 19 June. Laying appeared to be confined to about six weeks from mid-May to the end of June, and no obvious disparity was noticed for the rest of the nests in the area. Houston (1972) recorded a laying spread of 12 weeks for this species during one season in Tanzania.

One Lappet-faced Vulture egg was laid between 26 May and 6 June 1967. At three White-headed Vulture nests the chicks were estimated to

have hatched in the first week of September, indicating laying during the first half of July.

All the vulture nests examined contained a single egg, except for one White-backed Vulture nest which contained two. One of these was very stained, rotten inside and lying on the nest rim, and was thought to have been an addled egg from previous season. Two eggs have been found in nests of Ruppell's Vulture (North 1944) and Hooded Vulture (Boughton-Leigh 1932), but in each case it is exceptional. Thirty three White-backed Vulture eggs measured 82,4 (93,4–83,6) mm x 61,0 (71,5–63,6) mm; some were plain chalky white, but exactly two thirds had various amounts of faint purple and brown spotting, mainly at the obtuse end. One egg each of the Lappet-faced Vulture and White-headed Vulture measured 88,7 mm x 70,6 mm and 85,9 mm x 66,4 mm respectively; both were white with faint markings.

The incubation period of the White-backed Vulture, determined in two instances to the nearest day, was 56 and 58 days. This is about 12 days longer than the period given by van Someren (1956; as used by Houston 1972), but is then of the same order as other species of *Gyps* vulture for which it is known (Houston 1972). Hatching of the egg took up to three days. At one nest at 08h40 on 29 July the chick could be heard peeping and scratching but no cracks were evident on the shell. By 14h30 on 31 July there was a 2 cm diameter hole in the shell, and the chick had hatched by 09h10 on 2 August. At another nest the egg was cracked by 10h20 on 15 July, and a large hole was made by 09h25 on 16 July. The chick had hatched by 09h55 on 17 July, and the shell was still in the nest.

The nestling period of the White-backed Vulture was determined by observation from below for seven chicks as: 108±15, 126±2, 129±5, 130±5, 135±5, 135±15 and 140±10 days (average about 130 days). However, it is difficult to determine the fledging date accurately as the chicks spend much time in the nest after they can fly.

Chick development

Results are only available for a single White-backed Vulture chick, whose measurements at intervals are shown in Fig. 4. The tarsus was full grown by 55 days old, and body growth as indicated by the ulna and culmen was completed by 90 days old. The feather growth of the retrices and remiges was not complete by the last examination at 112 days old, and the chick left the nest for the first time at 126±2 days old. The decline in mass immediately after 55 days old is thought to be due to wood gatherers working in the immediate vicinity of the nest for three days, keeping the adults from feeding the chick. Development of the plumage of the chick is indicated by a series of photographs comprising Fig. 5.

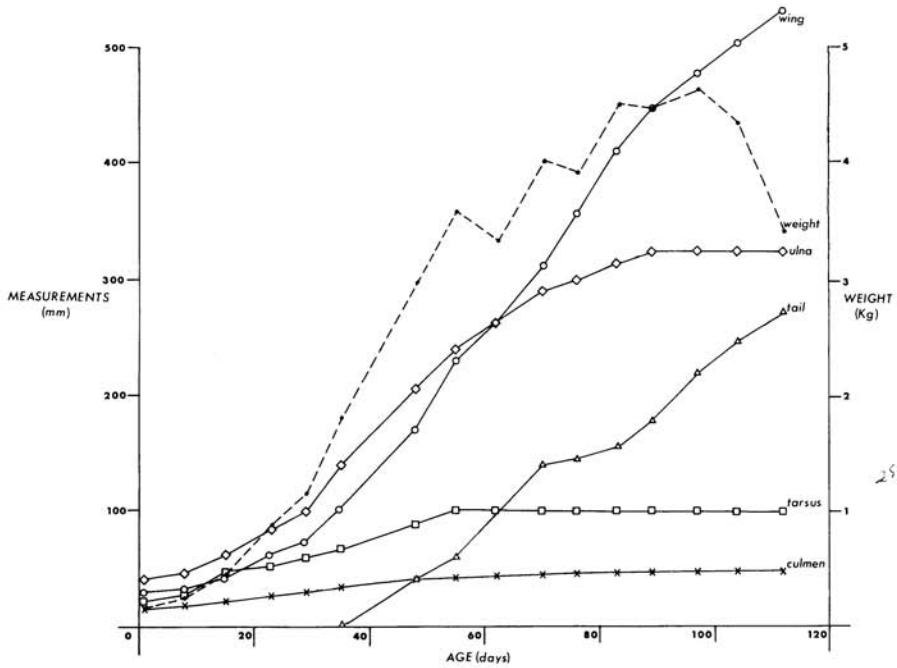


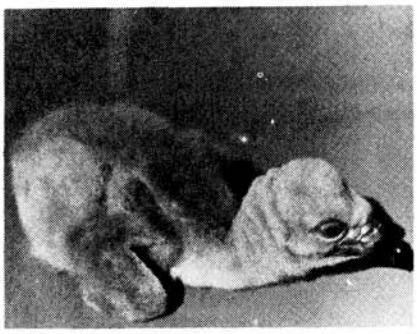
Fig. 4. Measurements of the wing, ulna, tail, tarsus, culmen and mass of a White-backed Vulture chick at intervals from 17 July to 7 November 1968. The crop was not emptied before determining mass.

Nesting success

During the 1967 season, seven (58 per cent) of the 12 White-backed Vulture nests under observation produced chicks to the flying stage. Of the unsuccessful nests, one had an addled egg. One on the canopy of a large *Acacia nigrescens* was predated by a Serval *Felis serval,* and in one the injuries to the chick indicated that it had been trampled by the parents who were still in attendance at the nest. In two nests the cause of disappearance of the 14 and 40 day old chicks respectively was unknown.

During the more general observations of 1968, of 56 nests where laying was thought to have occured, chicks were thought to have flown from 36 (64 per cent). The results were biased towards a high success since many nests were only noted as active once the chicks were at least six weeks old and could be seen from below. Of the unsuccessful nests, five contained addled eggs, two fell down in high winds, one nest tree was pushed down by elephants, two had fluff on the ground below indicating predation, two were deserted due to human interference, and in eight the cause was unknown.

These success figures appear to be lower than found for the same species in the Serengeti National Park, Tanzania, where comparable figures of 91 per cent and 83 per cent were recorded in successive seasons (Houston 1972). For a sample of 50 nests of the closely related Indian



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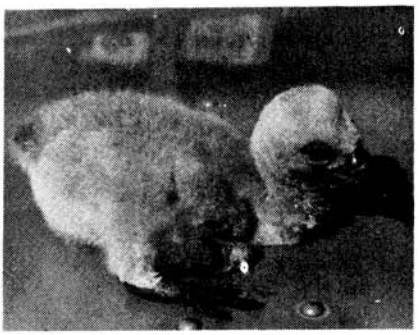

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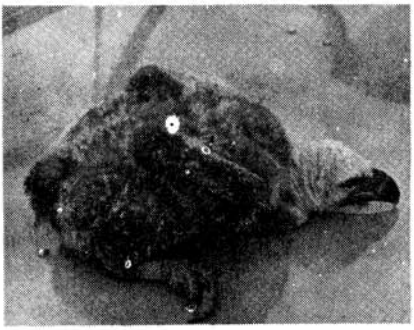

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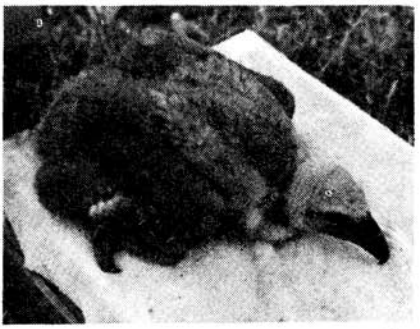

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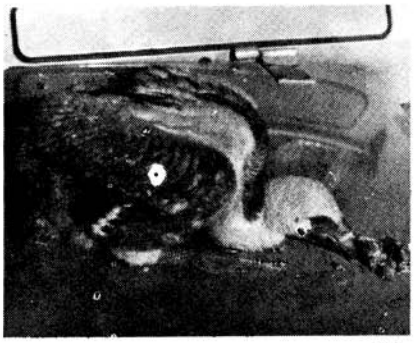

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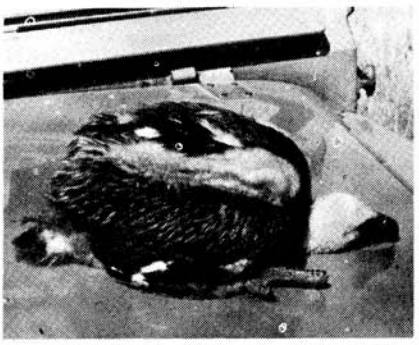

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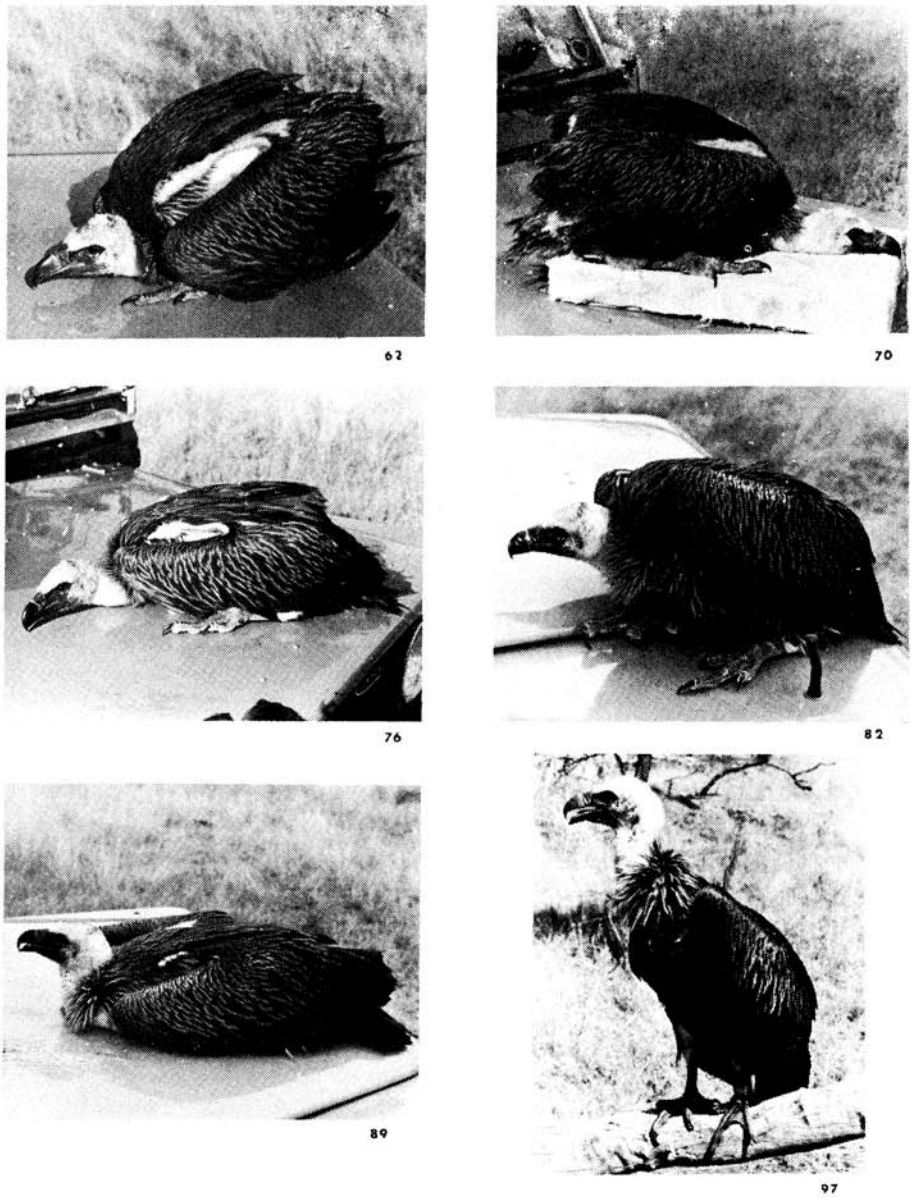

Fig. 5. Photographs at intervals of the same chick of the White-backed Vulture as measured for Fig. 4. The age in days is below each picture.

White-backed Vulture *Gyps bengalensis,* a success figure of 96 per cent is reported (Sharma 1970). For 23 nests of *G. coprotheres,* a success figure of 52 per cent is recorded (Ledger and Mundy 1973).

The only nest of a Lappet-faced Vulture studied in the Satara area had an infertile egg. Two nests of White-headed Vulture successfully produced chicks, but in a third the chick died when about two weeks old.

Feeding biology

The associations of scavenging birds recorded at food on 47 occasions in the central K. N. P. are shown in Table 3. The total numbers of each vulture species recorded may indicate their relative abundance in the area, as this is borne out by the relative numbers of nests of each species found. The figures for the K. N. P. are compared to others from elsewhere in Africa in Table 4.

Movements

From 15 May to 31 August 1967, 36 White-backed, one Cape, one Lappet-faced, three White-headed and six Hooded Vultures were trapped by tying nooses to the skin of carcasses at which they were feeding. The birds were ringed and individually marked by cutting the flight feathers (Snelling 1970). Six White-backed and two Hooded Vultures were seen again up to April 1969, an individual of each species being seen twice. The movements of the marked birds are shown in Fig. 6.

Discussion

The relative abundance of the vulture species in the central K. N. P. is similar to elsewhere in Africa (Table 4), with the White-backed Vulture predominating in all areas so far studied. It is interesting to note the similar relative abundance of the Cape Vulture in the K. N. P. and the Ruppell's Vulture in parts of East Africa. The latter two species dominate the White-backed Vulture at food, being larger (Kruuk 1967; *pers. obs.),* but they are colonial cliff-nesting species whereas the White-backed Vulture is a tree-nesting species. However, it appears that over much of the breeding range of these three species of *Gyps* vulture they do not overlap, and that overlap happens to be most evident in two of the areas so far studied, the K. N. P. and the Serengeti National Park (Houston 1972). Within the K. N. P. the movements of vultures appear to be so extensive that no regional variation in species abundance can be expected. Pennycuick (1972) has shown that *Gyps* vulture may have a foraging radius of over 100 km from their nests during dry season weather conditions. This means that even though the two *Gyps* species in the K. N. P. occupy separate breeding niches, the Cape Vultures from the Mariepskop colony can be expected to forage all over the Satara study area where the White-backed Vultures breed.

The White-backed Vulture must have evolved from or given rise to the closely-related colonial species, but there is some contention in the

Table 3

Number of scavenging birds recorded at food in the central Kruger National Park during 1967 and 1968

Food	Numbers of scavenging species*								Totals
	WBV	CV	LFV	WHV	HV	TE	B	MS	
Comatose impala* lamb with broken leg (birds waiting above)	9					1			10
Patch of bloody faeces			1	3					4
Remains of *Streptopelia* dove						1	1		2
Jackals* eating remains of *Lepus* hare	1				2	6	3		12
Polemaetus bellicosus eating impala lamb				1					1
Giraffe* female defending stillborn calf	36		1						37
Impala ram hidden in bushes					2				2
Cheetah* eating impala ram			2						2
Complete impala ewe	20		1						21
Complete impala ram	50								50
Complete impala ram	20								20
Complete impala ram	8	1	3			1			13
? with lions* present	35		2		4				41
Lions eating wildebeest*					1				1
Lions eating wildebeest	4		2		12				18
Lions eating wildebeest		1			6				7
Complete wildebeest and eaten remains of two others	60		2	2	4				68
SUB-TOTAL FOR: BEFORE FEEDING COMMENCED	243	2	14	6	32	8	4	0	309
Placental zebra* foal	5			2					7
Wildebeest afterbirth					7				7
Young duiker*	15					1	2		19
Juvenile impala ram	38	3	3	2	1				47
Impala ram forequarters	51		4						55
Juvenile wildebeest	10		7	1	2				20
Juvenile zebra	90	15	4	2					111
Juvenile zebra	48		4	1	1				54
Zebra	52								52
? zebra (across river)	100	5	2						107
Complete elephant* and heads and intestines of four others (numbers of birds estimated)	700	250	50	3	50			250	1 303

SUB-TOTAL FOR: ACTIVELY FEEDING	1 109	273	74	12	61	1	2	250	1 782
Cleaned bones of:									
? few bones	2			5		1			8
Steenbok*	11		3	2	5				21
Impala skull	16	1		2	4				23
Impala vertebral column	11		3		1				15
Impala	4			1					5
Impala	7		1	1					9
Impala ewe	17		2		6				25
Impala ewe	8	1		2			2		13
Impala ram	10		4	2	2				18
Impala ram	11	1	5	1	1			1	20
Juvenile wildebeest	30		5						35
Wildebeest	2				3				5
Wildebeest	6				3				9
Wildebeest	12		5	1	1				19
Zebra	28		1	1	2				32
Zebra	20			2	10	3			35
Zebra	9				6	1			16
Giraffe, with neck complete	13	1	1		3				18
Giraffe leg and vertebral column	20			1	3				24
SUB-TOTAL FOR: WHEN COMPLETED FEEDING	237	4	30	21	50	5	2	1	350
GRAND TOTAL:	1 589	279	118	39	143	14	8	251	2 441

* *abbreviations and common names:* WBV – White-backed Vulture; CV – Cape Vulture; LFV – Lappet-faced Vulture; WHV – White-headed Vulture; HV – Hooded Vulture; TE – Tawny Eagle; B – Bataleur; MS – Marabou Stork; impala – *Aepyceros melampus;* jackals – *Canis mesomelas;* giraffe – *Giraffa camelopardalis;* cheetah – *Acinonyx jubatus;* lion – *Panthera leo;* wildebeest – *Connochaetes taurinus;* zebra – *Equus burchelli;* duiker – *Sylvicapra grimmia;* elephant – *Loxodonta africana;* steenbok – *Raphicerus campestris.*

literature (Brown and Amadon 1968; Houston 1972) as to whether it nests colonially. Certainly it often nests singly, but on the other hand it does not appear to defend a territory other than for a few feet around the actual nest. Houston (1972) could find no aggregation of nests in the Serengeti National Park other than could be explained by the limited availability of suitable nest trees along rivers. However, in the K. N. P. there appear to be aggregations of nests in some areas (Fig. 1) which could not be explained by there being limited nest sites. These aggregations are mainly along the rivers or in *Acacia delagoensis* woodland, but some small aggregations of up to five nests are also apparent in more open savanna. The assessment that some of the areas, especially along the rivers, are suitable for nesting but are unused is purely subjective. The larger aggregations of nests also appear to be close to watering points, but this is not invariable and may be coincidental.

Table 4

Comparison of the relative abundance (as percentage of total numbers recorded at feeding association) of sympatric vulture species at six localities in Africa

Vulture species	Locality					
	Central Kruger National Park, South Africa *(Kemp ms)* n = 2 168 birds %	Luangwa Valley, Zambia *(Attwell 1963)* n = 467 birds %	Kafue National Park, Zambia *(Attwell 1963)* n = 356 birds %	Queen Elizabeth National Park, Uganda *(Petrides 1959)* n = ? %	Serengeti National Park, Tanzania *(Houston 1972)* n = 6 112 birds %	Serengeti National Park, Tanzania *(Kruuk 1967)* n = 1 737 birds %
Gyps africanus	70	92	85	85	70	64
*Gyps ruppellii**	–	–	–	2	18	13
Gyps coprotheres	12	–	–	–	–	–
Torgos tracheliotus	7	4	3	2	8	12
Trigonoceps occipitalis	2	1	3	1	0,3	3
Necrosyrtes monachus	9	2	8	10	3	8
*Neophron percnopterus**	–	–	–	–	0,03	1

* *Gyps ruppellii* Ruppell's Griffon; *Neophron percnopterus* Egyptian Vulture.

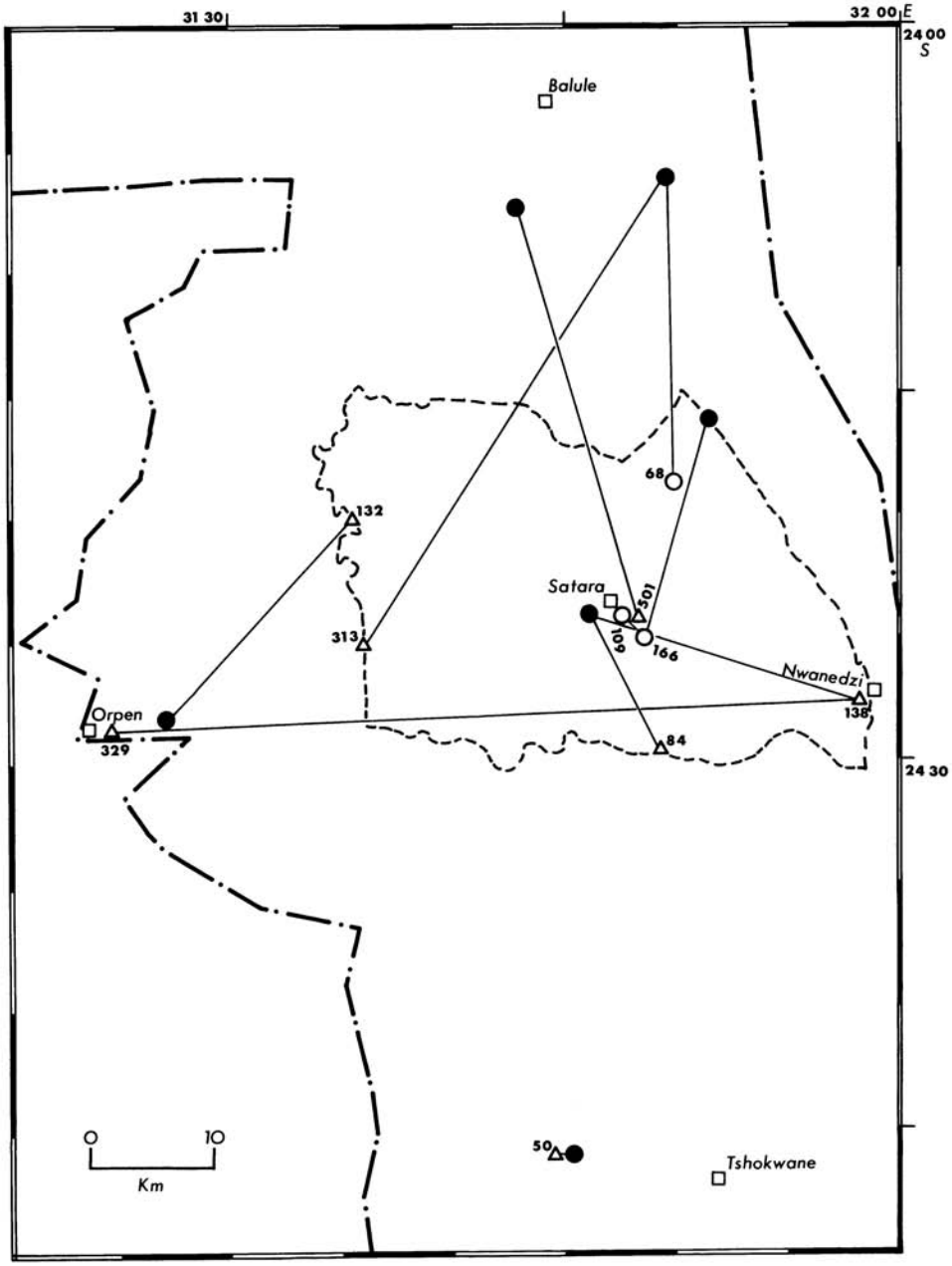

Fig. 6. Diagram of the central Kruger National Park (boundaries of dot-dash line) showing the position of the Satara study area (broken line) and movements of marked vultures. Solid circle – site of capture; open circles – resighting of Hooded Vulture; open triangles – resightings of White-backed Vulture. Numbers show the time elapsed in days since capture/last sighting.

All the vultures breeding in the Satara study area nest mainly on the canopy of trees, and the only other raptor nesting in the same site and at the same time is the Tawny Eagle. The choice by the White-backed Vulture of a nest site with some degree of protection, is thought to be important. Thorny trees are often used, but in riparian woodland non-thorny trees are used, which since they are not deciduous, make detection of the nest difficult from below. The proportion of nests associated with Buffalo Weaver nests is highest in the open savanna sites. The vultures nest-build and lay at a time when the weavers are absent from the area, although vulture chicks are still on the nest when the weaver return in summer (Fig. 3). This indicates that the association is chosen by the vultures when they build on weavers nests, and by the weavers when they build around vulture nests. It may render the nest less conspicuous from below, and is an association also common to the Bataleur in the area.

The breeding cycle and the development of the chick is comparable to the other *Gyps* species for which it is known (Houston 1972). The restricted period of onset of laying on the White-backed Vulture, and its constancy over two seasons, indicates a photoperiodic influence of onset during the six weeks preceding the austral winter equinox. This also fits the data for the Serengeti if the incubation period is increased by 12 days (Houston 1972), even though this is only between 1°S and 3°S of the equator, and so an internal circannual breeding cycle may be indicated.

The breeding success of the White-backed Vulture in the K. N. P. appears to be lower than the results for Serengeti. The reason for this is not apparent, but apart from natural factors operating outside the breeding biology of the species, addled eggs and predation of chicks appear to be the most important factors.

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