



Notes on the behavior of
Lappet-faced Vultures and Cape
Vultures in the Namib Desert
of South West Africa

by

E. G. Franz Sauer

Zoologisches Forschungsinstitut und
Museum Alexander Koenig, Bonn, Germany

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In his "Birds of the World", Oliver L. Austin, Jr. (1961) calls the vultures scientifically interesting, exceedingly useful and practical scavengers, "but not very nice critters." Though vultures may be practical and not very nice, they are a group of fascinating birds that have stirred the mind of man since ancient times. In spite of all the popular and scientific interest in birds, information on the natural history of vultures is still so scant that even modest chance observations in the field can yield new facts. Vultures include some of the largest of flying birds. By their keen senses they are able to locate carrion from afar and swiftly. This has sparked man's myth and imagination, but only modern science found answers. Old World vultures appear to locate carrion over long distances by sight, while the New World's Turkey Vulture (*Cathartes aura*) smells it from afar (Stager, 1964).

Watching vultures in the wild is an ever captivating adventure. While studying the South African Ostrich (*Struthio camelus australis*) in the inner Namib (Fig. 1), we recorded every encounter with Lappet-faced Vultures (*Torgos tracheliotus*) and Cape Vultures (*Gyps coprotheres*). We accumulated our data during our field research in the region of Tinkas and Hotsas Flats and at the Ganab and Hotsas water holes (Fig. 2), from 13 July to 13 December, 1964, and again during the months of September and December of 1969. Notes were taken at the water sites, game carcasses, rest areas of the two species, and at various nests of the Lappet-faced Vultures. We supplemented our observational data with photographic records both in color and black-and-white, using 35 mm still and 16 mm cine photography. We photographed the birds at close range from our well camouflaged blinds. The latter were imitations of termite mounds and natural outgrowths that left the birds uninfluenced by our presence so that they behaved completely naturally. Other reports on our research projects in the inner Namib provide information on the methods of study, on ecological features of the area, and on social contacts between ostriches and the vultures (Sauer, 1970; Sauer and Sauer, 1966 a, b; 67 a, b; 1970). This preliminary report presents data on the vultures' visits at the water holes and in communal areas, as well as descriptions of intra- and interspecific flock structures and the social status of the birds.

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GENERAL DESCRIPTION OF THE BIRDS

Literature provided little help. Our old friend the late Walter Hoesch (1955) restricted his list of South West African vultures to those verified by preserved specimens; thus he omits mention of the Cape Vulture. In fact, nesting records of the Cape Vultures in the Namib Desert Park and adjacent mountain ranges are still lacking, and the best guess is that they probably nest in the

rock faces of the mountains and inselbergs. General summaries in faunistic reports offer little help to a study of local distribution and ecology. Moreau (1966), for example, lists seven species of Aegypinae breeding in South West Africa. His information appears to be based on general handbook extracts or from very generalized distributional maps that typically cover whole regions but lack specific documentation for areas such as South West Africa. Fluctuations in the size of vulture populations and their sporadic migrations add further difficulties. The Egyptian Vulture (*Neophron percnopterus*), for example, is mentioned by McLachlan and Liversidge (1970), according to Roberts (1953), as "nowhere common" in South Africa. In the latter half of the last century Andersson (1872) found this species still "not uncommon" in South West Africa, "especially in the neighbourhood of the coast." During our extensive field studies in 1957, 58, 64, and 69 we never encountered a single Egyptian Vulture.

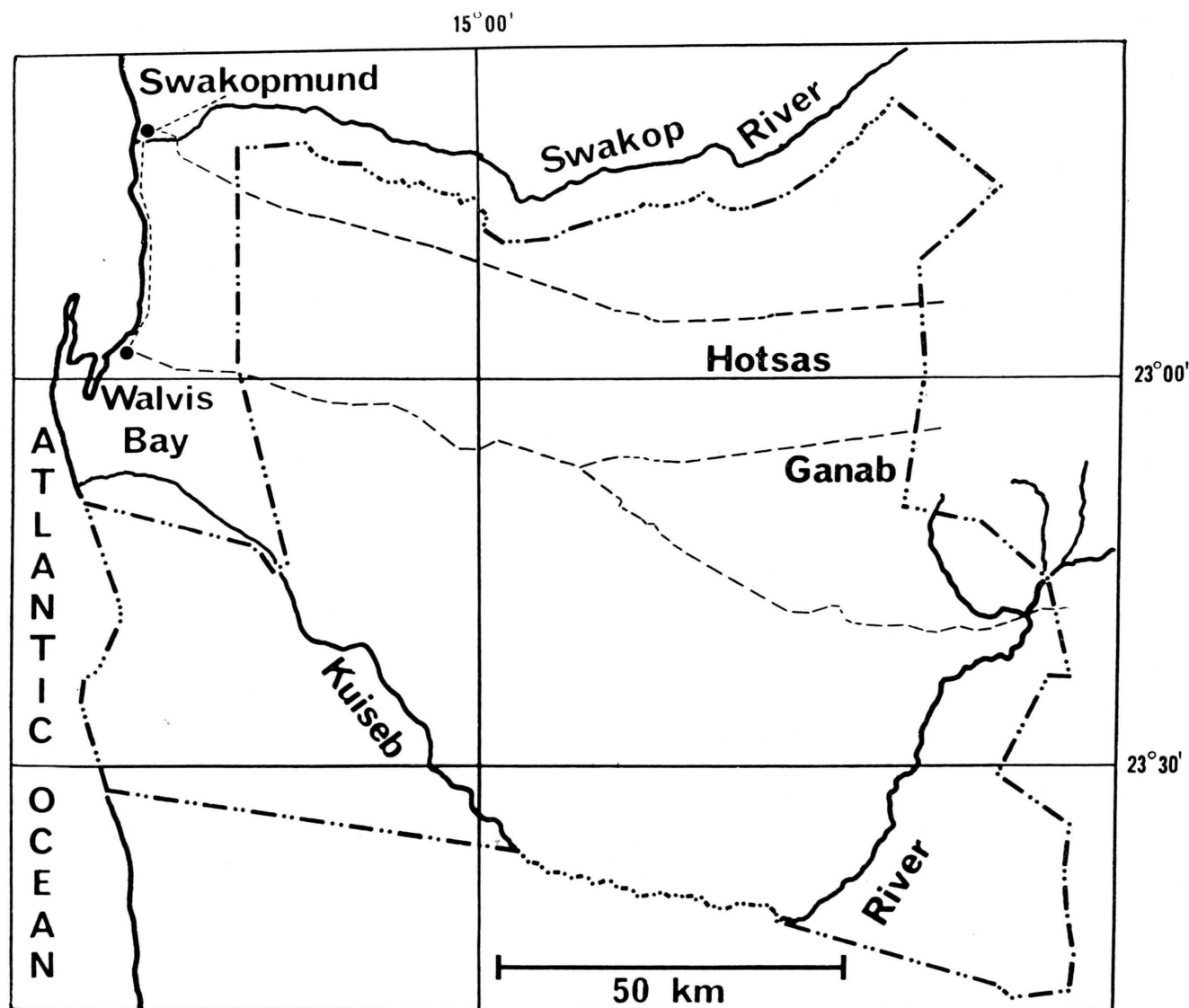


Figure 1. Namib Desert Park, South West Africa. The reserve covers an area of approximately 1 210 000 ha or 4 657 square miles; ... roads.

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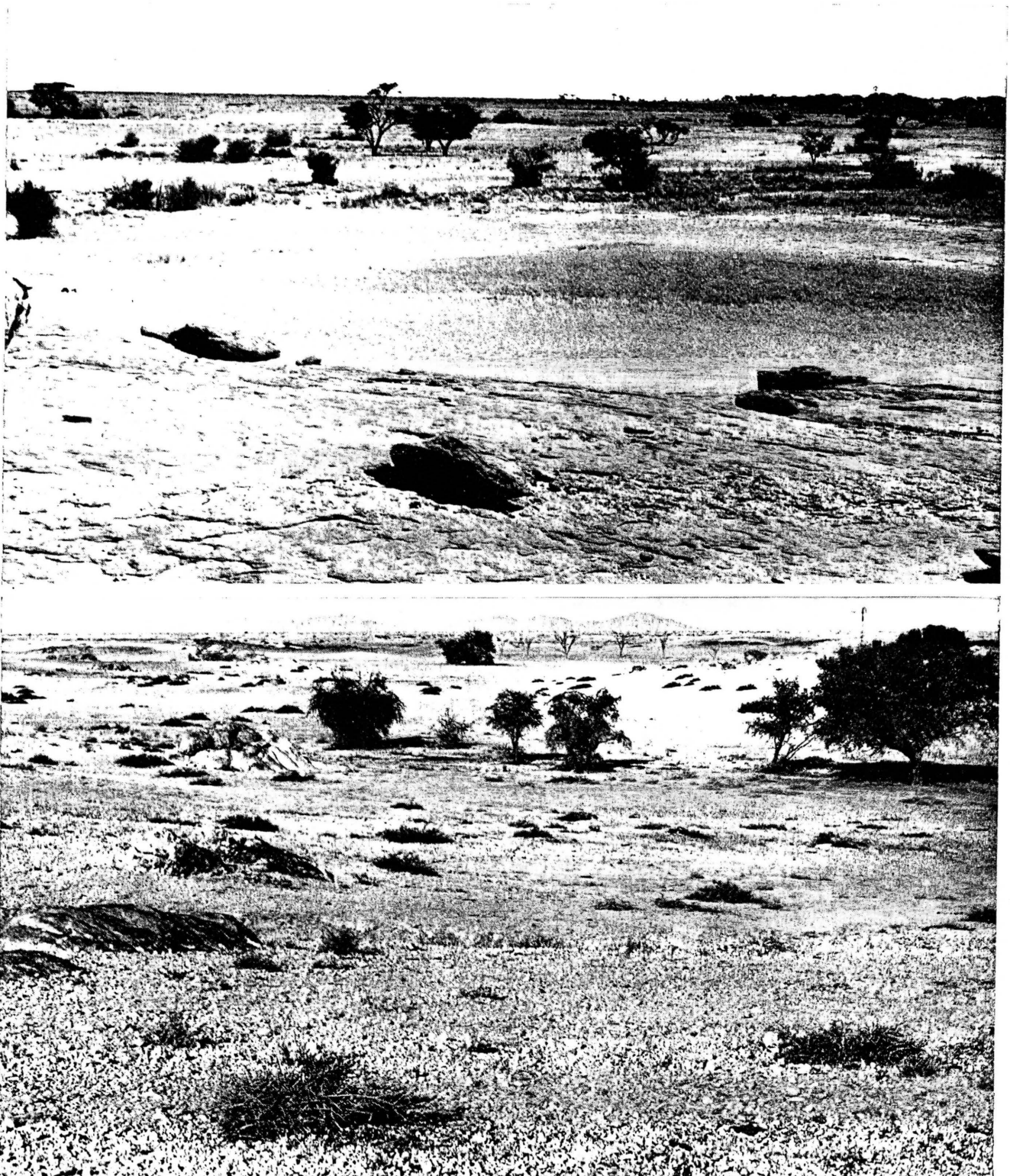


Figure 2. The habitat at (a) Ganab and (b) Hotsas with scatterings of acacia trees in the dry river beds. (Photographs and drawings by the author).

It seemed difficult to find the right names for the two species under discussion; initially we followed Roberts' usage to avoid the confusion caused by the widespread use of various common and scientific names. However, the Black Vulture, which is also known as the Eared Vulture, is now generally called the Lappet-faced Vulture. "The New Dictionary of Birds" (Landsborough Thomson, 1964) bestows the name Black Vulture to *Aegypius monachus*, and the New World has its own Black Vulture, *Coragyps atratus*. These are just a few examples of the nomenclatorial confusion.

The *Lappet-faced Vulture* of the inner Namib is a large, heavy bird whose enormous wings reach a wingspread of up to 300 cm; Mackworth-Praed and Grant (1962) list a measurement of 715–790 mm from the bend to the tip of the longest feather. The red of the bird's fleshy head and sparsely feathered neck and the purplish cere and cheeks form a colorful contrast to the dark brown plumage. The color of the beak is that of horn with some dark grey at the base, and the legs and feet appear bluish grey. Some of the birds in the inner Namib wear a uniformly dark brown plumage, others show scatterings of white feathers in the neck region, in the collar, on the chest, or among the brown feathers covering the thighs. Some individuals have a white-freckled back, some wear whitish "pants," and others show a little white in the otherwise brown primaries. The combinations are manifold; a freckle-back individual, for example, may have either solid brown or white "pants." While the age and molt of the birds are, in part, responsible for some of these variations, they can not be explained by age and molt alone. Various

white markings are not identical with the juvenile white. They are stable at least during the season and, therefore, very useful for individual recognition of the birds at close range.

McLachlan and Liversidge (1970), according to Roberts (1963), call the Lappet-faced Vulture "less sociable" than the other vultures. This may be so, but we can not confirm it; in the Namib we found this common vulture often very sociable. It provided us with a wealth of information on its intraspecific social system and on its interspecific relationships with other birds and mammals of the veld. Lappet-faced Vultures consorted freely and peacefully not only with their own kind but also with Cape Vultures. So we are not surprised to read that Andersson (1872) called the Lappet-faced Vulture the "Sociable Vulture." Aside from its social behaviour at the water sites and communal resting areas, we noted some of the Lappet-faced Vulture's nesting habits on top of acacia trees scattered along the dry washes on Tinkas and Hotsas Flats and studied its behaviour at carcasses.

The *Cape Vulture*, though rivalling the Lappet-faced Vulture in size, appears a trifle more slender-built and with shorter wings than its counterpart (680–690 mm after Mackworth-Praed and Grant, 1962). Both species associated frequently at the water site, when resting, and even while soaring. We sighted old and young birds of this species quite regularly in the inner Namib, and in 1964 one banded bird spent some time at our observation site at Hotsas. Since no vultures had been banded in South West Africa, this young bird must have migrated, possibly from a southern range where banding was carried out.



Figure 3. Lappet-faced Vultures and Oryx in the dry river bed at Hotsas.



Figure 4. Mixed flocks of Lappet-faced Vultures and Cape Vultures, a) 3:4 and b) 4:2 birds, peacefully crowded in small water holes at Hotsas.

The skin of the bare-faced head and long neck of the Cape Vulture is bluish. One of the young Cape Vultures had a distinctly purple rather than bluish throat and neck. The beak is dark, blackish in appearance; the legs and feet are of a gray to blackish color. The head is covered with hair-like feathers and the neck with a soft down, brownish in juvenile birds and white in the adults. At the base of its neck the Cape Vulture wears a brownish to white ruff. The crop patch looks brown.

The back is more or less pale buffish to greyish white. The feathers of the mantle, scapulars and rump show dark brown centers, while the primaries are dark brown to black, the secondaries more ashy brown. The underparts are buffy to creamy white. As in the Lappet-faced Vulture, the sexes look alike. The young birds are browner than the old birds. Some of the latter have a very pronounced ashy white appearance.

TIME SCHEDULE AND NUMBERS
OF LAPPET-FACED VULTURES
AND CAPE VULTURES
AT THE WATER SITE

Both species of vultures frequented the water sites of Hotsas and Ganab. The windmills, set up in the sandy rivers by the Nature Conservation Branch, provided a nearly always sufficient amount of fresh water in the otherwise dry veld. Most of our studies were done at the Hotsas water site (Fig. 3); frequent controls were made at Ganab. The vultures came to the water quite regularly for a number of purposes, for drinking, bathing, basking, and drying the wet plumage, preening and resting (Figs. 4–7). They displayed intra- and interspecific social activities when assembled at the water sites. Often after prolonged rests the vultures would take off again either in pairs or singly, spiralling skywards

for their communal soaring flights high above the plains or heading for their night roosts.

Lappet-faced Vultures were more common than Cape Vultures, though in 1969 the latter had significantly increased over the 1964 stock and sometimes dominated the former in numbers at the Hotsas water. Neither situation caused any significant amount of interspecific hostility between the two species; agonistic behaviour was chiefly limited to conspecific opponents. In general the Cape Vultures were subordinate to the Lappet-faced Vultures and gave way when one of them approached.

The regular appearance of the two species of vultures at the water sites of Ganab and Hotsas provided a means of estimating the numbers of birds inhabiting the area, to study various behavioural aspects, and to understand that part of their daily activity rhythm occupied with their visits to the water and surrounding communal areas.

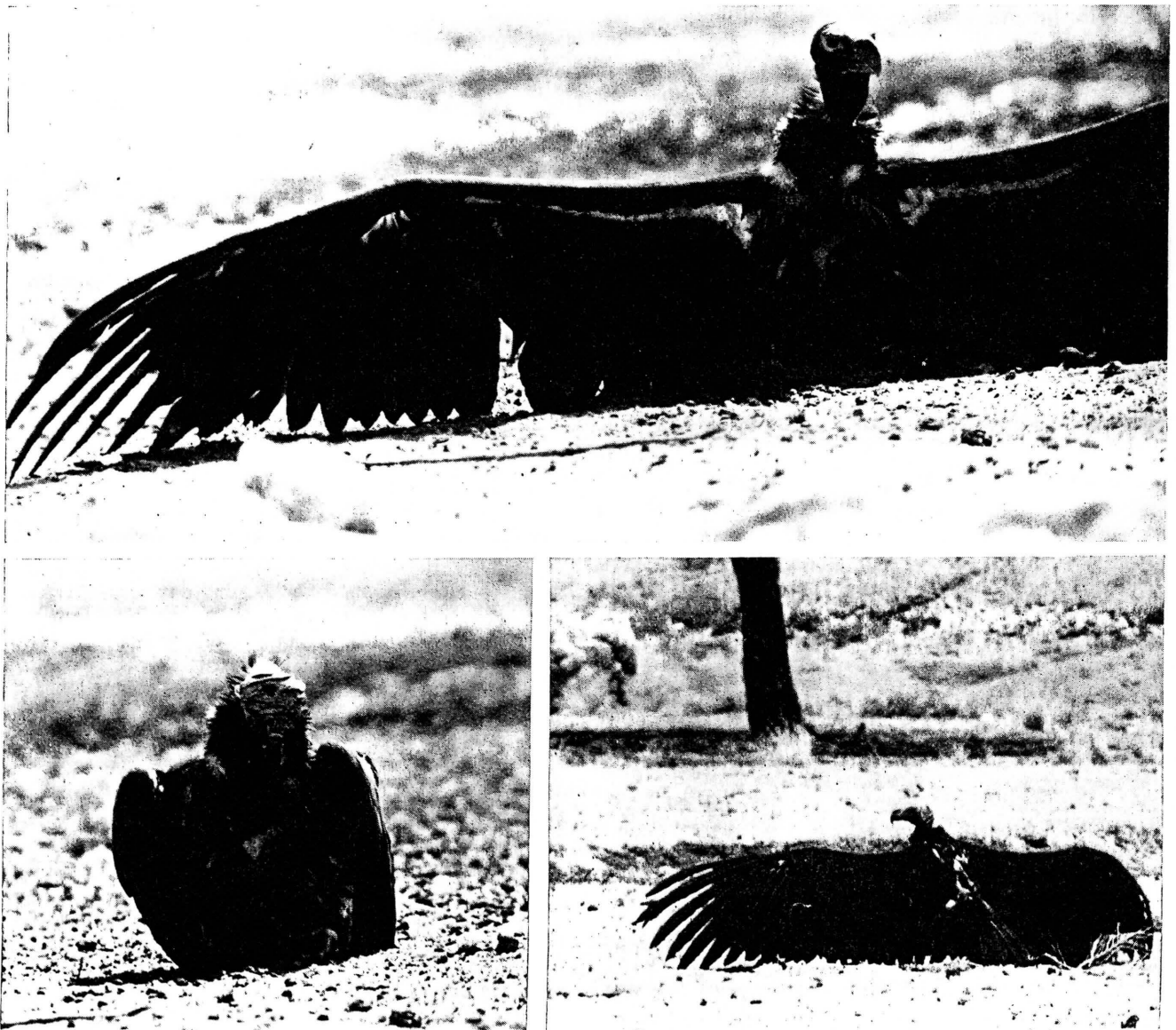


Figure 5. Basking Lappet-faced Vultures. a) and b) the same individual, resting on its tarso-metatarsi, in spread-wing posture and with closed wings. c) Rear view of bird in spread-wing posture.

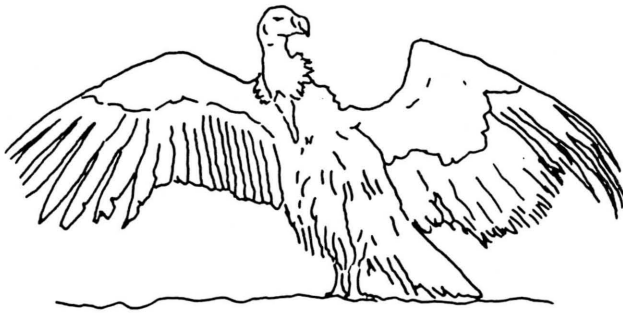


Figure 7. Cape Vulture in spread-wing posture for drying its plumage after bathing.

a) The Pattern in 1964

The example of the vultures' arrival times at Hotsas selected from our 1964 field studies is based on a 23-day check chosen at random between 14 July and 18 October (Fig. 8). The records are adjusted in the graph to the nearest 15-minute interval

and pertain to the arrival times of 194 birds, 153 Lappet-faced Vultures and 41 Cape Vultures, watched landing at the water site in the dry and sandy Hotsas River. The ratio of 3,73:1 matches that of the largest number of vultures from both species that we found assembled at one of the occasional carcasses, namely 26 Lappet-faced Vultures and 7 Cape Vultures (3,71:1) drawn to a dead ostrich near the eastern border of the Game Reserve. These ratios reflect the general balance between the two species roaming in the surroundings of Hotsas and Ganab in 1964, where Lappet-faced Vultures were about four times as plentiful as Cape Vultures. As expected, the assemblies of vultures at Hotsas varied considerably from time to time, ranging from an occasional solitary bird to the largest aggregation, which involved birds of both species and amounted to 14 Lappet-faced Vultures and 10 Cape Vultures. These figures, too, are representative of the local situation. While the above-mentioned dead ostrich had attracted the resident Lappet-faced Vultures of both the Hotsas and Ganab home ranges, the 14 Lappet-faced Vultures were resident

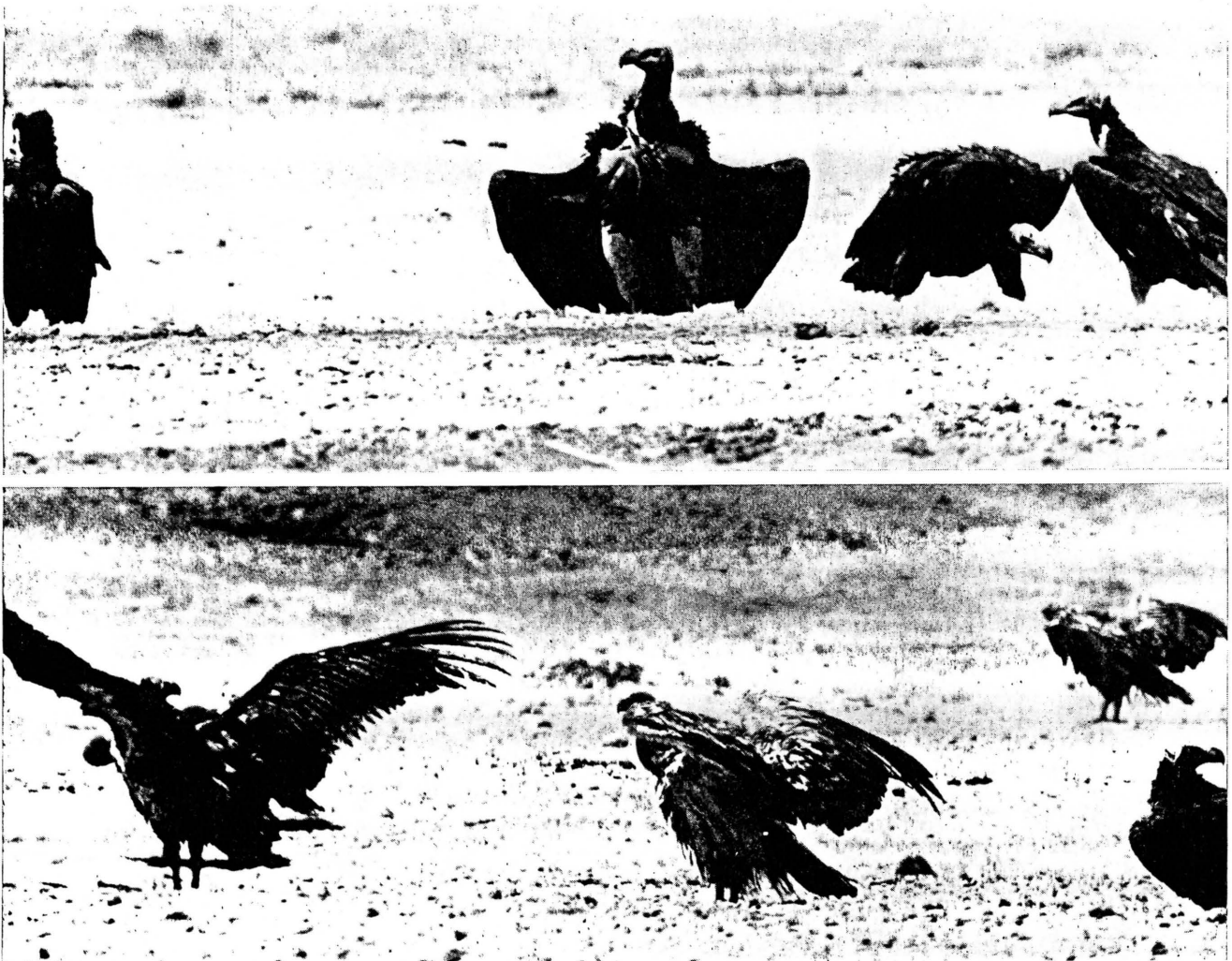


Figure 6. a) Lappet-faced Vulture basking with wings only slightly opened. b) Cape Vultures after their baths drying their wet plumages by spreading and fluttering their wings.

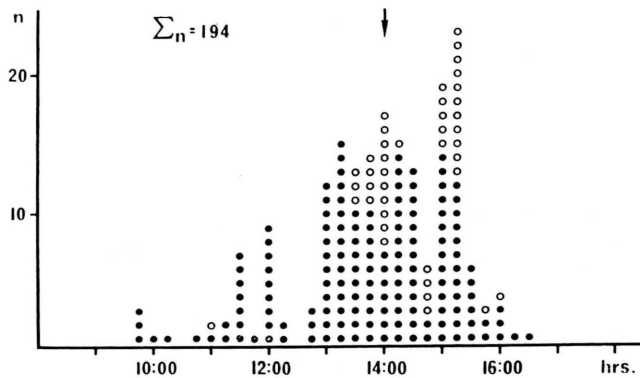


Figure 8. Arrival times of Lappet-faced Vultures (●) and Cape Vultures (○) at Hotsas in 1969. n number of birds.

in the close vicinity of Hotsas. The 10 Cape Vultures comprised the largest assembly of birds from this species during the entire observation period in 1964. As indicated before, they roosted in the nearby mountain range, and they appeared to scan a wider section of the flats than the Lappet-faced Vultures. They were also more attracted to the Hotsas water site than to Ganab; the terrain of Hotsas with a number of rocky rises surrounding the water site like an arena might be responsible for this.

Pairs and individual vultures showed a tendency to visit the water at Hotsas regularly for a number of days. Then when attracted by a large carcass like that of an adult ostrich, felled outside the vultures' regular home range, e.g. near Ganab, the birds would desert Hotsas for several days and utilize the water at Ganab.

In 1964 the earliest arrival of any vulture was at 09.45, the latest came to Hotsas at 16.30. Early arrivals, and sometimes those in the late afternoon too, usually came merely for a scoop of water and did not stay long. When the water sites were occupied by flocks of ostriches or groups of oryx, the Lappet-faced Vultures arriving early tended to flush the other animals from the water. These Lappet-faced Vultures would come in for a landing and sweep right over the heads of the ostriches or oryx, or they would perform brief and upsetting take-offs and flutter-walks toward them in their self-assured threat posture with the head lowered and the half-opened wings held in an angular position.

The birds that arrived from about 13.00 to 15.15 hours usually came for a prolonged stay and performed at leisure the behaviour mentioned above. Their presence at and near the water site could last for one to several hours. When they were brushed aside by groups of thirsty ostrich and oryx, they merely walked a few steps out of the way of the oncoming animals. When undisturbed they performed a sequence of activities ranging typically from drinking to bathing, basking with and without wing-flutter and various spread-wing postures typical of thermoregulation (Figs. 5 and 6a) and, after bathing, also for drying the plumage

(Figs. 6b and 7), to preening and resting. While resting they frequently lay flat on the ground right in the river sand, or they rested simply in an upright posture on nearby rocks and trees. In contrast to the Lappet-faced Vultures, the Cape Vultures were never seen resting in trees. (However in 1970, we found Cape Vultures at Hotsas also roosting on trees during daytime.) Early afternoon departures often meant a mass take-off for soaring flights, late afternoon departures dragged on and were mostly aimed toward the individual roosts and nest trees.

The diagram shows that the Lappet-faced Vultures arrived at the water site generally earlier than the Cape Vultures, with the 10% mark reached by 11.30 and 50% by 13.45. In comparison the Cape Vultures' 10% mark was at 13.30 and the 50% at 14.45. The Lappet-faced Vultures arrived frequently in twos, the second bird planing in some 30 to 60 seconds after its partner had landed (Fig. 9). The two birds would then go about their activities together or independently, yet keeping an eye on each other. Later they would depart in the same way, taking off in short succession, and unite for a soaring flight or follow each other in a low flight to their nest or to their night roost in an acacia tree.

The Cape Vultures arrived singly at intervals of several minutes. They mingled freely and peacefully with the Lappet-faced Vultures. When they departed (Fig. 10) they turned eastward and flew toward the mountain ranges (Fig. 2b) until they disappeared from sight.

There were days when no vultures came to the water at Hotsas, and then they would come again for days in succession. This, we believe, was primarily correlated with their feeding activity when carrion was located either outside or within the district. At times vultures carried bits of food to the water, or they regurgitated semidigested meat or intestines when they had just come from a carcass. Such food was either left or swallowed again once the birds had quenched their thirst. Left-overs remained either untouched and dried up, or they were taken by Pied Crows (*Corvus albus*), Black Crows (*Corvus capensis*), or Black-backed Jackals (*Thos mesomelas*), whichever came first.

b) The Pattern in 1969

Both Lappet-faced Vultures and Cape Vultures were more numerous at Hotsas in September and December of 1969 than at any time in 1964. The record of 433 arrivals on 12 days between December 2 and 18 pertains to 284 Lappet-faced Vulture and 149 Cape Vulture landings (Fig. 11), a 1,90:1 ratio compared to the 4:1 relation typical in 1964. The largest assemblies at Hotsas during the 1969 studies were 47 Lappet-faced Vultures and 25 Cape Vultures; for all practical purpose the ratio of 1,88:1 is identical with that of the total sample above.



Figure 9. Lappet-faced Vultures at Ganab. Two partners landing in quick succession alert the birds on the ground.

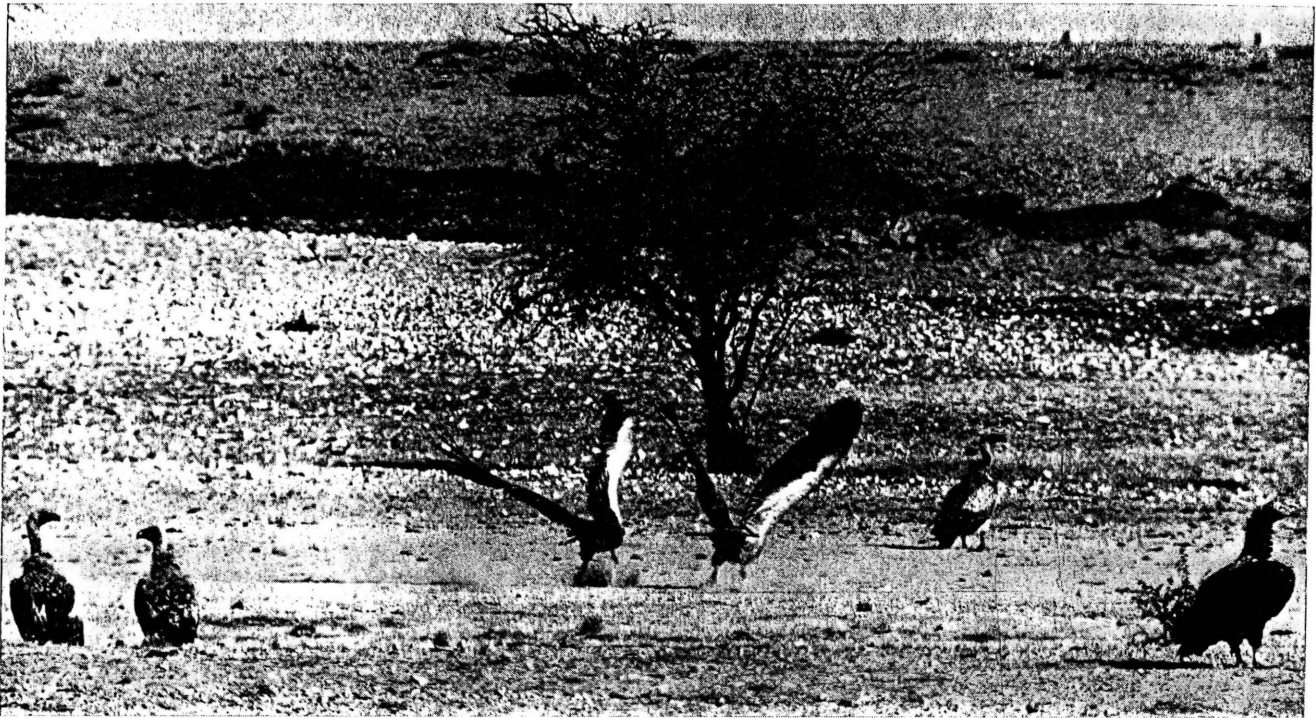


Figure 10. One pair of Cape Vultures taking off from the communal area at Hotsas.

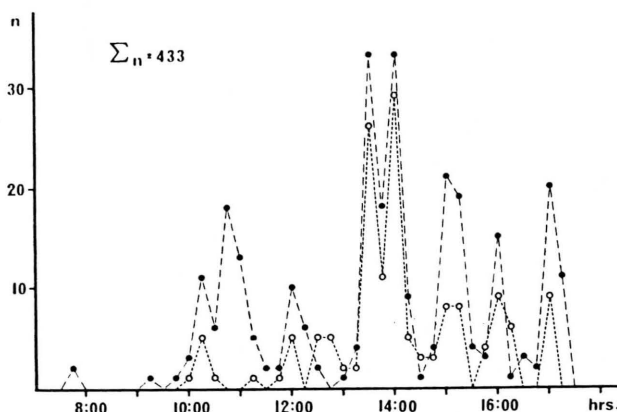


Figure 11. Arrival times of Lappet-faced Vultures (●) and Cape Vultures (○) at Hotsas in 1969. n number of birds.

Since the 1964 record of 194 vulture arrivals was based on a 23-day check from July to October, the two graphs span different periods and can not be compared directly. Certain comparisons seem nevertheless justified. It should be noted that the populations of the two species of vultures had remained the same in December 1964 as they were from July to October when the arrival times were recorded at the Hotsas water site. During the whole observation period in 1964 we never found any eggs or offspring and noticed no other immigrants aside from the young banded Cape Vulture. It should also be noted that the sample from the shorter period in 1969 is much larger than the long-term sample from 1964; it could be expected that the count in 1964 should have been larger if the birds had been more plentiful. Thus the records

in 1964 and 1969 reflect an equally reliable estimate of the total numbers of birds residing or appearing regularly at Hotsas.

The largest assemblies of vultures observed may well serve as a means to visualize their population increase. In 1964 we found the largest group of Lappet-faced Vultures composed of 26 birds, in 1969 the record number was 47 Lappet-faced Vultures. We consider both figures valid representations of the actual number of birds residing then in the neighbourhood of Hotsas and Ganab. Therefore, in 1969 we registered an increase by 1.8 over 1964. The comparable figures for the Cape Vultures, 10 in 1964 and 25 in 1969, reveal a growth factor of 2.5, which indicates that the Cape Vulture population had increased faster than that of the Lappet-faced Vulture.

The growth of the vulture populations is undeniable but difficult to explain without knowledge of the nesting success as well as the age and places of origin of the birds. Since records did not then exist, and since no banding program had then been carried out*, some guesswork seems justified.

The fact that the vultures are lawfully protected can not explain their population increase; the birds have been under protection ever since the area was declared a game reserve in 1907, and the law has been increasingly enforced for many years. The availability of water at Ganab and Hotsas, as well as in a few other places within the inner district

* Nest records and banding were initiated from July 1968 for Lappet-faced Vultures in the Namib Desert Park. However, none of the birds studied at Hotsas in 1969 was banded.

of the Namib Desert Park, provides no explanation either. The water sources utilized by the vultures have been available for more than a decade. The most likely cause underlying this population increase since 1964 seems the availability of increased amounts of carrion. As mentioned above, in 1964 we searched in vain for Lappet-faced Vulture eggs and young. Prior to 1964 there was a long period of drought, according to some statements since 1958, and all animal numbers had become very low. With the 1964 rains grazing became good and the herbivores recovered; in the following drought years they starved and vultures could thrive for some time. Then, food seemed to have become plentiful in 1969 after exceptional rains in March and April had created very favourable living conditions for herbivore animals in the inner Namib. The lush vegetation led to mass propagation, for example, among the ostriches. These birds began another reproductive cycle while their offspring were still very young and unwilling to leave the adult guards. Driven away and abandoned, many a deserted chick and juvenile ostrich died. Mountain Zebras (*Equus zebra hartmannae*), Springbuck (*Antidorcas marsupialis*), and other mammals, also Rüppell's Bustards (*Eupodotis rueppellii*) and Ludwig's Bustards (*E. ludwigii*), had considerably increased in numbers after the 1969 rains. Besides the propagations of some species, immigration seemed to be the major reason for the multitude of animals in 1969, and this was particularly so in the two species of vultures. With the increase in numbers of herbivores death occurred more often and carrion became available more frequently. By December 1969 the Lappet-faced Vultures, thriving at Hotsas, had built an amazing number of new nests indicative of the actions of the newcomers.

The graph reveals more data about the vultures frequenting Hotsas. Compared to the 1964 pattern, the arrival times of the vultures show a small but distinct peak in the forenoon and, after a characteristic mid-day drop, massive flights to the water in the afternoon. On the average the Lappet-faced Vultures arrived again ahead of the Cape Vultures, with 10% of the landings accomplished by 10.45 and 50% by 13.45. The latter reached the 10% mark by 12.30 and 50% by 14.00 hours.

The graph shows certain synchronizations in the pattern of the two species' arrival times. This happened usually when Lappet-faced Vultures headed for Hotsas in mass flights and thereby immediately attracted a following of Cape Vultures. One may assume that the latter, perched on high cliffs, had watched the flights of the former and followed suit when "something big and exciting" seemed to happen. The general social cohesiveness of the birds of the two species at the water sites was mentioned before. This flight phenomenon, too, was an expression of the interspecific social attraction whereby the Lappet-faced Vultures functioned as the socially attractive stimulus and played the role of the socially dominant partner during most of the contacts. Further, this flight behaviour of the Cape Vultures is also a typical example of their control of these maneuvers by sight.

In 1969 both kinds of vultures arrived frequently in the late afternoon, quite in contrast to the pattern in 1964. They often lingered and extended their stay at the water to less than an hour before sunset. Then the birds took off in quick succession for their night roosts. Though the Cape Vultures commonly left before the Lappet-faced Vultures flew to their nearby roosts, the bird departing latest was a Cape Vulture that left Hotsas at 19.00, i.e. 30 minutes before sunset, and headed swiftly eastward for the mountains. The late afternoon arrivals and evening departures did not occur in 1964 when the birds, on the average, seemed hungrier and more strongly motivated to take off for search flights in the early or mid-afternoon.

The frequent presence at the water site of more Cape Vultures than Lappet-faced Vultures at one time or another in 1969 may be explained by the large number of birds that could satisfy their social needs intraspecifically and gain a greater independence from the Lappet-faced Vultures during their daily maneuvers.

SOLITARY LAPPET-FACED VULTURES AND CAPE VULTURES AND THE INTRA- AND INTER-SPECIFIC FLOCK STRUCTURE IN THE COMMUNAL AREA

The following descriptions of the vultures' solitary states and diverse intra- and interspecific groupings show the sociability of the two species and the variability in the sizes and compositions of the flocks. The social attitudes of the birds varied in the course of the day, as well as over a period of time, and revealed a considerable social plasticity based on motivational changes and influenced by various environmental factors.

The water sites of Hotsas and Ganab were communal areas where the Lappet-faced and Cape Vultures assembled freely and generally peacefully. They performed their activities predominantly in close association, and solitary birds commonly sought and were permitted contact with individuals and flocks of either species. The largest group recorded in the communal area was at times exceeded by vulture assemblies at large pieces of carrion.

This suggested a still greater social tolerance, though not without tensions, than the one typically found in the community centers where the birds performed various maintenance activities. At the same time throughout the periods of our studies, the Lappet-faced Vultures kept their nest sites occupied, and there they maintained social distance from neighbouring pairs and solitary individuals. Most nests were separated by several hundred meters to several kilometers, but in 1969 some of the new nests occupied by different pairs were built in acacia trees less than 100 meters apart. Moving back and forth from the different locations the vultures switched from one social attitude to another in the course of a single day.

a) The Vultures at Hotsas in 1964

Solitary Lappet-faced Vultures and conspecific flocks up to 14 birds were recorded according to the following pattern and frequencies which include a total of 250 birds:

Numbers of Lappet-faced Vultures													
1	2	3	4	5	6	7	8	9	10	12	14		
16	13	7	4	7	2	1	4	3	2	2	1		

Frequencies of Observations (n=62)

The conspecific units of 40 Cape Vultures ranged from solitary birds to a flock of ten:

Numbers of Cape Vultures									
1	2	3	4	7	9	10			
5	1	1	1	1	1	1			

Frequencies of Observations (n=11)

In each of the two records the mode or unit of greatest frequency is that of the solitary vultures. They account for 25,8% of the observations of Lappet-faced Vultures and 45,4% of Cape Vultures. The sample of the latter is too small to yield a reliable evaluation of the distribution and frequencies of the observations; Cape Vultures were too few, and at the water they preferred mostly the company of Lappet-faced Vultures.

The counts of the conspecific aggregations of Lappet-faced Vultures suggest an exponential regression curve on which the frequency of the 2-vulture group deviates by -3,0 only insignificantly from the mode (the standard deviation is -8,16). This can be interpreted as an expression of the stable bond between paired birds that remain in close contact most of the time during their daily activity cycle. However, not all of the paired Lappet-faced Vultures arrived at the water together with their partners; in many instances one partner stayed in the empty nest or nearby while the other left for the water and communal rest area (p. 57).

Interspecific groupings of 89 Lappet-faced Vultures and 54 Cape Vultures at Hotsas in 1964 were recorded in the following 17 combinations and their corresponding frequencies:

		Numbers of Cape Vultures								
		1	2	3	5	7	10			
Numbers of Lappet-faced Vultures	1	1	1	1	1	1		5	Totals (Lappet-faced Vultures)	
	2	2		1				6		
	3		1	1				6		
	4	3						12		
	5	1			1			10		
	7			1				7		
	8	1						8		
	9		1					9		
	12	1						12		
	14						1	14		
		9	6	12	10	7	10	Totals (Cape Vulture)		

The frequencies and distributions of the interspecific flock combinations reveal no pronounced single preference or group structure, though statistically the association of 4 Lappet-faced Vultures and 1 Cape Vulture may be treated as the mode. Either species caused formations of interspecific flocks, whereby solitary or a few individuals of either one species were attracted by large gatherings of birds of the other species. Solitary Lappet-faced Vultures linking up with two or more Cape Vultures comprised a mere 4,5% of the sum of 89 Lappet-faced Vultures. In contrast, 14,8% of the 54 Cape Vultures were solitary birds that joined groups of two and more Lappet-faced Vultures. In other words, associations of solitary Cape Vultures with two and more Lappet-faced Vultures were three times as common at Hotsas as were interspecific flocks of solitary Lappet-faced Vultures with more than one Cape Vulture.

It should also be stressed that the vultures tended to flock in small groups when they came to the communal area for water and to perform their various maintenance activities. Seventy percent of the flocks were limited to a maximum of seven birds, and in 95% the largest group contained 13 birds. The exceptionally large flock of 14 Lappet-faced Vultures and 10 Cape Vultures came in the wake of a large carrion feast near Hotsas.

b) The Vultures at Hotsas in 1969

The following frequencies of solitary and flocked Lappet-faced Vultures, totaling 337 birds, were noted during the 1969 studies; they reflect the considerable increase of the population compared to the record of 1964:

Numbers of Lappet-faced Vultures																
1	2	3	4	5	6	7	8	9	10	11	19	20				
20	18	12	7	10	5	3	1	1	1	1	2	2				

Frequencies of Observations (n=83)

The solitary appearance and intraspecific flocks of 127 Cape Vultures were recorded as follows:

Numbers of Cape Vultures												
1	2	3	4	6	7	8	9	11	17			
7	3	3	1	4	1	3	2	1	1			

Frequencies of Observations (n=26)

As in 1964 the solitary vultures determine again the mode with 24,1% of the observations of Lappet-faced Vultures and 26,9% of the Cape Vulture counts. In contrast to the conditions in 1964, the increase in the numbers of Cape Vultures accounts for the reduction in the frequency of solitary birds.

The standard deviation from the mode of the distribution and frequencies of Lappet-faced Vultures is -2,8. The frequency of the occurrence of the 2-vulture flock is again close to the mode and based on a close contact between paired partners. This is less so in the Cape Vultures that occur nearly equally often in groups of 2, 3, 6, 8, and 9 birds.



Figure 12. Sections of large assemblies of Lappet-faced Vultures and Cape Vultures at Holsas.

The larger assemblies of vultures from both species (Fig. 12). displays were as slight as in 1964 and mainly directed to brief threats between conspecific pairs, mostly by Lappet-faced Vultures. Thus these gregarious birds easily and peace-

fully increased the flock size both in their com-

The interspecific grouping of 627 Lappet-faced Vultures and 485 Cape Vultures at Holsas in 1969 resulted in the following distribution of 56 combinations and their corresponding frequencies:

		Numbers of Cape Vultures															
		1	2	3	4	5	6	7	8	9	10	11 · 14	15 · 18	19 · 25			
Numbers of Lappet-faced Vultures	1	2	2		1	1		1		2	1		2		12		
	2	1	1		2			2				2			16		
	3	4	2		4		1								33		
	4		1		1	3									20		
	5			1	1		1								15		
	6	1				1		1	1					1	30		
	7			1											7		
	8							1							8		
	9	1												1	18		
	10	3			1	2					1				70		
	11		1												11		
	12						1							1	24		
	13	1								1					26		
	14									1					14		
	15							1							15		
	16		1							1	2				1	80	
	17								1							17	
	18								1							18	
	19								1							19	
	22								1							22	
	23												1			23	
	24											1				24	
	25								1							25	
	33													1		33	
	47														1	47	
		13	16	6	40	35	18	77	8	45	50	33	14	30	54	19	25
		Totals (Cape Vultures)															
																	Totals (Lappet-faced Vultures)

Totals (Lappet-faced Vultures)

Frequencies of combinations

As in 1964, the pattern of interspecific flock structure points out a tendency for small groupings but no preference for any one combination. As a result of the population increase in both species, the birds formed a number of flocks larger than those in 1964, and fewer solitary birds of each species joined groups of two and more birds of the other species, namely 1,6% of the Lappet-faced Vultures and 2,3% of the Cape Vultures. Compared with the situation in 1964 the reduction is particularly drastic in the case of the latter species (p. 54).

c) The Status of the Solitary Vultures

The preceding record showed that the communal area was visited regularly by numbers of solitary birds from each species regardless of the sizes of the populations. Some of these birds were juveniles. They were particularly evident in the small Cape Vulture population in 1964. Some immatures ap-

peared to be immigrants in the district, and at least one of them must have come from afar (p. 46). However, not all of the solitary vultures were juvenile birds. Judged by their plumage there were also subadults and adults among them, and some of the latter gave evidence that they were paired and had come to the water without their partners.

Though most of the adult Lappet-faced Vultures were paired and made their visits to Hotsas and Ganab together with their partners, single adults appeared quite regularly. Further, the frequencies of the 2-vulture groups and their multiples were not significantly different from that of the odd-numbered flocks. This points out that, in the presence of only monogamous bonds (we noted no polygamy), a substantial number of vultures had joined the flocks as solitary birds.

As stated above, the Lappet-faced Vultures had maintained their nests, although no eggs and no nestlings were present throughout the entire study in 1964 (no inspections of the occupied nests were

made during the short periods in 1969). The Lappet-faced Vultures used their nests for rests, sleep, and probably also as observation platforms. At times they displayed some weak interest in repairing the nest by pulling and rearranging a few twigs. Often one member of a pair remained on or near the nest while the partner was away and out of sight, performing a soaring flight in search for food or visiting a water hole and the communal center around it.

The single partner staying on or near the nest might have acted as a guard and defender had the nest site been invaded by a conspecific rival. But we saw no such case; the only active struggle about an occupied nest involved both partners that fought off an intruding pair of Lappet-faced Vultures. Though keeping the territory occupied and guarding the nest were most likely the main reasons for one bird to stay behind when the partner left, the guard seemed free to do whatever need might overcome it, as long as it could stay in the immediate vicinity of the nest. One occupant of a nest, becoming too hot on its exposed platform, found enough time even for a prolonged noon-day sleep and rest on the barren ground in the shade of a nearby bush (Fig. 13). This behaviour was quite different from the common thermoregulatory activity exercised through panting, spread-wing postures and water-baths.

Here and there a solitary adult Lappet-faced Vulture was joined at the water by its partner after a while. One could arrive at such a conclusion from

the couples' swift, perfectly tuned, and peaceful meeting, quite different from the threat-postures and threat-walks displayed between other birds, and also from the fact that the pairs acted in unison and later took off together for their roosts. Positive identification, however, was limited to a few familiar birds with individually distinct plumage patterns.

AGONISTIC BEHAVIOR

Agonistic behavior was essentially restricted to brief threats and the subsequent avoidance reactions of threatened birds. Lappet-faced Vultures, but rarely Cape Vultures, displayed threat-walks and threat-postures commonly when they arrived, flocked, and reorganized the flocks within the communal area at the water site. Though we shall publish a description of the behaviour together with analyses of our motion picture films, a brief account of the threat behaviour is given as far as it pertains to the regular events marking and influencing the flocking of the vultures in the communal district.

Vultures coming in for a landing at the water site commonly aimed for a spot near vultures already on the ground (Figs. 9 and 14a) and even landed in the midst of the flocks. Members of the assembled group expectantly viewed the approach and landing maneuvers of a new arrival. It would touch down, assume at once a self-assured threat posture, and displace another vulture right away (Figs. 14–16). With its wings slightly opened and



Figure 13. Lappet-faced Vulture resting in the shade of a bush near its nest on Tinkas Flats.

its head lowered the bird would walk toward one particular individual, seldom addressing all of the assembled vultures, and show off in front of all of them with a measured gait, thereby often pivoting exaggeratedly right and left.

As a rule, the threat displays were initiated by Lappet-faced Vultures and directed at other Lappet-faced Vultures. But they never broke up the

flock. The threatened birds rarely fought back, but gave way at once and permitted the new arrival to take its place at the water or else join and position itself in the flock. At times the threat display of the newcomer was curtailed by a quick and determined threat shown by one of the assembled birds that played a role of dominance within the flock. Some of the arrivals joined the flocks without signs of social dominance; they would approach



Figure 14. Threat displays of Lappet-faced Vultures at Hotsas. a) and b) Vulture landing at the water site displaces at once another bird. c) Threat display by new arrival. The threatened bird has turned away and walks a few steps to the side, while the dominant arrival switches from the threat posture to drinking without raising its head.



Figure 15. Lappet-faced Vultures; threat and alert postures.

other birds rather slowly and settle usually peripherally. These quiet arrivals were sometimes threatened briefly by the bird assuming the dominant position in the flock; though unchallenged it would show a threat display either to demonstrate its social rank within the flock or its determination to maintain its individual place.

Cape Vultures were hardly ever aggressive toward Lappet-faced Vultures when they landed or flocked with them; upon a threat from the latter they gave way immediately and accepted a subordinate position without signs of defense. Only when they crowded around a water hole they might briefly and defensively threaten both Cape and Lappet-faced Vultures.

Most of the time the vultures remained silent when they threatened one another. Occasionally they uttered a series of high-pitched shrieks, particularly when they had brief flare-ups of bill fencing. An excited bird might also give a single long-drawn shriek whereby it bent and stretched its neck in synchrony with the call.

There was never a case of agonistic excitement affecting all birds of a flock; threat behaviour did not seem correlated with the number of birds in a group. It was commonly restricted to individual rivalries fought out between two or three birds of a flock regardless of its size. However, the bystanders might become alert and watch the events. Since most of the threats were directed selectively toward one particular bird and not to just the nearest or any member of the flock, one had the impression that the birds knew one another individually and that the threats primarily served the purpose of maintaining the social status of a few high-ranking vultures (possibly males) of the district. Indeed, in many instances we found threat behaviour triggered not by the closeness (social distance) of any other bird, but rather by the individuality of particular birds. The lack of response of vultures standing along the path of a threat-walking bird suggests they knew the threat was not meant for them but for another vulture. The specificity of individual threats was so evident that one learned to predict accurately which vulture would threaten which other vulture. A Lappet-faced Vulture resting on a rocky rise several hundred meters from the water site would even fly over merely for the sake of threatening its particular rival when the latter had landed at the water. And

yet, after a brief threat display peace would be restored quickly even between rivals, and they would flock with each other and with other vultures with no further sign of hostility.

In summary, the threat behaviour displayed in the communal area by Lappet-faced Vultures, and rarely by Cape Vultures, was essentially an expression of social status which might involve a displacing of another bird merely for showing social strength or maintaining an individual distance or place.

DISCUSSION

The Social Status and the Time Schedule of the Vultures in the Communal Areas

This introductory and fragmentary report on the behaviour of Lappet-faced and Cape Vultures in the Namib of South West Africa deals with some preliminary findings concerning the time schedule and social status of the vultures when they flock outside their nest territories.

Nothing is known about the nesting of Cape Vultures in the district where the observations were made. Lappet-faced Vultures occupied nests in pairs and had them built on top of acacia trees. The pairs occupied and defended their nest territories, often including two nests or nests under

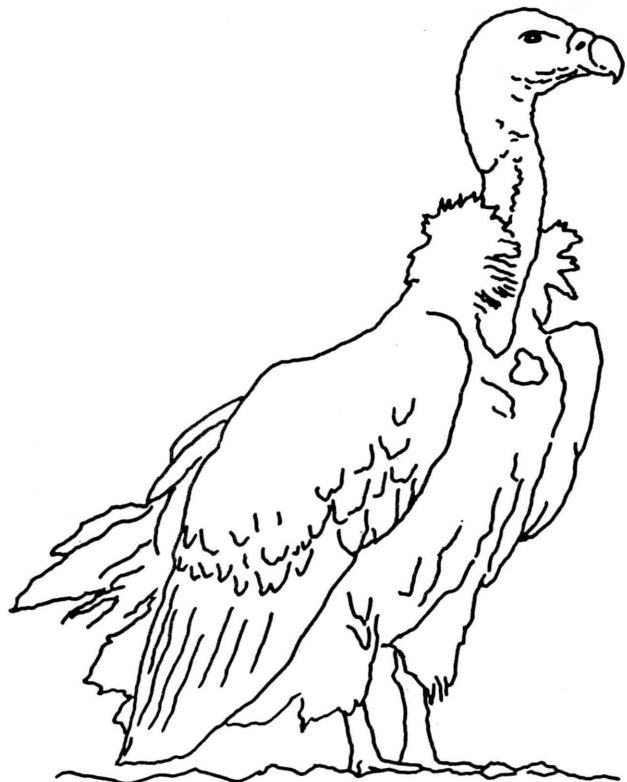


Figure 16. Cape Vulture; alert posture.

construction, and maintained their social (nest) distance from neighbouring pairs also when they were not in a reproductive state, that is when they had neither eggs nor chicks. In contrast to the social isolation of the pairs at their nest sites, the Lappet-faced Vultures were gregarious outside their territories and flocked readily with their own kind as well as with Cape Vultures. This signifies a typical change in their sociability in the course of their daily activity cycles.

Many birds of both species could be seen soaring together above the gravel plains of the inner Namib in their search for food. The birds were attracted to one another by sight; social induction was very strong. Search flights were usually initiated by one or a pair of vultures. Birds on the ground, occupied with various activities, would notice this, view the fliers for a while (Fig. 17), and then take off to join them. Others, possibly less hungry, might remain on the ground or become alerted only when the soaring birds suddenly descended toward a food source. In fact, this flight maneuver seemed to be a most important social stimulus to which other birds responded by sight. The basic reason for the vultures' sociability during the appetitive phase of their feeding drive must be the great selective advantage brought about by the relative ease and success with which a large number of vultures searching together could locate a usually single piece of food by sight.

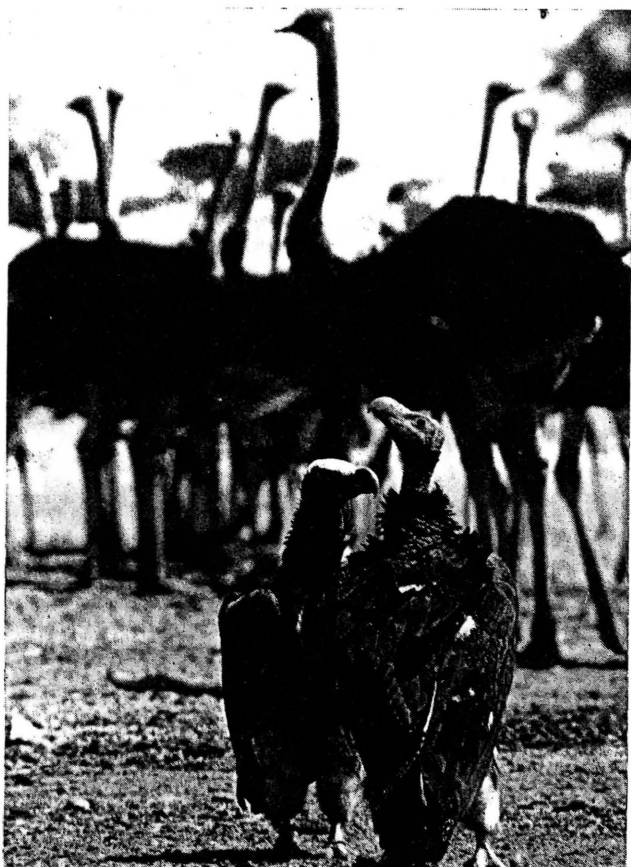


Figure 17. Pair of Lappet-faced Vultures viewing conspecifics and Cape Vultures that took off from Hotsas; moments before they joined the latter in their soaring flight.

Feeding, too, was a social event. Vultures of both species descended to the same carcass and fed side by side, though social tension kept the birds at individual and group distances. Social rank seemed responsible for the quality and quantity of food one bird or the other might take from a carcass. As a rule, Cape Vultures were subordinate to Lappet-faced Vultures when feeding on a piece of carrion. The non-aggressive partner of a high-ranking bird (male?) would profit from sharing the place with its partner. The intake of food was generally accomplished within a short time. This characterized the vultures as typical occasional feeders. When the occasion arose, they gobbled as much food as they could, even if it meant regurgitating part of it when they were so overstuffed that they could fly only clumsily and with great effort.

Feeding was followed by a lengthy resting period; much of it was spent outside the nest territories. This provided more and ample opportunities for social gatherings. Intra- and interspecific flocking was particularly favored since the birds preferred the few available water sites and their surroundings for a communal gathering place. Usually they were drawn to the water after a meal, but the attraction that the communal area held for the vultures must have been as great, for they came often without drinking any water, but seemingly rather for social contact, rest, and the performance of maintenance activities. The time the vultures spent in the undefended communal range suggests that the birds, after having feasted profusely on the carcass of a large animal, easily fasted for a couple of days before again becoming motivated to spiral skywards in search for more food.

When the vultures flocked during their flights either playfully for the sake of soaring and social contact or in search of food, when they flocked at a carcass to feed, or gathered for various maintenance and social activities in the communal area, the paired adult Lappet-faced Vultures maintained social contact with their respective partners. Solitary birds might abandon the flock practically unnoticed, but partners kept a close watch on each other and usually left together, taking off in quick succession. The discriminatory behaviour of the birds made it likely that they recognized not only their individual partners, but knew one another individually with the exception of new immigrants.

Between the two years of 1964 and 1969 during which we made our limited observations, the populations of the two species grew from about 26 to 47 Lappet-faced Vultures and from 10 to 25 Cape Vultures. Comparably, the largest mixed assemblies in 1964 amounted to 26 Lappet-faced Vultures and 7 Cape Vultures, or 14 and 10 respectively, and to 47 Lappet-faced Vultures and 18 Cape Vultures, or 16 and 25 respectively, in 1969. Though the vultures generally preferred to remain in small groups, the larger aggregations did not cause an increase in agonistic behaviour. They remained rather equally mild regardless of the size of the conspecific and interspecific flocks. One can say that the birds were socially extremely tol-

erant, that they were not overpopulated to cause any signs of social stress, and that their stable sociability might be a built-in behavioral mechanism of an important selective advantage. (Certainly no data whatsoever exist on how many vultures constitute a balanced population, or an under-, or overpopulation.)

Independent of the size of the populations, a fair number of juvenile and adult vultures came to the communal centers as solitary birds. Some, if not most of the adults coming solitarily were paired but had left their partners behind at the nest. This expresses, too, the strong motivation by which these birds were drawn to the communal centers.

The question arises what significance the regular intra- and interspecific social gatherings of the vultures might have. The most important reason seems to be the formation, maintenance and strengthening of the social bond, both intra- and interspecifically, that is the very basis for a successful and selectively advantageous collective search for food. No other reason for the vultures' regular and prolonged gregariousness seems as important as this one. The wide-spread protective advantage of flocking was unimportant as the birds under study were never attacked by any natural enemy. (*Genetta genetta* and *Felis libyca* are locally considered enemies of the vultures).

The process of intra- and interspecific socialization was particularly favored by the frequency and duration with which the vultures frequented the communal sites (graphs, p. 50 and p. 52), their mass arrivals, as well as the synchrony in arrival times of both species. It is also shown by the fact that the vultures reasserted their social rank quickly with brief and ritualized threats, but flocked peacefully otherwise. Their rest and various maintenance activities, which they performed side by side in their communal areas, might as easily be accomplished singly in the absence of any social partner; not one case of predation was noticed during the entire periods of observation. If adult vultures are preyed upon at all, it must be very minimal indeed. It seems a valid and useful hypothesis to view the intra- and interspecific socialization of Lappet-faced Vultures and Cape Vultures as a most efficient means of guaranteeing a selectively advantageous communal food gathering. Though many other events, such as the formation of pairs, take place during the social meetings within the communal areas, none of them can account for the regular and lasting assemblies.

SUMMARY

Lappet-faced Vultures (*Torgos tracheliotus*) and Cape Vultures (*Gyps coprotheres*) in the inner Namib of South West Africa were found to spend a considerable portion of their daily activities associated in conspecific (up to 20 Lappet-faced Vultures and 17 Cape Vultures) and mixed flocks (maximum numbers of Lappet-faced and Cape Vultures 47:18 and 16:25 respectively).

Birds of both species were attracted to one another by sight. They assembled during their soaring flights in search for food, while feeding on carcasses, and in their communal centers. The latter were suitably located around the few and much frequented water sites of Hotsas and Ganab.

The Lappet-faced Vultures lived socially isolated on their nests which they occupied and defended also during the non-reproductive season. Nothing is known about the nesting of Cape Vultures in the district where the observations were made. They had their roosts in the rocky faces of the mountains in the east where they supposedly nested.

While the birds gathered in the communal area, agonistic behaviour was kept at a minimum and was displayed more by Lappet-faced Vultures than by Cape Vultures when they entered a flock or reorganized it. The Cape Vultures were generally subordinate to the Lappet-faced Vultures. Threat-walks and threat-postures served to displace birds and especially to display social dominance by a few high-ranking vultures. The brief and ritualized threat gestures were quickly terminated through avoidance responses of the threatened birds which hardly ever stood up against the socially dominant vultures.

The social attraction and tolerance of the birds of both species guaranteed the maintenance of their flocks and remained stable regardless of the size of the gatherings. Data are given on the sizes of the flocks, pair bonds, social interactions, as well as on the occurrence and the status of solitary birds.

The regular and prolonged intra- and interspecific socialization of Lappet-faced and Cape Vultures is seen as an adaptation for the selectively advantageous method of communal food gathering these birds practiced.

The report contains also a general description of the birds and comparisons of population and flock sizes in 1964 and 1969. The maximum number of birds observed in the district were 47 Lappet-faced Vultures and 25 Cape Vultures.

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