rain-correlated variations in mean laying date that I documented. The markedly circannual laying date of particular pairs, certainly both identifiable partners at nest no. 63 where the date was exactly the same in both study years would, however, question the degree of influence of these proximate controls.

It must constantly be borne in mind that the food source of this colony is an "artefact" of stock-farming practices. As the food source has changed markedly within living memory, it is unrealistic to relate overall timing of the colony's breeding cycle to its current food source. In this regard, Houston (1976) concluded that the breeding season of the congener G. rueppellii in East Africa was so timed that the fledging date coincided with a relatively abundant period of food. This link certainly does not hold at Potberg, where fledglings appear during a time of relative decrease in food abundance.

It is of interest to note that throughout the Cape Vulture's range there is a gradation in laying dates, from earliest in the Transvaal (early May) through to latest in the southwestern Cape (mid June). This appears to be a reflection of environment-induced modification of what is largely the innately predetermined time of initiation of breeding, but the factors involved are unknown.

The accurately determined period length of 57 days compares favourably with the 56-day estimate of Mundy (1982:165) and the 57,6 day period of Boshoff & Currie (1981). It is clearly longer than the figures given in Brown & Amadon (1968) and McLachlan & Liversidge (1978).

4.3.3.The nestling period

Immediately after hatching, the tendency was for both parents to stay at the nest together for longer stretches than during the incubation period. Nestlings were essentially guarded all the time by at least one parent (this study, Mundy 1982), and this contrasts with attendance behaviour of other vulture species (Mundy 1982, Pennycuick 1976). Predation may account for a substantial portion of egg and nestling loss in colonial situations, e.g. gulls , reviewed in Hunt & Hunt (1976). The high parental attendance by G. coprotheres, for the stage of the period after the nestling is dorsally feathered, could then reflect an anti-predator response ; more likely it is an effect of coloniality and the traffic of strangers to the nest (Mundy 1982). For example, the ability of parents to repulse Black Eagle predatory attempts is enhanced as a result of their colonial nesting habit (4.2.6., appendix b).

That attendance stints of both sexes were shorter than during the incubation period reflects the increased attendance of both parents, as well as not such close attendance by any one parent. This made changeovers more difficult to discern and resulted in a greater proportion of "within-day" stints being documented. The earlier changeover time reflects the weather conditions of approaching summer, as compared to the previous period (see chapter three), as well as the stimulation provided by the nestling to return to the nest earlier.

Nestling growth and condition, as well as aspects of the quality of food as it affects nestlings, are considered in chapter three (3.2.4. and 3.3.).

Nestlings of the Lappet-faced Vulture are known to be parasitised by Hippoboscid flies Icosta meda (Anthony 1976), and in 1981 Potberg nestlings were heavily fed on by simuliid flies. As parents remove flies, the number of flies that I observed was probably greater than it would have been had the parents not been disturbed (by me). Simuliid flies require water in which to breed (Ledger 1979), and the stream in the kloof provides a suitable habitat. The Potberg colony is the only one I know of with a suitable breeding ground for these flies within some 400 m of the breeding ledges (see also Mundy 1982, Tarboton & Allan in press). That the degree of nestling infestation is related to preceding precipitation, is indicated in Figure 25, although other factors may influence their presence.

Simuliids are known to be vectors of protozoan parasites (Fallis et al. 1973), and are likely vectors of avian haematozoa into vulture nestlings (Boshoff & Currie 1981, Boshoff 1981). Blood smears of 1979 nestlings (a year of heavy infestation) contained one or more species of Leucocytozoon, with the degree of infection varying from low-grade in some samples to a higher parasitaemia in others (Boshoff & Currie 1981). The fact that the early blood film taken from a 22-day old nestling revealed no *Leucocytozoon* presence probably reflects an aspect of the flies' life cycle. For example, gametocytes of *L. neavei* were first seen in peripheral blood of Guinea Fowl *Numida meleagris* nestlings 14 days after infection from sporozoites from *S. adersi* (Fallis *et al.* 1973). The subsequent fledging success of those Potberg nestlings with high parasitaemia is unknown, thus whether *Leucocytozoon* contributes to Cape Vulture mortality or morbidity remains undetermined. The nestling that exhibited a low-grade *Leucocytozoon* infection (and which was fed on by a large number of simuliids) in this study was last seen flying six days after it fledged, and it did not have a PFDP. Given the necessity of at least some supplementary aid from the parents during this stage of its life (4.3.4.), even if it dispersed, the chances are that it did not live long. However, no link between its probable demise and the parasitaemia is suggested ; the nestling certainly lived for some three months with this infection. Thus more observations of the fate of fledglings known to be infected with blood parasites are needed before any conclusion regarding the effects of either parasite can be reached.

In a previous study of haematozoa from southern African vultures, the Cape Vulture was the only species that was not infected with blood parasites (Greiner & Mundy 1979). This was ascribed to its unique nesting habit, as well as the timing of its breeding season. In their first weeks of life, nestlings have a relatively soft skin and are either naked or sparsely covered with feathers ; consequently it is at this stage that they are particularly vulnerable to the attentions of biting insects (Markus 1974). My observations of the different extent of feeding by flies at two sequential visits to the nest would tend to support this. Greiner & Mundy (1979) sampled nestlings from summer rainfall colonies, during which time "appropriate ornithophilic vectors are evidently scarce or absent .. precluding transmission of potential pathogens ..". These results then indicate another unique effect of this colony's location, and consequent implications for the members. The adults display a behavioural trait related to the presence of the flies in that they remove flies with their bills, and it has been reflected upon previously that many hosts may be evolutionarily adapted to their blood parasites (Markus 1974).

4.3.4.The post-fledging dependence period

Parental care extends beyond the pre-fledging periods in a wide variety of birds (Ashmole & Tovar 1968, Burger 1981, Diamond 1975, Feare 1975, Nelson 1976, Skutch 1976), including raptors (reviewed in Brown & Amador 1968, Newton 1979, see also Sherrod 1983). It is, however, largely unstudied due to obvious difficulties in observing the juveniles after they fly. Particularly lengthy individual PFDP lengths have been observed in Crowned Eagles Stephanoaetus coronatus (11,5 months)(Brown 1966), Harpy Eagles Harpia harpyja (10 months) (Fowler & Cope 1954), and the California Condor (7 months) (Koford 1953). In most members of the Accipitridae, much shorter periods have been documented (e.g. Johnson 1973, Newton 1979:Table 18, Sherrod 1983, Snyder & Wiley 1976). New World Black Vultures Coragyps atratus have been observed to continue to feed juveniles away from the nest site some six months after fledging (Jackson 1975); similar behaviour (away from the site) has not been observed in any accipitrid species. Individual PFDPs have also been documented for Old World vultures (Anthony 1976, Mundy 1982, Mundy & Cook 1975, Pennycuick 1976), although observations are minimal. As a general rule in raptors, the larger species remain dependent longer (Newton 1979).

The occurrence of prolonged parental care certainly seems to be correlated with the use of skilled feeding methods, exploitation of scarce foods and proficiency in accurate flying (Ashmole & Tovar 1968, Koford 1953, Stonehouse & Stonehouse 1963), and the improvement of these with age and experience (Dunn 1972, Lack 1968, Orians 1969). A surplus of fat, laid down during the nestling and post-fledging periods, would serve to tide the juvenile over during periods of early self-feeding when its skills were not mastered to the point where hunting was more likely to be successful (Cade 1982, Drent & Daan 1980, Sherrod 1983). Using these reserves, a juvenile may survive approximately three weeks without food. In the instance I documented, after this length of time the juvenile was some two-thirds of its "normal" body weight.

The lack of proficiency in flying is probably accentuated in young griffons, whose wing loadings approach the possible maximum (Pennycuick 1972). This was illustrated by the number of days that lapsed before the first observed foraging attempt in three of the 1981 PFDPs (Table 9). Lack of proficiency in the factors listed above would act to increase the probability of mortality of this age-class, and this would account, partly, for the variation in length of PFDP that is often observed (this study, Newton 1979). The lengths would also be influenced by the particular, local, food conditions : it is clearly advantageous to the juvenile to attain efficiency in feeding as soon as possible.

In practice, it is very difficult to document the proportion of food supplied by the parents compared to the proportion obtained by the juvenile through the different stages of the PFDP. A relatively higher concentration of available food would facilitate this transition (see also chapter six). This was borne out in observations of Oystercatchers Haematopus ostralegus, where the age at which parental feeding ceased varied with the habitat, and consequently with food (Norton-Griffiths 1969).

Juvenile Cape Vultures initiate contact with their parents, and not vice versa. In the breeding kloof this occurs at the natal site only. The behaviour of the juvenile that never revisited its site, and consequently starved, emphasised this aspect : its parents made no attempt to visit it at its often used perch point 15 m below them. Also, juveniles spent very little time alone at their nest sites, and were clearly stimulated to visit them by the presence of the parents. Juveniles may solicit food from adults other than their parents, however my circumstantial evidence indicates that parents differentiate between similarly-aged offspring and supply food to their own offspring only. Given what I consider the necessity of parental feeding aid during this critical period, this trait is of adaptive value in increasing the probability of the parents' reproductive success. It is surely significant that the

Aasvogelvlei immatures arrived at Potberg some 2,5 months after fledging : their "dispersal" presumably followed a PFDP, rather than taking the place of it.

Although Newton (1979) cites two references of "well authenticated" cases of adults terminating the period by driving their young away, these do not in fact refer to such behaviour. The overt aggressive terminations that I observed, together with Rowe's (1947) observations of a juvenile Black Eagle, would then appear to be the only recorded instances in the Accipitridae.

The traditional view of the relationship between parent and offspring assumes unilateral parental investment (Wilson 1975); however, the phenomenon of parent-offspring conflict was apparently clarified by Trivers (1974), who interpreted it as the outcome of natural selection operating in opposite directions on the two generations. The timing of the period of conflict is explained in terms of the inclusive fitness of the juvenile, and of the reproductive fitness of the parent ; both fitnesses are defined in Wilson (1975). In vultures with such an extended breeding cycle, the cost to the female in terms of her ability to produce an egg in the next season becomes clearly apparent as the PFDP approaches that season's laying date. This was illustrated by the increase in frequency of copulations during the PFDP as it overlapped with the pre-laying period.

In overall terms, a "choice" must be made between deferring the next season's breeding attempt and continuing to supply the juvenile with food, or terminating the PFDP. If the former, the juvenile's inclusive fitness diminishes, but its reproductive fitness is enhanced only if it could not have survived without the additional parental help, ceteris paribus. Factors influencing this "switch" are those that necessitated the (lengthy) period in the first place : the juvenile's requirements, and its proficiency in flight in relation to its ability to obtain its particular food-type. My observations indicate that Cape Vultures, at least at Potberg, attempt breeding in the season following a successful cycle, thereby opting for the latter.

The aggressive interactions between parents and their offspring (recognisable to me) formed a subset of all the intraspecific interactions that I observed. The observations of overt aggressive termination of the period are then consistent with parent-offspring conflict theory (Trivers 1974), and are not neccessarily "anthropomorphic and erroneous" (Brown & Amadon 1968). The case of the juvenile that was chased off the site and subsequently fed at the site, is indicative of the extended time-period of conflict of fitnesses of either "participant" (as illustrated in Wilson 1975: Figure 16-2).

CHAPTER FIVE : POPULATION DYNAMICS

5.1.Introduction

This chapter is concerned with breeding rates, survival rates and the effects of the consequent reproductive rate on the southwestern Cape (sub) population. Directly concerned with numbers of individuals, it documents the state (including influx and efflux) of the population as it was during the study period, and provides a framework for population trend prediction.

Griffon vultures, together with sea-birds and other large raptors, have a very low reproductive rate (Amadon 1964, Wynne Edwards 1955). Individuals can be differentiated according to breeding status and capability ; the non-breeding segment then includes non-breeding "breedable" adults, sub-adults and immatures, e.g. four year olds, and other immatures, e.g. juveniles. The term "breedable" refers to individuals that are capable of breeding, but for various reasons are not active in a particular year, and is used because some immature plumaged individuals are fully capable of breeding (this study, see Newton 1979:Table 21). The demographic parameters associated with the dynamics of this population (including those given by Brown & Cade 1972) are then considered separately. Breeding success during the study period and for the previous six years is documented in chapter four (4.2.5.).

5.2.Information concerning the demographic parameters

5.2.1.Population size and structure

Information pertaining to colony size prior to this study is collated in Boshoff & Currie (1981). The number of active Potberg nest sites for the 1975 - 1983 period, as well as Aasvogelvlei 1981-1983, are depicted in Figure 30. The totals of all birds present in the colony were very constant (Figure 17), save for the drop of some 17 per cent of the total following the helicopter incident (see 4.2.6.). Simultaneous counts at

Aasvogelvlei produced 82 (Potberg 57) in 1981 and 74 (Potberg 59) in 1982 (A.F.Boshoff, N.G. Palmer pers. comm.). Figure 17 documents counts made just before dark at Aasvogelvlei during the study period.

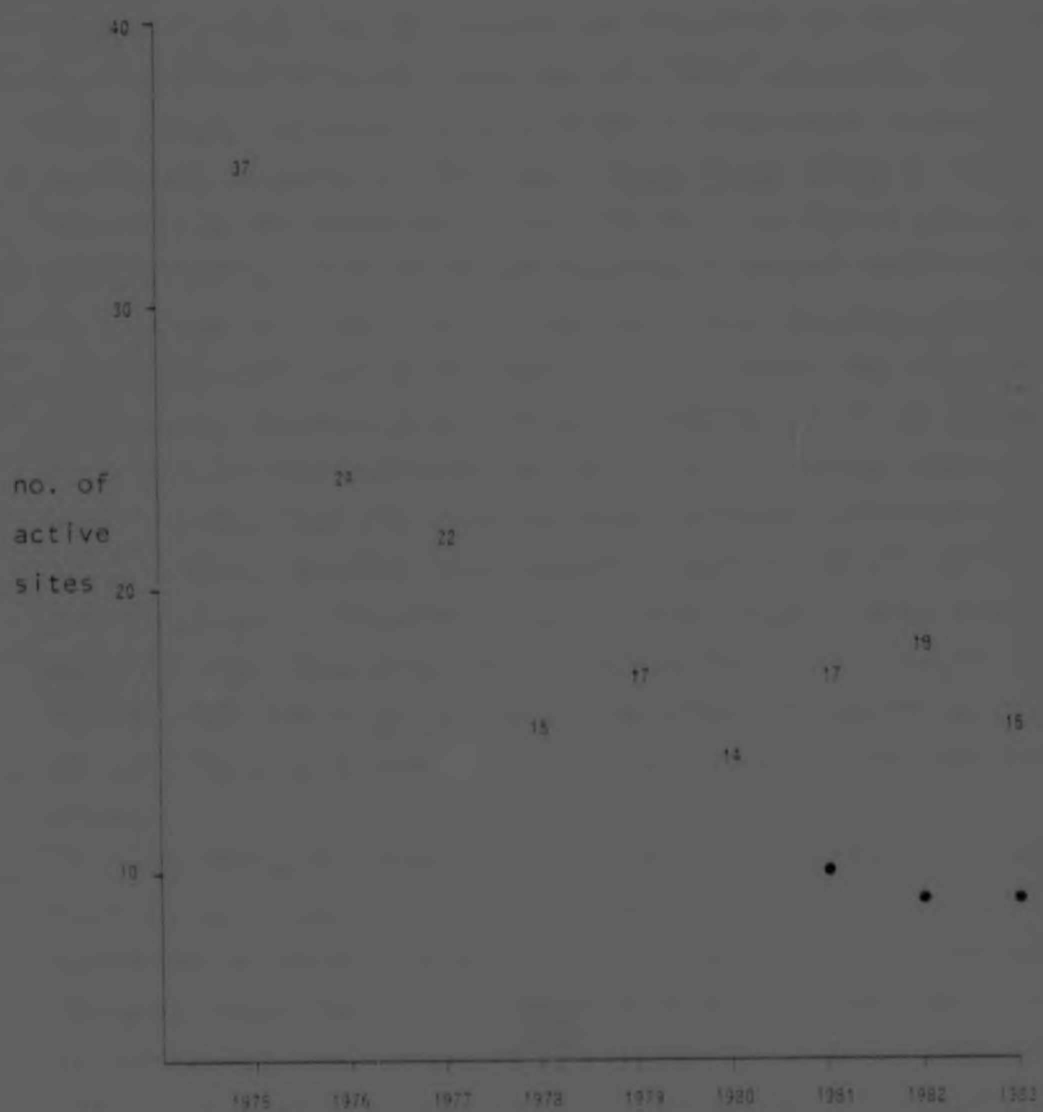

Figure 30. The number of active nests at Potberg (numbered) and Aasvogelvlei for the last nine years.

Three immatures, ringed as nestlings at Aasvogelvlei in 1981, were resighted at Potberg (4.2.4.), and this confirmed inter-colony movement. As the colonies are 120 km apart (line of sight), this involves some 2,5 hours flying time, using an average speed of 50 kph (Boshoff, Robertson & Norton in prep., Pennycuick 1972). These two colonies were therefore assumed to constitute a single population. This population was, in turn, assumed to be discrete in terms of influx of birds from other colonies : no ringed bird from any other colony has ever been found in the area, nor has any colour ringed "foreigner" been resighted (this study, Boshoff & Currie 1981). However one immature, sighted in 1982 at Potberg and age-estimated as having fledged in 1981, was not ringed and therefore not from Potberg or Aasvogelvlei. This incident was the only suggestion of influx from other, unknown, areas. After a newspaper report which documented vultures at Perdeberg (Cape Times 15 April 1983), an old site in the Langeberg range (33 57S ; 21 32E), I checked the area, which is 18 km SW of Aasvogelvlei, in April 1983. I counted 28 vultures and saw one Aasvogelvlei 1982 immature. The amount of "whitewash" suggested that this location was used fairly frequently. Considering efflux, a number of birds ringed at Potberg have been resighted or recovered in various areas of the Cape Province (but not near any other colonies) before initiation of this study (Boshoff 1981,Boshoff & Currie 1981:5). No similar incidents were documented during this study. These instances confirm that immatures may disperse from their natal colony (Mundy 1982, Piper et al. 1981), and therefore cannot be assumed as dead merely because they are no longer resighted at the colony.

The foraging range of the Potberg vultures was recorded indirectly (postal survey) and directly (radio-tracking) : the following instances document sightings made away from the defined foraging range (see 3.2.1.). Separate sightings were made of one vulture (same individual ?) in February and April 1982, 105 km WSW of the kloof and ca 40 km SE of Aasvoelkop, a defunct vulture roost (Boshoff & Vernon 1980, I. Bell, ex P. Steyn in litt., Martin 1983). A single adult was observed 45 km SSE of Aasvogelvlei (118 km ENE of Potberg) in August 1982 (A.F. Boshoff in litt.). The three other sightings given by Martin (1983) were within a 60 km radius of the kloof, some 1,5 hours vulture-flying time distant. Records for the decade 1970 - 1979 are given in Boshoff et al. (1983:Figure 17).

Age estimations of all birds in the colony (divided into two classes) were made at the start of each breeding cycle . Thus at the start of the 1981 cycle, 43 (75 %) were estimated as five years old and older ("breedable" age). Seventeen breeding pairs comprise 34 breeders, which constituted 61 per cent of the then current total of 57 birds. The proportion documented at the start of the 1982 cycle was of 40 birds five years and older (70 % of the then current total). Thus 34/43 (79 %) of "breedable" birds were active in 1981, and 36 / 40 (90 %) in 1982.

At Aasvogelvlei, a maximum of 19 vultures was counted in 1981, of which at least two were clearly immatures. Probably one of these was active (5.2.2.) and in that year, ten sites were active, i.e. 20 breeders at the colony. In 1982, 16 was the highest count, and of nine breeding pairs, eight eggs were laid.

5.2.2.Deferred maturity

Vultures are included in the group of birds which show a deferred maturity by not breeding in their first few years, and this obviously affects the breeding dynamics of the population in question. In 1981 then, of 34 active breeders 2 were estimated by plumage characters as immatures and 2 of 36 in 1982. Certainly at two sites that were activated for the 1982 cycle, both females had brown eyes and were estimated as no older than four years (and into their fifth). Of seven ringed breeders in 1981, and six in 1982, only two were of known age (Robertson 1983b), as others had either a metal ring (four), or had missing colour rings (two). Of the known age pair in 1981, the male was six years old (and into its seventh) and the female four years old ; it is possible, but unknown, whether this same pair used the same (active) site the previous cycle. A female, with a missing ring and only observed in 1981, was either ringed in 1974 or 1975 if ringed at Potberg : more likely the latter, it was then five years old when it produced an egg in 1981. And the age of another (male) with missing rings could not be determined with adequate accuracy. All three breeding adults with metal rings could have been ringed in any year between 1951 and 1973 (Boshoff & Currie 1981). A female ringed in 1977 at Potberg commenced breeding in the 1983 cycle (possible mate replacement, see 4.2.1.), then six years old and into its seventh year. It was observed as not breeding in the previous two years.

No ringed birds bred at Aasvogelvlei in either year. In 1981, A.F. Boshoff and I classed only one breeder (subsequent dead egg) as an immature, and estimated it at four years old.

5.2.3.Frequency of active sites, and of breeding

As with other raptors, individuals show breeding periodicity by not breeding in particular years : this is particularly evident in a colony where all "breedable" birds are visible. If it is assumed that pairs (or at least one of the pair) occupy the same site when active in two consecutive years, breeding frequency can be determined by examining active sites as well as observing recognisable individuals. Considering 64 sites over eight years (average annual increment of 1,6 new sites documented per year from 1975), the same site was active in two consecutive years 15 times (2 years : 15) ; in 3 years : 8 times ; in 4 years : 4 times ; in 5 years : 4 times and in 6,7 and 8 years : twice (data from CDNEC records). If two adjacent years are considered over the seven cycles, 67 per cent or two thirds of the sites that were active in one year were active in the next (range 45% - 83%). Fourteen of seventeen (82%) active 1980 sites were active in 1981 (15/18 or 83% in 1982). Thus during the study period, one fifth of the sites "laid off" between the two years, as compared to a factor of one third for the years 1975-1982. This corresponds to a pair breeding at a specific site at a frequency of about two in every three years.

Of seven recognisable individuals active at six sites in 1981, five were active at the same site (four sites) the following year, a decrement of less than one third. Both birds of the colour ringed pair were active at the same site in both years.

5.2.4.Age-class survival rates

The following evidence concerns survival of marked individuals, first-year immatures and other age groups separately, by documenting how long each was seen in the colony (depicted in Figure 31). The alternative reason (to death) of non-sighting, of dispersal and ring loss, must be borne in mind. One opened metal ring, of a bird colour ringed in 1975, was found at the base of NW1 cliff in 1982. It is possible that this individual was active in 1981 (Figure 31, 'YW').

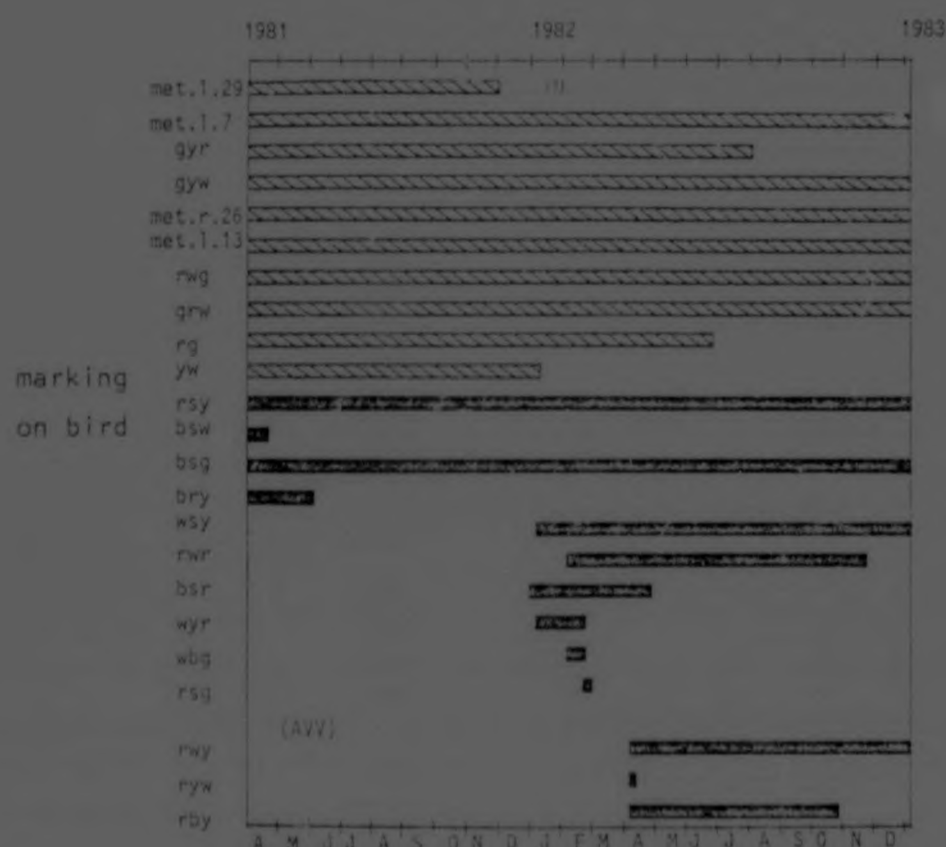

Figure 31. Diagram depicting the length of time ringed vultures were resighted in the kloof. The dark shading indicates birds ringed in 1980 (rsy, bsw, bsg, bry) and during the study period. Three immatures ringed at Aasvogelvlei were resighted from April 1982. For met.l.29, see text "Adult survival".

Immature survival

Only two of eight 1980 fledglings were definitely seen in the kloof up to one year after fledging ; however two others were not ringed. Thus no more than four remained alive and in the kloof throughout their first year, although this figure is most likely 2/8 (Table 13.). As observations began some three months after fledging, the average of 44,7 per cent is probably lower than the "true" value.

Table 13. The number of months, in the year after fledging, that juveniles were resighted in the kloof. As birds from nests 55 and 30 were not colour ringed, their presence in the kloof was uncertain.

Year	Bird	no. months after fledging that bird was resighted	% of max. possib.e
1980	RSY	12	100
	BSW	3	25
	BSG	12	100
	BRY	4	33
	n.55	min.6	50 (?)
	n.30	min.6	50 (?)
	BRG	0	0
	WYB	0	0
	Average :	5.4	44.7
1981	[illegible]WR	10	83
	BSR	4	33
	WYR	2	17
	WBG	0.5	4
	RSG	0.3	2.5
	WSY	12	100
	Average :	4.8	40.0
Combined average :		5.1	42.7

In 1981, all nestlings were ringed and only one was resighted in the kloof one year after fledging. On average, immatures remained for 40 per cent of the maximum possible period in their first year. The mean for the two years is one of 43 per cent "survival" in the first year (Table 13).

Of seven that fledged in 1982, only one was present in the kloof six months later. Three were recovered dead within one month of fledging.

Thus, for these three years combined, four (or a maximum of six) of 21 immatures were resighted alive one year after they had fledged, a "survival" rate of some 19 - 29 per cent for this age class.

Adult survival

Of the seven recognisable individuals active at six sites in 1981, five were present one year later. One "missing" bird had a metal ring only, thus could have easily been missed as it was no longer seen at a nest site in 1982 and could have been confused with other, similarly ringed, birds (Figure 31: met.1.29). Adult survival is also indicated in the total counts (Figure 17). Although the speed of mate replacement is unknown, no breeder was considered to have died whilst engaged in a cycle ; certainly no ringed partner went missing. One (non-ringed) adult that died during the study period was found (an estimated six weeks after death) 4 m from the top of the waterfall at the head of the kloof.

General survival

Table 14 documents the birds that were resighted in 1981, according to when they were ringed. I spent a large amount of time in observation and, as all perch areas were visible from the observation point, am confident that I observed every ringed bird. Assuming that the colour ringed vultures had not lost all their rings, of 123 birds that had been ringed up until 1980, 14 (11,4%) were sighted in 1981. If "breedable" colour ringed birds alone are considered (i.e. 1974 - 1976), four of 48 (8,3%) survived to breed in the kloof. Of course, an unknown number of non ringed birds from those years may or may not be breeding.

Table 14. The number of nestlings that were metal ringed and colour ringed at Potberg (data from Boshoff & Currie 1981, CDNEC records), and the number that were subsequently resighted during the study period. Two individuals (x^{a}, x^{b}) with missing rings could not be accurately placed.

Year	no. nestlings metal ringed	no. nestlings colour ringed	no. nestlings not ringed	no. resighted in 1981	no. resighted in 1982	no. breeding
pre-'72	12	-	?			
1972	14	-	?	} 4	3	3
1973	14	-	min. 6			
1974	-	22	2	1^{a}	1^{ab}	1^{ab}
1975	-	15	8	$-^{a}$	$-^{ab}$	$-^{ab}$
1976	-	11	5	1	1	1
1977	-	13	2	1	1	-
1978	-	7	2	-	-	-
1979	-	9	1	1	1	-
1980	-	6	2	4	1	-
Total :	40	83	28 (min.)	13	10	7

5.3. Discussion

5.3.1. Population structure

The colony has certainly declined in numbers within living memory, but it appears to have stabilised. The drop in the number of active sites between 1975 and 1976 (Figure 30) would suggest a sudden decline in colony strength, and it is not unlikely that this was due to an indirect poisoning event. Breeding activity in the subsequent years suggest an absence of any form of persecution and, as a result of discussions with farmers in the area (chapter three), I would consider such an event to be unlikely in the future. Nonetheless, the colonial nesting and feeding habits of this species do render a colony of this size very vulnerable to sudden extermination by as little as a single, albeit unintentional, poisoning event. That the available evidence suggests that it is a discrete population increases the possibility of such a "clean sweep", and also raises questions concerning the viability, in genetic terms, of the population. These aspects are discussed further in chapter six.

A figure of some 30 per cent of immatures in 1982 reflects either a high adult survival or a relatively low juvenile survival rate : the (suggested) high mortality of ringed birds would indicate the latter. However, the numbers of birds at Aasvogelvlei serves to emphasise that colonies may differ in the proportions of certain age-classes counted, particularly if the colony is checked only sporadically. That even less birds than double the number of active nests were counted in both years (save for one count) indicates a different foraging behaviour to that at Potberg (or a very different breeding strategy !). Also, it is known that the population of Cape Vultures is spatially heterogeneous with at least four components (Mundy 1982, Piper et al. 1981). However at Potberg, where colony numbers were very stable, the proportion of "breedable" birds breeding in either year cannot be considered low, if it is remembered that factors such as an (unknown) skew in the male : female ratio in a colony this size would influence partner availability considerably. For example, in the California Condor population of some 60 individuals in 1946, Koford (1953) documented a 62 per cent proportion of males.

Both the location and the presence of an Aasvogelvlei immature suggested that the vultures at Perdeberg formed part of the 1982 Aasvogelvlei population. It is possible that at least one breeding attempt occurred in the Langeberg in 1981 (e.g. Perdeberg ?), and this may explain the presence of the non-ringed immature I saw at Potberg. As only three vultures were counted at Aasvogelvlei in January 1983 and the two colonies are so close together, I assumed that the birds counted at Perdeberg were the same as those that were at Aasvogelvlei in 1982.

5.3.2.Deferred maturity

The (successful) four year old female breeding record is the youngest age of a documented griffon vulture breeding attempt ; a European Griffon Vulture Gyps fulvus was found breeding in the wild at five years of age (Terrasse 1977) and a captive G. coprotheres bred unsuccessfully in its sixth year (Mundy 1982). Mundy (op. cit.) then assumed the age of first breeding for the species to be six years. But why do birds not breed in their immature years ? According to Lack (1968:297) ".. they (birds) have evolved physiological regulating factors to prevent earlier maturity because this .. enables them to leave more offspring than if they mature earlier. This view implies, first, that any individuals which attempt to breed when younger are unlikely to succeed and, secondly that the attempt to breed exposes the birds to a higher mortality than if they do not attempt to breed." This view (correctly) stresses certain constraints of natural selection, and it also defines the phenomenon of deferred maturity as an adaptation (sensu Williams 1966).

It is known that young birds have a high mortality rate (e.g. Piper et al. 1981, 5.2.4.), presumably because they are less efficient in finding food than older birds (Lack 1968, chapter four). A transition to efficient feeding as a result of experience gained could then be viewed as tiding the individual over a series of levels (Newton 1979:136) or energy thresholds (Drent & Daan 1980, Vernon & Robertson 1983). The end result is an individual capable of accumulating sufficient reserves so that it is able to accommodate each level, and thereby exceed the (summated) breeding threshold. The balance of an individual's energy budget is then expected to vary seasonally (e.g., with relative food abundance in relation to requirements, q.v. Houston 1976), annually and with age, where age is linked with increasing experience (Vernon & Robertson 1983). Viewed in its correct perspective then, deferred maturity is a consequence (sensu Williams 1966) of inexperience.

Individual variations in the age of first breeding would then result from environmental variations, and consequent food availability (Lack 1968, Newton 1979), as well as intraspecific relations (e.g., availability of mates and nest sites) that influence attainment of the breeding thresholds. These factors can be expected to vary between the different colonies throughout southern Africa.

5.3.3.Survival

Given the assumption that ringed vultures have not lost all their rings, whether the "missing" vultures are dead, or alive elsewhere, the fact remains that they do not constitute part of this population's breeding segment.

Survival estimates for this species have been made, based on ring recoveries (Houston 1974b, Piper et al. 1981), although the authors have criticised the results (op. cit.), e.g., "clearly nonsense" (Mundy 1982:267). Indeed, if based solely on recoveries of dead birds, all estimates of age-specific survival, that assume a constant survival rate for particular age-classes, are liable to be untrustworthy (Lakhani & Newton 1983). Also, in the absence of reliable estimates, prediction of population numbers constitutes little more than a numerical exercise. For example, the expected annual increment of "breedable" vultures from the Potberg colony was calculated using past breeding data and estimated age-specific survival rates of 40 per cent p.a. for first years, 85 per cent p.a. over the next four years and 92 per cent p.a. for adults. From December 1982 to December 1987, the population "dropped" by five birds : if the adult survival estimate was increased to 95 per cent p.a., the population would show an increase of two ! These considerations do, however, emphasise the overwhelming importance of high adult survival rates, for animals with such a low reproductive rate. As with the Andean Condor Vultur gryphus and the California Condor, these vultures display ".. such low reproductive rates that their populations could not persist except for the extraordinary longevity of the adults" (Mertz 1971).

CHAPTER SIX : GENERAL DISCUSSION

The evolution of exclusive scavengers is proposed to have occurred under certain conditions, as described by Houston (1979). The proposal is based on studies of griffon vultures and other scavengers in the relatively undisturbed (by man) situation in the Serengeti in East Africa (Houston 1972, 1974a, 1976, Kruuk 1967, Petrides 1959, Pennycuick 1972). In a previous paper, Houston (1974a) remarked that the situation in the Serengeti ".. may not be typical of the activities of griffon vultures in other regions of Africa today". As one stands on top of the Potberg today (Figure 3), it is indeed difficult to re-create, in one's mind, the scenario of Coastal Rhenosterbosveld supporting numbers of Bontebok and other bovids (chapter two). And if the degree of man's influence on life communities in general is viewed as a continuum (Myers 1979), the remnant vulture population in the southern-southwestern Cape is surely positioned towards an extremity. This statement needs, however, to be qualified. In terms of their feeding, the birds are totally dependent on the stock farmer, whereas in the breeding area the situation in the kloof remains remarkably undisturbed. Throughout their range then, Cape Vultures have undergone a marked transition in feeding ecology in the last two to three centuries and the aim of this study was to examine the nature and effects of this altered food supply on the reproductive performance of a particular colony.

Food is considered limiting if it prevents a population from increasing and if sufficient, it must be so in quantity, quality and availability to the animal concerned (Newton 1980). I attempted to determine how much food would be available to the vultures in the area surrounding the colony by incorporating the various factors that influence its availability. I then attempted to determine how much food individuals, and the whole colony, actually obtained. The former was determined by (informal) personal interviews with farmers, as well as a postal survey ; I consider that both of these methods fulfilled a valuable extension role. The limited nature of the feeding range determined by these methods, and subsequently supported by the radio-tracking study was expected, given that its size is dependant on the (summated) requirements of individual colony members. In passing, it is of interest to note that the existence of a feeding range is not necessarily an effect of man's influences. Although griffon vultures originated under and are most suited to certain conditions (Houston 1979), peripheral populations, in areas of low or no migratory ungulate concentrations, would have fed on the carcasses of resident species. The southern-southwestern Cape would have been such an area (chapter two).

Practical difficulties with the estimation of crop content of individual birds resulted in this section being not as accurate as I had originally hoped. In retrospect, I should have concentrated, during the observations, on a more rigorous documentation of a smaller number of nests (e.g.those on NW2).

Thus in contrast to the Serengeti, where food varies seasonally in distribution and abundance (Houston 1974a), food at Potberg varies in abundance only. The level of variation in the quantity available within an area of some 60 km radius of the colony (excluding south !) is considered highly unlikely to fall below the colony's requirements : in general terms there is thus a spatial sufficiency. A similar conclusion was reached with <u>Gymnogyps californianus</u>, another large-carcass scavenger (Miller <u>et al</u>. 1965). In terms of temporal availability of food, the evidence I obtained indicated that both adults and nestlings obtained sufficient quantities during the nestling period. Although this period coincides with inclement weather , and 1981 was exceptionally wet in this respect, the condition of nestlings as indicated by growth in both wing length and body mass suggested that the nestlings nonetheless recieved sufficient quantities of food.

But is this food available to all age groups ? Young vultures are less efficient at obtaining food than older birds (Houston 1976, Mundy 1982), and at Potberg young birds have a very low survival rate (chapter five). Juveniles may also have very lengthy PFDPs, and if the length of the PFDP is indicative of the availability of food to that age class (chapter four), then my observations reflect a difficulty that those juveniles experience in obtaining food. Are the chances of an immature individual being behaviourally excluded by adults from ingesting food greater at a small (e.g. sheep) carcass than at a large (e.g hartebeest) carcass ? Two factors could reinforce this disadvantage. Firstly, the smaller carcass would presumably be eaten up faster, and by fewer birds and secondly, adults, which outnumber juveniles by a ratio of some three to one (chapter five), generally initiate feeding at the carcass (Mundy 1982). This proposal is essentially a corollary of that of Fisher's (1952), which accounted fc the surge in numbers of the Fulmar Fulmarus glacialis : the initiation and development of whaling provided a rich and easily available food source (discarded offal) that acted to increase the survival rates of the younger age classes. The very small numbers of ringed birds surviving to breed at either colony (Table 14) highlighted the current lack of recruitment (and, consequently, an important advantage of the ringing programme !). A flaw in my study was then a lack of carcass-watches that would have provided relevant information. Comparative PFDP lengths from other colonies, e.g. those in the Transvaal where the food source is different, would also illuminate this aspect. This proposal is, however, testable. A limited supplementary feeding scheme, specifically designed to assist juveniles through this period of transition (chapter four) has been initiated at Potberg, and is outlined in appendix a. Nestlings will continue to be colour ringed for at least five years, and during the months after fledging, the juveniles' use of this source as well as their survival, will be monitored (CDNEC-A.F. Boshoff pers. comm.). Other things being equal, documentation of subsequent juvenile survival rates will then allow for a conclusion regarding the proposal's validity. These vultures have thus achieved a transition in their food source, but I suggest that this transition has not been achieved with equal sucess by all age groups.

The evidence indicates that this sub-population constitutes a discrete entity (chapter five) : distribution maps should incorporate this (e.g. Newman 1983, Steyn 1982), as the nearest known breeding conspecifics are i. the northeastern Cape, some 500 km from this area. In the Cape Province, this species has undergone fluctuations in numbers in the past, although it is likely that its range was continuous until approximately one century ago (Boshoff & Vernon 1980). If one assumes isolation since then, and this is most likely an over-estimate of the time-span, some five isolated generations are involved. What then are the consequent implications for the remnant group ? Obviously a smaller size increases the chances of elimination in a particular area, and the CDNEC has attempted to reduce the likelihood of such an event, e.g. indirect poisoning, by means of considerable extension work with farmers. Less apparent are biological effects of such size and isolation, and as these two attributes are unique to this population it is relevant to consider them in some detail here. For example, in small populations heterozygosity decreases through the action of genetic drift, although in population sizes of 100 to 1000 the loss of variability is slight in each generation (Roughgarden 1979). Also, only one individual migrating between "isolated" groups per generation is enough to counter the effect of drift (op. cit.) : it is therefore highly unlikely that these vultures display any phenotypic disadvantage resulting from this effect alone. Secondly, a recent analysis of the effects of inbreeding accounted for the higher mortality rates of inbred captive young ungulates (Ballou & Ralls 1982). The frequency of inbreeding in the colonial (e.g. griffon vulture) situation, where birds appear to breed in their natal areas (chapter four), is presumably greater than that in solitary breeders, other things being equal. Consequently, on the basis of this alone, i.e. excluding any possible behavioural traits that might prevent inbreeding, one would expect a relatively low level of heterozygosity in this sub-population. Ballou & Ralls (1982) concluded by emphasising that an awareness of the effects of inbreeding, such as decreased fertility, is vital to the sound conservation management of small (isolated) populations. Genetic drift and inbreeding then result in decreased heterozygosity, and a recent electrophoretic study of allozymes and soluble proteins of Cheetahs Acinonyx jubatus revealed dramatically low levels of variation (O'Brien et al. 1983). These levels could not, however, be linked to any (deleterious) phenotypic effects. Nevertheless, it should be borne in mind that deleterious effects are not of necessity a direct consequence of reduced variability : the link certainly has been demonstrated (Ballou & Ralls 1982 & refs. therein), but not (as yet) to be causal. Furthermore, any study of this interesting aspect (e.g. between southern Cape and northern Transvaal vultures ?) should critically question which proteins the study is to be based on : O'Brien et al. (1983) did not consider this.

Colonial nesting provides opportunities for individuals to observe where others go in search of food (Loman & Tamm 1980, Ward & Zahavi 1973) and, given the proposed link between a migratory food source and the evolution of these scavengers, the advantages accruing to an individual nesting near conspecifics are apparent. Furthermore, where the food source is evenly distributed throughout a particular area (e.g. feeding range), the network of individuals spreading over the area (Houston 1974a) together with local enhancement (Hinde 1970) at a carcass clearly facilitate the discovery of food. Where numbers in the colony decline, is there a critical level below which these advantages effectively break down ? The radio-tracking study vividly demonstrated the capability of an individual to cover large tracts of ground rapidly and a personal, "visceral", understanding is that under this altered food regime the advantages of colonial breeding, in terms of actually finding the carcass, are not as great as they were under the conditions of the "Serengeti scenario". The Potberg colony is currently at a reduced level, i.e. there are vacant nest sites in the kloof that have been successful in the past, and in an area of apparent food abundance. Is the tendency of this southern-southwestern Cape population to splinter into smaller breeding groups a reflection of this decreased advantage, in combination with other, unknown, social factors?

This study has demonstrated that these vultures are essentially self-sustaining under the conditions of the "farmland scenario", given a lack of persecution and a continued willingness on the part of the farming community to (indirectly) support them. The results of the limited feeding programme should provide for a conclusion as to whether manipulative management procedures are neccessary in order to maintain their presence in the area. Of equal importance, I trust that the study has illustrated aspects of their life history, and indicated those that warrant further investigation.

APPENDIX A

An active management plan for the colony, of which the limited feeding programme forms a major part, was accepted in principle by the CDNEC at a meeting in April 1983. The location of the feeding sites on private property was accepted by the farm owner in October 1983. Most of the points listed in the section "Publicity campaign" have been attended to. The management proposals are outlined in this appendix.

Aims

a. To improve the survival rate of first year birds.
b. To increase the breeding success.
c. To remove, or lessen, the threat of poisoned carcasses in the foraging area, as well as reduce the pesticide levels that are currently found in addled eggs.

Manipulation of the food supply

Although research indicates temporal variations in the quantity of food available to the vultures, a spatial sufficiency is concluded to exist in the area surrounding the colony. The time of year during which newly fledged birds are in particular need of an adequate and easily available food supply (due to inexperience in flying and foraging abilities) coincides with one such period. This study highlighted the critically low recruitment to breeding displayed by the Potberg colony, mortality being highest during the months following fledging. The rationale for a limited feeding programme is discussed further in chapter six. It is therefore considered that a supplementary feeding programme be implemented during the January to June period.

The supply of uncontaminated food will also act to reduce the levels of contaminants currently found in eggs as well as ensure an adequate supply during the months preceding laying.

Details of the feeding programme

A supplement of no less than 100 kg of carcass per week should be provided. A supply of bone fragments in the size range 1-5 cm obtained from previous carcasses should be made available at the site. This supplement must be in the form of whole carcasses to attract the birds, provide a balanced diet and simulate natural feeding behaviour. Carcasses must be slit along the stomach to allow the vultures entry into the body cavity, and must be removed for burning or burial not later than two days after placement so as to prevent the accumulation of blowfly eggs (and consequent farmer antagonism).

To ensure that the vultures retain their foraging behaviour, three alternate feeding sites should be used. The approximate location of these is shown in Figure 1.

Figure 1. The approximate location of the feeding sites (marked as stars) in relation to the colony (arrow).

Although it would be ideal to have three sites in the De Hoop Nature Reserve, this is not possible as the colony's foraging area, determined (to an unknown extent) by prevailing winds and the orographic effects of the Potberg, falls mainly to

the north of the reserve. In all cases the sites must :
- be large enough to allow the vultures to take off after feeding, and an area of at least 50x50 m is suggested.
- be positioned on top or on the high slopes of a hill, to facilitate take-off.
- be fenced off to prevent the entry of mammalian scavengers.

Duration of the feeding programme

It is imperative that basic research/monitoring of the colony be continued in order to determine the effectiveness of the management plan outlined above, and thereby allow for a conclusion on its duration. The following information is considered vital :
- first year survival rate
- number of eggs laid per year
- number of birds fledged per year
- number of adult birds present per year
- degree of dependance of the colony on the supplementary feeding scheme.

Past research indicates no harmful disturbance effects to nestlings between the ages of 40 and 70 days as a result of ringing by small parties. In order to monitor the survival rates of immature birds, the colour ringing programme must be continued for a minimum of five years.

Disturbance at the colony

The breeding kloof must remain totally undisturbed by human presence. If control of access is not rigorously maintained, the breeding success becomes seriously endangered. This is of particular importance during the months May through January, when disturbed adults may leave eggs and/or young nestlings and expose them to depredation, climatic effects and the risk of premature fledging. During the breeding months, one person walking quietly along the base of the cliffs is enough to chase every incubating adult off its nest. If necessary, the cliffs can be viewed from the opposite sides of the kloof (i.e. on the southwestern slopes), without disturbing the birds.

Publicity campaign

The aim here is to reach every stock farmer within the foraging range of the Potberg and Aasvogelvlei colonies. The plight of the vultures should be made aware to the farmers as well as the advantages which vultures have for them. The colonies remain extremely vulnerable to the threat of poisoned carcasses in the foraging area to combat insect plagues, e.g. blowfly ; here, one carcass has the potential to kill half the breeding segment of the Potberg colony. Thus an appeal must be made to prevent a (albeit accidental) poisoning event.

Conclusion

Mortality during certain stages of the breeding cycle currently limits recruitment to the reproductive segment of the colony. Even in the absence of other mortality factors (e.g. a poisoning event, or human disturbance), such critically low recruitment levels will eventually result in extinction of the colony. The programme outlined above is designed to alleviate stress at the particular stages that exhibit high mortality rates. Monitoring the essential demographic aspects of the population will enable an evaluation of the programme after five years and a decision on its future.

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APPENDIX B

The accounts of the following observations that I made at Potberg are taken from "Predatory attempts on Cape Vultures by Black Eagles" (Mundy, Robertson, Komen & O'Connor in prep.).

At 15h45 on 24 July 1981 a subadult eagle swooped down towards a cliff and caused 25 roosting vultures to fly off, but (the) two incubating birds remained on their eggs. At 15h30 on 14 January 1982 a juvenile entered the gorge and dived down to within 10 m of a breeding ledge, eliciting hoarse calls and extended necks from the vultures and causing 9 of 12 birds to fly off, including a fledgling which had fledged a week earlier. The three that remained were attending the only active nests on that cliff, although a nestling of 114 days was the only nest occupant at the time. The eagle then dived past another breeding area and elicited further hoarse calls, causing four more birds to fly off.

At 08h40 on 13 December 1981 loud calls anounced the arrival of a female eagle on a vulture site where the vultures had failed in their breeding attempt in July. The site was 4 m above an adult attending a 116-day old nestling. Within 30 seconds, further hoarse calls accompanied the landing of the male eagle on a ledge 3 m higher. At 08h50 a juvenile vulture also landed at this last site and aggressively chased the eagle off by jabbing at it vigorously with its bill and emitting a high-pitched staccato call. The female eagle left three minutes later and between 09h02 and 11h55, and together with the male, the eagles elicited aggressive responses 11 more times from four attendant parent vultures by soaring past their section cliff repeatedly.

At 10h03 on 24 December 1981 an eagle dived at five vultures perched on a cliff, causing a juvenile to fly off; no call was heard. The eagle repeated the behaviour and caused three of the remaining four adults to jump off. As it soared in the vicinity of the cliff once again, the last vulture jumped off and the eagle dived after it, extending its legs as it passed over the vulture, but no contact was made. The vulture winced slightly, flexed its wings, thereby increasing its speed, and flew on. At

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10h11 the male eagle landed 1,5 m from a 133-day old nestling and 2 5 m from similar aged nestling on either side. All three attendant adults rushed towards the eagle and noisily jabbed at it, and the eagle was finally forced off the ledge eight seconds after it had landed.

APPENDIX C

The following is a copy of the letter, reduced in size, that was used in the postal survey (chapter three) :

PROVINCIAL ADMINISTRATION OF THE CAPE OF GOOD HOPE

DEPARTMENT OF NATURE AND ENVIRONMENTAL CONSERVATION

Telephone: Napkei 5430

Potberg (De Hoop Nature Reserve)
P.O. Bredasdorp
BREDASDORP
7280

Dear Sir

I am employed by the above Department to carry out research on the Cape Vulture. As you may know, Cape Vultures have undergone a dramatic decline in the past few decades, especially in the Cape Province where there are now no more than 65 breeding pairs. The major aim of my research is to try and understand the factors causing this decline; these Vultures occur only in Southern Africa and are therefore our conservation priority.

I would like to estimate the foraging area of the vultures from the Potberg mountain, which is the only remaining vulture colony in the south-western Cape Province. I would therefore be extremely grateful if you could answer the question below, detach and return the slip in the pre-addressed envelope. I would also appreciate hearing from you about any vultures found in distress on your farm.

In order for me to make full use of the information supplied by you it is essential that you supply your address as requested below. I thank you in anticipation of your co-operation.

Yours faithfully

A.S. Robertson

A.S. ROBERTSON

---------------------------- TEAR HERE ----------------------------

PLEASE TICK APPROPRIATE ANSWER

How often do you see vultures on your farm?

About once a day
About once a week
About once a month
About once a year
About once per five years
About once per ten years
Never

NAME ....

ADDRESS ....

....

....

B.O. ASB. VIR AFRIKAANS

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About once per five years
About once per ten years
Never

NAME ....

ADDRESS ....

....

....

S.O. ASB. VIR AFRIKAANS

APPENDIX D

The following thicknesses of shell fragments were measured directly, by the Western Foundation of Vertebrate Zoology, California, using a Federal Bench comparator thickness guage (L. Kiff _in litt._). Ten measurements were made of each sample and, where known, the fate of the sample is indicated (hatched^f : nestling subsequently fledged). The original position of the fragment, where known, is also indicated (x^e : equatorial ; x^p : polar).

Nest	Date	Thickness (mm)		Fate	Collector
		membrane present	membrane absent		
10	1974	0,671	0,626	addled	CDNEC
40	1974	0,564	-	addled	CDNEC
3	1975	$0,668^e$, $0,610^p$	0,626	addled	CDNEC
4	1975	$0,708^e$	-	addled	CDNEC
42	1975	$0,641^e$, $0,661^p$	0,562	embryo dead	CDNEC
55	1975	0,760	$0,627^p$; $0,649^p$	addled	CDNEC
13	1981	-	0,649	addled	ASR
16	1981	-	0,622	hatched^f	ASR
29	1981	0,759	0,661	addled	ASR
63	1981	-	0,680	hatched^f	ASR
17	1982	-	$0,852^e$;$0,850^p$	addled	ASR
13 AVV	1982	-	$0,646^e$;$0,588^p$	addled	ASR

APPENDIX E

The following is a list of poisons used in the farmlands surrounding the colony, in order of amounts sold at the Bredasdorp-Napier Co-operative (S. Lambrechts pers. comm.). From discussions with farmers in the area, it would appear that "Dazzel" is, or certainly was, the most frequently used poison to combat Blow flies.

Brand	Main component	Manufacturer
1. Sheep dips		
Super Golden Fleece	Diazinon, Amitraz	Coopers
Sumifleece		Shell
Dazzel NF	Diazinon	Agricura
Sarna dip	Phoxim	Bayer SA
Topclip purple (Primatex, Parecto)	Diazinon, Rotenone	Ciba Geigy
Diazinon	Diazinon	Coopers
Zip dip	Triazophos	Hoechst
γ-BHC Dip	Lindane, Trichlorophenol	Agricura
2. Sheep blow-fly strike		
Vetrazin SP 50	Vetrazin	Ciba Geigy
Dazzel	Diazinon	Agricura
PAB	Dichlofenthion	Milborrow
Inject	Fenthion ethyl	Bayer SA
Karbadip	Carbaryol	Agricura
Nexa jet	Bromophos-ethyl	Hoechst
Bromex DFF	Dichlofenthion	Coopers

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