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THE FEEDING ECOLOGY AND BREEDING BIOLOGY OF A CAPE VULTURE COLONY IN THE SOUTHWESTERN CAPE PROVINCE

Alistair Stuart Robertson

A dissertation submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, for the degree of Master of Science.

Johannesburg 1983



"Then with a sudden lift of the one great pinion,
Swung proudly to a curve and from its height
Took half a mile of sunlight in one long sweep."

"Buzzards"
Martin Armstrong

ABSTRACT

Cape Vultures Gyps coprotheres at Potberg obtain their food from stock farms, within a limited area surrounding the colony. The size of the foraging range was determined by means of a postal survey, and the quantity of food available within it was estimated to exceed the colony's requirements. Data pertaining to daily feeding forays of individuals, monthly foraging patterns and the growth of nestlings indicated no seasonal shortages in the amount of food obtained.

One complete breeding cycle and another two post-fledging dependence periods were observed during 165 days. Results concerning deferred maturity, frequency and success of breeding, a sex-linked difference in behaviour, nestling parasites, behaviour of dependent juveniles, aggressive terminations of the post-fledging period and survival of marked individuals, were obtained. It is suggested that the transition to feeding exclusively on sheep carcasses has not been achieved with equal success by all age groups.

DECLARATION

I declare that this dissertation is my own work
and that it has not been submitted to any other university.

A.S. Robertson.

ACKNOWLEDGEMENTS

The outline of this study was proposed by Dr André Boshoff of the Cape Department of Nature and Environmental Conservation, and I was employed by that department for two years. In 1983, I was supported by bursaries from the CSIR and the University of the Witwatersrand. I thank numerous members of the CDNEC, in particular Wally du Preez and Kobus Muller, for their help with administrative matters. André guided me unobstrusively, and I offer my sincere appreciation for all his encouragement and help throughout this study.

I thank Professor Hugh Paterson for assuming supervision after the initial supervisor left, and for criticism of the manuscript. I am also grateful to Carl Vernon and Dr Peter Mundy for their enthusiasm in the study, and for commenting on drafts of the manuscript. Pete's red pen was much in evidence in the drafts, and his attention to detail was greatly appreciated. My thanks to Marc Centner for help with statistics, Neil Caithness for help with the word processor, Professor Miles Markus for analysis of the blood smears and Ms Ansie de Kock of the University of Port Elizabeth for analysis of the addled eggs.

Cape Vultures live on cliffs and, as a climber, I was introduced to them in 1977 by a Belgian expatriate, in order to partake in the Vulture Study Group's ringing activities. I consequently thank Dr John Ledger and other VSG members for those fragrant and instructive trips, as well as the VSG for the loan of photographic equipment used during this study.

Living alone next to a vulture colony was an intense experience, and it would have been a very lonely one were it not for friends such as the Februarys, Peter and Jenny Steyn, John and Alison Michler, and Tony and Kitty Metselaar, all of whom suffered my intrusions into society with a warmth that deeply impressed me. Mr and Mrs Feb. provided an "always-welcome" home in Cape Town which I greatly appreciated.

I share these remote places with the memory of my father, and my mother cares ; I am particularly grateful to both for supporting my education in the direction of my choice.

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CHAPTER ONE : INTRODUCTION

The Cape Vulture (Gyps coprotheres Forster 1798) is the heaviest member of the family Accipitridae that occurs as an endemic species throughout southern Africa (Mundy 1982). Aspects of its life history include a low breeding rate, deferred maturity, prolonged parental care, high adult survival and low juvenile survival rates (Houston 1974b, Mundy 1982, Piper et al. 1981). It breeds in colonies on cliff faces and is the only vulture species to do so in southern Africa (Mundy 1982). A combination of the colonial and cliff-nesting habits then renders this species convenient to study the consequences of large size and low reproductive rates on the biology of avian species ; the results may therefore be applicable in general terms to a wider assemblage of animals.

Along with the six other griffon species distributed throughout the Old World (listed in Brown & Amadon 1968) Cape Vultures are described as specialist feeders on the carcasses of large migratory ungulates (Houston 1974c). The evolution of this exclusive scavenging behaviour is postulated to have occurred under conditions (Houston op. cit.) which probably no longer occur throughout any griffon species' range in Africa (Houston 1974a). Houston's (1972) study of the feeding and breeding ecology of two griffon species inhabiting relatively natural conditions in East Africa is then especially relevant when considering the congeners that range over areas of industrial and agricultural development in southern Africa. In particular, his study of Rüppell's Griffon G. rueppellii (Houston 1974a, 1975, 1976), that area's ecological counterpart to G. coprotheres (Mundy 1982), provides numerous points of potential comparison.

In a comparative study of the biology of the five southern African vulture species, Mundy (1982) highlighted the decline of the Cape Vulture and listed a variety of man-induced factors to account for the decline in numbers. This decline was described as "accelerating" and giving "cause for concern" (Siegfried et al. 1976), and the vulture is now listed as "a vulnerable endemic species of southern Africa which has lost much of its population" (Brooke in press). That review documents estimated numbers and

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population trends, and concludes with a total of some 2000 breeding pairs throughout the subcontinent. In the Cape Province alone, some 65 breeding pairs were estimated in 1979 (Boshoff & Vernon 1980), and the Transvaal Province now constitutes the main stronghold (Tarboton & Allan in press). The temporal gradation in the degree of man's impact on the food supply and numbers of the Cape Vulture, including its past and present distribution in the Cape Province, is described in Boshoff & Vernon (1980).

Although the Cape Vulture is one of the best studied of South African rare and endangered birds (Brooke in press), certain aspects of its (and raptors in general) life history remained "totally uninvestigated", e.g. the post-fledging dependence period (Mundy 1982:234, Newton 1979). More importantly, the possibility of the food supply being the factor limiting the population "remains to be fully investigated" (Mundy 1982:275). In essence, this was the rationale behind this study : to examine the nature and effects of the current food supply on a particular colony's reproductive performance, as well as to determine the degree of influence of various factors that have been documented as influencing numbers in different areas of the species' range. The aim, therefore, was to provide a detailed, and essentially conservation-oriented, case study of a colony.

I studied the Potberg colony in the southwestern Cape Province, and monitored breeding at another colony 120 km away in the Little Karoo. Evidence indicated that these vultures likely constituted a discrete group of the species' population (Boshoff & Vernon 1980). Situated in sheep country (Jarvis et al. 1974), the area including the kloof was purchased in 1978 by the Cape Department of Nature and Environmental Conservation (CDNEC), and now forms part of the De Hoop Nature Reserve. It is unique in that it is the only remaining regular breeding colony within the winter rainfall region, and lies on the periphery of the species' current range. Although the colony had been under sporadic observation, and ringing visits, since 1951, annual monitoring began in 1974 with the colour ringing of nestlings. Available data for the period 1951 - 1980 are collated in Boshoff & Currie (1981) and Boshoff (1981) My study commenced in March 1981, with the emphasis in the first year on observing the birds in their

breeding area. Thereafter, more time was spent in the foraging area of the surrounding farmlands. I was involved in a radio-tracking study of juveniles and of the foraging behavior of an adult vulture from October 1982 through 26 February 1983, although this was not part of the study per se (Bushoff, Robertson & Norton in prep.).

CHAPTER TWO : STUDY AREA

2.1. Potberg

2.1.1. Location

The Potberg ("berg" is Afrikaans for mountain) (34 22S; FU 31E) lies some 10 km north of the Indian Ocean, 40 km SSE of Swellendam and within the magisterial district of Bredasdorp (Figure 1). This elongated mountain, some 25 km in length, is oriented in a southeasterly/northwesterly direction and is 611 m above sea level at its highest point.



Figure 1. The study area. The location of the Potberg (PB), Aasvogelvlei (AVV) and Perdeberg (PDP) colonies are indicated.

The vultures inhabit the largest bluff in the mountain thereafter referred to as the vulture bluff [illegible]ated on its

southern slopes and 4 km from its western extremity. Within the kloof, the birds use southeast- and southwest-facing cliffs for nest sites and roost areas (see Figures 18, 19 and 20). Situated as it is in a kloof, unlike many other Cape Vulture colonies (Mundy 1982), this colony is suited to an observational study as all breeding and roosting areas are clearly visible from a vantage point on the southeast side.

The quartzite cliffs of the Table Mountain Series (Heydorn & Tinley 1980) are approximately 70 m high and the kloof is about 1 km in length. The nesting cliffs are some 60 m high.

2.1.2. Climate

The study area is situated within the bimodal rainfall region as defined by Heydorn & Tinley (1980), close to the junction of this region with the winter rainfall area.

	25 Year Average	H0	H1	H2		25 Yr Av.	H0	H1	H2
JAN	31.3	57.9	113.1	[illegible]	JUL	52.8	2.8	[illegible]	47.7
FEB	[illegible]	21.8	38.5	25.1	AUG	61.0	36.[illegible]	[illegible]	38.7
MAR	51.3	16.4	64.3	73.1	SEP	39.2	40.[illegible]	[illegible]	33.9
APR	51.0	41.6	246.9	197.[illegible]	OCT	40.0	58.[illegible]	13.1	36.6
MAY	57.9	34.9	34.9	11.8	NOV	29.2	80.[illegible]	59.0	21.7
JUN	51.3	71.8	62.3	29.7	DEC	25.9	45.1	28.5	38.1

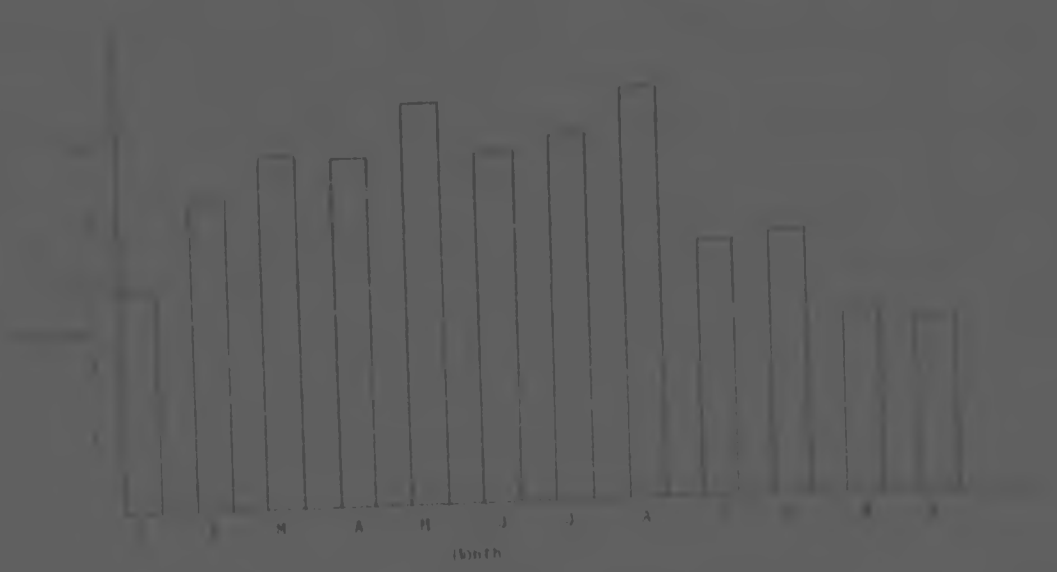

Figure 2. The percentage of rainfall each month as a proportion of the total annual rainfall, averaged over a period of [illegible] years (1955-1979). Actual monthly amounts in mm are given above the figure (J. C. Michler pers. comm.).

In general, the area exhibits a temperate Mediterranean climate similar to that of the southwest Cape coast. The area receives the bulk of its rainfall from about May to September and has a warm to hot and dry summer. Mean annual rainfall is 520 mm and its mean monthly distribution is shown in Figure 2. These figures were obtained from the farm 'Elandspad', situated on the southern slopes of the Potberg and 13 km east of the kloof. The year 1981 was exceptionally wet in that 64 per cent more rain fell than the average obtained for the last 26 years. As demonstrated in Heydorn & Tinley (1980), a marked feature of rainfall in the Cape coastal region is the strong orographic control, where rainfall curves follow the relief undulations closely. This influence was observable at the Potberg where, on numerous occasions, the mountain was covered in cloud while the surrounding farmlands were relatively clear. The incidence of precipitation and cloudy conditions is therefore higher in the kloof than in the surrounding area.

The strongest winds occur in midsummer, with the autumn and early winter being the seasons with the least wind (Schulze 1965). Prevailing summer winds are southeasterly whereas in winter northwesterly winds are frequent.

In 1982, the farm Driefontein (14 km W of the Potberg) received an average of 7,2 hours of sunlight per day (range 5,2-9,6 hrs) : only in April, June and July did this figure fall below six hours per day. Between the months of October and March, the average was not less than seven hours per day. These and other data were obtained from the Swellendam Extension Officer of Agricultural Technical Services (ATS) ; where this source is used in the text, it is acknowledged as "ATS-J.P. Pietersen pers. comm."

2.1.3. History

Before the arrival of European settlers in the southwestern Cape, bovids that frequented the area in relatively large numbers included Bontebok Damaliscus dorcas dorcas (Pallas), Red Hartebeest Alcelaphus buselaphus (Pallas) and Eland Taurotragus oryx (Pallas) (du Plessis 1969, Skead 1980). Being of relatively

large size, these would have provided a likely food source for griffon vultures. Carnivores included Hyaena spp., Leopards Panthera pardus (L.) as well as Lions P. leo [illegible] cit.). The vegetation type in the slightly undulating to [illegible] dissected lowlands that surround the Potberg on all flanks except the southern is (or rather, was) Coastal Rhenosterbosveld (Acock 1975, Day et al. 1979). The limestone hills and sand plains comprising the coastal forelands were, and are largely still, of the Coastal Macchia (Fynbos) vegetation type (Day et al. [illegible].

In the late eighteenth century, a group of pure-bred merino sheep were introduced to the (Bredasdorp) area. Pastures were introduced as a crop rotation in the late 1930's, and sheep farming intensified. Wheat farming was introduced in the early nineteenth century and in 1892 the first bags were transported to the Cape Town markets (B. Brynard in litt.). With the exception of the south, the area around the mountain is now a patchwork of wheatfields and stock pastures (Figure 3).



Figure 3. View from the top of the Potberg. The Langeberg range is visible in the background.

In fact, some 70 per cent of the area that was previously coastal Shenosterbosveld has been cultivated and the combined Bredesdorp and Swellendam area now contains, inter alia, some 500 000 sheep and 15 000 cattle (ATS-J.P. Pietersen pers. comm.). The effects of the initiation and development of agricultural practices on the status and distribution of the Cape Vulture throughout the Cape Province are described in Boshoff & Vernon (1980), and specifically for the southwestern Cape in Boshoff & Vernon (1979: 6-8).

In 1976, that part of the Potberg containing the vulture kloof was incorporated into the De Hoop Nature Reserve and is now controlled by the CDNRC. Prior to 1981, the kloof had constituted part of the farm Potberg.

2.2. Assessment

2.2.1. Location

This colony (33 52S; 21 38E) is situated on the cliffs formed by the Gourits River, 4 km north of the confluence of the Gourits and Groot rivers. This position is 8 km north of the Langeberg range, and is 120 km (line of sight) from Potberg, at an altitude of ca 150 m (Figure 1).

The nest sites face south-east, i.e. on the western side of the river, and are easily viewed from the eastern bank. This observation point is reached via the farm "Grootplaas" (resident owner P. Beukes) ; the nesting cliffs are included on this farm's property. The cliffs are ca 90 m in height and the nests are located, on average ca 30 m above the water. During the study period, the nests were spread along some 1,5 km of cliff face.

2.2.2. Climate

Situated in the rain shadow area of the Little Karoo, this area receives slightly in excess of 400 mm per year (Heydorn & Tinley 1980, ATS-J.P. Pietersen pers. comm.). Maximum amounts of precipitation are recorded in the months November and March (Heydorn & Tinley op. cit.).

CHAPTER THREE : FEEDING ECOLOGY

3.1.Introduction and methods

The aim of the study of the feeding ecology was to determine *where* colony members obtain *how much* of *what* food, as well as *how* and *when* this food is ingested, in order to describe its influence on the reproductive dynamics of the colony. The investigation was divided into two sections, viz. a study of the potential food available and a study of the foraging behaviour and amount of food obtained by the vultures. The former was carried out in the farmlands surrounding the colony and the latter in the vulture kloof, during the days of observation. Observations commenced in May 1981, for 12 days per month regardless of weather conditions, and ended in May 1982. In total, 165 days were spent at the observation point, averaging some 8,5 hours per day. A small tent, camouflaged in brown hessian, was erected at the observation point to provide shelter from inclement weather.

Potential food available

Four methods were used to determine the size of the feeding range around the colony :

a. A questionnaire, requesting information on sightings only, was posted to the farmers within the magisterial districts of Bredasdorp, Swellendam, Heidelberg, Riversdale and Albertinia (see appendix C).

b. Personal interviews were conducted with 45 farmers within a 40 km radius of the colony.

c. Individual feeding sites were located by means of a radio-tracking study of the foraging behaviour of an adult vulture.

d. Individual feeding forays, defined as the length of time taken by an individual to leave the nest site, locate and consume food and return to the site, were documented on a random basis for breeding birds. These times provide an indirect measure of the distance travelled to a food item. The times were grouped into calendar months and analysed by Multiple Range tests, using a Hewlett Packard HP-41 calculator.

Information pertaining to the availability of carcasses to the vultures was obtained by personal interviews with the farmers within the foraging range. The farmers were questioned on, inter alia, sheep mortality rates (and temporal variations thereof), carcass management procedures and their personal attitudes to the vultures.

Food obtained, and foraging behaviour

To determine the range of food used by the colony, the bases of the breeding and roosting cliffs were searched for regurgitated pellets and artefacts and farmers were interviewed in order to obtain their personal observations. Artefacts and other indicators of the nature of the food obtained were collected during visits to the nests. The Potberg breeding areas were visited four times in 1981 and five times in 1982, although individual nest sites were visited no more than three times in any one year. The Aasvogelvlei sites were visited once in each year.

A number of carcasses consumed by the vultures were located by searching the farmlands close to the colony.

Various methods were used in an attempt to determine the actual amount of food obtained by the birds, as well as give an indication of its availability. One of these, the visual estimation of crop content of returning foragers, has been attempted before (Houston 1972, 1976). The crop, a diverticulum of the oesophagus which functions as an elastic food store, projects beyond the contour feathers when full and is observable in both flying and perched birds (e.g. the small bulge in the neck of the vulture in the frontispiece, also Houston 1976:Figure 3). Captive birds were fed measured amounts of meat and the resultant crop bulge was photographed in order to obtain a visual estimate of the degree of distension. During the day-long observations, estimations were made of the proportion of the colony considered to have obtained food that day. Individual breeding sites were monitored each observation day and the degree of crop distension of each occupant was scored into one of the following three categories, whenever possible :

0 : No food obtained.

1 : Food obtained, less than ca 700g.

2 : Food obtained, more than ca 700g.

At each visit to the nests, nestlings were weighed and their wing lengths were measured. As nearly all 1981 and 1982 nestlings from Potberg were of known age, these figures were then directly comparable to the correlations of weight and growth obtained at numerous colonies during the southern African ringing programme.

During the observation days, counts were made every 10 minutes of the total number of birds present in the kloof in order to document whole colony foraging times and the proportion of time spent in the search for food. Estimates of cloud cover and wind speed were made throughout each day. The results were grouped by calendar month, and compared by Multiple Range tests using a HP-85 calculator.

3.2.Results

3.2.1.The foraging range

A breakdown of the postal survey is given in Table 1.

Table 1. Breakdown of the postal survey.

	Total	Per cent
Questionnaires mailed	1173 (A)	-
" returned (viable)	556 (B)	47 (of A)
" " (incomplete)	51	4 (of A)
Unsolicited information supplied	156	28 (of B)

The results of the postal survey are depicted in Figures 4, 5 and 6 . Vultures sighted by farmers in the farmlands surrounding the Potberg are presumed to be colony members. Figure 6 includes sightings of birds that are presumed to have foraged from the Aasvogelvlei colony, as the sightings were made in farmlands close to that colony. Figure 6 also includes an outline of the



Figure 4. Results of the [illegible], giving the location of farmers that reported to "never see" vultures. The star marks the location of the Selsby, and [illegible], [illegible], RD-[illegible] and [illegible] (also Figures [illegible] & [illegible]).

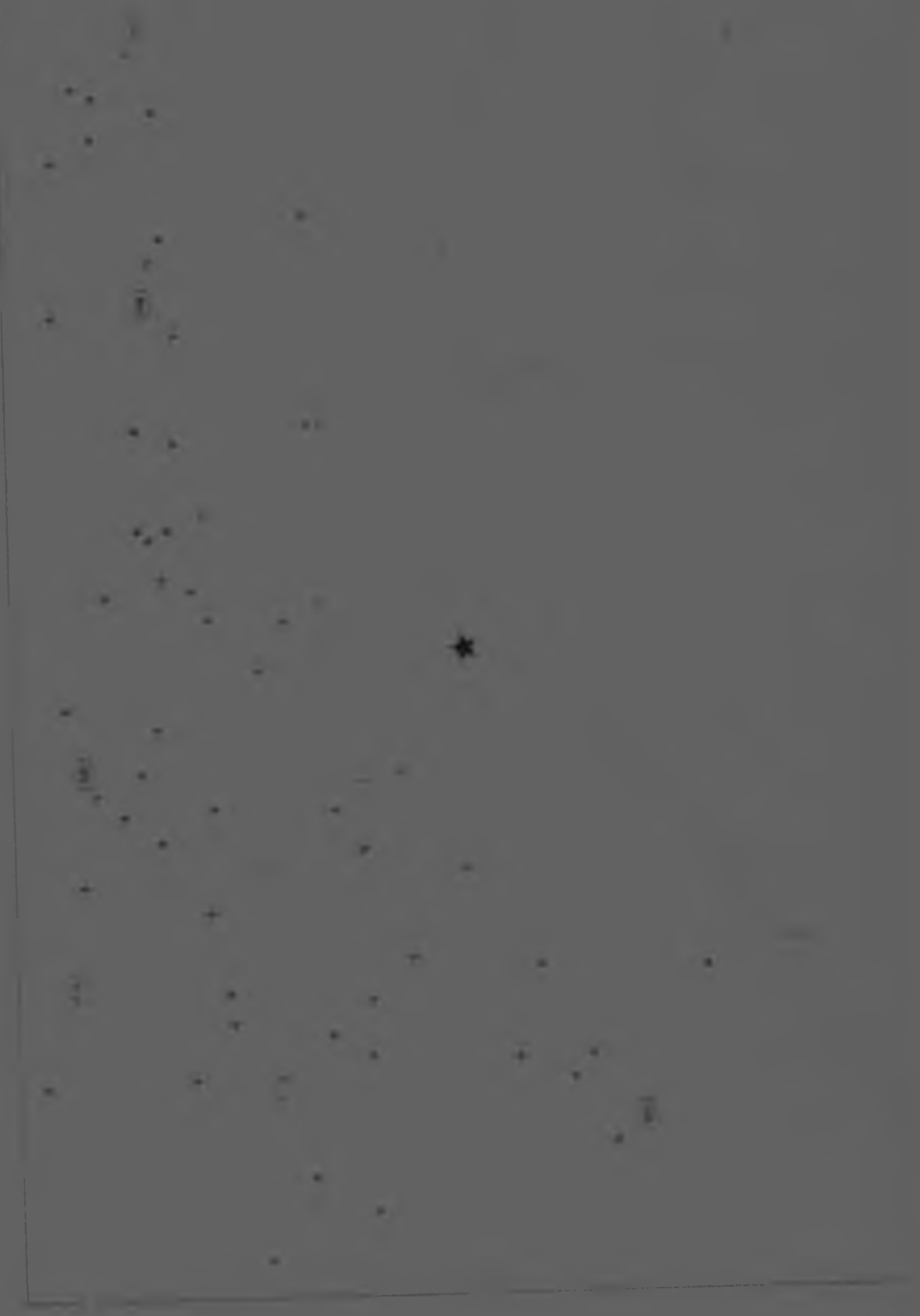

Figure 5. Results of the postal survey, giving the location of farmers that reported to see vultures "once every 5 years" (5), or "once every 10 years" (6).

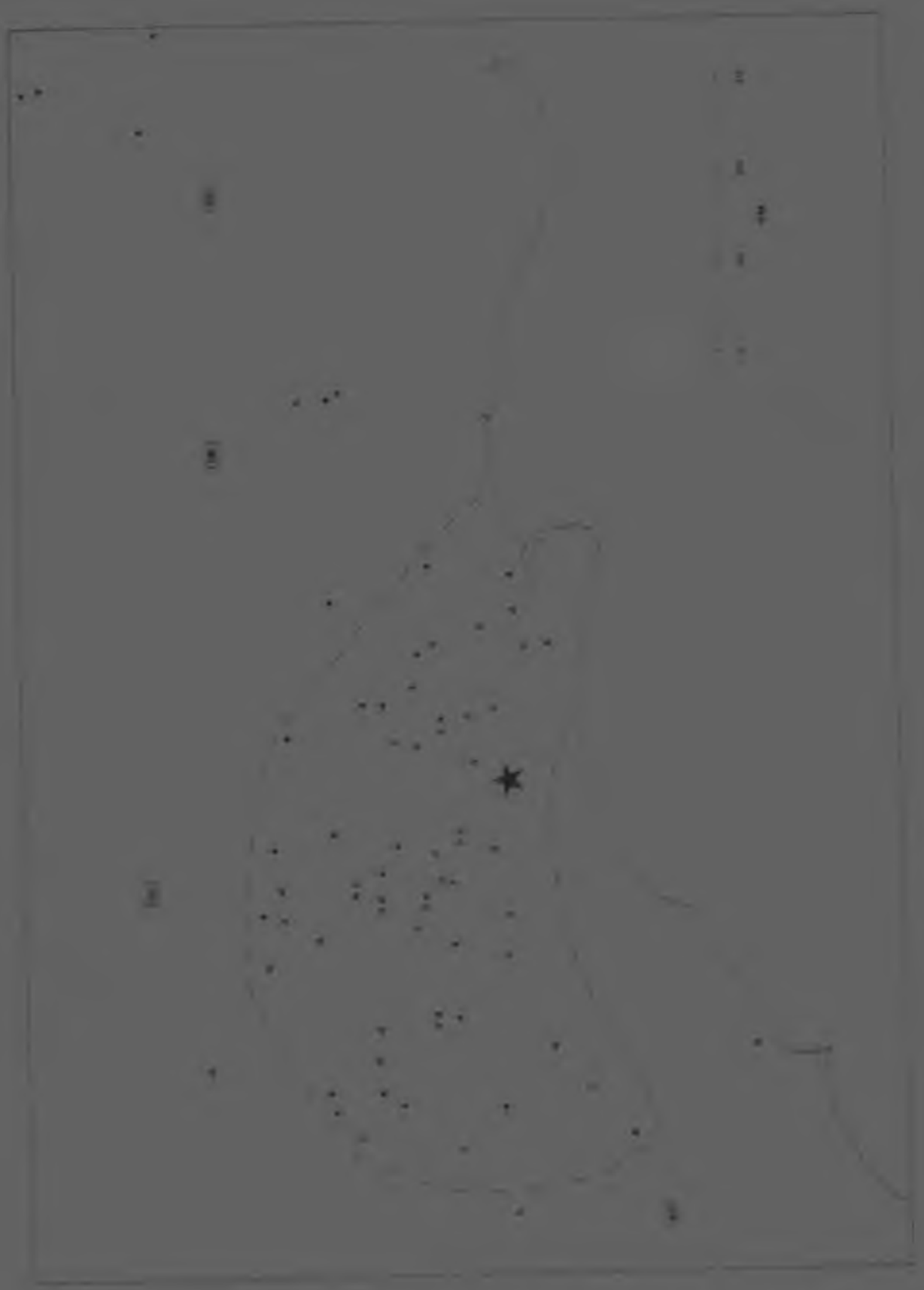

Figure 9. Results of the postal survey, giving the location of farmers that reported to see vultures "once a year" (4), or more often (2, 3). The dotted line encloses the daily foraging range.

current foraging range, an area of approximately 200 000 ha, as determined by comparison of this Figure with Figure 4. The limestone ridge is uncultivated, supports a comparatively low number of stock and is not included within the foraging range in the calculations of potential food. This figure therefore differs from that given in Robertson (1983a). The De Hoop Nature Reserve is also excluded due to its low ungulate content at the time of the study, behaviour of the radio-marked vulture and the observation that vultures "are never" seen over the De Hoop area (P. van der Westhuizen pers. comm.). Sightings of vultures outside of this range are documented in chapter five (5.1.). Although certain farms where the residents replied that they never saw vultures could not be located, all farms where vultures were seen "once a year" or more often were located, and are included in Figure 6.

All "feeding" sites located during the radio-tracking study were situated within the boundaries of the outline in Figure 6 (Boshoff, Robertson & Norton in prep.).

The overall average feeding time was 3 hours 42 minutes (range 52 minutes - 7 hours 5 minutes, n=323), and these are presented in Figure 7. Analysis indicated significant differences between various months, in particular shorter forays for months during which lambing occurred, as compared to out-of-lambing season months (Tukey's Multiple Range test, 1% level). Months of lambing are included in 3.2.3. On 28 August 1982, a group of vultures was observed to feed on a farm 6 km from the kloof. After feeding, 10 birds (of 16 present) lay down and were stationary for 35 minutes, some 35 m from the carcass. The weather was overcast and when a breeze picked up and a light drizzle started, all flew off ; the observation is included to illustrate how the feeding times may be influenced by a range of behavioural (and other) factors (see Mundy 1982). From the radio-tracking study, a factor of distance to feeding site per feeding time was obtained (Boshoff, Robertson & Norton in prep.). Using this factor, the above average time of 3 hours 42 minutes corresponds to feeding sites located approximately 13 km from the kloof.

Figure 7. Feeding forays of individual vultures, averaged per calendar month. The sample sizes and means (±s.d.) are given. Months that are significantly different share the same number (Tukey's Multiple Range test, 2. at level), and where the number is encircled, the difference is significant at the 0.01 level.

3.2.2 Nature of the food source

A range of artefacts, bones and bone fragments, presumed to have been brought back to the kloof by the vultures was found at the bases of the breeding and roosting cliffs (Table 2); all regurgitated pellets were of sheep's wool. Seven sheep ear tags were found at the base of the breeding cliffs during the study.

Table 2. Ma[illegible] found at nests. Where possible, the bones were identified: vertebra (v), metatarsal (mt) or rib (r).

		1981	[illegible]
Bone	intact	[illegible]	[illegible]
	fragment	[illegible]	[illegible]
Horny hoof covering		[illegible]	
Other			1 - glass 20x30
Regurgitate		[illegible]	[illegible]
		[illegible]	
Bone	intact		[illegible]
	fragment	[illegible]	40x10(r)
Horny hoof covering			[illegible]
Regurgitate		[illegible]	[illegible]

All of the 45 farmers that were interviewed considered that the vultures currently feed exclusively on sheep carcasses, although five were of the opinion that dead cattle could very likely supplement this diet.

All carcasses visited by vultures, that were located during the radio-tracking study, were of sheep (Boshoff, Robertson & Norton in prep.).

3.2.3.Stock contained within the foraging range

A large amount of stock, of which sheep and cattle are the most numerous, is farmed in the area. Sheep and cattle totals for the last six years are presented in Table 3.

Table 3. Livestock totals for the Bredasdorp-Swellendam area. These data were obtained from ATS-J.P. Pietersen pers. comm. and the yearly reports of the Swellendam State Veterinarian.

Period of census	Swellendam		Bredasdorp	
	sheep	cattle	sheep	cattle
'981/2	306091	'6230	315020	'8740
'980/'	297304	'5912	335691	'9554
'979/80	354868	'6449	332230	'9779
'978/9	336361	'6445	296974	21660
'977/8	333090	'6098	240600	'8800
'976 -	214160	'5039	238077	'8584

In the calculations of the theoretical amount of food available to the vultures, only sheep are considered. This was because evidence obtained during this study indicated that the Potberg vultures feed almost exclusively on sheep carcasses (3.2.2.).

The average annual adult sheep mortality estimate obtained from these interviews was 2,2 per cent. All farmers interviewed considered sheep deaths to be temporally dependant, with a peak at the time of lambing. In addition, in the winter rainfall region an average of 16,9 per cent of lambs die between birth and

weaning (Louw 1970). Of 45 farmers interviewed, the dates of lambing seasons were obtained from 38: all of these considered the months of March-April to constitute the main lambing season, while 34 (89%) indicated that approximately 30 per cent of one year's lambing occurs in the September-October period. Also, losses to diseases such as lamb dysentery and, especially, enterotoxaemia are heaviest during the winter months (Monnig & Veldman 1976). Figure 8 outlines the factors influencing the availability of these carcasses to the vultures.

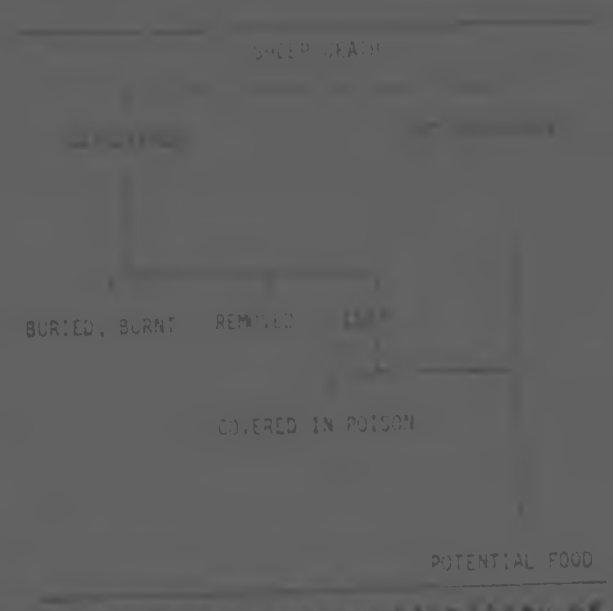

Figure 8. Factors influencing the availability of carcasses to the vultures.

The farms of all the farmers that were interviewed were situated within the boundaries of the foraging range in Figure 6.

An estimated average of 1,7 sheep per hectare of cultivated farmland as obtained from these interviews. This is probably an underestimate, e.g. on the farm Mopama (35 km N of Potberg), some 8500 sheep are pastured on ca 2000 ha, an average of 4,2 sheep per ha (M.G. Lourens pers. comm.). The potential number of sheep deaths that can be expected in one year is then calculated as follows:

Foraging area :	194 [illegible]0 ha
74% under cultivation :	143 560 ha
1,7 sheep per ha :	244 052 sheep
Mortality estimate :	5369 sheep

The figure of 74 per cent of the area surrounding the colony being under cultivation was obtained from ATS-J. P. Pietersen pers. comm. Of the 45 farmers questioned, 29 (62%) considered it important to remove the carcass from the grazing lands as soon as it was found. If the carcass was reasonably fresh, it would always be removed, but 16 farmers replied that carcasses in an advanced state of decomposition would either be left or covered with poison. If the factor of two-thirds is applied to the figure reached in the above calculations, 1790 carcasses are calculated as being theoretically available to the vultures within the foraging area in one year. This must be considered a minimum estimate : not all carcasses are located and not all those that are removed are rendered unavailable to the vultures (pers. obs.).

A recent study of the daily requirements of Cape Vultures (Komen 1983) confirmed an earlier estimate (Houston 1972, Mundy 1982) of 300-500 g of lean meat per day, thus the amount required by the whole colony may be estimated (Table 4). In addition, each nestling requires some 76 kg of lean meat between hatching and fledging (Komen 1983).

Table 4. Colony food requirements, based on an average daily metabolic rate (ADMR) of 0,47 g per day (J. Komen pers. comm.) and a factor of 1,5 taken from Gessaman (1973). One sheep is taken as the equivalent of 15 kg of meat (Jarvis et al. 1974).

			Week		Year	
	ADMR	1.5 x ADMR	kg	sheep	kg	sheep
[illegible]	0.47	0.70	4.9	0.3	257.3	17.1
[illegible]	28.2	42.3	[illegible]	19.7	15439	1920

3.2.4. Amount of food obtained by the vultures

The results of the visual estimation of the proportion of the colony considered to have obtained food during a particular observation day, expressed as averages for each calendar month, are presented in Figure 9. The overall monthly average of 40 per cent translates into an individual bird feeding approximately every two and a half days. Difficulties were experienced with this method (3.3.).

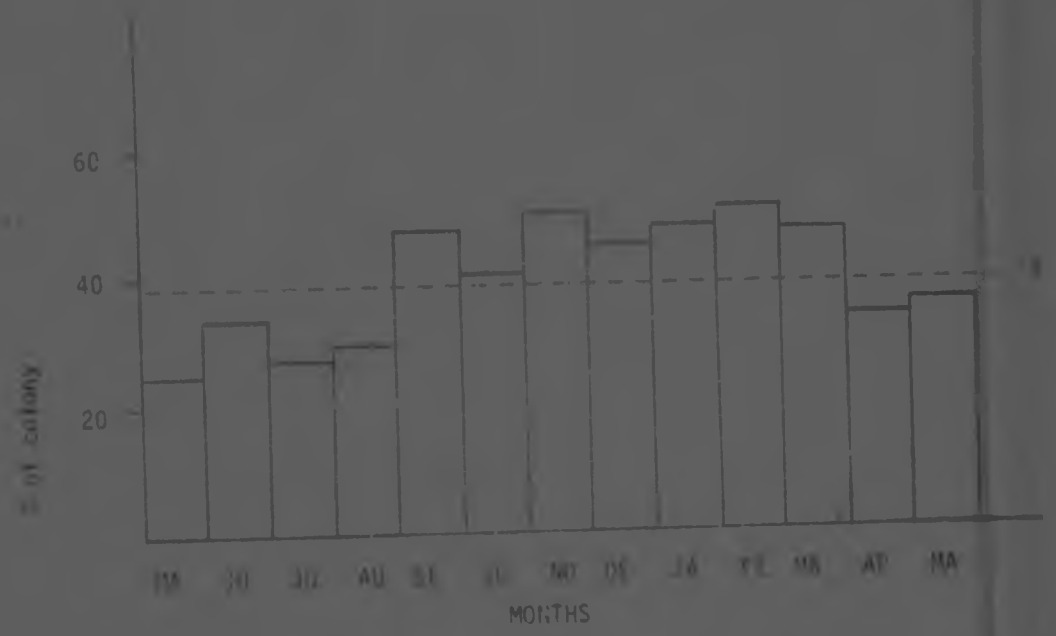

Figure 9. Daily estimations of the proportion of the colony considered to have obtained food in an observation day. The proportions are averaged per calendar month. The mean estimate is indicated ($\bar{x}$).

Although members of a pair that have failed during the breeding cycle may retain their nest site, the level of occupancy drops after the point of breeding failure (chapter four). The not all site occupants could be constantly monitored throughout one year. As most birds at nest sites were not individually recognisable, only breeding sites where a fledgling was raised in the 1981 season were monitored. The results of this individual

Table 5. Results of estimation of crop content of individual birds. Column B gives the number of observation days per nest, and e.g., column D the number of days in which the site occupants were considered to have obtained food.

Nest	No. chick estimates	B	No. days not fed	No. days fed	No. days chicks fed	No. days crop estimated	No. days fed	A/B	C/B	D/B	E/C	F/B
	A		C		E		F					
1	12	11	11	10	11	10	10	1.0	1.0	0.91	1.0	0.91
2	11	10	10	10	11	11	10	1.0	1.0	1.0	1.0	1.0
3	11	10	10	10	11	11	10	1.0	1.0	1.0	1.0	1.0
4	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
5	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
6	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
7	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
8	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
9	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
10	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
11	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
12	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
13	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
14	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
15	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
16	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
17	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
18	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
19	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
20	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
21	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
22	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
23	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
24	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
25	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
26	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
27	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
28	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
29	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
30	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
31	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
32	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
33	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
34	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
35	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
36	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
37	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
38	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
39	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
40	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
41	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
42	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
43	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
44	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
45	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
46	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
47	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
48	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
49	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
50	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
51	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
52	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
53	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
54	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
55	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
56	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
57	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
58	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
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60	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
61	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
62	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
63	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
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66	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
67	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
68	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
69	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
70	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
71	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
72	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
73	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
74	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
75	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
76	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
77	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
78	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
79	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
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109	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
110	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
111	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
112	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
113	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
114	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
115	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
116	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
117	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
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127	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
128	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
129	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
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132	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
133	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
134	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
135	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
136	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
137	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
138	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
139	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
140	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
141	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
142	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
143	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
144	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
145	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
146	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
147	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
148	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
149	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
150	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
151	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
152	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
153	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
154	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
155	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
156	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
157	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
158	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
159	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
160	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
161	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
162	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
163	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
164	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
165	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
166	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
167	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
168	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
169	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
170	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
171	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
172	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
173	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
174	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
175	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
176	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
177	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
178	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
179	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
180	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
181	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
182	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
183	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
184	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
185	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
186	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
187	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
188	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
189	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
190	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
191	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
192	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
193	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
194	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
195	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
196	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
197	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
198	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
199	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91
200	12	11	11	10	11	11	10	1.0	1.0	0.91	1.0	0.91

Table 5. Results of estimation of crop content of individual birds. Column B gives the number of observation days per nest, and e.g., column D is number of days in which the site occupants were considered to have obtained food.

Nest	no. crops estimated	no. days	no. days not fed	no. days fed	no. days [illegible]	no. days [illegible]	no. days [illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
	A	B	C	D	E	F	G					
4	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
6	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
7	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
16	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
17	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
61	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
63	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Total :	[illegible]	[illegible]					Mean :	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

crop [illegible] Table 5, where an overall average of 1,[illegible] crop estimations were obtained per nest per day (Table 5, column A/B). Of all crops recorded, 53 per cent were classed as empty (C/A) ; this indicates that individuals obtain food in one of every two attempts. The difference between the number of times birds were recorded as having obtained food, compared to returning with an empty crop, was not significant (χ^2 = 2,65, 6d.f., p>0,25). Of the birds recorded as having obtained food, 69 per cent were estimated as having obtained more than their daily requirement (E/D). On 64 per cent of the observation days, crop estimations of both members of a pair were obtained (C/B) and on 17 per cent of these days, both birds were concluded as having obtained food in the one day. At changeovers during the incubation period, the incoming partner had obtained food on 64 per cent of the post-11h30 changeovers (4.2.2.).

Weights and wing lengths of Potberg nestlings of known age are presented in Figures 10 and 11, compared to the curve of similar measurements made at the Magaliesberg and Botswana colonies (original graph supplied by P.J. Mundy). Figure 12 documents the body mass - wing length correlation measured during the study period at Aasvogelvlei, in relation to the mean curve of Transvaal nestling growth. In 1981, four Potberg nestlings were visited twice, and one was weighed once. In 1982, two nestlings were visited three times; the age of one of these was not known accurately, but was estimated and included in the figure due to its exceptional mass. The weight of another nestling was not obtained. Thus all (but one) nestlings were heavier than the mean weight at the same age that was recorded at the Magaliesberg colonies, and all but two had longer wing lengths for their age (in the two "shorters", feathers had not yet appeared). One 1981 and one 1982 nestling had exceptionally long wing lengths for their age: nestling periods were 139 days and 124 days (shortest recorded in this study) respectively.

Three large nestlings vacated their nests in November 1982, most likely the result of human disturbance (see chapter four, 4.4.5.). Two were located, one alive but seriously injured, within 1 week of the event and post-mortems on both were carried out by a veterinary surgeon (N. Drager). The level of fat storage



Figure 10. Growth of [illegible]otberg nestlings in body mass, [illegible] to the mean curve [illegible] Magali[illegible]sberg colonies. Munday [illegible]



Figure 11. Growth of Potberg nestlings [illegible] relation to the mean curve from the Magalie[illegible] 1982).

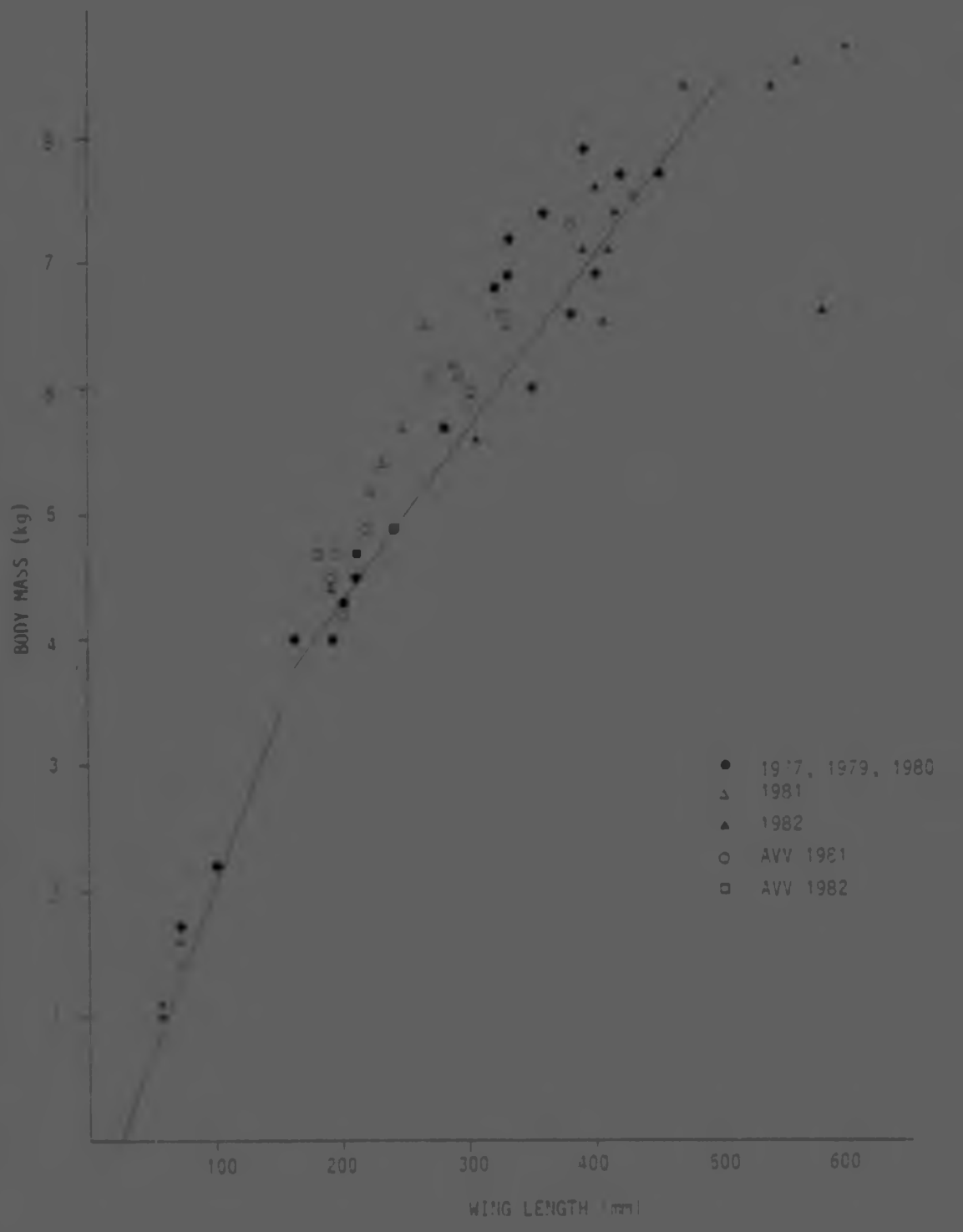

Figure 12. The relationship between body mass and wing length of nestlings. This includes nestlings weighed during the study period at Potberg and Aasvogelvlei (as indicated), as well as Potberg nestlings weighed in 1977, 1979 and 1980 (data from CDNEC records). The straight line of the relationship obtained from the Magaliesberg colonies was supplied by P.J. Mundy.

was considerable in both and was classed as score 6 and score 7 (highest possible score of 9, see Houston 1976:17). The stomach of one contained several sticks, the largest measuring 180 x 10 mm, an end of which had caused an ulcer in the pyloric region and most likely a small rupture in the left liver lobe (localised fibrinous peritonitis seen). No parasites were found in the intestinal tracts of either nestling.

All farmers more than 15 km from the colony that were questioned noted that the proportion of carcasses they located that had been consumed by the vultures was particularly small.

Allegations concerning vulture attacks on sheep are discussed in 3.3.

3.2.5. Foraging behaviour

Proportion of time spent foraging

The numbers of birds present in the kloof during each observation day have been averaged for each calendar month and are presented in Figures 13 - 16, as an indication of the proportion of each day that the whole colony spent foraging. During the summer months (October - March), at least 50 per cent had left the kloof by 09h30 (3 months) or 10h00, and the winter months (May - August) reflected a shift of at least half an hour later in the day. Conversely, 50 per cent or more had returned by 13h30 or earlier (three months) or 14h00 in the summer months, and by 14h00 (five months) or later in the winter months. At the 10h00 time count, significantly more birds were present in May 1982 than during each month from September through to February inclusive (Tukey's Multiple Range test, 5% level). The same situation held for the 11h00 count between May 1982 and October, November, December and March. There were no significant differences at the 5 per cent level between the other hourly counts.



Figure 13. Monthly foraging pattern of the whole colony : May 1981. The means (±s.d.) of vultures present in the kloof at each time interval are averaged per calendar month. Figures 14, 15 and 16 have the same format as this Figure.

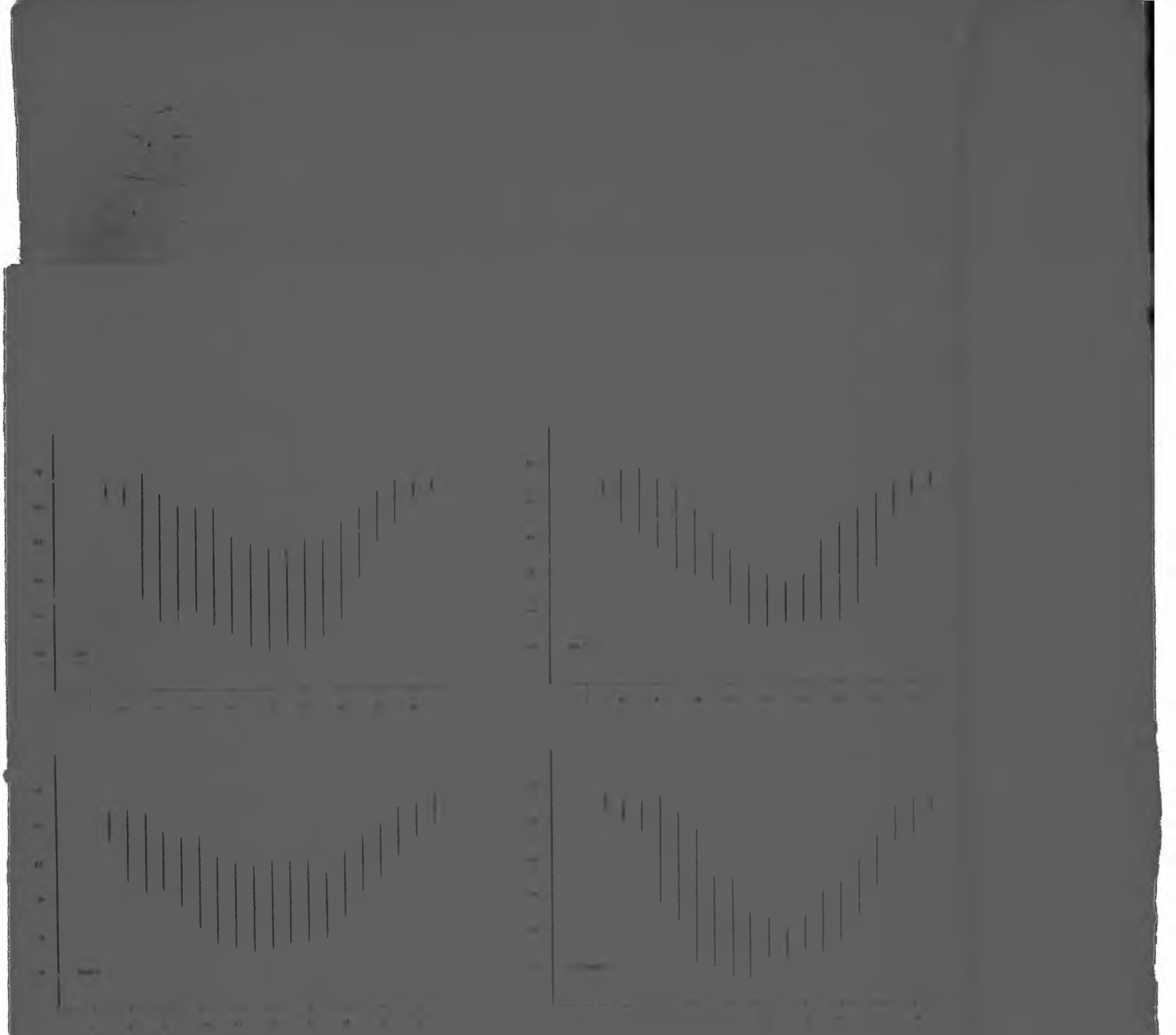

Figure 14. Monthly foraging pattern of the whole colony : June - September 1981.

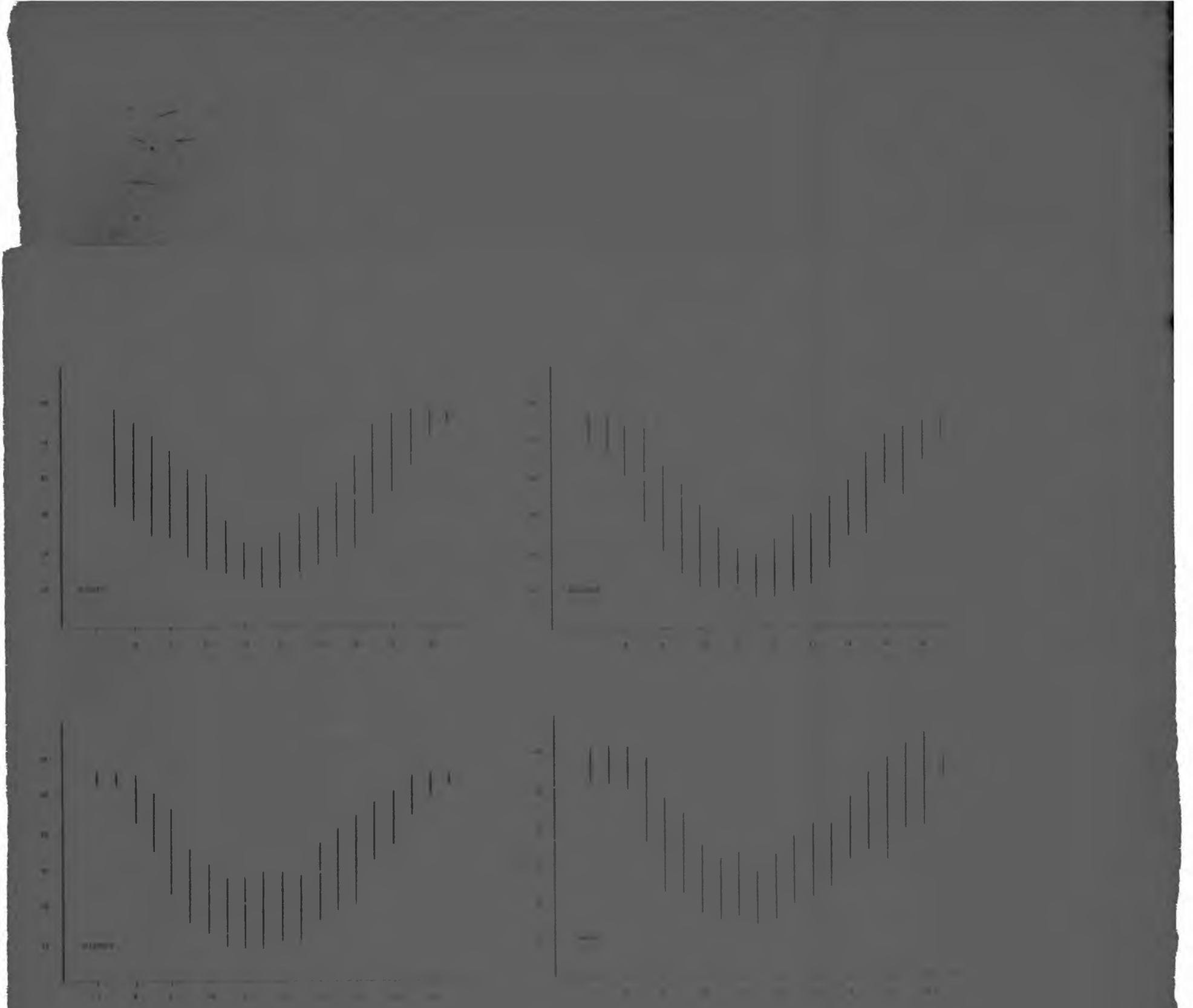

Figure 15. Monthly foraging patterns of the whole colony
October 1981 - January 1982.

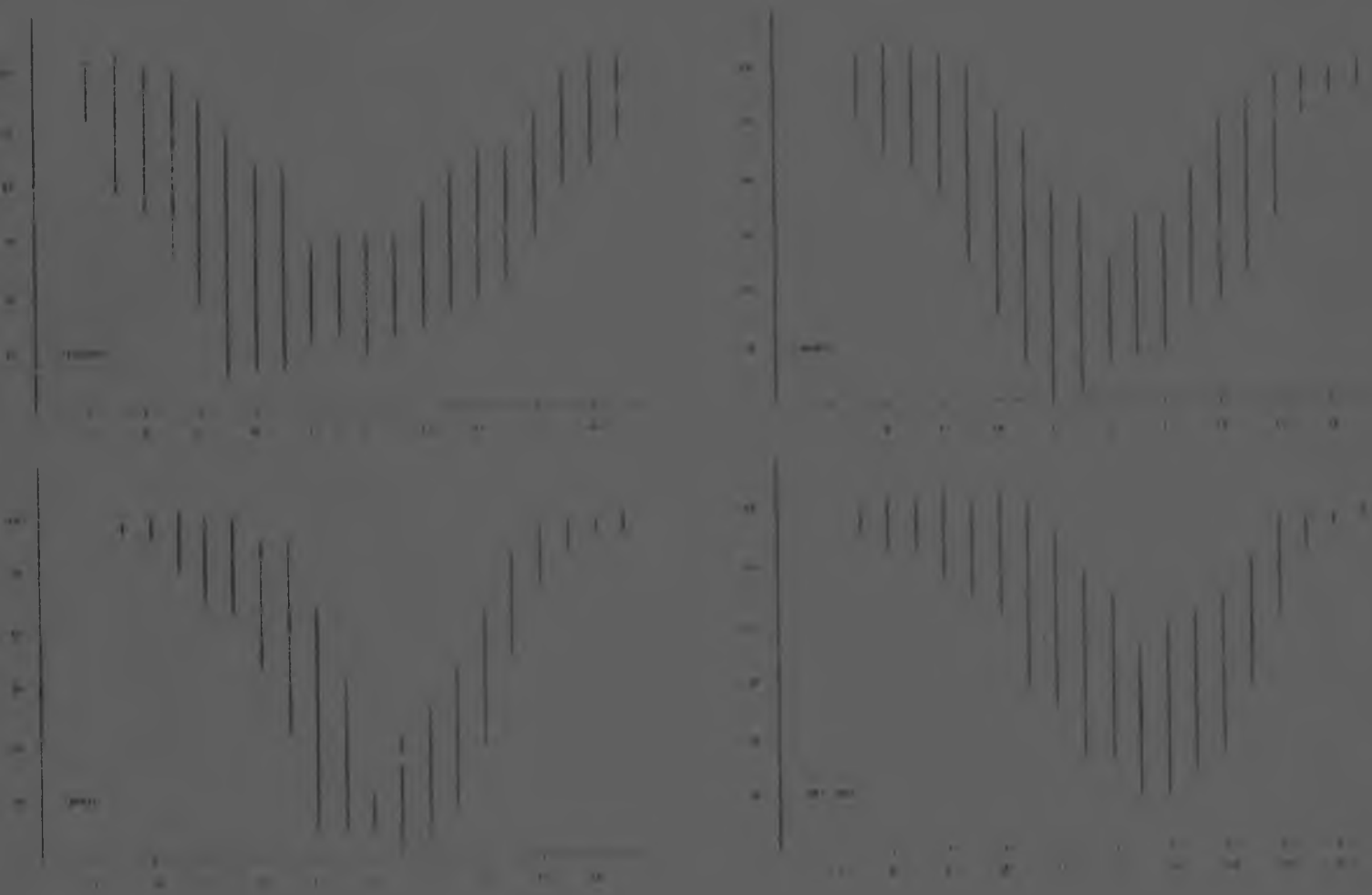

Figure 16. Monthly foraging patterns of the whole colony : February - May 1982.

Most vultures returned to the kloof after each day s foraging, as established by the counts made at the end of each day (Figure 17). The average of the monthly standard deviations of vultures present at the last count of each day was 2,04 individuals. This contrasts with behaviour observed at Aasvogelvlei where, at the few times birds were counted, breeding birds appeared to stay away from the colony overnight (chapter five, 5.2.).

Vultures at carcasses

Eight reports of vultures that were counted on the ground at a sheep carcass were obtained, and I observed a further 10 instances. The average number of birds on the ground in all cases was 9,8 (range 4-21). At six of the instances that I observed, a pair of White-necked Ravens Corvus albicollis (Latham) was present.

I located seven vulture-consumed lamb carcasses, less than one month old, in September 1982 on the farm adjacent to the Potberg. Of these, only one carcass had bones other than leg bones present and four of the skulls, or portions thereof, had been removed - presumably by the vultures.

A feature of the older carcasses which had been eaten by vultures was that even from nearby they did not appear to have been fed on at all. Closer examination revealed gaps in the base of the legs and around the posterior, where the birds had made their entry. Four of the 10 older sheep still contained decomposing viscera. Also, on every carcass (including a donkey and Springbok Antidorcas marsupialis (Zimmerman) that I had placed) the skin around the lower jaw was missing. A three day old carcass that had been completely emptied out weighed 18 kg ; its live weight (seven months old) was estimated at 60 kg.. Two four month old lamb carcasses, attended by vultures weighed [illegible] kg and 9 kg.

3.2.6.Contamination of the food source

Two repercussions of food contamination were considered : the ingestion of small amounts of poison that accumulate and

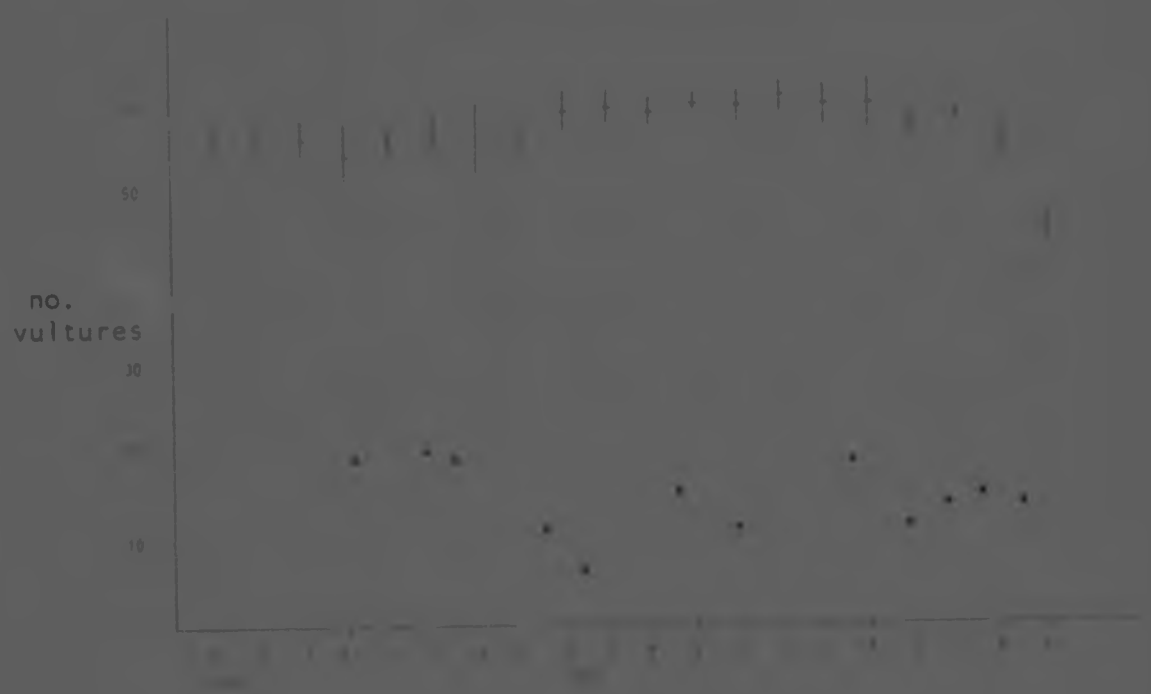

Figure 17. Total counts of vultures made in the evening at Potberg and Aasvogelvlei (●). For the Potberg counts, the mean (±s.d.) for each month is given, single counts were made at Aasvogelvlei.

subsequently affect an individual's breeding, and the sudden ingestion of a lethal or near lethal dose (a "poisoning event"), e.g. Ledger (1980) and Morris & Mundy (1981).

The range of poisons used in the area on sheep is presented in appendix e. The modes of application are via dips or directly externally (e.g. in the prevention of blow fly myiasis). Blow flies (family Calliphoridae) primarily breed in carrion, but also lay eggs in live sheep , larvae then digest meat externally and if the sheep remains untreated, it may eventually die (Ledger 1979). The chief area of attack is between the hind legs (ibid.) Thus vultures entering a carcass through a treated anal area would come into direct contact with the poison.

The results of analysis of eggs for pesticide contamination are presented in Table 6.

Table 6. The results of analysis of eggs collected during the study period, expressed as mg /kg wet weight.

Sample	α-BHC	γ-BHC	p,p'DDE	p,p'DDD	p,p'DDT	Dieldrin
PBS7	0,003	0,005	0,03	0,04	Trace	0,002
PB3		0,003	0,02	0,002	0,008	0,02
PB17			0,49	0,17	0,02	0,05
AYV13	-		0,37	0,07		0,02

Another method of diminishing blow fly presence is to treat carcasses with poison, and this is the origin of a potential poisoning event. One such carcass was located 30 km NW of the kloof. Of 45 farmers interviewed, six admitted to this practice, but only "infrequently".

Without exception, each farmer considered the White-necked Raven a pest for its alleged attacks on young lambs, lambing ewes and sheep in distress. This species is rarely seen in the area

(pers. obs.), although it was considered common in the past. The opinion of 42 of 45 farmers was that it declined in status as a direct result of the poisoning of carcasses set out for it. In most cases the poison "Dazzel" (active ingredient Diazinon) was said to have been used. No farmer reported ever having found a dead vulture, and no poisoned vultures were found during this study.

3.3.Discussion

3.3.1.The foraging range

With their efficient method of soaring, griffon vultures are capable of covering vast distances in search of food. Pennycuick 1972) documented an average speed of 47 km/hr for a foraging Ruppell's Griffon, and a similar speed for the Cape Vulture was obtained from the radio-tracking study (Boshoff, Robertson & Norton in prep.). Griffons breeding in the Serengeti were found to travel up to 150 km from their nest site to reach the concentrations of food (Houston 1976, Pennycuick 1972). Pennycuick (1972) estimated a foraging radius of some 110 km for breeding G. rueppellii in the Serengeti, and Jarvis et al. (1974) calculated a theoretical daily foraging radius of 130-225 km from the Potberg colony. This resulted in a feeding range, i.e. an area within which members obtain most or all of their food, of ca 200 000 sq. km. Jarvis et al. (1974) concluded that it was possible that the colony's requirements were met within an area of 35 km radius, although the study did not consider that the Indian Ocean reduces this potential foraging area to one half.

The methods used to define the size of the current daily foraging range indicated that it was smaller than a theoretical maximum :

a. As areas of vulture "presence" indicated by the postal survey were surrounded by areas of "absence", the boundary was defined with relative confidence. Also, the area covered by this survey was clearly sufficient to encompass the daily foraging movements. With a maximum radius of some 40 km, this boundary is within one hour's flight of the colony. Individuals may occasionally exceed the boundaries, e.g. the radio-marked vulture roosting on the Langeberg (Bosnoff, Robertson & Norton in prep.), and other sightings (e.g. Martin 1983). These extra-feeding range movements are documented in chapter five (5.1.).

b. The radio-marked vulture's foraging behaviour was not considered atypical, as it was found to obtain food successfully as well as forage with other members of the Potberg colony (Boshoff, Robertson & Norton in prep.).

c. If the factor of "time spent away from the kloof" per distance to "feeding" site is valid (3.2.1.), the average of 13 km to "food" sources (as measured by the individual feeding forays documented in the kloof) is obviously well within a vulture's foraging capabilities. As the feeding forays were documented for breeding birds, this distance is probably longer : active breeders would be expected to return to their nests and nestlings sooner (Drent & Daan 1980).

In essence, the feeding range constitutes the summated effect of the individual requirements of colony members : comparison of colony requirements (Table 4) with the expected number of carcasses available to the vultures in one year within the range (3.2.3.) tends to reflect this. Similar inverse correlations are documented between the home ranges of individual raptors and the numerical density of their prey (reviewed in Schoener 1968).

The shape of the range is probably influenced by two topographical features of the area, viz. the orientation and elongated shape of the Potberg, and the presence of the limestone ridge to the west of the colony. Winds are strongest and southeasterly in summer (Schulze 1965) and the shape of the mountain would provide considerable wave lift over the surrounding northwestern farmlands. According to a farmer whose farm lies on the northern slopes of this ridge and 15 km from the kloof, the vultures use the ridge as a "highway" and are often seen flying close to the slopes, in parallel with the ridge (J. van Eeden pers. comm.). This is consistent with the expectation of vultures exploiting orographic lift, in this case ridge lift, produced by winds incident on the southern side of the ridge. For birds with a particularly high wing-loading (Pennycuick 1972), orographic-induced assistance in flight would be expected to influence flying activity.

It would seem likely that birds from Aasvogelvlei forage over farmlands south of the Langeberg range, as indicated by the postal survey returns. Also, a single adult was observed 45 km SSE of this colony in August 1982 (A.F. Boshoff in litt.). These sightings are actually very near the Perdeberg location (chapter five, 5.2.).

3.3.2.Food obtained

Quantity of food

Difficulties were experienced with the visual estimation of the proportion of the colony considered to have obtained food during a particular day. Houston (1972) has discussed some of the inaccuracies with this method, viz. the accuracy of the visual scoring and the time taken for food to be digested (i.e. a bird that obtained a full crop in the afternoon of the previous day would still display a bulging crop). Roosting birds tended to perch facing the cliff (away from the observer), thus estimations were made largely on flying birds as they returned. Perched birds would frequently leave perch sites and circle in the kloof, thus individuals could be seen more than once. Inaccuracies also arose when considering birds that have ingested 500 g or less : the crop distension is difficult to discern when the bird is perched, and, not being visible as a clear bulge when in flight, is easily missed. A full crop may contain some 1400 g of meat and viscera (Houston 1972, pers. obs.). Houston (1972, 1976:Figure 3), acknowledging these deficiencies in the method, proceeded to document average crop contents of returning G. rueppellii foragers to an accuracy of 250 g and greater ! Bearing these various points in mind, the result of birds feeding every 2,5 days is considered a minimum figure. Given the inaccuracies of the method, this overall view of the food situation (of ca 600 g obtained every 2,5 days) corresponds to some 240 g obtained per day. This approximates to half the daily adult requirement (Komen 1983, Mundy 1982).

A more time-specific measure of the frequency of food obtained was the number of times an incoming adult was documented, at a post-11h30 changeover, as having obtained food during a particular period of the breeding cycle (4.2.2.). During the 1981 incubation period, at two-thirds of all post-foraging changeovers, the incoming adult had obtained at least 500 g of food. During the nestling period (up to an approximate nestling age of 100 days in each case) this proportion was four-fifths. However during the nestling period, parents would be more likely to visit the nest after feeding (to feed the nestling) than if

they had not fed, and this figure may be skewed as a result.

Correlations of weight and winglength with known age provide an indication of the quantity of food obtained, as well as "chick condition", during that particular stage of the cycle (Mundy & Komen 1983, Newton 1980). Certainly, the overshoot in body mass that is found in many nestlings is primarily a matter of fat deposition (Bryant & Gardiner 1979), which occurs after the period of maximal growth. Figures 10 and 11 then indicate a period of sufficient food during the early to mid nestling period. This is reflected in the enhanced growth rate during the early phase of the period (0-70 days), and above-average (for the Magaliesberg) accumulation of reserves during the deposition phase of 70-100 days (J. Komen pers. comm.). The latter was confirmed by results of the post-mortem. This fat is a reserve intended to ease the transition to self-feeding following fledging, as well as to bridge gaps in parental food delivery that may occur during the nestling period (Drent & Daan 1980).

Quality of food

Houston (1978) considered that the particularly lengthy nestling period of griffon vultures was related to an aspect of the quality of food they obtained. Parents have difficulty in meeting the calcium requirements of the nestling, due largely to their food source which contains a mere 0,01 per cent calcium (Houston 1972). Parents then meet the requirements by providing calcium-rich food items, such as bone-chips, to their nestlings (Mundy 1982). In most areas, "natural" as well as ranching areas that contain large animals only, an intermediate is needed to reduce large bones to an edible size ; where those intermediates have disappeared, consequent forms of bone-diseases have been documented (Mundy & Ledger 1976). At the Potberg colony, only one instance of bone deformation has been documented, and Boshoff & Currie (1981) concluded it possible that the diet of the birds was such that bones small enough to swallow are obtained. Furthermore, approximately one third of each year's lambs appear in September, certainly on one large farm adjacent to the Potberg. Thus given their high mortality rate and the observation that vultures clearly visit the lamb carcasses (this study,

Boshoff, Robertson & Norton in prep.), the timing of this lambing season enables the parents to supply the calcium requirements of their young. On two occasions in September, and one in October 1982, I observed groups of less than ten vultures on the ground at old sheep carcasses (where only bleached bones and some wool remained). This may suggest that vultures revisit old carcasses in order to obtain bone pieces, although this needs substantiation.

3.3.3.Foraging behaviour

The foraging patterns of the colony as a whole (Figures 13 - 16) are remarkably consistent over the observation period, given the, albeit slight, change in colony numbers (Figure 17), the variation in hours of sunlight between winter and summer, and the change in breeding status of some 36 birds throughout the year ("tying" them to sites). This is in marked contrast to Rooks Corvus frugilegus (L.) for example, which spent more than 90 per cent of the daylight feeding during summer when food was scarcest (Feare 1972). The standard deviation of the mean of each month's daily counts provides an indication of the variability observed during individual days : as a general rule, this variability was greater during the morning than it was in the afternoon (except January). This variation likely reflects the birds' dependance on lift (thermals or orographic lift induced by wind) : in the mornings they would generally congregate on specific cliffs and "wait" for suitable flying conditions. Those cliffs, incidentally, were hardly ever used in the afternoon.

The shortest proportion of time spent foraging , in terms of theoretical food available, would be expected during the lambing season (March - May), a period of above average mortality. This would result in a higher probability of a food item occurring within a given radius of the colony. Birds returned at very similar times during these months (standard deviation of the 15h30 means of vultures present of 4.2, 2.7 and 3.0). The length of the feeding forays documented during these months (Figure 7) support this indication of increased food availability. In contrast, the variability in numbers returning at the end of the

day was greatest in January and February, and along with the reasonably lengthy individual feeding forays documented during these months, this probably reflects a relatively lower availability of food. Similarly, the radio-marked vulture's mean furthest foraging site and mean furthest "feeding" site in summer were on the average more than twice as far as those in winter (Boshoff, Robertson & Norton in prep.).

If 10 birds on average visit carcasses (3.2.5.) and each carcass supplies ca 15 kg (Jarvis et al. 1974), then if each bird removes ca 1200 g (Houston 1976), no food remains. Adult merino sheep weigh ca 50 kg (ATS-J.P. Pietersen pers. comm.) ; presumably more than 33 per cent of this weight is edible to vultures, e.g. 65 per cent of an Impala Aepyceros melampus is edible to griffon vultures (Mundy et al. 1983), then a carcass will obviously supply more food. The figure of 15 kg per sheep is thus a mimimum estimate, as an adult merino sheep could supply some 30 kg of food.

3.3.4.Contamination

With regard to contamination of the food source, the effects of gradual accumulation are considered first. Only dead eggs were analysed during this study : the results therefore do not reflect the levels for all eggs (or rather, the levels in females - Newton 1979:241). No tissues were examined. A Potberg egg collected in 1975 displayed the highest DDE content (ca 3,5 mg/kg wet weight) of vulture eggs that had been analysed by that date (Mundy et al. 1982). DDE, a stable metabolite of DDT, causes shell thinning and egg breakage as well as increasing mortality of embryos in unbroken eggs (reviewed in Newton 1979). The results in Table 6 are likely to be below the critical concentration ; in the Peregrine Falcon Falco peregrinus, hatching failure due to DDE contamination starts at 15 mg/kg wet weight (Peakall & Kemp 1976). The use of DDT was restricted in 1970 and withdrawn from agricultural use in 1976 ; these levels likely reflect continued use on a much reduced scale, possibly as a result of stockpiling.

The dieldrin level of PB17 (Table 6) is below the threshold

of 1 ppm above which upsets to breeding occurred in the Golden Eagle Aquila chrysaetos (Lockie et al. 1969). The Potberg egg collected in 1975 contained a higher concentration of ca 0,9 ppm (Mundy et al. 1982), although that study did not question the possible effects of this level. In the study of organo-chlorine residues in Golden Eagles in Scotland, dieldrin (described as the most toxic and abundant residue) was concluded as having caused a substantial decline in breeding success. In a situation similar to that at Potberg, the contaminant was ingested as the eagles fed on sheep carcasses. After it was banned from sheep dips in 1966, the eagles' breeding success consequently improved (Lockie et al. 1969). The evidence, albeit scant, then implicates dieldrin as a possible cause of reduced hatching rates in the past.

3.3.5. Allegations concerning sheep attacks

Much has been documented concerning allegations that vultures attack live sheep, in particular lambs and lambing ewes, and this aspect is reviewed in Boshoff & Vernon (1979, 1980) and Mundy (1982). None of the 45 farmers interviewed remembered such an instance in the previous ten years in the study area, and virtually all differentiated between vultures and ravens in this regard (3.2.5.). I did not observe lambing ewes for any length of time, but was assured by the shepherd of a large farm bordering the Potberg that vultures "leave the sheep alone". The only time I observed vultures (from some 700 m) in sheep grazing lands where no carcass was present, they remained perched for 20 minutes some 15 m from the nearest sheep before disappearing. I was left with the impression of them "waiting in anticipation"!

CHAPTER FOUR : BREEDING BIOLOGY

4.1.Introduction and methods

The broad aim here was to study breeding at the Potberg colony through all its stages in order to determine and understand recruitment to the population. Breeding at the Aarvogelvlei colony was also monitored in both years.



Figure 18. NW1 cliff. Nests active during the study period are numbered.

All active nest sites and roosting ledges were visible from the observation point, although certain sites were more easily observed than others. Thus nests on NW1 cliff were easier to

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All active nest sites and roosting ledges were visible from the observation point, although certain sites were more easily observed than others. Thus nests on NW2 cliff were easier to



Figure 19. NW2 cliff. Nests actve during the study period are numbered.



Figure 20. NE cliff. Nests active during the study period are numbered.

monitor than those on NE cliff (see Figures 18-20). Nonetheless, an attempt was made to monitor events at all sites and, for example, the presence of birds at all sites and roosting ledges was documented every thirty minutes during each observation day. The proportion of each class, i.e. one, both or neither occupant present at each count during an observation day, was determined and subsequently converted to an arcsine transformation (Schefler 1969). These figures were then compared within sites (e.g. proportion of counts of a single occupant versus the proportion of both occupants) as well as between different sites by Multiple Range tests, using a Hewlett Packard HP-85 calculator. Individual vultures were age-estimated using the characters given by Mundy (1982:43-44). Observations began in May 1981, for 12 days each month regardless of weather conditions, and ended in May 1982. Thus observations included the tail-end activities of the 1980 breeding season, all stages of the 1981 season and the initiation of the 1982 season. In addition, nine consecutive days of observation were conducted from 26 July to 3 August 1982. In total, 165 days were spent at the observation point, where one 'day' represents the time period 07h00-16h30. Nests were regularly inspected in order to obtain dates of fledging and observations of juveniles.

All nestlings at Potberg and Aasvogelvlei were colour ringed, weighed and measured as part of the national colour ringing programme on Cape Vultures (Ledger 1974). Nests were visited on five other occasions in order to collect addled eggs or shell fragments and, on 23 June 1981, to replace an egg that an adult had knocked out of the nest cup. In 1981, blood samples were obtained from both colonies and on both nest visits at Potberg. Smears were prepared by the method described in Greiner & Mundy (1979) and subsequently scanned for the presence of blood parasites by M.B. Markus.

Although most of the breeding pairs were not individually recognisable, there were a number of ringed breeders present and, at nest no. 63 where both were colour ringed, strangers alone at the nest for longer than five minutes were seen on only three occasions. Thus unless shown to the contrary, vultures observed at a site were documented as the occupants.

Addled eggs were analysed for the presence of pesticide residues by gas chromatography (A.C. de Kock in litt.), and the thickness of shell fragments was determined using a Federal Bench comparator thickness guage (L.F. Kiff in litt.). A radio-tracking study of the post-fledging dependence period of three 1982 juveniles was attempted ; the results of this study have been written up separately (Boshoff, Robertson & Norton in prep.).

The breeding cycle has been divided into its successive stages of pre-laying, incubation, nestling, and post-fledging dependence periods (Newton 1979) and each is considered separately, as is retention of a nest site from a previous year's breeding, the stages and causes of failure in breeding, and various inter- and intra-specific interactions. Unless stated otherwise, all observations were made at the Potberg colony.

4.2.Results

4.2.1.The pre-laying period

For raptors in general, the main activities in the period preceding laying include nest-site inspection, nest-building, various courtship procedures and copulation (Newton 1979). Due to the length of the breeding cycle, certain nests displayed an overlap of post-fledging and pre-laying periods (see 4.2.4.), whereas other pairs that failed in breeding retained their nest site from the date of failure.

Figure 21 depicts the average occupancy of 10 nests for the 1981 pre-laying period. As observations ceased before eggs were laid in 1982, no similar figures for that year are available. Certain sites that failed in 1981 were active in 1982 and were occupied to varying degrees in the interim period. These birds were clearly retaining the site, as they were observed to repel intruders from the site (see 4.2.6.). Nest sites were left vacant five per cent of the observation time during this period (n=10), as indicated in Figure 21. Analysis indicated significant differences at the 0.01 level in the degree of occupancy between nests, e.g. two nests on the NW2 breeding ledge. However, two other nests on the same ledge on NW1 cliff were occupied by one

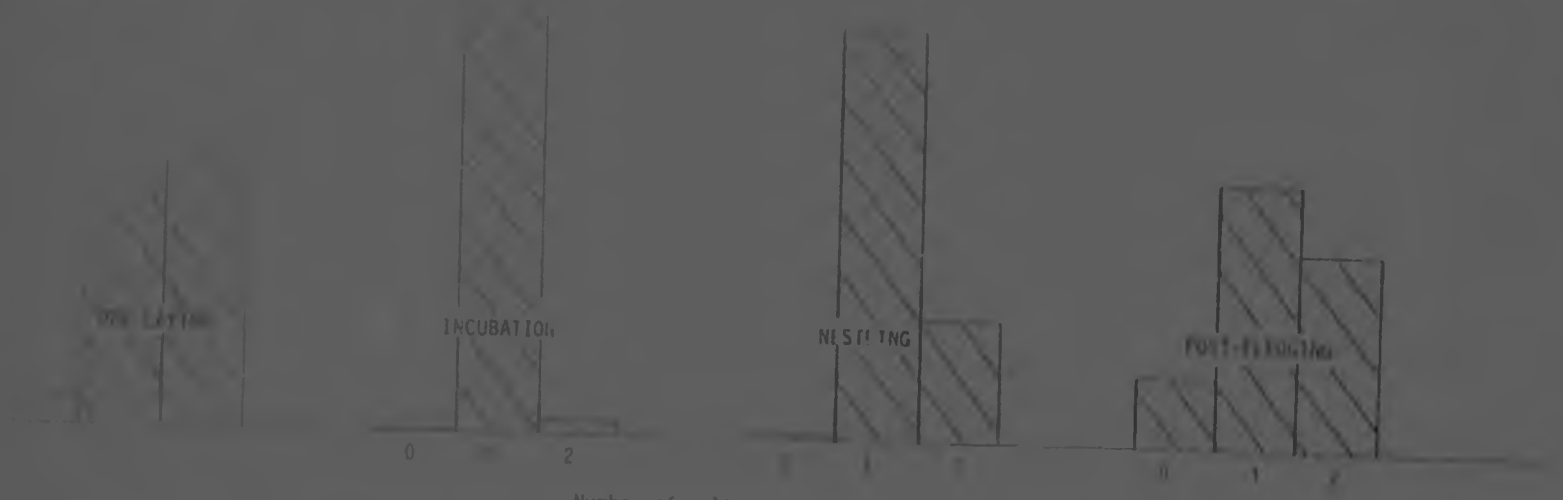


Figure 1. The average level of occupancy of nests during different periods of the breeding cycle. The number of nests used in the calculations for each period is indicated.



Figure 21. The average level of occupancy of nests during different periods of the breeding cycle. The number of nests used in the calculations for each period is indicated.

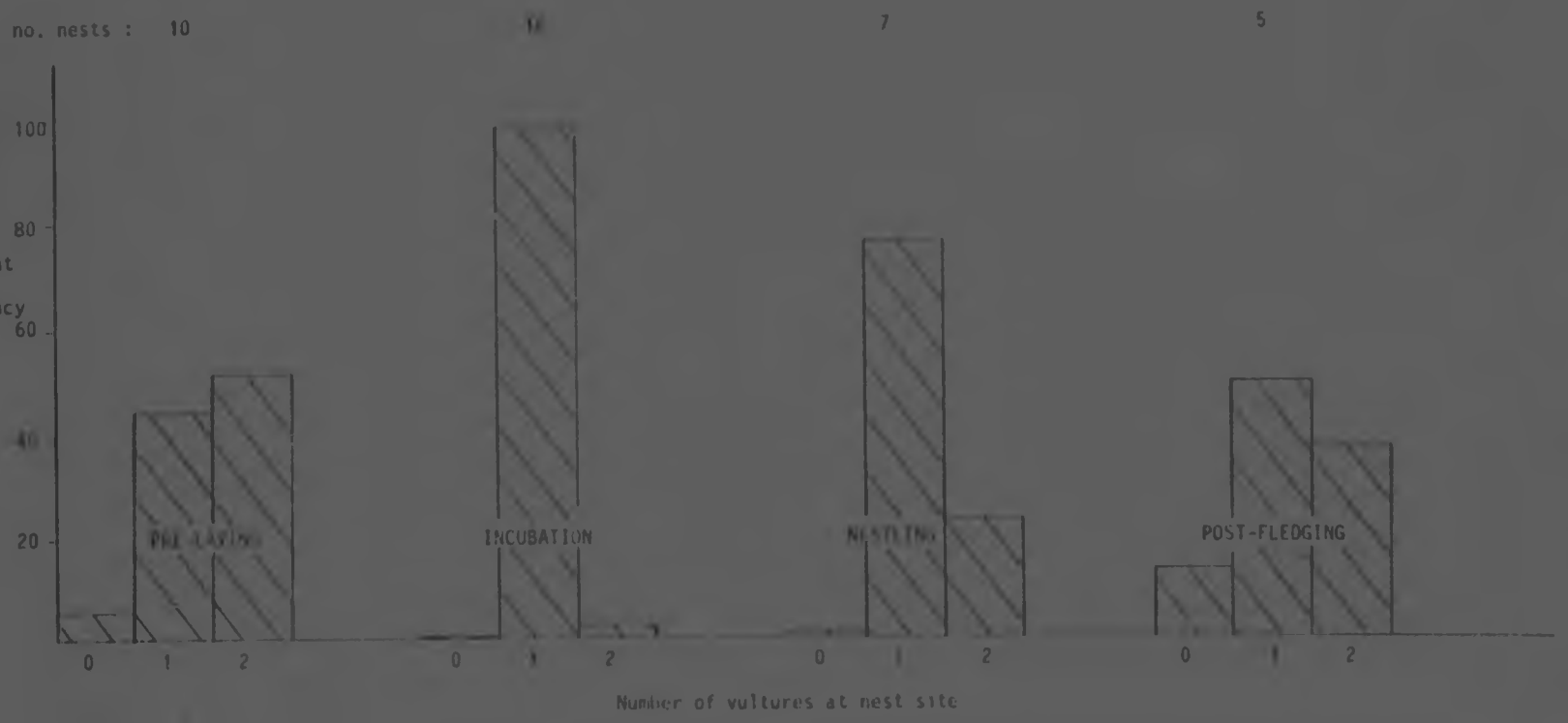


Figure 21. The average level of occupancy of nests during different periods of the breeding cycle. The number of nests used in the calculations for each period is indicated.

or both adults for similar amounts of time.

Activation of nest sites

Of the 17 breeding sites that were active in 1981, 14 (82 %) were active again in 1982. Of the additional four that became active in 1982, one had been active in 1980 (see chapter five). Thus only three sites were initiated during the observation period. An occupied site can be distinguished from an area used for roosting by intruder repulsion beha.iour (4.2.6.).

A pair of non-ringed birds was observed at a site, the real female occupant of which had a metal ring, on 29 October 1981: both stood very close togetner and bent over the site, facing inwards and picking at sticks on the surface. Seven minutes later, the female occupant landed at the site and repulsed both, who then repeated this behaviour at another (vacant) site. The impression gained was of a pair "prospecting" a possible future breeding site, some seven months before the next season's average laying date.

At another site, a pair comprising an immature male (est. 3 rd year) and female (est. 4 th year) was observed to copulate 36 times between 30 June and 30 December 1981. On most occasions after the attempt, both birds would bend over and pick at the "nest" contents : this was examined on 8 October and found to consist of a few sticks and fresh green sprays - an "intermediate" nest structure. The first intruder repulsion event observed at this site was on 20 December. This site produced a fledgling in 1982/3, thus it effectively was activated in mid-1981, if the parents are assumed to be the same individuals.

A probable mate replacement occurred at one site in 1983, where a colour ringed, six year old female was observed at nest no.61, from late December 1982. This site was active in the two previous years (both partners adult and non-ringed). The six year old's sex was determined by observation of a copulation attempt with an unknown adult male at a perch point on 18 May 1982. This female was hatched at nest no.57 on NW1 (Figure 18), and was often sighted perched on NW1 cliff during 1981 and 1982.

Copulation

Copulation attempts, which precede the initiation of nest building, were easily noted due to the male's distinctive hoarse call as he grips the female's ruff while balancing on her back (as described for the White-backed Vulture in Mundy 1982 ; see also Figure 22). With lateral motions of his tail, the male knocks the female's tail from side to side before leaning back and pressing his tail down to achieve coition. While on the nest, both birds spend much time bending over and pecking at the nest contents (e.g. Figure 22) : this would, in effect, position the female's back for the male, who would then mount from her side or rear. Of 32 attempts that were timed, the male was on the female's back for 42 seconds (range 22 - 56 seconds), although in at least 12 other cases, the male stood on the female's back for longer than three minutes before being jabbed off . Some males gave the impression of being 'inexperienced' by moving around on the female's back and not attempting to juxtapose cloacas. Thus in 17 of 31 observed attempts (55 %) at nest no. 57 in 1981, no cloacal contact occurred. This was observed to lesser extents at other sites, and not at all at some sites, although it is 'often difficult to judge' (Green 1976).

As with the White-backed Vulture (Houston 1976), no discernible display occurred at the nest before or after copulation, although pairs were occasionally seen to allopreen necks gently, both before and after the event (for the latter, see Mundy 1982). A form of "scapular action" display (Berruti 1981) generally occurs just after a bird has landed at a site, where it turns its head and places its bill at the junction of its wing and body. Less often, both members of the pair were engaged in this behaviour, and it is often accompanied by autopreening.

In the period May 1981 - May 1982 (154 observation days), 1783 copulation attempts were observed, of which 1706 (95.7 %) occurred at nest sites (Table 7). A peak in frequency occurred just prior to the average laying date of each season. For seven successful nests in 1981, 67,9 per cent of observed attempts occurred during the pre-laying period (Table 8) ; this includes one site (nest no. 61) where the nestling disappeared at 111/2

Site	A No. before egg laid	B Total observed May 81-Dec 81		A/B	Total observed Jan 82-May 82	
7	112	113	E	99,1	38	E
13	31	35	E	88,6	18	E
16	42	53	E	79,2	54	E
6	30	39	E	76,9	34	E
26	49	61	E	80,3	53	E
[illegible]	44	55	E	80,0	64	E
63	59	59	E	100	22	E
55	44	45	E	97,8	25	E
17	48	57	E	84,2	51	E
61	17	30	E	56,7	54	E
30	38	49	E	77,5	5	E
18	39	49	E	79,5	48	E
57	31	31	E	100	46	E
29	39	57	E	68,4	4	-
45	21	21	E	100	0	-
3	54	54	E	100	1	-
2	-	32	-	[illegible]	30	E
50	-	8	-	-	25	E
25	-	24	[illegible]	-	71	E
64	-	0	[illegible]	[illegible]	19	E
8	-	117	-	-	21	-
57[a]	-	34	[illegible]	-	-	-
ROOST POINTS		56			21	
		Σ x = 1079			Σ x = 504	

Table 7. Copulation attempts observed in the colony. This Table also documents the sites that were active during the study period (E : egg laid). Nest no. 57[a] is adjacent to nest no. 57, but has never known to be active in the history of the colony.

days of age.

Three hundred and seventeen (17,8 %) attempts occurred at sites or roost points where no egg was produced ; e.g. at nest no. 8, 138 attempts were observed without an egg appearing in either year. Eleven attempts (0,6%), where a male that had jumped onto an assumed female's back was aggressively jabbed off, that occurred on roost points, were classed as "resisted matings" (Estep & Bruce 1981). Similar incidents, although not at the nesting area, have been observed in White-backed Vultures (Mundy 1982). In six of the eleven cases, one of the birds was from a known nest site (4 males, 2 females). These contrasted with three cases of "cross matings" (0,05 %), where the male achieved cloacal contact and was not aggressively jabbed off. For example, nest no. 13 female was thus involved (26 June 1981) some six days before laying an egg, and on 23 June, nest no. 17 male was observed to copulate with an unidentified adult female at a roost point while his partner incubated the egg.

Table 8. Copulation attempts observed per period of breeding cycle. The figures for nest no. 61 are in brackets as the nestling disappeared before fledging, and the total for successful sites excludes this site.

Nest	Pre-lay. A	A/E %	Inc. B	B/E %	Nestl C	C/E %	PFDP D	D/E %	Total
6	31	76	8	20	0	0	2	5	41
17	47	63	8	11	20	27	0	0	75
16	42	39	2	2	15	14	49	45	108
18	37	-	1	-	-	-	-	-	38
29	38	-	5	-	-	-	-	-	43
4	44	73	0	0	13	22	3	5	60
26	47	-	6	-	-	-	-	-	53
61	16	(59)	0	0	(11)	(41)	-	-	27
30	38	-	0	-	-	-	-	-	38
13	27	-	2	-	-	-	-	-	29
57	30	-	0	-	-	-	-	-	30
55	46	-	0	-	-	-	-	-	46
45	21	-	0	-	-	-	-	-	21
3	45	-	0	-	-	-	-	-	45
63	49	69	0	0	2	3	20	28	71
7	112	96	0	0	3	3	1	1	116
Mean		69		5%		11%		15%	52,4
						Total for successful sites :			471

Nest-building

No sign of nest building at any site was observed before the end of March 1982 and at only two sites, successful in the previous cycle, were there any remains of the nest structure. In fact, by the end of December 1981, nest material on the sites of all failed breeding attempts had disappeared, presumably removed by wind and rain.

Collection of nest material in earnest was first observed on 25 April 1982, some ten weeks before the average laying date. This is similar to Lappet-faced Vulture behaviour (Pennycuick 1976). Branches comprising the nest structure were collected, in most cases, from two separate areas on the slopes of the kloof and carried back to the nest in the bill (contra Houston 1976:20 for Ruppell's Griffon, where all the branches used for building were seen to be stolen from other sites.). Filching was seen on two occasions in the pre-laying period in 1981 and on several occasions in the same period in 1982. In total, nest material was seen to be taken from other sites on 18 occasions, by occupants of eight different sites. Only twice was the site occupant present when the material was taken, and on 13 occasions the material was taken from an adjacent site.

At six nests where male and female could be distinguished (sexes determined by observation of copulation, at least one partner ringed), the frequency of collecting forays by either sex could be determined. Collecting forays were mainly determined for three nests only - those situated on NW2 cliff where the collector's sex could be determined with greater certainty. Of 98 collections, males collected 75 times, significantly more (76 %) than did females (χ^2 "=" expected values test, $p<0,01$) although at one nest, the difference was not significant ($p=0,05$, $n = 31$). The female generally packed the material into the structure, although both sexes were often seen bending over and rearranging the contents (Figure 22).



Figure 22. A view of the NW2 breeding ledge. Nest no.16 juvenile, head lowered in begging posture, stands near its nest (16) while its parents copulate. Its colour rings are faintly visible. Eleven days after the photograph was taken (mid-May 1982), this 270-day old juvenile was aggressively chased off the ledge by one of its parents. At another site (18), an adult bends over and packs at the nest material. The parents of the light brown juvenile adjacent to this site are both colour ringed, and consequently of known age (nest no. 63, chapter five, 5.2.2.).

4.2.2 The incubation period

In 1981, 356 nest-days of observation of 16 nests with eggs were made, and I accumulated a further 99 nest-days of 17 nests during an eight day consecutive period in 1982.

No double clutches (Mundy & Ledger 1975, Mundy 1982) or replacement clutches were recorded during the actual study period, although the egg at nest no. 55 was laid significantly later (on 14 July 1980, which was exactly two standard deviations later) than the estimated mean of 5 June for that year and was thus likely to have been a replacement clutch.

For 16 incubation periods in 1981, which includes one egg lost after 41 days, one adult was at the site at 97,7 per cent of the counts (range 91,2%-100%) and sites were unoccupied only 0,09 per cent of this observation period, an average of 359 thirty-minute counts per nest. This behaviour is indicated in Figure 21. At all nests, the frequency of a single adult at the nest was significantly higher than for any other stage of the breeding cycle (Sheffe's test, $p<0,01$). A partner remained at the site 2,0 per cent of the time (range 0%-8,8%). Birds generally incubated the eggs very tightly and on only one occasion did one adult leave an egg unoccupied , for 182 minutes, for no apparent reason (but see 4.2.3.).

Of an average of 78,5 copulations observed at six nests throughout the breeding cycle, 5,3 per cent occurred during the incubation period (Table 8).

The results of analysis of eggs for pesticide contamination are presented in chapter three (Table 6), and the thickness of shell fragments measured are given in appendix d.

A White-necked Raven was observed to cause an incubating adult to stand, but remain on its nest, and jab aggressively as the raven landed on a nesting ledge at Aasvogelvlei. Two ravens then landed 1,5 m above another incubating adult, which remained tight on its nest. One subsequently landed at a third nest and pecked at the outlying nest material : the attendant adult jabbed aggressively but remained in an incubating position. At least four ravens were seen over the Potberg kloof, but no predatory attempts were observed.

Laying dates

Laying dates for 1981 and 1982 were determined by checking the colony regularly, although precise dates for three nests were not obtained in 1982. Dates for 1977, 1979 and 1980, as well as the dates of laying in both 1981 and 1982 at Aasvogelvlei were estimated using an average incubation period of 56 days and a known-age / wing length curve (Mundy 1982). Wing lengths of nestlings measured before 1981 were obtained from CDNEC records. Thus only laying dates of sites that produced large nestlings were obtained for years other than 1981 and 1982. These laying dates are depicted in Figure 23, and significant differences (Student's t-test) between the means of any years are indicated; both the Potberg and Aasvogelvlei means are compared here.

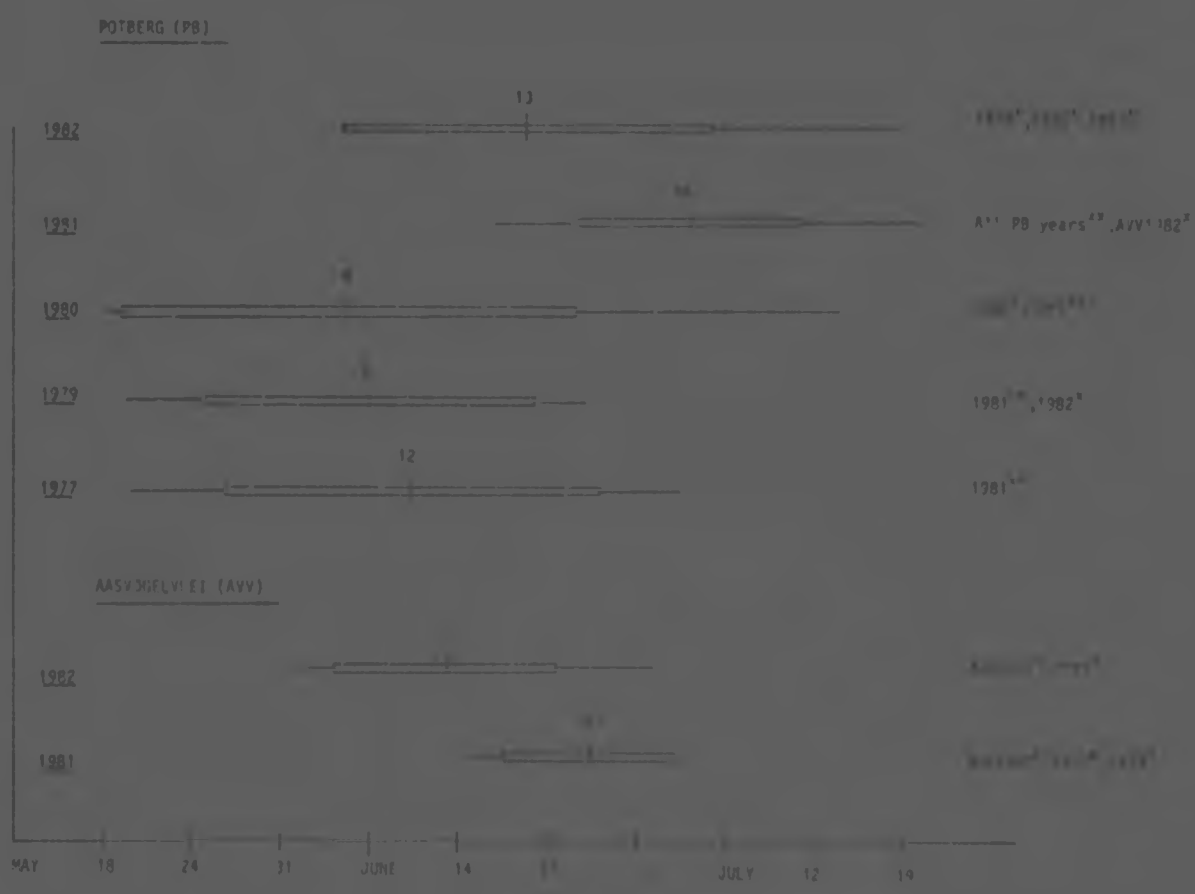


Figure 23. Dates of egg laying at Potberg and Aasvogelvlei. The mean (±s.d.) and range are shown, as well as significant differences (1% level : year^{xx} ; 5% level : year^{x}).

In 1977 only, did the link of higher rainfall and later mean laying date not occur, although the differences are very slight. Considering this relationship however, in 1980 alone was the preceding six months' precipitation significantly less than that of 1981 (t-test, p=0,05). The extreme example was the 1981 mean date, which was significantly later than any other year at Potberg (Figure 23), and similar only to the mean date for the same year at Aasvogelvlei (t-test,20 d.f., p=0,09). The overall average laying date for the five years is 17 June (no. eggs=58, s.d.=17,5), and this is clearly later than the early-May average for the Sterpoort, Magaliesberg colony (Mundy 1982:171) and the similar average for the Colleywobbles, Transkei colony (Vernon et al. 1982).

The following considers the evidence as to whether raising an offspring successfully might delay egg-laying in the following year. All 1981 eggs were laid significantly later than in 1980, except the likely replacement clutch mentioned. Of the three long post-fledging dependence periods in 1980/1, an egg was laid at the same site before the mean 1981 laying date on one occasion and after it on another, neither date being significantly different ; the third site was not active in the subsequent season . After the post-fledging dependence periods observed in 1981/2, eggs were laid at the same sites before the mean 1982 date on four of the five occassions and significantly later by the confirmed same adults (Robertson 1983b) in one instance. At the site with the longest 1981 PFDP, the following year's egg was laid before the mean date.

The most accurate times of laying were obtained for three eggs in 1981, where both were laid between 16h30 and 07h30 the next day. At one of these sites (nest no. 63), the same colour ringed female laid an egg in 1982 between 17h30 and 15h00, on exactly the same date as the previous year.

Changeovers, and incubation of the egg

Changeovers were generally accomplished within about three minutes of the mate's arrival at the nest, although certain partners gave the impression of being "keen" to relieve an incubator which was "reluctant" to leave. In such cases,

changeovers recorded after the incubator had been gently nudged off the nest; this behaviour was more frequent during the nesting period. During what was most likely the first changeover at nest no.16, the incoming adult allowed the egg to roll out of the cup by standing on the rim. After a few feeble attempts at replacing the egg with its bill, it continued to "incubate" the empty nest. During the next 90 minutes, the bird attempted on three occassions to replace the egg, which lay some 8 cm from the rim. I replaced the egg at 15h40, after it had been exposed for 450 minutes (clear weather, 9-13 knot breeze). This egg subsequently produced the begging juvenile in Figure 22 | A pair of California Condors Gymnogyps californianus was also observed to allow the egg to roll out of the nest, although in that case the egg shattered (Anon 1982). This was possibly the fate of the egg from nest no. 25 in 1982 (see 4.2.5.1.

A total of 186 changeovers of birds incubating eggs were noted in 1981, averaging 11,5 per site ,or 0,5 per nest-day of observation. However, a number of changeovers at the outlying sites were probably missed: if the NW2 ledge (directly opposite the observation point) is considered in isolation, 61 changeovers were documented for four incubation periods during 38 nest-days, i.e. 0,7 changeovers per nest per day. As an extreme example, at one site, three changeovers on the same day were observed on two different days. Changeovers occurred in the morning, before a day's foraging or, in the afternoon, after foraging. The earliest instance noted where the incoming partner had fed that morning was 11h30 : if the changeovers are then divided into pre-11h30 (51, 33%) and post-11h30 groups (125, or 67%), then the incoming adult had obtained food on 64 per cent of the latter (8,6% cases unknown). The overall average changeover time was 12 hrs 54 mins, 50 mins earlier than that documented for the Skeerpoort, Magaliesberg colony (Mundy 1982:161). The two average changeover times of 10h10 and 14h12 probably reflect the situation more accurately, and the four-hour separation agrees with the average of the feeding forays (3 hrs 42 mins) obtained for the colony (3.2.2.).

Incubating birds occasionally stood up to stretch, flap [illegible] wings, repulse intruders (4.2.5.), or move the egg (along

its long axis, Mundy 1982: 161), and the longest period in such cases that the egg was exposed was 4 minutes (1 instance timed, average 1,2 mins).

Measured incubation stints, i.e. the length of time between two changeovers at a site, were obtained whenever possible when changeovers were observed during consecutive days of observation. As with changeovers, these measured stints are divided into those where two changeovers occurred within one observation day ("within-day"), and longer stints. In 1981, the mean "within-day" stint was 3 hrs 15 mins (n=44) and this was not significantly different to the 1982 figure of 3 hrs 31 mins (t-test, 60 d.f., p=0,30). The mean of 1981 "long" stints was 26 hrs 21 mins (n=72) and this was significantly longer than the 1982 mean of 22 hrs 35 mins (t-test, 98 d.f., p=0,01), due to the inclusion of 11 "extra long" stints (mean = 44 hrs 3 mins, range 40 hrs 45 mins- 48 hrs 8 mins). If these 11 values are excluded, the 1981 mean of 22 hrs 48 mins is not significantly longer than those obtained in 1982 (t-test, 86 d.f., p=0,37). In five of these extra-long cases, the individual concerned was identifiable (ringed), confirming that no changeover had been missed.

Sexes could be distinguished at five nests due to the presence of either a metal ringed (two nests) or colour ringed partner. I only those instances where the ring/s was/were clearly resighted at both changeovers, are the corresponding stints used in analysis of any sex-related differences in length. The mean for males (1981 and 1982 figures combined) was not significantly longer than the mean for females (t-test, 30 d.f., p=0,32), and the observed frequencies of either sex was not significantly different (χ^2="expected values test, p=0,72).

Five addled eggs ocurred in two years, three during the observation year. In two of these three cases no change in incubation behaviour after the expected hatching date was noted. For example, adults at nest no. 29 continued to incubate normally for 18 days after the expected hatching date, until I collected the egg for analysis. At one nest however, the incubating adult tended to stand over the egg, rather than sit on it, from some 14 days after the expected hatching date. Twenty four days after the expected hatching date, the incumbent adult (male) deserted this

egg for 152 mins, returned to stand near it for 355 mins, to leave it unattended that night (I collected the egg the next day).

Length of the period

At six sites in 1981 where both laying and hatching dates were accurately obtained, an average incubation period of 57 days (95% C.L.s 55,6-58,4) was documented.

4.2.3.The nestling period

A total of 377 nest-days of observation of ten sites with nestlings were made in 1981 and 15 nest-days, at four nests, in 1982. In 1981, seven nestlings lived longer than 11 days and six fledged, and of ten nestlings colour ringed (average age=76 days) in 1982, seven fledged (see 4.2.5.).

Eleven per cent of copulation attempts observed at successful sites through the 1981 cycle occurred during the nestling period (Table 8). The mean hatching date for the years 1977 and 1979 - 1982 was then 14 August, calculated using the mean laying date of 17 June and a 57-day incubation period.

Parental care of the nestling

During observations of the seven nests in 1981, nestlings were left unattended for 1,2 per cent of the observed nestling period (range 0,1%-4,5%), and one nestling was unattended for significantly more time than three other nests (Scheffe's test, $p<0,05$). Six nestlings were seen unattended at least once during the period (i.e. one never), and the average age at the first such instance was 71,7 days (range 41-93 days). Nestlings were accompanied by one adult 76,4 per cent of the counts. Both adults were at the nest 22,4 per cent of the time: in all cases this was significantly greater than during the incubation period and, in three of the five cases, significantly less than during the PFDP (Scheffe's test, $p<0,05$) (Figure 21).

During this period in 1981, sexes were distinguishable at

only one active nest and both parents attended the nestling for similar lengths of time (t-test, 21d.f., p=0,43). Both male and female attendance stints were significantly shorter than those obtained during the incubation period (t-tests, p<0,01).

The mean "long" attendance stint of 21 hrs 56 mins (n=71) documented was not significantly shorter than the similar mean obtained during incubation, if the 11 "extra-long" stints are excluded (t-test, 129d.f., p=0,09). If these values are included, the difference becomes significant. The mean "within day" stint of 3 hrs 39 mins (n=53) was not significantly longer than the figure for the incubation period (t-test, 95d.f., p=0,17). The average changeover time documented for this period is then 12h29, which is significantly earlier than that documented for the incubation period (t-test, 375d.f., p=0,49). Of 193 changeovers, 65,8 per cent occurred after 11h30 and on 86 per cent of these, the incoming adult had obtained food (4,6% of cases unknown).

For its first few weeks, the nestling is brooded closely by the adult, making the precise time of hatching difficult to discern. There is subsequently a gradation in attendance behaviour of the parents, particularly after the nestling is dorsally feathered. This behaviour varied between nests, e.g. at one site adults often "incubated" the empty nest while the nestling stood nearby. A four month old nestling wandered 2m to an adjacent site containing a five month old nestling on three occasions: both pecked gently at each other's necks before being aggressively jabbed at by an attendant adult. Similar behaviour was never observed for adults of adjacent sites. Partners continued to bring fresh green sprays to the nest during this period.

Most feeding bouts were mouth to mouth, with the nestling actively calling and tapping the parent's bill while drawing food from its mouth. On at least seven occasions, parents that had not fed were observed to go through the motions of regurgitating without any food appearing, although in observation it is difficult to be accurate about this (chapter three, 3.3.). The "ex-attendant" partner consumed food that was regurgitated onto the nest by the forager on six occassions.

Nestling development is described in Mundy (1982), and the

correlations of wing and body mass with age are presented and discussed in chapter three. The particularly lightweight individual was the bird which did not visit its nest site after fledging (4.2.4.).

Predatory attempts on nestlings, as well as intraspecific behaviour with other vultures are described in 4.2.6.

Parasite infestation

All nestlings visited on 8 October 1981 were infested with Black flies Prosimulium spp. (identified by J.S. Paterson). The average age of these nestlings was 43 days (range 22-55 days). The heaviest infestation was observed on a 47-day old nestling, where one half of the head was fully covered, with relatively light infestation on the other (Figure 24). The main area affected was the crown, but one nestling showed two areas under the wing. The infestation on one nestling, that was unattended while adjacent nestlings were ringed, increased on its head and back, i.e. the presence of the adult affected the degree of infestation. This was confirmed later by observing attendant adults removing flies from nestlings with their bills. When all nestlings were visited 34 days later, only one fly was observed on the head of an 83 day old nestling. One 55 day old nestling had a very low grade Leucocytozoon infection (two gametocytes seen on a blood smear) ; no infection was noted for the same individual in two smears taken 34 days earlier. Plasmodium spp., microfillariae and other protozoa were searched for but not found.

No simulids were observed at Aasvogelvlei in either year, and examination of samples from four nestlings did not indicate the presence of any blood parasites.

In 1982, of ten nestlings examined, less than ten Black flies were present on the crowns of only two nestlings.

Figure 25 records the degrees of simulid infestation for the years 1976 - 1982, in relation to the rainfall total for the six months preceding September. Heavy infestation was documented in 1976, to a lesser extent in 1977, absent in 1978, again heavy in 1979 and, finally, absent in 198[illegible]ff & Currie 1981, CDNEC records).



Figure 24. Simuliid infestation of a 47-day old nestling.

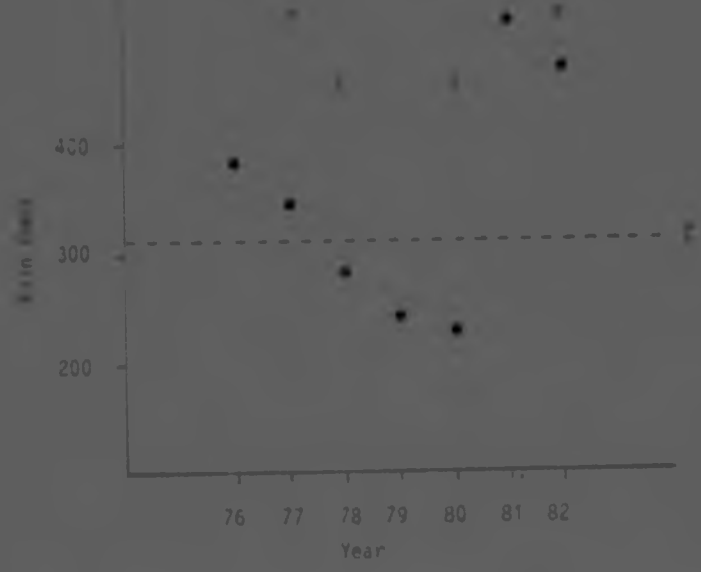


Figure 25. Simuliid presence related to the amount of rain in the six months preceding September (●). The degree of infestation is classed as heavy (H), medium (M) or absent (A), and the mean amount of rainfall for these months is shown ($\bar{x}$).

Length of the period

Where no days of observation preceded the day the fledgling was first seen away from the nest, the fledging date was not accurately known (four cases known to within five days). Where at least two observation days preceded the date of first observed flight, that day was taken as the fledging date. Some fledging dates were only known to within an accuracy of three days. In 1981 mean nestling periods were 148,0-150,3 days (range 139-171) days). Both these means were significantly longer than the 1982 mean of 137 days (range 125 - 147 days) (t-test for mean of 148, 11d.f., p=0,04).The individual with the 125-day nestling period died an estimated three weeks after fledging. It was found, under foliage in the kloof river, an estimated two weeks after its death (P.v.d. Westhuizen pers. comm.). The next shortest nestling period I documented was 136 days, and this bird survived at least five months.

The mean for all available period lengths is then 142 or 143 days ; this compares well with Mundy's (1982:188) estimate of 140 days. The mean 1981 fledging date was 21-23 January 1982, and this contrasts with 28 December 1982 for 1982 fledglings.

4.2.4. The post-fledging dependence period (PFDP)

After fledging, young raptors may visit the nest site and remain dependent on their parents for what is known to be a very variable length of time (Newton 1979). In this study, termination of the period was taken as the date of the last recorded visit of the juvenile to its natal nest site. Parent-juvenile interactions were observed at the breeding area only ; it was not attempted to observe any such interactions, if these occur, at feeding sites, as is the case e.g., in the Black Vulture Coragyps atratus (Cathartidae) (Jackson 1975).

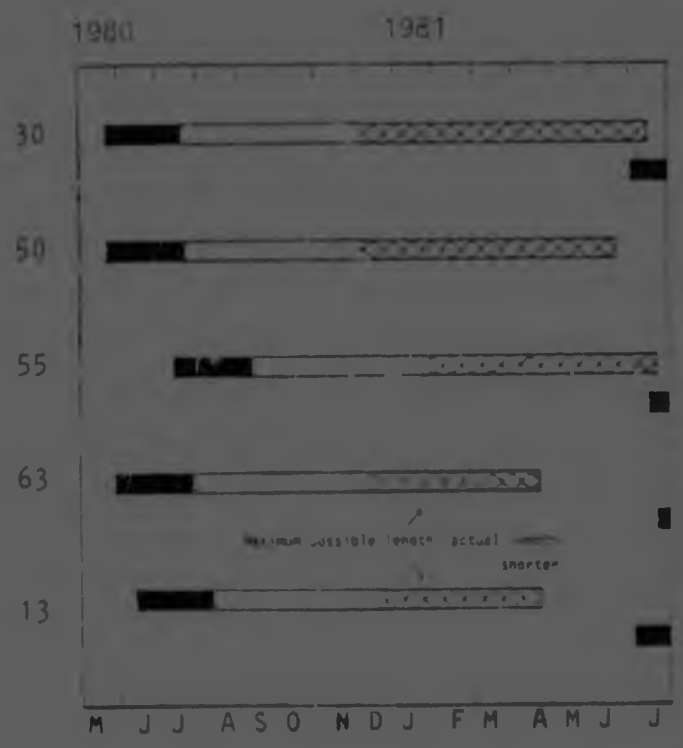
From 8 May 1981, 118 PFDP-days of observation were made of three 1980 juveniles (i.e. nestlings in 1980), and 137 PFDP-days of six juveniles in the following season. A minimum of three hours of observation every day between 21 December and 13 January 1983 (23 consecutive days) were made of 1982 juveniles around the time of fledging. Juveniles are clearly distinguishable in the field by various plumage characters (e.g. black-brown eye colour and a long, lanceolated and streaked ruff), as documented in Mundy (1982:43). Colour ringed as nestlings, each juvenile was then individually recognisable. The observed PFDPs are depicted in Figure 26.

Length of the period

In 1981, three juveniles continued to visit the nest sites for 221, 194 and 175 days after fledging, although they were last seen receiving food at 210, 189 and 159 days respectively. The PFDPs of three other juveniles did not exceed 117 and 133 days in length (i.e. two of these juveniles were resighted in the kloof, but never seen at their nests).

In 1981, five juveniles (of six that fledged) held PFDPs of longer than 13 days: 15-19 days, 22-25 days, 83 days, 120-124 days and 139-142 days. The sixth juvenile (nest no. 7) was last resighted in the kloof six days after fledging, and one day after fledging at its site.

Three 1981 juveniles from Aasvogelvlei held periods of no longer than 82, 84 and 85 days (estimated ages from wing lengths at ringing, using a 143-day nestling period), as they were



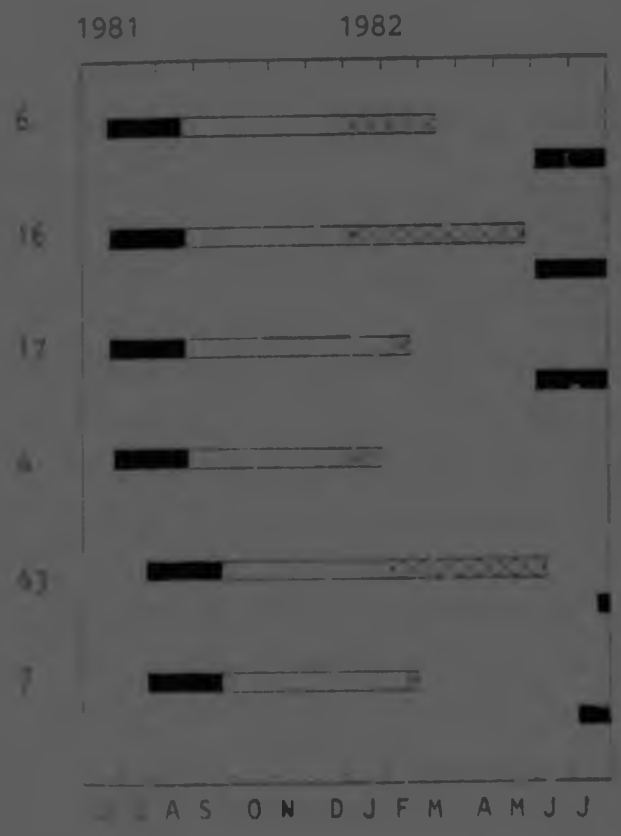
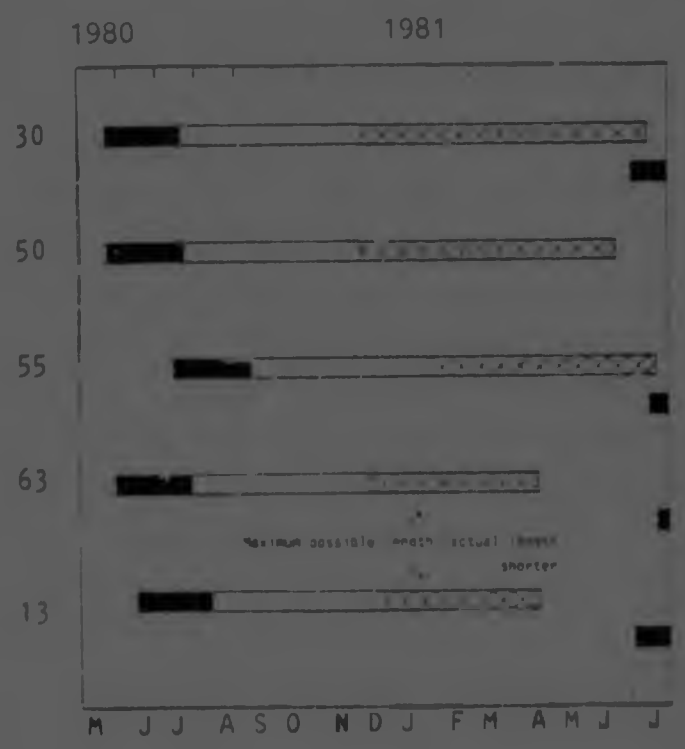


Figure 26. Diagram of the breeding cycles of individual nests (numbered on left). The incubation period is represented by dark blocks, the nestling period by empty blocks and the PFDP by hatched blocks.



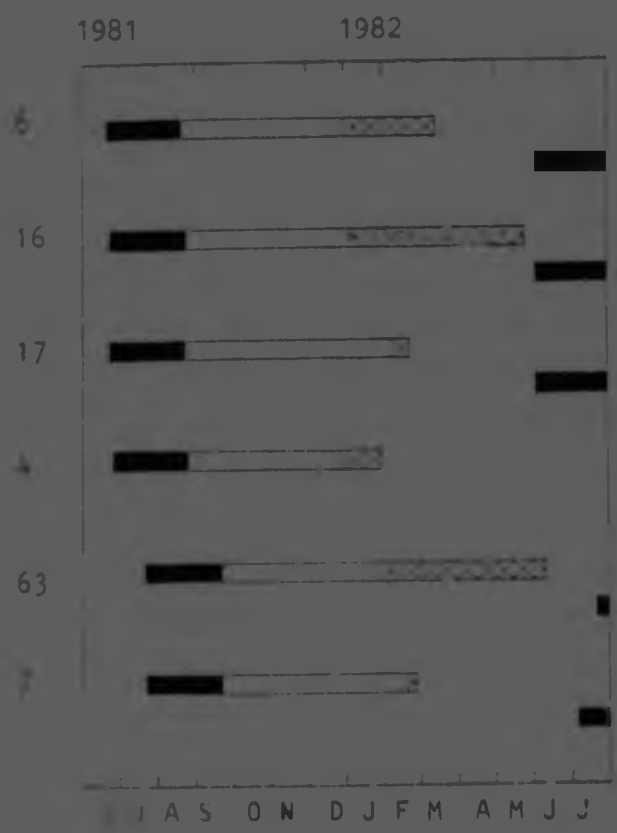


Figure 26. Diagram of the breeding cycles of individual nests (numbered on left). The incubation period is represented by dark blocks, the nestling period by empty blocks and the PFDP by hatched blocks.

resighted at Potberg from 6 April 1982.

Although observations were made of 1982 juveniles, no PFDP lengths were obtained, except for those that were recovered dead. Only one juvenile was resighted in the kloof five months after fledging (A.F. Boshoff pers. comm.).

At nest no. 30, the 1980 PFDP overlapped with the next season's incubation period by two days; the juvenile visited the site eleven days later but was aggressively chased off by the incubating adult. At nest no. 55, there was a similar overlap of four days, as illustrated in Figure 2 . No feeding was observed at any nest during this period of overlap. For the three 1981 PFDPs of longer than 82 days, the next season's egg was laid 41 days after the periods had ended (range 6-79 days).

Behaviour of juveniles

The presence of juveniles at their nests is displayed for three nests in Figures 27 - 29. On average, the five 1981 juveniles were at their natal sites at 36 per cent of the counts made on days during their respective PFDPs. If the three long periods are considered alone, this figure is 26 per cent. For the three long PFDPs, juveniles were alone at their sites 1,8, 1,9 and 2,5 per cent of the counts.

Individuals were often seen to land (clumsily) at various places on the slopes of the kloof, where they would spend time perched. During the course of the study, two juveniles were extricated from undergrowth that had trapped them, and it is likely that at least one other had died as a result of landing in vegetation. One of those captured had landed on top of the parked Combi at the mouth of the kloof ! Thus if a juvenile was not at its site or visible in the kloof, it could not necessarily be concluded as foraging. A radio-tracking study was initiated with an aim of documenting the transition to full foraging capabilities, but lapsed after two marked individuals died and the transmitter on the third stopped functioning (Boshoff, Robertson & Norton in prep.). Given this consideration, the number of days during which juveniles were considered to have foraged, as a proportion of the number of days observed, are presented in Table 9. As if to emphasise the variability in

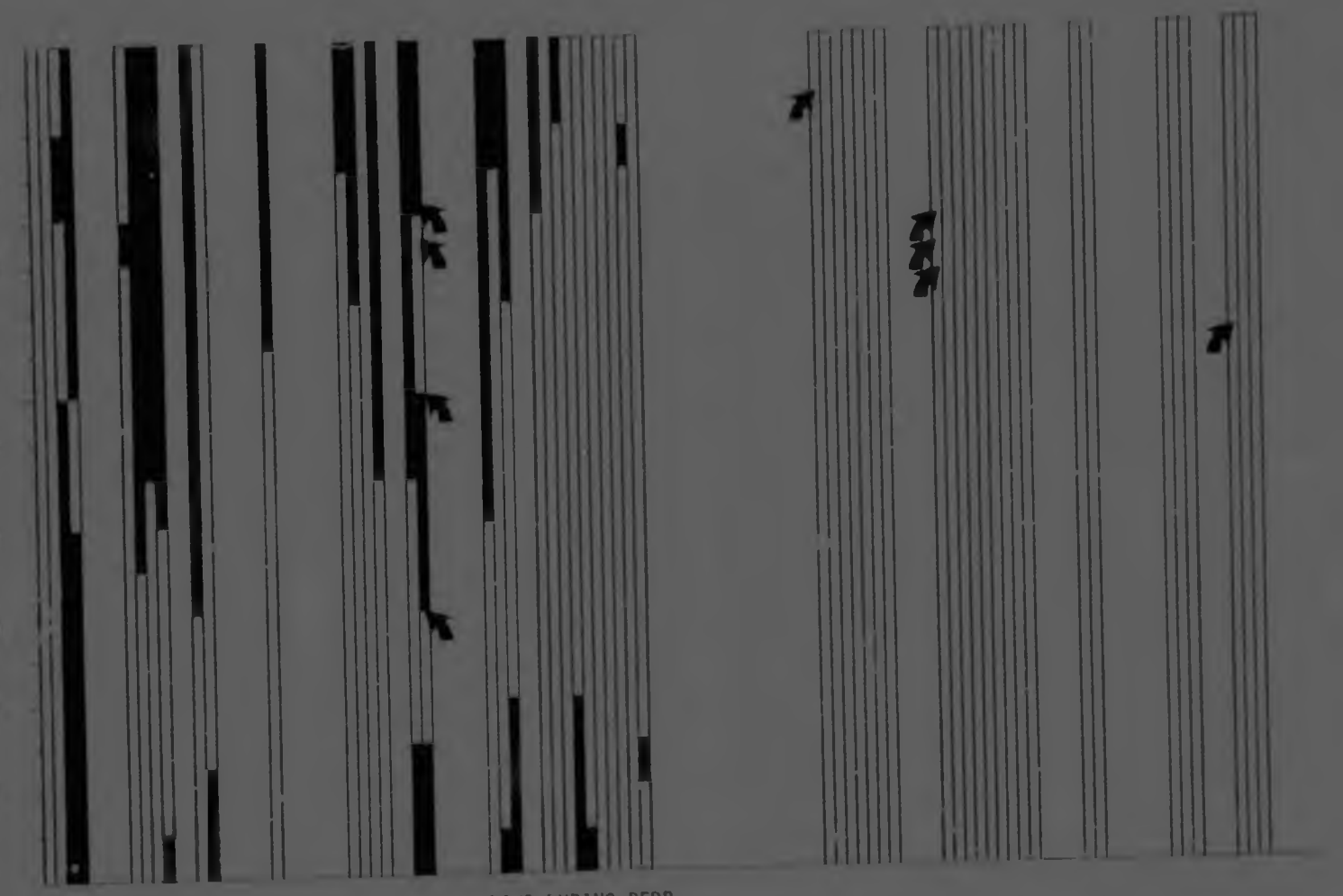


Figure 27. Diagram depicting the periods when a juvenile (nest no. 61 was at its nest during its PFDP (shaded areas). Each empty block represents an observation day, and days of no observation are equally spaced between these; Figures 29 and 30 have the same format. Aggressive interactions between the juvenile and its parents were observed at the points indicated by arrows.

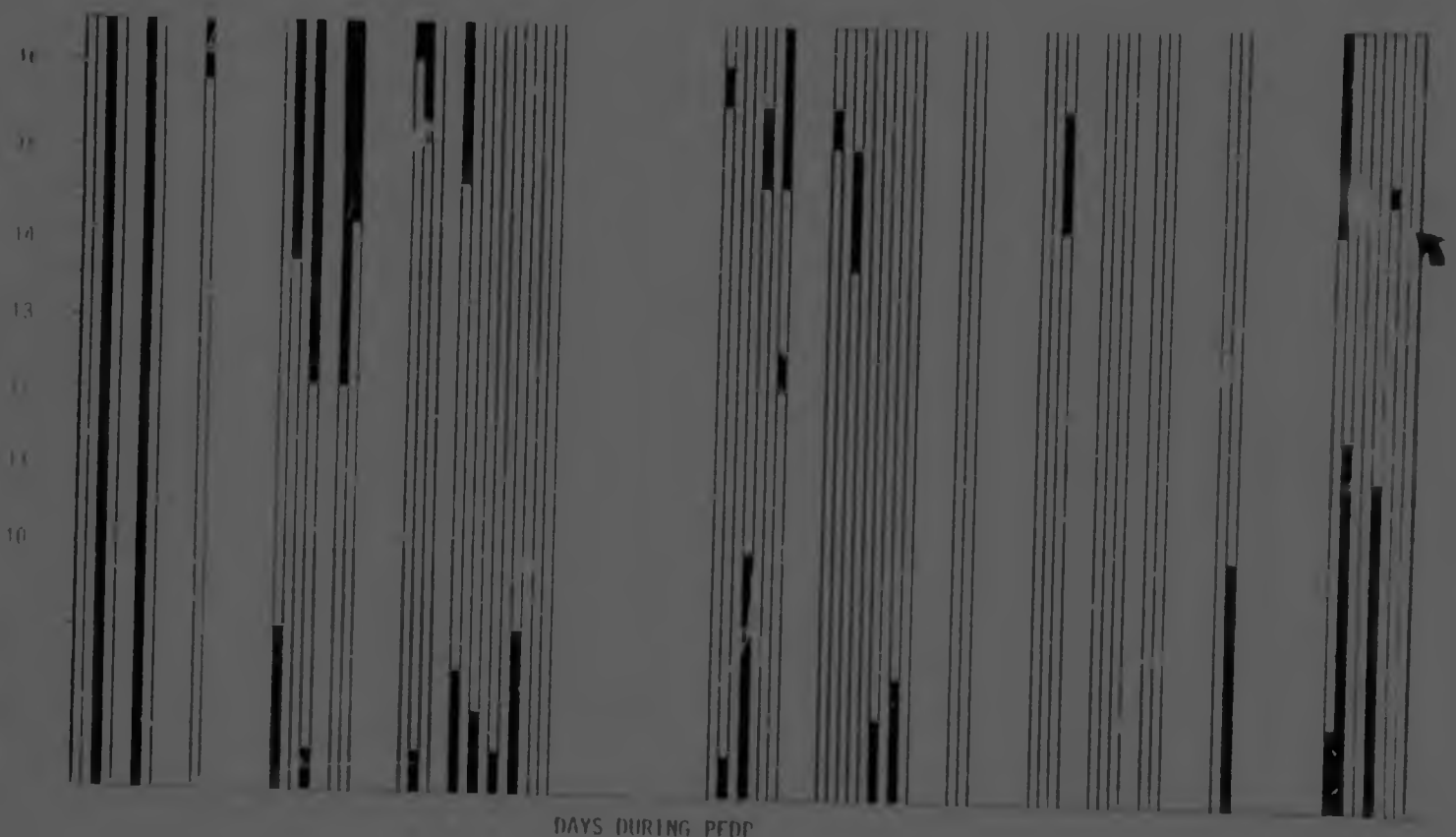


Figure 28. Diagram depicting the periods when a juvenile (nest no. 16) was at [illegible] nest during its PFDP (see Figure 28). An aggressive interaction between this juvenile and its parents was observed at the point indicated.

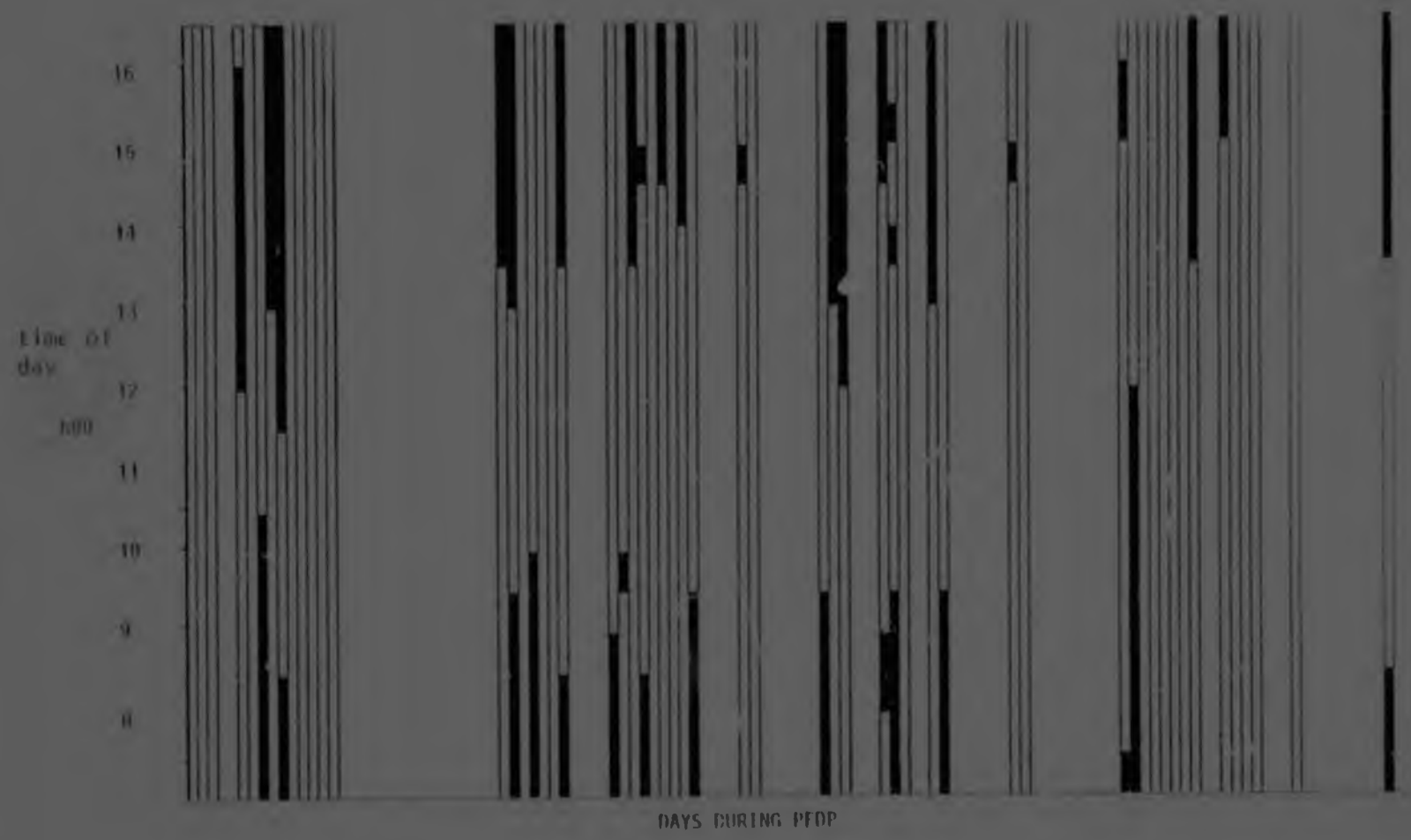


Figure 29. Diagram depicting the periods when a juvenile (nest no. 63) was at its nest during its PFDP (see Figure 28). Observations ceased before termination of this PFDP.

behaviour during this period, nest no.7 juvenile returned to the colony with a full crop the day after it fledged! This individual was not observed after this day.

Table 9. The number of days that juveniles, during their PFDP, were considered not to have foraged. Column A gives the number of days between fledging and the first observed foraging attempt ; in brackets is the number of observation days between these two events.

Nest	No. days juv. observed	No. days juv. did not forage	prop.%	col. A
6	26	16	62	43 (16)
16	49	14	29	17 (6)
4	9	8	89	25 (8)
17	8	6	75	1 (1)
63	43	15	35	2 (1)
7	2	1	(50)	1 (1)

At the nest site, juveniles solicit for food by means of a range of signals, including neck-stabbing, hoarse-calling, crouching and wing-shaking (Mundy 1982:189)(see Figure 22). Only once was a perched juvenile heard to call hoarsely away from the site (no adult nearby); no neck-stabbing or wing-shaking was observed away from a site (although see "Parents at the nest"). On six occasions with two individuals, the juvenile called in the air some 15 secs before landing. Juveniles indicated recognition of a parent by commencing soliciting behaviour before the parent landed. If the adult flew off while the juvenile was begging, that behaviour would cease. The occurrence of food-soliciting behaviour is given in Table 10, as is the proportion of days

Nest	A No. days observed	B No. days juv. visited nest	B/A %	soliciting behaviour am only	pm only	am + pm	C No. days soliciting seen	D No. days ad[illegible] 'motions'	D/C %	C/8
[illegible]	26	22	85	3	10	5	18	11	61	82
16	49	32	65	2	12	2	16	10	63	50
[illegible]	[illegible]	[illegible]	44	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	33	75
17	8	6	75	1	3	-	4	[illegible]	50	67
63	43	29	67	4	20	2	26	15	58	90
			$\bar{x}$ = 67%	Σx=12	Σx 46		Σx=67		$\bar{x}$=53%	$\bar{x}$=73%

Table 10. The occurrence of food-soliciting behaviour during the PFDP of five juveniles in 1981/2. Column D gives the number of days that adults were observed to go through the motions of regurgitating food.

Nest	A No. days observed	B No. days juv. visited nest	B/A %	soliciting behaviour am only	pm only	am + pm	C No. days soliciting seen	D No. days ad lt 'motions'	D/C %	C/B
6	26	22	85	3	10	5	18	..	..	82
16	49	32	65	2	12	2	16	10	63	50
4	9	4	44	2	1	-	3	1	33	75
17	8	6	75	1	3	-	4	2	50	67
63	43	29	67	4	20	2	26	15	58	90
			$\bar{x}$ = 67%	Σx=12	Σx=46		Σx=67		$\bar{x}$=53%	$\bar{x}$=73%

Table 10. The occurrence of food-soliciting behaviour during the PFDP of five juveniles in 1981/2. Column D gives the number of days that adults were observed to go through the motions of regurgitating food.

during each 1981 PFDP that the juvenile visited its site (col. B/A).

Adults with an empty crop were seen to go through the motions of regurgitating , and juvenile soliciting behaviour would continue after this had ceased (although up to some 500g of food is not visible as a distension - see 3.3). As both birds often fe nto the cliff, actual transfer of food was difficult to ascertain from the observation point. Even when the juvenile had apparently received a substantial amount of food, the soliciting behaviour would continue sporadically through the afternoon. The number of days where an adult was observed to "go through the motions" are indicated in Table 10 (col. D/C): these are likely to be minimum figures, as such instances are easily missed by an observer.

All juveniles that had PFDPs visited their sites within a maximum of four observation days of their respective fledging dates: a 1982 juvenile, equipped with a radio-transmitter, did not visit its site once during the 17 days that it remained in the vicinity of the kloof (i.e. it did not forage). Each day it made a number of exploratory flights in the kloof and often soared past its site where an adult (which on at least eight occasions had a bulging crop) was present, but landed most times at a point ca 15 m below its site. On its second to fifth flights it landed in vegetation, and was caught and weighed two days after fledging (weight 6,9 kg). After 19 days of not obtaining food, it was found dead 4 kms from the kloof (weight 5,2 kg).

An interspecific interaction between a juvenile and two Secretary Birds Sagittarius serpentarius is described in 4.2.6.

Parents at the nest

During the PFDP of each 1981 juvenile, adults left the nest vacant for 14 per cent of th observation period (Figure 21) ; there was no significant difference between any of the five nests (Scheffe's test, $p > 0,05$). At three of the five nests, each site was unoccupied for significantly more time than during the incubation or nestling periods (Scheffe's test, $p < 0,01$), while not significantly different from the pre-laying period or

behaviour shown during retention of the site.

On average, 15,0 per cent of copulations observed through the breeding cycle occurred during this period (six nests, Table 8). At nest no. 16, an egg was laid six days after the juvenile's last recorded visit ; 45.4 per cent of copulations observed at this site occurred during that PFDP (the site with the copulating adults in Figure 22). A male parent mounted a 225 day-old juvenile in a copulation attempt, and emitted a loud groan before the shrieking juvenile jabbed it off. The parent then pecked gently at the juvenile's back. This was the only incident of this kind observed. Similar behaviour has been observed in Gannets Sula bassana (Nelson 1978).

Two observations indicated that adults differentiated between juveniles and recognised their own offspring. In one case, nest no. 16 juvenile (no. 16 juv.), 12 days after fledging, landed near nest no. 57 and walked onto the vacant nest. A juvenile had fledged from this site seven days before, and was in full view of the site at the time. At 09h30 an adult landed and no. 16 juv. initiated normal food-soliciting behaviour. After the adult gave it two aggressive jabs on its wing, the soliciting stopped and the adult stood in an aggressive posture over it, neck extended for four minutes, before moving off the nest. Sixteen minutes later, no. 57 juv. landed on the site ledge, looked at the intruder and stood facing out. Twelve minutes after this, the adult jabbed aggressively at the intruder and repulsed it from the site. In the second case, no. 63 juv. (8 days after fledging) landed between two nest sites, one of which (nest no.6) held a dependant juvenile 30 days older than the intruder; no. 6 juv. was not at the site at the time. Both adults aggressively jabbed at no. 63 juv.'s head and back and stood over it, whilst the juvenile crouched and shrieked submissively, with their necks extended in classic threat posture (Mundy 1982:188). Four minutes after landing, the juvenile was aggressively pushed off the ledge by nest no. 6 adult. On three other occasions, a juvenile during its PFDP was aggressively repulsed after landing at a site other than its own, although these instances differed from the two cited above in that the sites concerned had produced no similarly aged offspring that cycle.

Termination of the period

Aggressive interactions were noted in five of eight observed PFDPs during this study: observations ceased before the end of one long 1981 PFDP, thus this ratio is more correctly five of seven cases. One 1981 PFDP is excluded from this as the juvenile was at the site for one day only. In that case it appeared to have foraged successfully the day after fledging and it is not known whether it dispersed or died after that day, but it was never resighted in the kloof again. The aggressive encounters ranged from a parent jabbing sharply at the soliciting offspring while allowing it to remain at the site (7 instances, 2 nests), to the parent chasing the juvenile off the site (11 instances, 4 nests), or preventing it from landing at the site (4 instances, 1 nest). In three of the seven instances, the juvenile jabbed back at the adult but ceased to solicit. During the 11 instances that the juvenile was chased off the site after landing, it was not at the site for longer than three minutes. Parents prevented the offspring from landing by extending their necks (3 instances within 15 minutes at one site, both adults present), or by moving quickly to its projected landing spot and calling loudly, causing it to veer off.

At the first recorded aggressive encounter in each case, the average age of the juvenile was 290 days (range 175-361 days). This translates into some 147 days, or five months, of PFDP. The first recorded case of aggressive jabbing at nest no. 6 occurred 36 days before the period ended, and the juvenile was also chased off the site five times that day and prevented from landing once (Figure 27). Six days later it was fed by a parent at the site, after two bouts of aggressive jabbing (lasting a few seconds each). In three of the other cases, the juvenile did not spend time at the site after aggression was recorded (one individual visited the site 10 and 11 days after it had been chased off, but it neither solicited nor was offered any food).

Retention of the site

Of the nine sites that failed in breeding in 1981, six were active in 1982. At two of these sites, one partner had a metal ring and both birds were active in both cycles. After the pair at

nest no. 63 failed during the incubation period in 1982, both (colour ringed) partners were seen to spend time at, and repulse intruders from, that site. These instances served to confirm behaviour that was indicative of retaining a specific nest site for the purposes of breeding in the following season.

Sites that failed in 1981 and were active in 1982 were unoccupied for 43 per cent of the counts (range 12%-50%, 537 site-days of observation, mean of 91 site-days per site), and only one site was attended significantly more than any other site (Scheffe's test, $p < 0,01$). On average for six sites, a single adult attended the site for 24 per cent of the counts, one site being significantly less attended than the other five. Both sites were attended by adults for 33 per cent of the counts on average, and there were no significant differences between sites in this respect.

For 11 per cent of the counts at sites that produced juveniles in 1981, adults were not at the site after the PFDP had ended.

4.2.5.Breeding success

As all breeding sites and roosting areas at Potberg were clearly visible, the difficulties in measuring the various parameters associated with the production of young (see Newton 1979:128-130) were ameliorated to a considerable extent. Thus it is certain, at least at Potberg, that during the study period the relevant information on active sites, eggs laid, nestlings hatched and the numbers of non-breeding birds was obtained; it was assumed that breeding occurred only at Potberg and Aasvogelvlei (chapter five). Success is then expressed as the mean number of young produced (nestlings fledged) per territorial pair. This corresponds to Howard's (1979) quaternary level estimate of reproductive success. The survival of juveniles until termination of parental care (Howard's op. cit. fifth level estimate of reproductive success), and the proportion of birds breeding, is considered in chapter five. In both years at nest no. 8 where a complete nest was built and the (non-ringed, presumed same) adults copulated frequently (Table 7), no egg was laid but the site was included as active. The partially active site discussed in 4.2.1. was not taken as active in 1981.

Table 11. Breeding data for 1981 and 1982 at Potberg (PB) and Aasvogelvlei (AVV).

Colony	PB				PB				AVV		
Cliff	NW1	NW2	NE	Σ x	NW1	NW2	NE	Σ x	1981	1982	Σ x
(A)Breeding pairs	10	5	2	17	11	6	1	18	10	9	
Eggs laid	9	5	2	16	10	6	1	17	10	8	
Eggs hatched	5	5	-	10	10	4		14	?	?	
Nestl. ringed	4	3	-	7	7	3		10	6	5	11
(B)Nestl. fledged	3	3		6	5	2		7	4	5	9
(B/A)Success				0,35				0,39	0,40	0,55	

Breeding data for 1981 and 1982 for Potberg and Aasvogelvlei are presented in Table 11, and separated according to the location of each site for the Potberg colony (see Figures 18, 19 and 20). The Potberg success figures for the two years were not significantly different (χ^2=0,043, 1d.f., p>0,25). Considering both colonies for the two years of the study period (54 pair-years), 22 nestlings fledged, an average of 0,41 nestlings per pair (or 0,39 as I 'improved' this figure by replacing an egg in 1981 (?), described in 4.2.2.); for the purposes of statistical calculations, this site is taken as successful. Due to the low expected frequencies involved, the figures for Potberg and Aasvogelvlei were not compared statistically; in all chi-square tests, Yates' correction factor is used (Schefler 1969:95).

The Potberg 1981 success figure is significantly lower than the Kranzberg figure for the same year (χ^2=4,67, 1d.f., p<0,05) as well as the Colleywobbles figure (χ^2=5,81, 1d.f., p<0,025); figures were taken from J.C. Dobbs and P.C. Benson (pers comm.) and Vernon et al. (1982) respectively. It was not significantly lower than the previous two years combined (χ^2=1,32, 1d.f., p=0,25). The 1982 Potberg figure was significantly lower than that of 1981 at Colleywobbles (χ^2=4,85, 1d.f., p<0,05), but not significantly lower than the 1982 Kranzberg figure (χ^2=2,86, 1d.f., p>0,05). Between 1975 and 1982, nestlings were documented at 98 of 165 active sites (1975-1980 data from CDNEC records), a figure of 0,59 nestlings per site. As 13 eggs were documented, and their outcome unknown, this figure is more accurately given as 0,51-0,67 nestlings raised per active site, or pair. This figure is not significantly higher than a mean success figure for the Magaliesberg colonies (Mundy 1982:193) (χ^2= 0,19, 1d.f., p>0,2).

Of sites that were active in both study years at Potberg, 2 out of 13 (0,15) produced fledglings in both years, 7 out of 13 (0,54) produced one fledgling, 4 out of 13 (0,38) produced large nestlings, and 3 out of 13 (0,23) never produced one. Obviously, sites that produced fledglings also produced large nestlings : the categories are not separated here. The difference in the success of attempts between NW1 and NW2 cliffs was not significant (χ^2=3,34, 1d.f., p>0,05). The frequency of breeding

at particular sites is included in chapter six (see also Table 7).

Causes of breeding failure

Possible causes of breeding failure are listed in Table 12, linked to observed causes of failure for the two years and both colonies, and are discussed in this section. Many of the categories are directly linked, and an attempt was made to differentiate between proximate and ultimate causes (Newton 1979: 129), and include both.

Table 12. Possible causes of breeding failure and their estimated occurrence at Potberg (PB) and Aasvogelvlei (AVV) during the study period.

Category	Incidence in 1981		Incidence in 1982	
	PB	AVV	PB	AVV
1. Dead egg	3	2	2	1
2. Depredation	-	-	2	-
3. Nest content knocked off nest	-	1	1 ?	-
4. Weather	3	-	-	-
5. Parent death	-	-	-	-
6. Human disturbance	-	-	3	-
7. Unknown	-	1	1	2
Total :	9	4	9	3

Category one. This grouping includes eggs that are infertile and those that died as a result of pesticide contamination or changes in the micro-climate of the egg, the latter a result of incubating birds vacating the nest (see categories four and

eight). The effects of pesticide contamination are discussed in chapter three (3.3.). A proportion of all eggs laid must be infertile (Brown & Amador 1968). No nest site at either colony produced an addled egg in both years.

The thickness of eggshell fragments, as well as sections of eggs that were collected for contaminant analysis, were measured directly and are presented in appendix d.

Category two. Ravens and Baboons Papio ursinus are known to prey on vulture eggs (P.C. Benson pers. comm., Green 1977, Houston 1976, pers. obs.) and Black Eagles Aquila verreauxii on nestlings (Bowen 1970, Mundy et al. in prep., Steyn 1973). No successful predatory attempt was observed during this study : the breeding failures comprising this category are those that were most likely a result of depredation. Examples include the sudden disappearance of a young nestling which could not be located after searching the base of the cliff, or the discovery of egg and content remains in the nest whose measured shell thickness was concluded unlikely to have been extra-thin. The attempts that I observed are documented in appendix b.

Category three. Incidents included here may occur as a result of disturbance (category six) causing the adult rapidly to vacate the nest, or during changeovers (e.g. incident described in 4.2.2.), or as a result of intruder repulsion behaviour. Either of these was likely the fate of nest no. 25 in 1982, as remains of the shell and contents were found within 0,5 m of the nest.

At one nest at Aasvogelvlei in 1981, a downy white nestling was found dead at the base of a relatively high nest structure (some 0,7 m off the sloping ledge), partially in a horizontal crack. It is probable that it had fallen out of the nest (adults disturbed ? -see category six) and consequently starved to death. A Martial Eagle Polemaetus bellicosus nestling that fell out of its nest in the same year at Potberg was attended and fed on the ground (pers. obs.). It is possible that the vulture nestling died as a result of the actual fall ; in either case, the ultimate cause is unknown.

Category four. Direct effects of inclement weather include physical destruction of the nest and consequent mortality, as well as starvation of nestlings at critical stages of growth, or

at hatching, through inhibition of foraging by the adults. In 1981, Potberg experienced the highest incidence of rainfall in 26 years (2.1.2.): located within the winter rainfall region, this precipitation is thus highest during the egg and young nestling periods.

Category five No evidence of parent death was noted, certainly not one of the eight ringed birds died during a breeding cycle in either year.

Category six Three large nestlings vacated their nests between 18 and 21 November 1982 and a helicopter was observed to pass through the kloof on 24 November. Although not definite, it is likely that helicopters had entered the kloof during the previous week. Subsequent post-mortems of two of the nestlings revealed substantial fat reserves (chapter three), thus three out of 18 of the 1982 breeding attempts were concluded as having been lost due to direct human disturbance. With the exception of disturbance during ringing operations (4.1.) and five searches of the cliff bases (3.2.1.), this was the only disturbance incident observed, in marked contrast to some other colonies (J.C. Dobbs & P.C. Benson pers. comm., Komen 1983). I emphasise that one person walking quietly along the bases of NW1 and NW2 breeding cliffs during the cycle results in every attendant adult vacating its site. Although Aasvogelvlei is located on private property, the disturbance there is considered minimal.

4.2.6.General behaviour

Intraspecific behaviour

Repulsion of intruders from the nest site

The behaviour of the colour ringed pair in particular, and at other nests where one partner was ringed, served to confirm that intruders landing near an occupied nest site are aggressively chased off. Consistent acts of repulsion may then be used to indicate an occupied site. Between 1 July 1981 and 31 May 1982 (139 observation days), 437 such cases were noted at 22 different sites. A further 74 instances were noted (14 sites

during the nine day observation stint from 26 July to 3 August 1982.

The agonistic behaviour was clearly graded : as a first sign of aggressive intent, the site occupant would stand, and peer into the nest. A few aggressive jabs in the direction of the intruder would lead to the occupant jumping off the structure, giving a hoarse call and engaging contact by jabbing, until the intruder left. In five instances where juveniles landed at foreign sites and remained for longer than a few seconds, the occupants jabbed at and stood over them with necks extended in the threat posture : two such instances are described in 4.2.4.

Significantly more instances occurred after 12h00 than before that time (χ^2 "=" expected values test, $p<0,001$). In all but 67 cases (15%), the intruder left immediately : of these 67 instances, the intruder was age-estimated as an immature 54 times. Thus an adult intruder landing at a site is more likely to be repulsed immediately than if it were in immature plumage. In at least 11 instances, immatures were "allowed" to remain within 3 m of the site. Not all intruders were age-estimated however. Thirty per cent of the 131 instances occurred at sites with no egg, nestling or dependent juvenile (i.e. pairs that had failed in breeding, or where no egg was produced). After failure in breeding, repulsions were documented at all sites except one, which was abandoned after failure, and was not active in the following season. Members of adjacent sites recognised each other and no aggression was recorded save for when a member wandered too near to its adjacent site.

Intruders landing on a communal nesting ledge were generally chased off by the occupants of more than one site, resulting in a summated repulsion effect. This effect was particularly evident when interspecific predatory attempts were observed ("Interspecific behaviour", and appendix b). Intruders were not tolerated at any point on the NW2 breeding ledge (Figure 22) by a member of any nest on that ledge.

An adult from the site that was active in both years but never produced an egg, was repulsed from various sites with eggs on 19 observed occasions in 1981 and 15 in 1982 (observed during the nine day stint). On two of the occasions in 1981, both

members visited foreign sites together. An extreme case occurred 21 days after the 1981 average laying date, when one nest no.8 occupant was aggressively repulsed ten times from four different sites within 200 m of its own. Each site it visited had an egg, and in each case the incubating adult jumped off the nest structure to repulse it. Ten days before the (estimated) 1982 average laying date, an incubating adult was off its egg 11 times in 14 minutes to repulse the pair that kept on landing at the site : this pair finally landed at nest no.8. This behaviour was not observed by the occupants of any other site.

The only time that a colour ringed immature was observed to visit its natal site (one breeding attempt had passed since it fledged), it carried nest material to the site but was aggressively chased off twice by the attendant adult.

Interspecific behaviour

Predatory attempts on nestlings by Black Eagles are described in detail in appendix b.

Both eagles often soared past the vulture breeding ledges (within some 20 m), and this elicited clearly aggressive responses on occasions observed between November 1981 and February 1982, i.e. when there were large vulture nestlings present. On seven other occasions when the eagles soared past the breeding ledges, I recorded no discernible aggressive response : these occasions occurred when there were either eggs (four instances) or empty nests.

The eagles' nest was situated between NE and NW2 cliffs and vultures consequently passed it frequently. On eleven of these ocassions, one of the eagles dived at the vulture causing it to flex its wings. These aggressive interactions, initiated by the eagles, were only observed during the eagles' breeding cycle. After the eyas disappeared in July 1981, I observed no similar incidents until May 1982, the onset of that season's breeding attempt.

On 23 February 1982, I observed an aggressive interaction between a six month old juvenile and two Secretary Birds in an open field 5 km from the kloof. I disturbed the juvenile, which

landed 40 m from the two birds : both ran towards it and attempted to stamp on it in characteristic fashion. The vulture responded with loud staccato calls and after some 40 secs the two wandered off.

Interactions betweer vultures and White-necked Ravens are documented in 4.2.3.

Although Peregrine Falcons Falco peregrinus nested within 5 m of one vulture nest, and often perched close to vultures, no aggressive interactions were observed.

Chacma Baboons were observed periodically in the kloof and when near (e.g. below) the breeding ledges, vultures would watch them closely. No predatory attempts were observed.

4.3.Discussion

4.3.1.The pre-laying period

On the evidence available, sites are activated some six months or more before egg-laying. I can only conclude that pair formation preceded occupancy of a site : single vultures were not seen consistently at the few sites initiated during the study period. All biparental species possess mechanisms for bringing mates together and achieving copulation, essentially a signal-response reaction chain (Paterson 1982). I discerned few courtship procedures except, perhaps, mutual preening and scapular action (Berruti 1981). Obviously, many signals perceived by either sex may not be perceived easily by human observers. The characters of the specific-mate recognition system function effectively in the normal or recognised habitat of the species (Paterson op. cit.), and for raptors in general, pair formation for instance is associated with potential breeding places (Newton 1979). In the Cape Vulture this is the breeding colony, and specifically the nesting ledges, where 95,7 per cent of all copulation attempts occurred. In contrast to the feeding area which, certainly in this colony's case, is totally man-influenced (chapter three), the breeding area is unaffected by humans. Thus aspects of breeding behaviour that I observed that are not directly linked to feeding, e.g. nestling attendance and foraging times, should be representative of the species throughout its range.

As nest material disappeared from some sites before the next season's cycle, the site rather than the nest structure (Newton 1979) would appear the more valuable resource. This was emphasised by intruder repulsion behaviour throughout the year.

Houston's (1976) observation of a sex-related difference in behaviour during this period is confirmed, and as a number of individuals were recognisable, males were documented to collect nest material more frequently than females. I emphasise that the behaviour is not distinctive for Cape Vulture males ; very similar behaviour occurs in Gannets (Nelson 1978). Such behaviour would, in effect, reduce the female's energy expenditure ; is it

then related to production of the egg ? A range of raptor females increase in weight prior to egg production (Newton 1979:Figure 15). However, in griffon vultures that share parental attendance duties, the increase occurs in both sexes (Houston 1976). Thus energy is accumulated not merely to enable the female to produce eggs, but to supplement the energy budget of both during the subsequent cycle periods (Newton 1979). Also, the griffon vulture clutch of one egg weighs between three and five per cent of the female's body weight (Mundy 1982) and, in contrast to smaller raptors, places a relatively small demand on her reserves. These considerations indicate that the bias in collecting forays is related to some other factor, such as courtship (akin to Gannet behaviour ?).

Far more copulation attempts occur than may be considered adequate for insemination, and this has been noticed in a number of species (reviewed in Newton 1979 and Steyn 1982). It certainly occurs at Potberg in the majority of pairs, albeit at a reduced frequency, throughout the year (also Mundy 1982) ; this contrasts with Houston's (1976) observation of none after a month past the mean laying date. As I spent more time in observation, and was consistent through the length of one cycle, I would gain a more accurate reflection of the birds' behaviour.

The act itself is considered to serve biological functions other than immediate fertilisation (Power 1980), including induction of ovarian activity (Erickson & Zenone 1976) and inducement of endocrine changes facilitating successive stages of nesting (Hinde 1970). It has been implicated in pair-bonding (Newton 1979), but anomalies such as high frequencies of attempts, in species with weak pair bonds, are documented (e.g. Black-shouldered Kite Elanus caeruleus, reviewed in Steyn 1982). Noting the strong tactile stimuli in Gannet copulations, Nelson (1978) suggested them to be a prolonged source of sexual stimulation ; similar stimuli, both tactile and auditory, are apparent in vulture matings. The effect, if any, of the male's loud calls on adjacent pairs would be incidental.

Erickson & Zenone (1976) consider that many copulations spread over a long time reflect an attempt by the male to increase his confidence of paternity. This is based on Trivers'

(1974) suggestion that in species where the male contributes extensively to parental care, it is important, in evolutionary terms, to the male that the eggs are fertilised by his own sperm. Limiting copulations to the female's time of ovulation opens the possibility of her being inseminated prior to his efforts. Across a range of species then, the greater the male's parental investment, the stronger the behaviour that would ensure his genetic paternity. If this holds, the occurrence of colonial breeding would again emphasise the importance of this behaviour, as coloniality effectively raises the female's chances of contact with with other males (e.g. at the roost points). Copulations certainly occur at areas other than nest sites (this study, Houston 1976).

4.3.2.The incubation period

Given the often markedly circannual rhythm of laying (e.g. this study, Mundy 1982), vultures clearly respond to certain proximate factors that provide a genetic-based stimulus to initiate breeding behaviour (Lack 1954). Food availability at the time may then result in minor modifications in the laying date. For raptors in general, mean laying dates are earlier in good as opposed to poor food conditions ; food therefore acts as both a proximate and ultimate controlling factor (Newton 1979). For example, Yom-Tov (1974) advanced the laying date of the Crow Corvus corone by offering supplementary food in the pre-laying period and comparing the results with controls, although the effect was subtle (Drent & Daan 1980). Also, under good food conditions one would expect an increase in the number of breeding attempts, other things being equal (chapter five, 5.3.2.). However, long periods of precipitation or heavy cloud, through inhibiting vultures' foraging, effectively reduces the rate of accumulation of the necessary (4.3.4.) body reserves in the period preceding laying. This would act to delay the date of laying, and if this consideration influences the date to a considerable extent (i.e. if it alone were largely responsible), the late 1981 laying date then indicates a period of reduced food availability. This explanation seems the most feasible for the

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 [illegible] 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 [illegible] 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 the 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 thus 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.

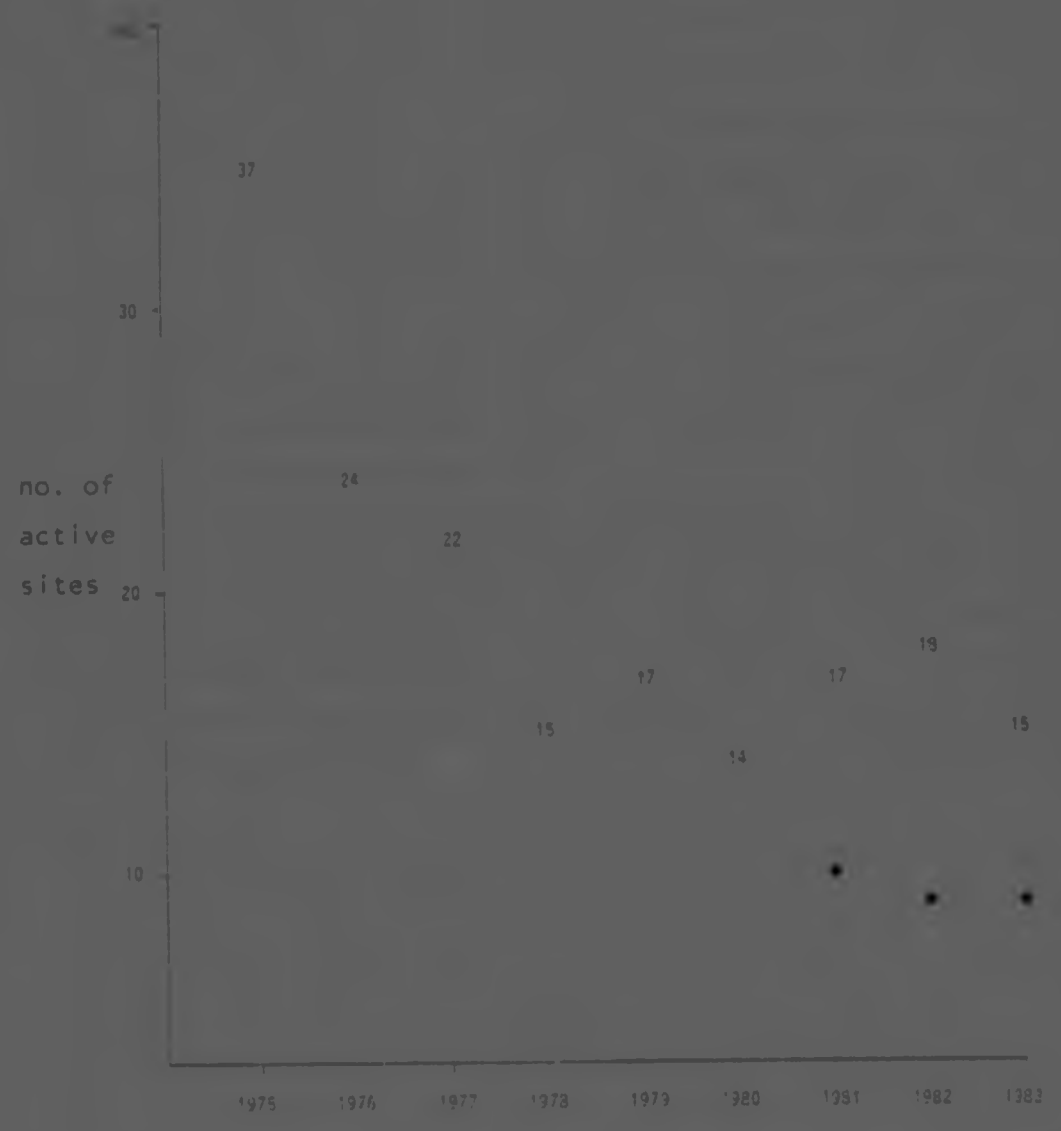


Figure 30. The number of active nests at Potberg (numbered) and Aasvogelvlei for the last nine years.

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 rate.

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').

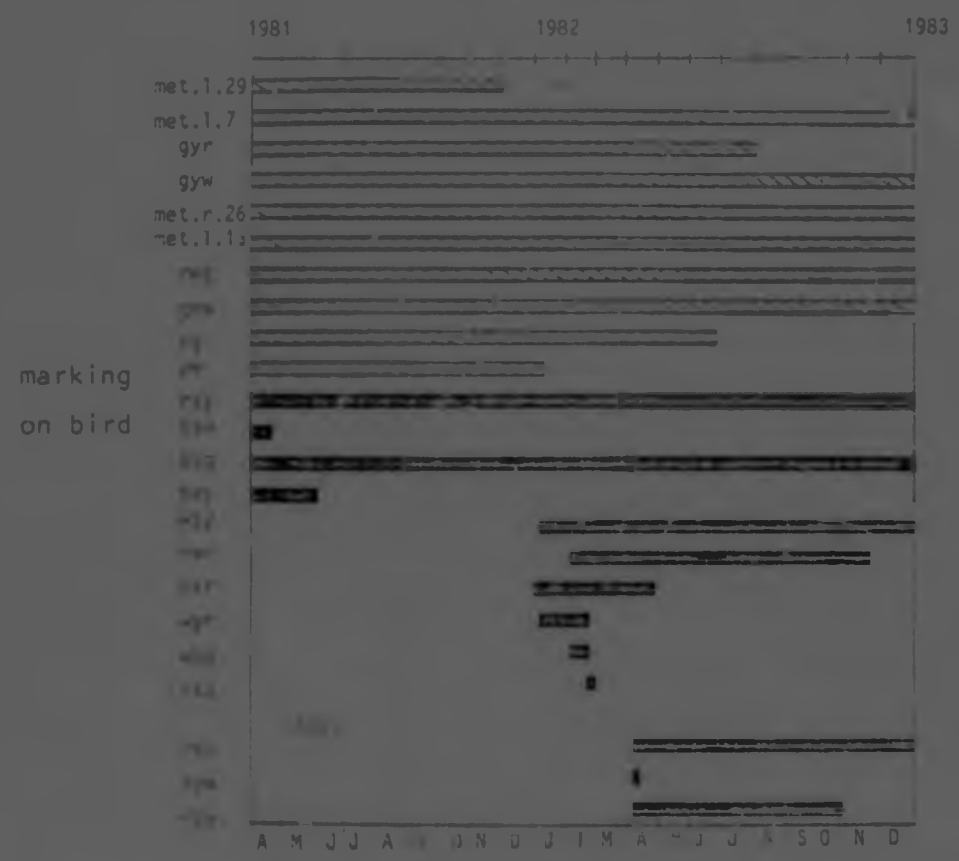


Figure 31. Diagram depicting the length of time ringed vultures were resighted in the kloof. The dark shading indicates birds ringed in 1980 (rsy, bsw, bsg, bry) and during the study period. Three immatures ringed at Aasvogelvlei were resighted from April 1982. For met.1.29, see text "Adult survival".

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.

[illegible]	Bird	no. months after fledging that bird was resighted	% of max. possib.e
[illegible]	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
[illegible]	PWR	10	83
	BSR	4	33
	WYR	2	17
	WBG	0.5	4
	RSG	0.3	2.5
	WBY	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		?			
1973	14		min. 6			
1974	-	22	2		[ab]	[ab]
1975	-	15	8		[ab]	[ab]
1976	-	11	5			
1977	-	13	2			-
1978	-	7	2			
[illegible]	-	9	1			-
1980	-	6	2	4	1	-
Total	40	[illegible]	[illegible]	13	18	1

5.3.Discussion

5.3.1.Population structure

The [redacted] 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 (1957) [illegible] per cent proportion of males.

Both the location and the presence [illegible] 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, 5.2.4.1), 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 beer 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 leve. f 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 co clusion was reached with Gymnogyps californianus, another large-carcass scavenger (Miller et al. 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 a' 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 fo 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 in 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

[illegible], w[illegible] [illegible]

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 announced 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 [illegible] ENVIRONMENTAL CONSERVATION

Telephone: Napkei 5430

Potberg (De Hoop Nature Reserve)
P.U. 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 6[illegible] breeding pairs. The major aim of my research is to try and understand the factors causing this decline. Vultures occur only in Southern Africa and are therefore our conservation priority.

I would like to estimate the foraging area [illegible] vultures from the Potberg mountain, which is the only breeding 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

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 .....
.....
.....

P.O. ASB. VIR AFRIKAANS

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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.

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A.S. ROBERTSON

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About once a week .....

About once a month

About once a year

About once per five years

About once per ten years

Never

B.V. 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) membrane present	Thickness (mm) membrane absent	Fate	Collector
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	$0,627^p$; $0,549^p$	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	-	$0,646^e$;$0,585^p$	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. Lambrecht, 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
Y-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 UFF	Dichlofenthion	Coopers

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