



# Mathematical Demography of the Cape Vulture

Volume 2

Steven Edward Piper B.Sc.Eng. (Natal), M.Sc. (Witwatersrand)



A thesis submitted to the Faculty of Science, University of Cape Town in partial fulfillment  
of the requirements of the degree of Doctor of Philosophy

Submitted : Westville, Natal. Ides of March, 1993

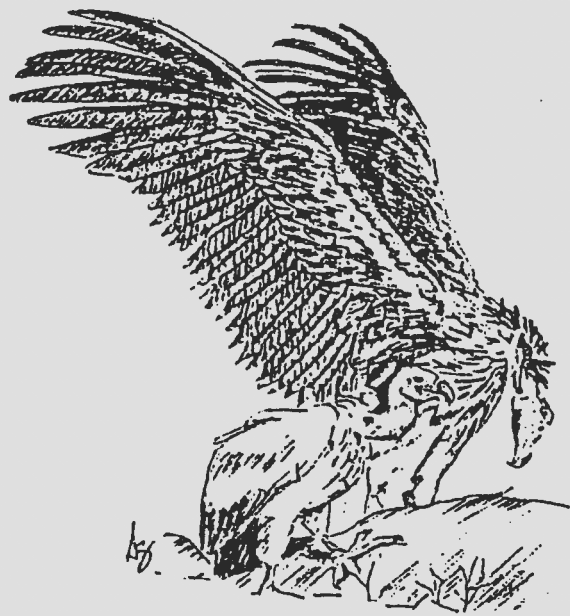
Examined : 11 October, 1993

Corrected : 31 December, 1993

The University of Cape Town has been given  
the right to reproduce this thesis in whole  
or in part. Copyright is held by the author.

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.



# Movements

## Contents

6.1	Patterns of recoveries .....	282
6.2	Location of unnatural mortality .....	334
6.3	Patterns of resightings .....	341
6.4	Models of movement .....	362
6.4.1	Theoretical framework and terminology. ....	363
6.4.2	Drift, dispersal and exploration. ....	368
6.4.3	Nursery areas. ....	378
6.4.4	Nomadism, vagrancy, irruptions and colonization. ....	379
6.4.5	Migration. ....	381
6.4.6	Natal fidelity and philopatry. ....	382
6.4.7	Home range and foraging. ....	383
6.4.8	Age-sets and spat-falls. ....	384
6.5	Summary .....	387

## Abstract

Movements of Cape Vultures are inferred from the 'displacements' of uniquely identifiable marked birds. A 'displacement' is the line joining the point at which a marked bird was located with the point at which it was next located. Marked birds are located when they are seen alive and their colour-rings are sighted accurately (i.e. a resighting) or when they are found dead and a ring-number is read accurately (i.e. a recovery). From an analysis of the spatial distribution of ring-recoveries of birds ringed as nestlings in the south-central Transvaal, southern Botswana and the Transkei it is clear that most fledglings wander out into the eastern Cape, Karoo, northern Cape and south-western Transvaal. It is shown that when fledglings leave their natal colony they move away from concentrations of adults, presumably to avoid competition. It is also shown that they move towards 'nursery areas'. The spatial locations and concentrations of birds dying from a number of unnatural causes of mortality are investigated. The patterns of resightings tend to confirm the conclusions reached from the study of ring-recovery data. Finally, a word-model of dispersal is presented for the Cape Vulture.

# Movements

In the simplest of population models it is assumed that the population is made up of a single, homogeneous unit in which all members of the population mix freely (see Lebreton & Clobert 1991: 76). The next level of sophistication is to assume that the population is made up of a series of discrete groups, or demes, within which there is free mixing and between which there may be some transfers (Blondel 1991: 62-64). For the Cape Vulture it is clear that the population is not uniformly distributed over southern Africa. The variations in density may be seen from distribution maps derived from the locations of roosts and colonies (see sections 3.1.1 and 3.2.1) or from the SABAP-based reporting rate (see section 3.2.5). It is also clear that the Cape Vulture population is disjoint. It is likely that the population has small and probably isolated concentrations in the south-western Cape and Namibia (section 3.2.1), while the Zimbabwean concentration is not isolated (P.J. Mundy pers. comm.). In addition, there are two large concentrations, the first is in the Transvaal and eastern Botswana while the second is in the Transkei, Lesotho, the Eastern Cape and Natal. The primary aim of this chapter is to determine the directions and magnitudes of the movements between various concentrations of the population.

Considerations of territory and its effects are central to the study of the population dynamics of many avian species (e.g. Smith, Arcese & Hochachka 1991). Because the Cape Vulture is a colonial nesting species, it is likely that breeding pairs hold only a small territory around the nest itself (Mundy 1982: 161; pers. obs.); this territory is so small, relative to the daily foraging range, as to be irrelevant in terms of the population dynamics. This observation is useful because it means that the smallest spatial unit which needs to be considered is a whole roost or colony, rather than a single breeding territory.

How will it be possible to understand the spatial processes within the Cape Vulture population? From an analysis of the seasonality of sightings (using data from the SABAP-based bird-watchers, section 3.2.4), it is clear that there are no gross seasonal movements within the population. This is to be expected because the breeding adults are tied to the nest (actually to the egg, nestling or fledgling) for at least eight to ten months of the year (i.e. mid-April to early January in the Magaliesberg, see Mundy 1982: 160-189). Thus if there are birds within the population that move great distances then these movements are more likely to be undertaken by those birds not yet breeding, nevertheless, it clearly is possible for adults to move about the subcontinent, especially if they are not breeding. The only way to detect these movements is by monitoring individuals which are uniquely identifiable. To this end the patterns of ring-recoveries from each colony will be examined to gain insight into the geographical distributions of death while the patterns of resightings will be used to get some

idea of the nursery areas (see definition below) and whether birds from different colonies use the same areas for foraging. In a summary of methods used to study '*lifetime tracks*', Baker (1982: 24) has provided the following comment.

It is no accident that most descriptions of lifetime tracks are concerned with ranges rather than with the tracks themselves. This is because, until very recently, most of the methods available for studying migration gave information concerning ranges, but not tracks.

For over a decade, the concept of 'nursery areas' has been bandied about by members of the Vulture Study Group (see review in section 6.4 below). It is hypothesized that young birds move away from their natal colonies to avoid competing with adults, and go to those areas which are predominantly populated by sub-adult birds and which have an abundant food supply, for at least part of the year. These are called nursery areas. If nursery areas exist, then a number of questions arise.

- 1) When birds are in a nursery area, do they stay in one place or do they move about in some way which could be called nomadic?
- 2) Is there any evidence to suggest that young birds return to their natal colonies a number of times before they attain their adult plumage? If they do so, it may be to assess their chances of finding a mate or a breeding site.
- 3) If young birds return to their natal colonies, is there any evidence that they do this on a seasonally regular pattern which could be called migration?
- 4) Do sub-adult birds visit breeding colonies other than their natal colony? Do they do this to assess and compare conditions at other colonies, or do they just use these colonies as convenient roost sites?
- 5) How do young birds find nursery areas in the first place?

It will be shown in this chapter that sub-adult birds move far and wide from their natal colonies in the first four to six years of their lives, much further away than breeding adults could ever do while still tied to their nests. In the light of this, it is interesting to ask what evidence is there that birds find new food sources, and further if these turn out to be permanent, then whether they establish a colony there. In other words do Cape Vultures have a well developed ability to colonize new areas?

Initially consideration will be given (section 6.1 below) to the patterns which arise from mapping the locations at which ringed birds have died. This will be followed with an investigation of the patterns revealed by various causes of mortality, e.g. electrocution (section 6.2). An analysis of the patterns of resightings (section 6.3) is used to investigate the extent to which young birds move out from their natal colonies and then return to them. These empirical analyses are then brought together and examined in the light of the theoretical issues surrounding movements (section 6.4).

## 6.1 Patterns of recoveries

Rings have been put on Cape Vultures from 1948 (see section 5.2.1 above) in the hope that the resulting pattern of recoveries would show where the birds travelled. It was not a planned experiment: nestlings were ringed opportunistically and no effort was devoted to finding them subsequently (Ashton 1979). The patterns of ring-recoveries that resulted are portrayed and explored here, and various suggestions are made as to how these patterns were generated. In subsequent sections of this chapter, specific models are developed and hypotheses tested.

A total of 7289 Cape Vultures have been fitted with rings at 28 different sites over the 41-year period from 1948 to 1988, both years inclusive (Table 6.1 and summaries in section 5.2.1 above). Up to the end of 1990 these have generated 597 recoveries, i.e. birds found dead and reported (see summaries in section 5.2.2). Of these, 192 (i.e. 32%) are 'useful', where a recovery is termed useful if it contributes meaningful spatial information. This is defined as the bird having moved at least 10 km from its place of ringing, having survived beyond the January in the year after ringing and having definitely fledged (see definition and motivation in section 5.2.2 above). Of the 28 sites at which birds have been ringed only ten sites have produced one, or more useful recoveries (Table 6.1). These useful recoveries are plotted on separate maps, one for each colony of origin (Table 6.1). The transformation of the radial-arm lines (i.e. representing the arc joining the points of ringing and ring-recovery on the map) from latitude and longitude to Albers' Equal Area map projection coordinates is illustrated in Appendix 1. A brief summary of the spatial pattern of the useful recoveries from birds ringed at each colony is provided.

*Colleywobbles.* All 23 ring-recoveries from Colleywobbles (Table 6.1) are to the west spread through an arc of just over  $90^\circ$  from the south-west through to north-north-west (Figure 6.1 A). The recoveries are the from the eastern Cape, Karoo, O.F.S. and western Transvaal. Surprisingly, there are no recoveries in the Transkei itself, except at the foot of the Colleywobbles Cliff (pers. obs.). This lack of recoveries in the Transkei cannot be due to the territory being unsuitable for vultures, for many Cape Vultures are known to roost, breed and forage there (see sections 3.1.1 and 3.2.5 above). It is more likely that ringed birds do die there, but are not reported because most of the people are too poor to afford the postage needed to report the rings. They are also not literate and there is no 'bird-ringing tradition' among them (see arguments in section 5.2.2 above). Some 74% (i.e. 17 out of 23) of the recoveries lie inside the current distribution of the Cape Vulture (Table 6.2). The current distribution is defined as the envelope enclosing all the  $\frac{1}{4}^\circ * \frac{1}{4}^\circ$  grid-cells with a Cape Vulture (smoothed) reporting rate of 3% (see section 3.2.5 above), based on the SABAP sightings data.

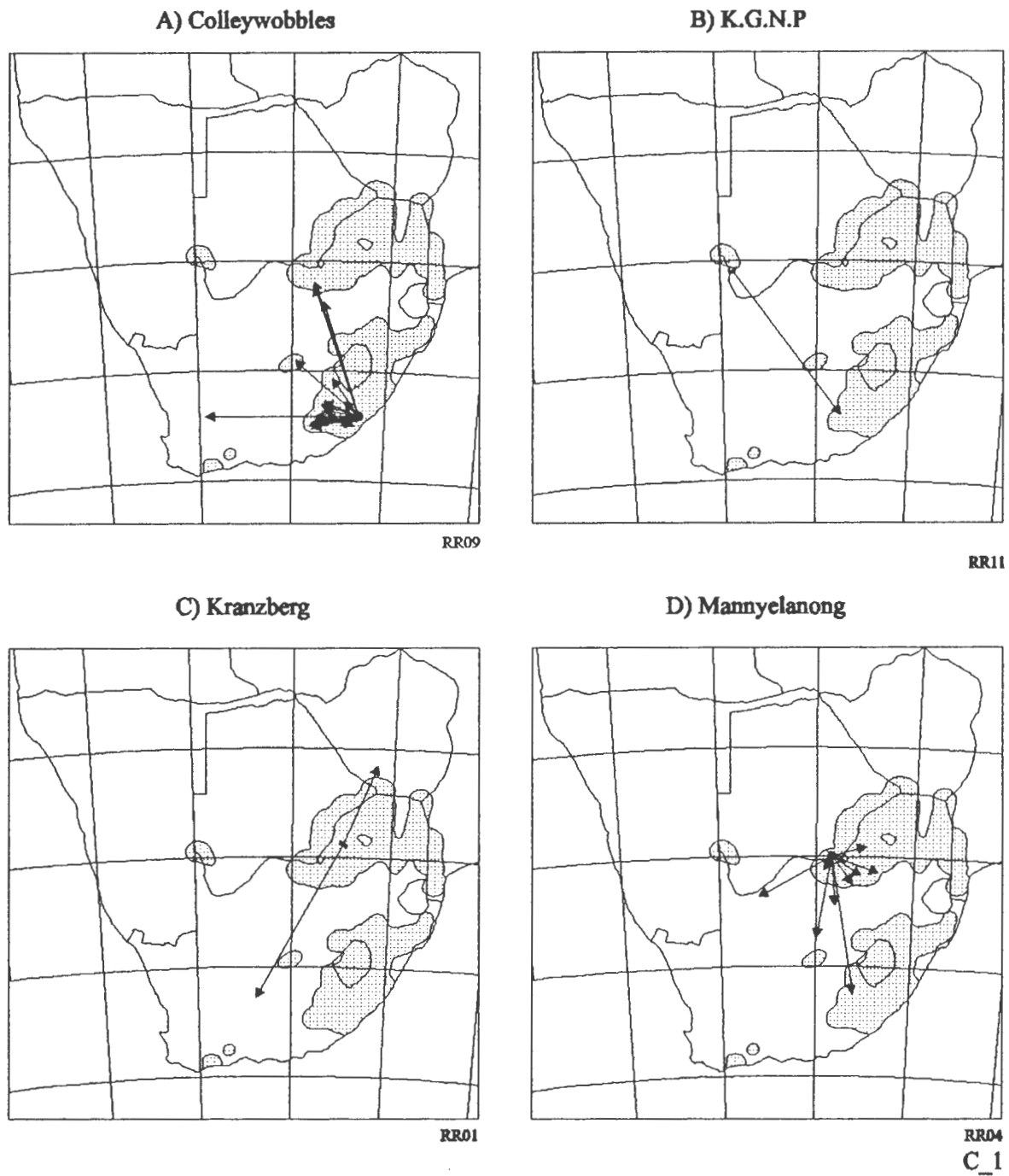


Figure 6.1 Spatial location of recoveries from birds ringed at the following sites. A) Colleywobbles, B) Kalahari Gemsbok National Park, C) Kranzberg and D) Mannyelanong. The enclosed stippled region approximates the current Cape Vulture distribution.

Table 6.1  
List of ringing localities producing useful recoveries.  
(‘Useful’ means the bird moved more than 10 km having definitely fledged)

Site	‘G’-prefix rings	Other rings	Total rings	Useful recoveries	Figure
Aasvogelvlei	38	0	38	0	
Baratani Hill	3	0	3	0	
Bellair (CROW)	3	0	3	0	
Colleywobbles	418	0	418	23	6.1 A
Debshan Shangani	1	0	1	0	
Giant’s Castle	12	0	12	0	
Gonarezho	11	0	11	0	
Kalahari Gemsbok	1+?	?	1+	1	6.1 B
Karnmelkspruit	17	0	17	0	
Kranzberg	0	56	56	2	6.1 C
Mannyelanong	430	162	592	11	6.1 D
Manoutsa	363	0	363	5	6.2 A
Manyana	53	0	53	1	
Mlengana	2	0	2	0	
Nooitgedacht	0	55	55	1	6.2 B
Pilanesberg	3	0	3	0	
Potberg	160	12	172	3	6.2 C
Roberts’ Farm	1107	1258	2365	64	6.2 D
Sengwa	1	0	1	0	
Skeerpoort	1432	1592	3024	78	6.3
Sparta Baby Beef	1	1	2	0	
Tuli Block	1	0	1	0	
Unknown	2	0	2	0	
Waterberg	3	0	3	0	
Zastron	8	0	8	0	
<b>Totals</b>	<b>4069</b>	<b>3136</b>	<b>7206</b>	<b>189</b>	<b>6.4 A, B</b>

Note. Some small sites at which adults only were ringed have been omitted.

*Kalahari Gemsbok National Park.* Although there is only one ring-recovery from the Kalahari Gemsbok National Park (Table 6.1) it is of interest because of the great distance travelled (Figure 6.1 B). The bird was recovered within the current Cape Vulture distribution in the eastern Cape.

*Kranzberg.* There are two ring-recoveries from Kranzberg of the 56 birds originally ringed (in the 1950s; see section 5.2.1 and Tables 5.2.1.2 and 3 above; Table 6.1). They are of interest because of the great distances travelled (Figure 6.1 C). Both recoveries were from areas outside the current Cape Vulture distribution (Table 6.2).

Table 6.2

Proportion of recoveries from each colony found within the current Cape Vulture distribution<sup>1</sup>.

(‘Current range’ of the Cape Vulture is defined in section 3.2.5.)

Colony	Outside present range	Inside present range	Total	Proportion within range	Lower 95% limit	Upper 95% limit
Colleywobbles	6	17	23	73.9%	51.6%	89.8%
Kalahari Gemsbok	0	1	1	100.0%	-	-
Kranzberg	2	0	2	0.0%	-	-
Mannyelanong	5	6	11	54.5%	23.4%	83.3%
Manoutsa	1	4	5	80.0%	-	-
Manyana	1	0	1	0.0%	-	-
Nooitgedacht	1	0	1	0.0%	-	-
Potberg	2	1	3	33.3%	-	-
Roberts’ Farm	33	31	64	48.4%	35.8%	61.3%
Skeerpoort	45	33	78	42.3%	31.2%	54.0%
Total	96	93	189	49.2%	41.9%	56.9%

*Mannyelanong*. All but one of the 11 ring-recoveries from Mannyelanong (Table 6.1) are from south of the natal colony and are spread through an arc from east-north-east through to west-south-west (Figure 6.1 D) and lie in the eastern and northern Cape, Karoo, Botswana and western Transvaal. Surprisingly, there are few recoveries in Botswana itself, though it is known that Cape Vultures are recorded throughout the dry Kalahari (Borello 1987). The reasons for the lack of recoveries may be both cultural (see above) and a low human density (human population in 1990 was about 2 561 000, density approximately 22 per 1000 ha compared with 282 per 1000 ha in South Africa; World Bank Atlas 1991: 6 Anon. 1990: 268). Six of the 11 recoveries (i.e. 54%) are inside the current Cape Vulture distribution (Table 6.2) and there is one recovery in an area of high reporting-rate (i.e. near the Kranzberg colony).

*Manoutsa*. All five ring-recoveries from Manoutsa (Table 6.1) are to the edge of the species’ range (Figure 6.2 A) and one is outside the current limits (Table 6.2). Two are from the Kruger National Park in the east and three are from the western Transvaal.

*Manyana*. The single recovery for Manyana is so close to the natal colony that it does not show on the map.

<sup>1</sup> The decision as to whether a recovery is within the current Cape Vulture distribution is based upon the SABAP reporting rate of the  $\frac{1}{4}^{\circ}$  by  $\frac{1}{4}^{\circ}$  grid-cell in which the recovery is found. Note that the stippled regions shown on the maps have been smoothed and this has altered the boundaries slightly

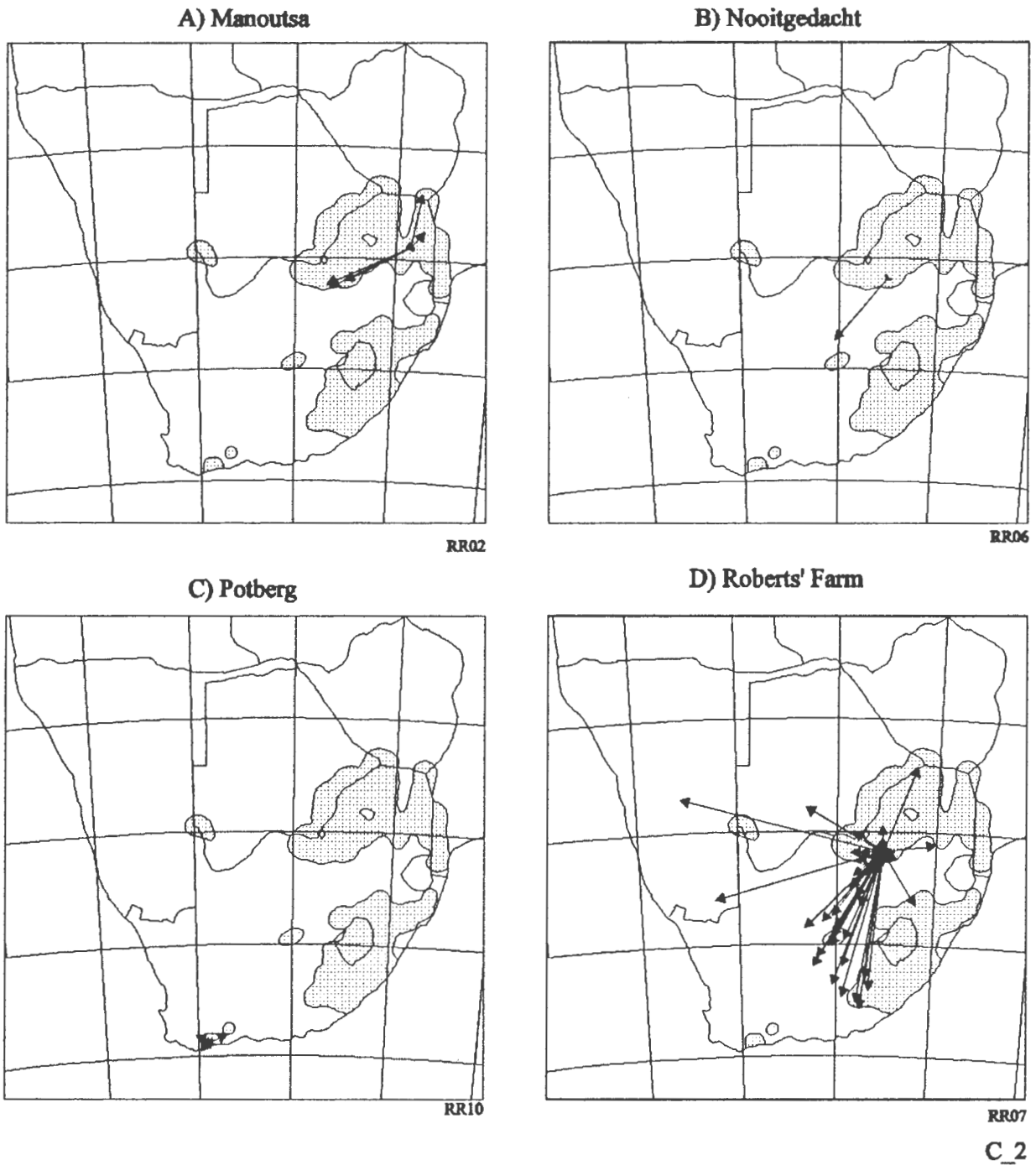


Figure 6.2 Spatial location of recoveries from birds ringed at the following sites. A) Manoutsa, B) Nooitgedacht, C) Potberg and D) Roberts' Farm. The enclosed stippled region approximates the current Cape Vulture distribution.

*Nooitgedacht*. The one recovery from the 53 birds originally ringed (Table 6.1) is in the northern Cape (Figure 6.2 B) at some considerable distance from the colony and outside the Cape Vulture's current distribution (Table 6.2).

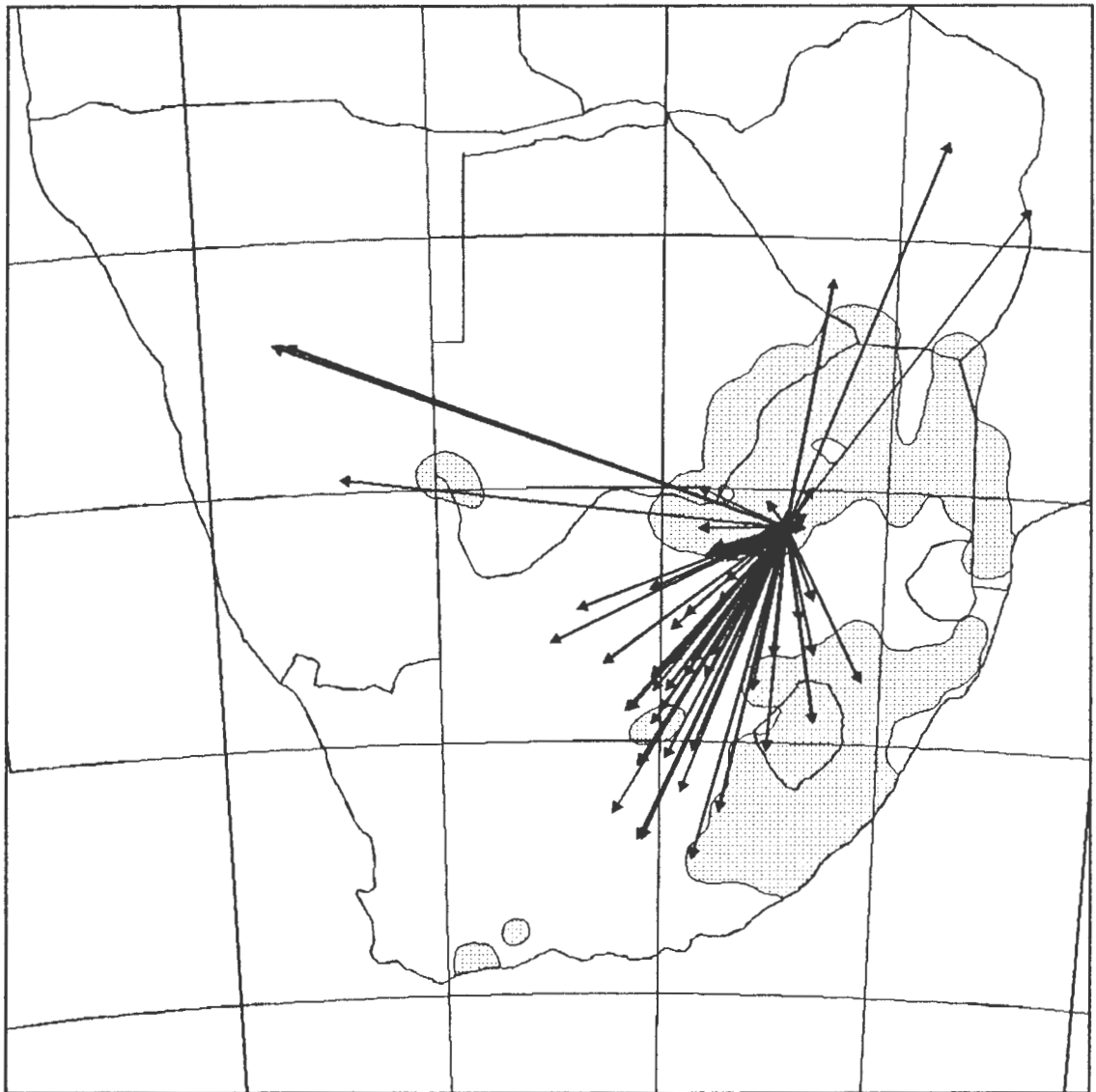
*Potberg*. Two of the three ring-recoveries from the 173 birds ringed in the Potberg (Table 6.2) are just outside the species' range (Figure 6.2 C) but all are confined to the region around the colony (Table 6.2).

*Roberts' Farm*. The 64 ring-recoveries from Roberts' Farm (Table 6.1) are spread around all points of the compass, but are concentrated in the south-west (Figure 6.2 D). There are recoveries from the eastern Cape, Karoo, northern Cape, Namibia, Botswana and the Transvaal. Nearly half (31 of 64 = 48%) of the recoveries are inside the current species range (Table 6.2) and some are from the central Transvaal 'core' areas.

*Skeerpoort*. The 78 ring-recoveries from Skeerpoort (Table 6.1) are spread out in a pattern similar to those of Roberts' Farm (cf. Figures 6.2 D and 6.3). There are recoveries from all the regions reported for Roberts' Farm and in addition from Lesotho and Zimbabwe. Many of the recoveries (45 of 78 = 42.3%) are from outside the species' current range (Table 6.2). Some are from very far afield while a few are from the central Transvaal 'core' areas.

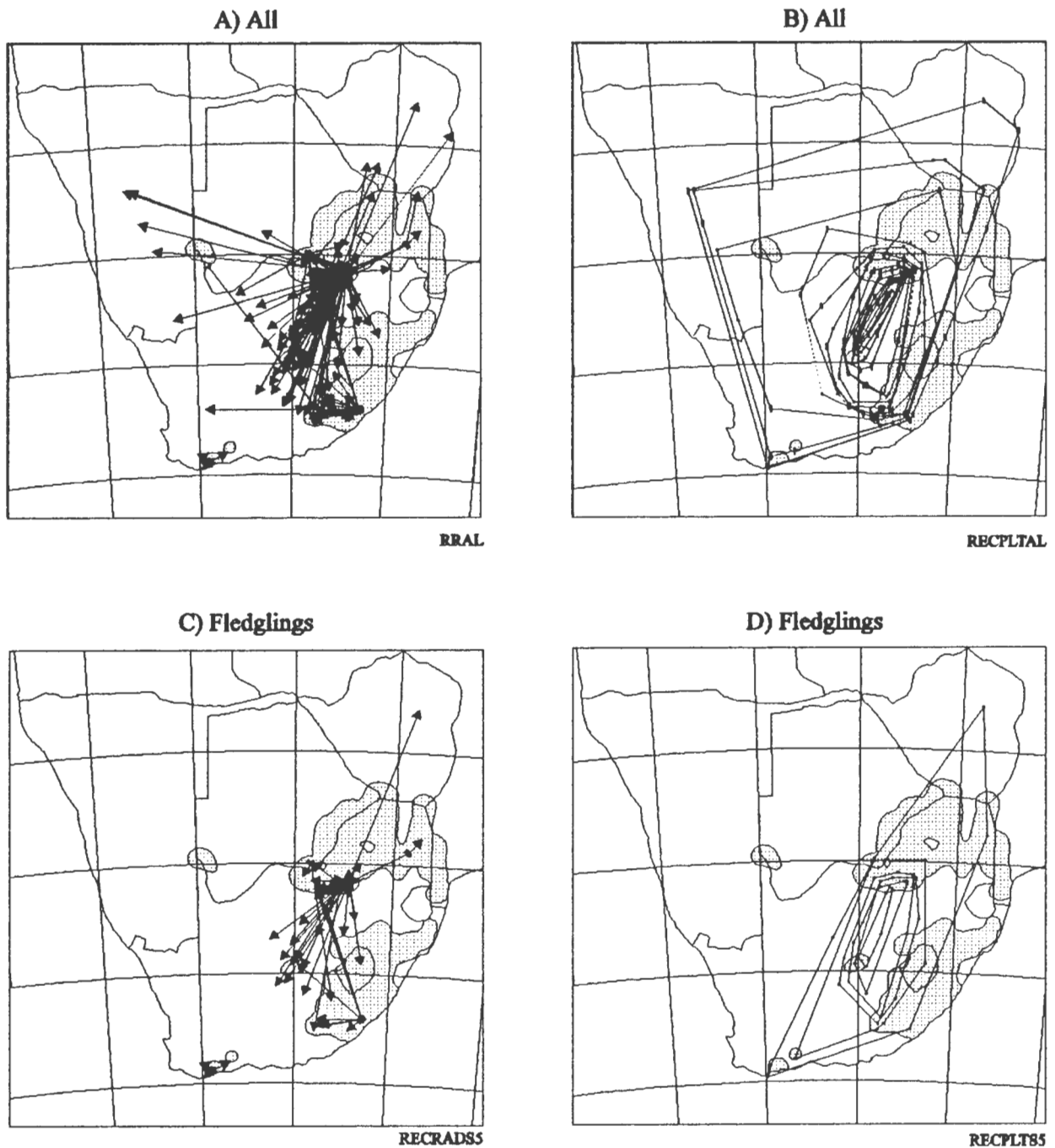
From an inspection of the foregoing maps it is possible to conclude that some colonies produce similar patterns of ring-recovery 'radial arms'. The first group is Roberts' Farm and Skeerpoort, and possibly Nooitgedacht as well as Kranzberg. The second group is Mannyelanong and Manyana. It is also noted that some colonies produce ring-recoveries which are mostly within the current species' range (e.g. Colleywobbles, Mannyelanong, Manyana and Manoutsa) while others produce most ring-recoveries from outside these limits (e.g. Roberts' Farm and Skeerpoort; Table 6.2). Possible processes giving rise to these patterns will be investigated below. Having displayed all the useful ring-recoveries on a colony by colony basis, it is also possible to display them all on a single map. This may be in the form of a radial-arm plot (Figure 6.4 A) or as a collection of point recovery localities (Figure 6.4 B; computation of these localities are illustrated in Appendix 1). The radial-arm plot (though too cluttered, cartographically) shows that many birds go to the Karoo, northern Cape, eastern Cape and O.F.S. - these are the possible 'nursery areas' to be investigated below (section 6.4). Also, it is seen that many birds go great distances, often more than 1000 km, before dying. From the map in which the recoveries are shown as points (Figure 6.4 B) it is readily concluded that about half (i.e. 96 of 189) of the ring-recoveries are outside the Cape Vulture's current range.

Skeerpoort



RR05

Figure 6.3 Spatial location of recoveries from birds ringed at Skeerpoort - the site with the greatest number of recoveries. The enclosed stippled region approximates the current Cape Vulture distribution.



C\_4

Figure 6.4 Spatial location of all useful recoveries. A) Radial-arm plot. B) Point plot with a peeling of convex hulls. Recoveries of Fledglings. C) Radial-arm plot. D) Point plot with a peeling of convex hulls. The enclosed stippled region approximates the current Cape Vulture distribution.

Table 6.3

Distances at which useful recoveries are reported compared among age classes. (Gamma distribution fitted to each age class,  $a = b = \text{fit} = \text{goodness-of-fit}$  by chi-squared, none significant)

Age class	Sample	Mean km	Median km	Upper quartile km	Max km	Gamma $\alpha$	Gamma $\beta$	fit %
05 Fledglings	59	260	164	454	909	0.967	3.721	7.2%
06 Older first-years	40	351	291	454	1226	1.647	4.695	38.2%
07 Second-years	38	424	438	613	1033	1.825	4.305	3.7%
08 Third-years	19	264	192	369	890	1.581	5.989	-
09 Four+ years	33	213	108	264	925	0.909	4.267	19.6%

Gamma distribution parameters are  $\alpha$  (shape) and  $\beta \cdot 10^{-3}$  (scale). The goodness-of-fit is measured by chi-squared,  $p\text{-value} < 5\%$  indicates inadequate fit (in bold). Recoveries of third-years were not tested because there were too few degrees of freedom.

Table 6.4

Proportion dying close to natal colony compared among age classes. (Second number in each block is column proportion%)

	Fledgling	Older First-year	Second-year	Third-year	Four+ years	Totals
Die at colony	49 45.4%	9 18.4%	10 20.8%	8 29.6%	13 28.3%	89 32.0%
Away	59 54.6%	40 81.6%	38 79.2%	19 70.4%	33 71.7%	189 68.0%
Totals	108 38.8%	49 17.6%	48 17.3%	27 9.7%	46 16.5%	278

(Chi-squared = 16.2, 4 df,  $p=0.0028$ )

Table 6.5

Proportion dying close to natal colony: fledglings compared with older birds. (Second number in each block is column proportion%)

	Fledgling	Older birds	Totals
Die at colony	49 45.4%	40 23.5%	89 32.0%
Away	59 54.6%	130 76.5%	189 68.0%
Totals	108 38.8%	170 61.21%	278

(Chi-squared = 13.5, 1 df,  $p=0.00024$  with Yates' correction)

---

The recoveries span the whole subcontinent and include recoveries from almost every country in the region (Figure 6.4 A). While this distribution is easily seen, it is not as easy to detect the core of the recoveries. To make this more visible, the recoveries are surrounded by the minimum convex hull (this is the figure which would result if the recoveries were marked by drawing pins in a map which were then enclosed by a tight elastic band - the band would contract to take up the shape of the minimum convex hull). If the points lying on the hull are removed then a new minimum convex hull can be constructed which lies completely within the previous hull. This process is called the *convex hull peels* of the data (Green 1981), and is used to provide a robust and non-parametric estimate of the core of a spatial distribution. This process is analogous to the use of box-and-whisker plots with univariate data. The peelings were performed using GENSTAT 5 (Anon. 1988). Taking all the Cape Vulture recoveries together (Figure 6.4 B), it is clear that the core of the distribution lies on an axis from the south western Transvaal through to the central Karoo.

Given these patterns of recoveries, the next step is to investigate those factors which are likely to influence the way in which they are generated. Factors to be investigated in this section are *age*, *epoch* and *natal colony*, while *cause of death* is investigated in the next section (6.2).

*Age effects.* Are there any differences in recovery pattern between different age classes? What evidence is there to suggest this factor merits investigation? From a study of the Pied Flycatcher *Ficedula hypoleuca*, in Finland, it was discovered that those juveniles found dead during their first winter migration were spread over a wider front and at greater distances from their natal territories than birds dying during their second, or subsequent winter migrations (see Baker 1982: 11-13). It is also known that young Bald Eagles, raised in Florida (in the southeastern U.S.A.), move far away from their natal areas in the summer after they were hatched (Newton 1979: 183-185), and it is possible that their parents do not go as far. Thus it is sensible to investigate whether different age classes are recovered in different regions. Age dependency has been observed elsewhere and so it is to be investigated here.

The recoveries from each age class are summarized by inspecting their spatial distribution from a map, by comparing the recovery patterns with the species' current distribution and by comparing the statistics of the distances travelled (i.e. mean, median etc.) among the age classes which are defined as follows.

- Fledglings. Found dead in the year following ringing and 1-6 months old. Most of the recoveries were found close to the natal colony, with only one at a great distance (Figure 6.4 C), in Zimbabwe. Over half (i.e. 33 of 59 = 56%, Table 6.6) were found within the species' current distribution (Figure 6.4 D). Performing a convex hull peels of this data-set reveals that the recoveries lie in a north-east to south-west band loosely centered on the north east Cape (Figure 6.4 D).
- First-years. Found dead in the year following ringing and 7-12 months old. More birds are recovered further out than for fledglings (cf. Figures 6.4 C and 6.5 A). A third (14 of 40 = 35%, Table 6.6) are found within the species' current range (Figure 6.5 B). Not only are there more birds further out, but the core of the distribution is more diffuse (cf. Figures 6.4 D and 6.5 B).
- Second-years. Many birds far away from the natal colony (Figure 6.5 C). Just over a third (i.e. 14 of 38 = 37%, Table 6.6) were found within the species' current distribution (Figure 6.5 D). The convex hull peels reveal that the second-years have an even more diffuse distribution than that for younger birds (Figure 6.5 D): however, the core is in approximately the same region.
- Third-years. A few far away from the natal colony (Figure 6.6 A). Over a half (i.e. 10 of 19 = 53%, Table 6.6) were found within the species' current range (Figure 6.6 B). The distribution of birds dying in their third year is more compact overall, but has a slightly more diffuse core than that exhibited by second-years (cf. Figures 6.5 D and 6.6 B).
- Fourth+ years. A few far away from the site of ringing, but many close to the natal colony (Figure 6.6 C). The majority were found within the current 3% reporting-rate boundary (Figure 6.6 D). The convex hull peels of those birds dying at four+ years is more compact than that for third-years (Figure 6.6 B) and resembles most closely those dying in their second year (cf. Figures 6.5 D and 6.6D).

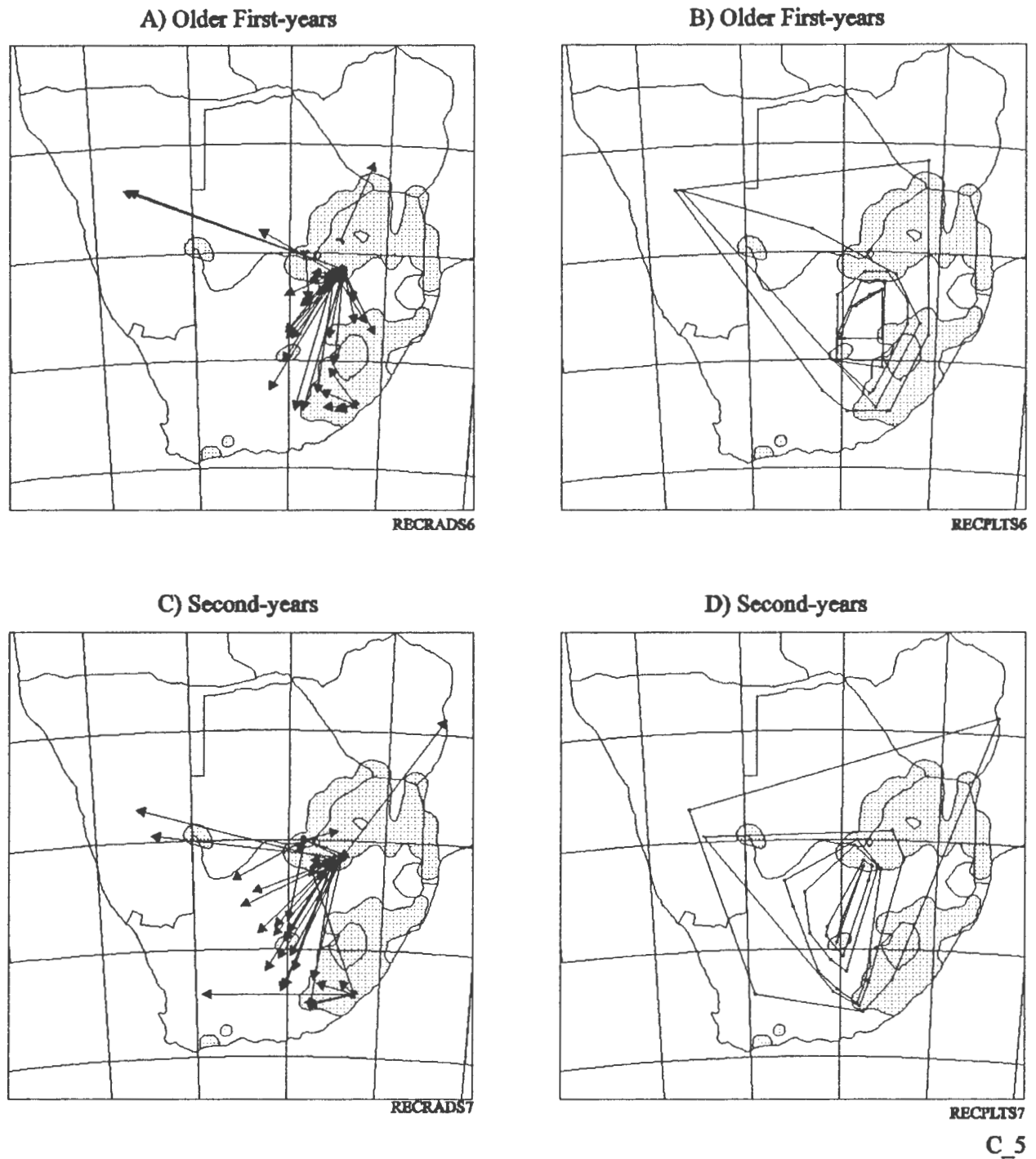


Figure 6.5 Recoveries of older first-years. A) Radial-arm plot. B) Point plot with a peeling of convex hulls. Recoveries of second-years. C) Radial-arm plot. D) Point plot with a peeling of convex hulls. The enclosed stippled region approximates the current Cape Vulture distribution.

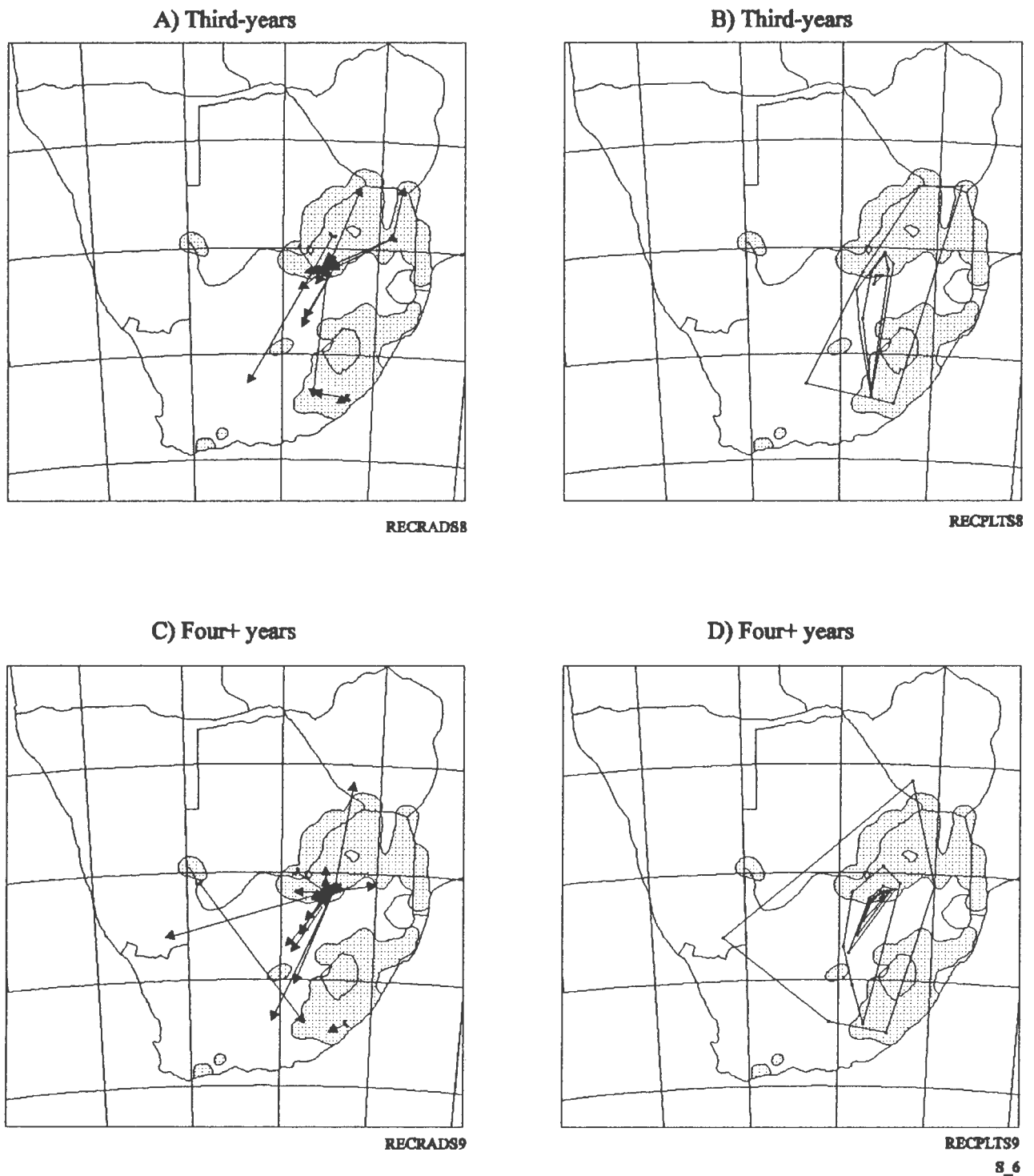


Figure 6.6 Recoveries of third-years. A) Radial-arm plot. B) Point plot with a peeling of convex hulls. Recoveries of four+ years. C) Radial-arm plot. D) Point plot with a peeling of convex hulls. The enclosed stippled region approximates the current Cape Vulture distribution.

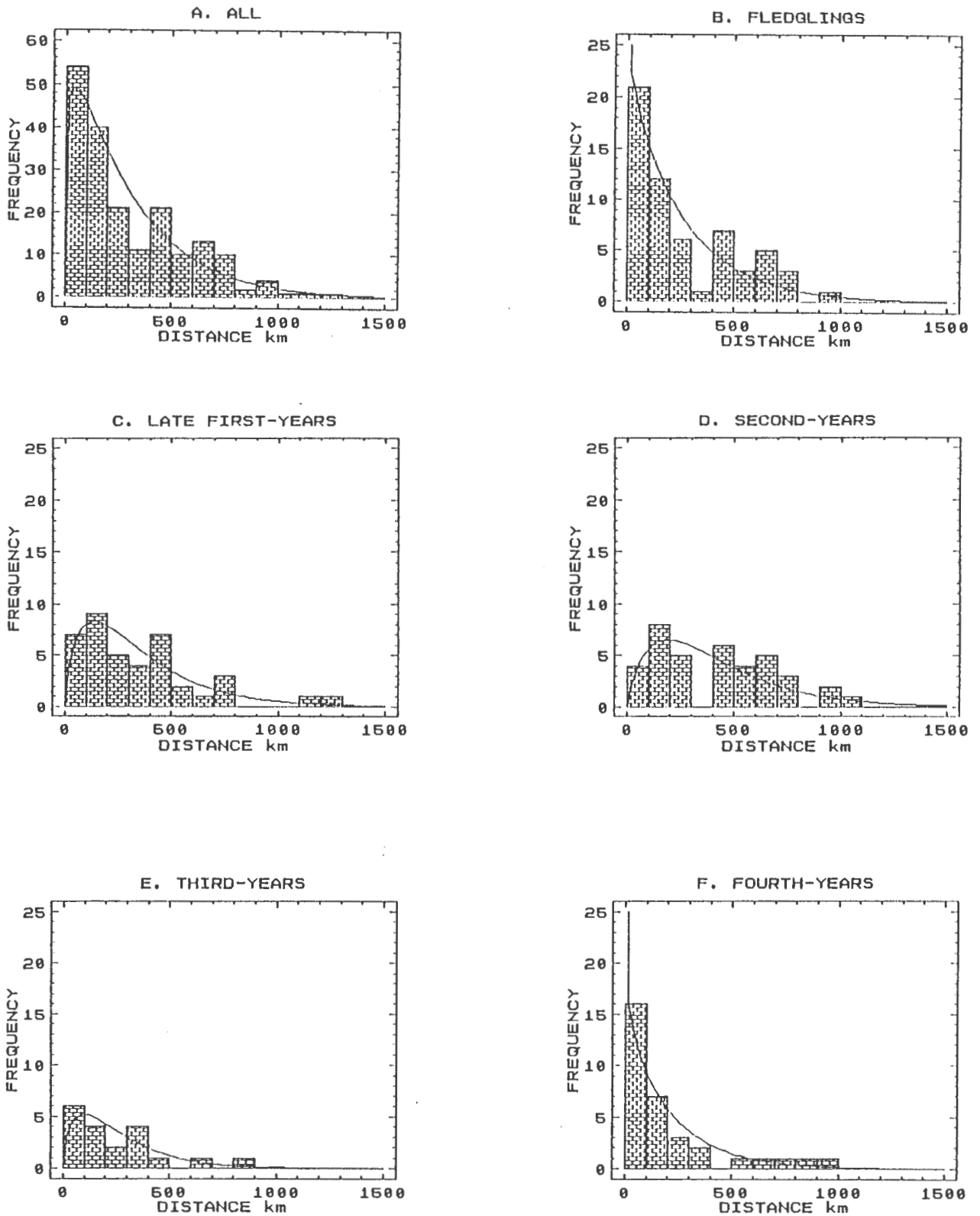


Figure 6.7 Distance (km) travelled by ringed birds recovered from natal colony as a function of age class. Histogram overlaid with the best-fit gamma distribution. A. All birds. B. Fledglings (age class 05). C. Late first-years (age class 06). D. Second-years (age class 07). E. Third-years (age class 08) F. Four + years (age class 09).

Table 6.6  
Proportion of recoveries from each age class found within the current Cape Vulture distribution.

Age class	Outside present range	Inside present range	Total	Proportion within range	Lower 95% limit	Upper 95% limit
05 Fledglings	26	33	59	55.9%	42.4%	68.8%
06 Older first-years	26	14	40	35.0%	20.6%	51.7%
07 Second-years	24	14	38	36.8%	21.8%	54.0%
08 Third-years	9	10	19	52.6%	28.9%	75.6%
09 Four+ years	11	22	33	66.7%	48.2%	82.0%
Total	96	93	189	49.2%	41.9%	56.9%

(Chi-squared = 10.7, 4 df,  $p = 0.0296$ )

It is possible to compare directly the distances travelled by birds in each age-class, both graphically (Figure 6.7) and numerically (Table 6.3). The distributions of these distance-at-death data (i.e. Table 6.3) are tested against the gamma distribution so that they be used in a diffusion-type model. The mean distance at which ringed Cape Vultures are recovered increases in the first three age classes, thereafter decreasing, in near-adults, to approximately the same distance as for fledglings (Table 6.3, Figure 6.8 A). Conversely, it is seen that the proportion of fledglings dying within the species' current distribution is over 50%, but this figure drops to 35% for older first-years then rises slowly through the age classes to those four+ years old where 67% die within the species range (Table 6.6, Figure 6.9). The perception is that young birds drift out from their natal colony for the first two to three years then they start returning. Once attached to their breeding colony, they seldom wander far afield.

If the perception of juvenile movements presented above is accurate then it seems probable that the proportion dying in the immediate vicinity of the natal colony (i.e. < 10 km) should decrease initially as more birds move away and then increase in later years as they return (Table 6.4, Figure 6.8 B). Just over 45% of the fledglings die near their natal colony whereas only 18% of the older first-years die close to their natal colonies. Thereafter the proportion rises slowly for older age classes (Figure 6.8 B). The proportion dying near the natal colony differs significantly between the age classes (Chi-squared test,  $p < 0.05$ ). However, there is no difference between age classes when fledglings are excluded (Chi-squared test,  $p > 0.1$ ) indicating that only the fledglings differ from older birds (Table 6.5).

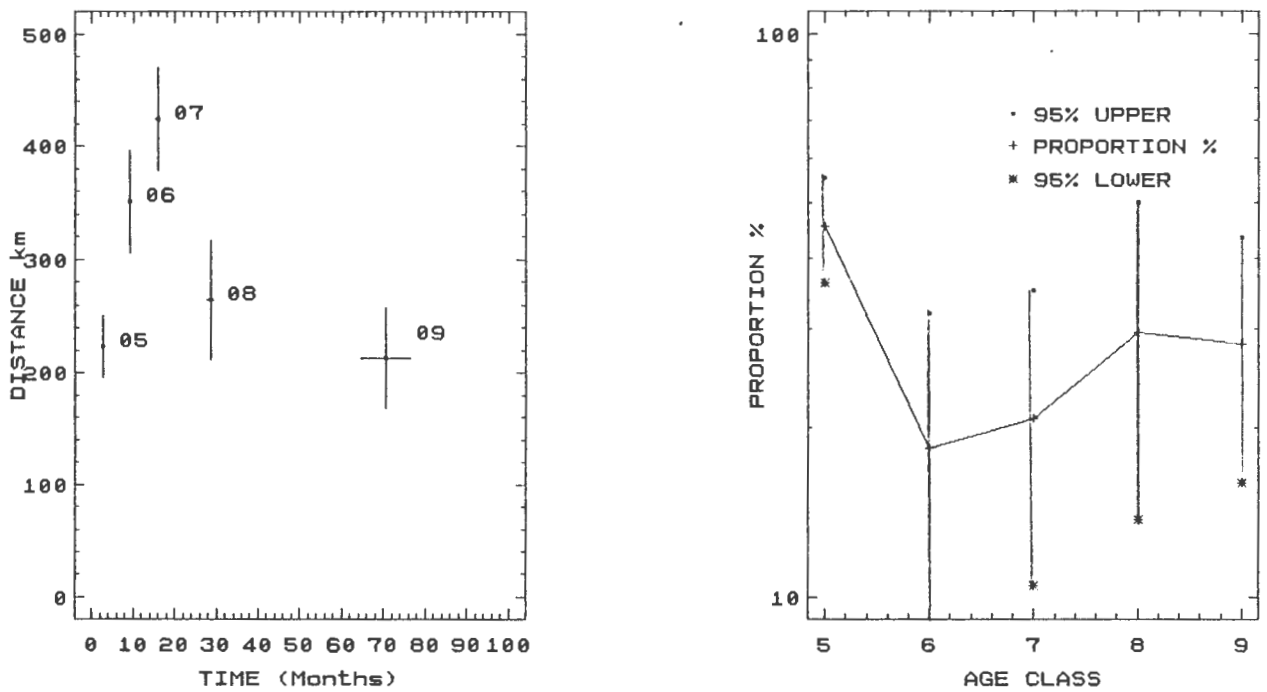


Figure 6.8 A) Mean distance  $\pm$  s.e. (km) travelled by all birds of a given age group plotted against mean lifetime  $\pm$  s.e. (months). B) Estimated proportion (with 95% confidence limits) of birds dying within 10 km of the natal colony. The age classes are: 05 = Fledglings, 06 = Late first-years, 07 = Second-years, 08 = Third-years and 09 = Four+ years.

Table 6.7  
Distances (km) at which useful recoveries are reported compared among Decades.

Decade	Sample	Mean	Standard error	Quartiles			Maximum
				lower	median	upper	
1950*	22	465	56	224	491.5	639	907
1960	39	426	50	110	422	584	1192
1970	96	232	23	76	142	310	1226
1980	32	261	40	79	207	423	925

\* One recovery from the 31 birds ringed in 1948 is included.

Table 6.8  
Elapsed times (months) at which useful recoveries are reported compared among Decades.

Decade	Sample	Mean	standard error	Quartiles			Maximum
				lower	median	upper	
1950*	22	33.4	8.7	9.0	18.5	45.0	157
1960	39	14.9	2.9	4.0	9.0	17.0	82
1970	96	21.9	2.8	5.0	11.5	26.0	127
1980	32	19.1	3.8	5.5	11.5	24.5	101

\* One recovery from the 31 birds ringed in 1948 is included.

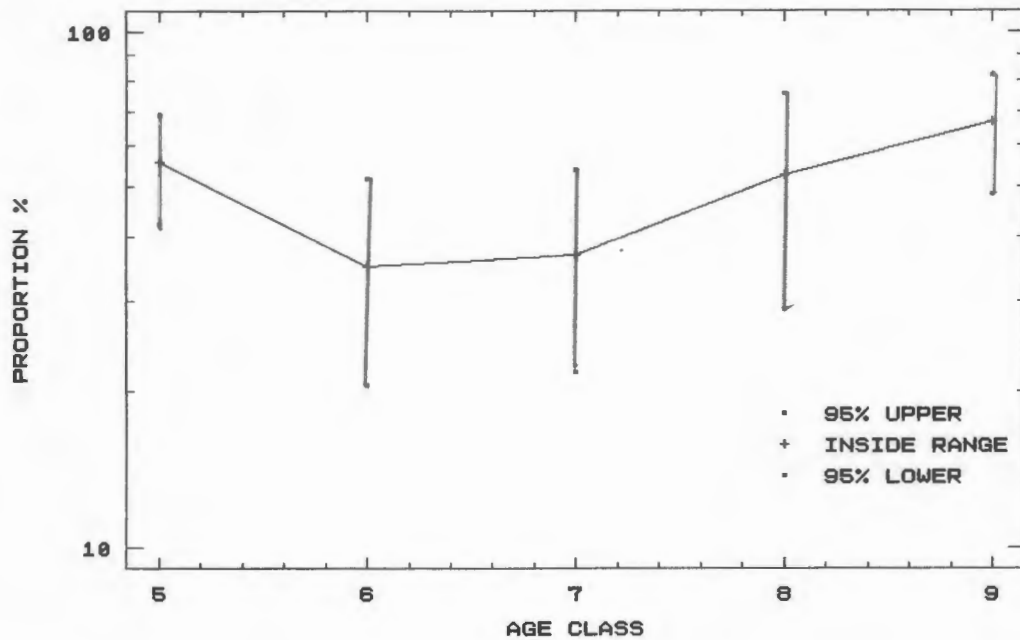


Figure 6.9 Proportion of recoveries found within the species' current range as a function of age-class.

*Epoch effects.* The proportion of Transvaal-ringed Cape Vultures subsequently recovered in the Cape Province (south of  $29^{\circ}$  S) decreased from 42% in the 1950s to 11% in the early 1970s (Vernon 1978). Reasons suggested for this are (loc. cit.: 19):

the vultures gradually decreased their rate of dispersal to the Cape or recoveries of vultures in the Cape were not reported. There has been a decline of the Cape Vulture populations in the Cape in the 1970s but the causal factors are not known. Two possibilities, decreased food availability and persecution, could both speed the decline and shift the recovery locality. The dispersive vultures from the Transvaal may have gone elsewhere to better food supplies and/or they may have been poisoned by Cape farmers and not reported.

This line of investigation, initiated by C.J. Vernon, will now be expanded to cover all Cape Vultures ringed at all colonies. Specifically the following questions will be asked.

- 1) How can the increased search effort by Vulture Study Group members from 1973 onwards be accounted for?
- 2) Has there been a decline in the distance travelled *per se*, by Cape Vultures found dead as recoveries, since ringing began?
- 3) Has the distance decreased because Cape Vultures no longer live so long, or because they no longer travel so far?
- 4) Are there areas that ringed Cape Vultures went to in the earlier decades (i.e. the 1950s and 1960s) that they no longer go to?

When the Vulture Study Group started its intensive search campaign in 1973 its members concentrated their searches for dead birds at the major breeding colonies and the scree slopes below the breeding cliffs (P.J. Mundy pers. comm.). Thus, by excluding all those recoveries within 10 km of the natal colonies the potential bias of this increased effort will be reduced.

By plotting separately the straight-line distance from the point of ringing to the point of recovery against lifetime, for birds ringed in decades beginning 1950 (including one recovery from the 31 birds ringed in 1948), 1960, 1970 and 1980, the following trends are suggested (Figure 6.10).

- 1) In the 1960s there were fewer birds living beyond 40 months and more birds dying closer to the natal colony than in the previous decade.
- 2) During the 1970s there were more long-lived birds than ever before but they were dying closer to their natal colonies.
- 3) The distance travelled during the 1980s started to increase with fewer birds dying so close to the natal colonies, when compared with the 1970s.

Summarizing the elapsed distance and longevity data separately (Figure 6.11) reinforces these suggestions, which may be tested. By comparing the average distances travelled in each decade (Table 6.7; differences statistically different,  $p < 0.01$ , ANOVA) with the average lifespan, (Table 6.8, Figure 6.12; only 1950s significantly longer,  $p < 0.05$ , ANOVA) it is seen that while there was a decrease in average distance moved from the 1950s to the 1960s it was not nearly as dramatic as the drop in average lifespan. During the 1970s the average distance travelled nearly halved but the average lifespan increased when compared with the 1960s. In the last decade average lifespan decreased slightly over the previous decade while average distance increased.

It is suggested that the following forces acted on the Cape Vulture population to give rise to the above patterns.

- 1) Mortality factors (notably starvation from decreased food supply in the Cape, see Boshoff & Vernon 1980: 238) increased regionally during the late 1950s and 1960s causing increased mortality across the whole population. This led to an overall drop in survival without influencing the distance travelled by individuals.
- 2) During the late 1960s and early 1970s there was a general collapse of the Cape Vulture population along its outer fringe, e.g. the eastern Cape, Karoo, northern Cape and Namibia causing the species' range to contract dramatically. However, at the same time conditions improved slightly in the species' 'heartland' and this caused an increase in longevity. There may be a bias in this apparent change, however, because the 1970s saw the introduction of new metal rings and these lasted longer than the old aluminium rings thus giving an apparent increase in lifespan.
- 3) During the 1980s the range of the species started to expand slightly thus allowing the young birds to move further afield. There are recoveries still to be reported from this last decade (i.e. the recovery data-set is not complete) and these will increase the average lifespan.

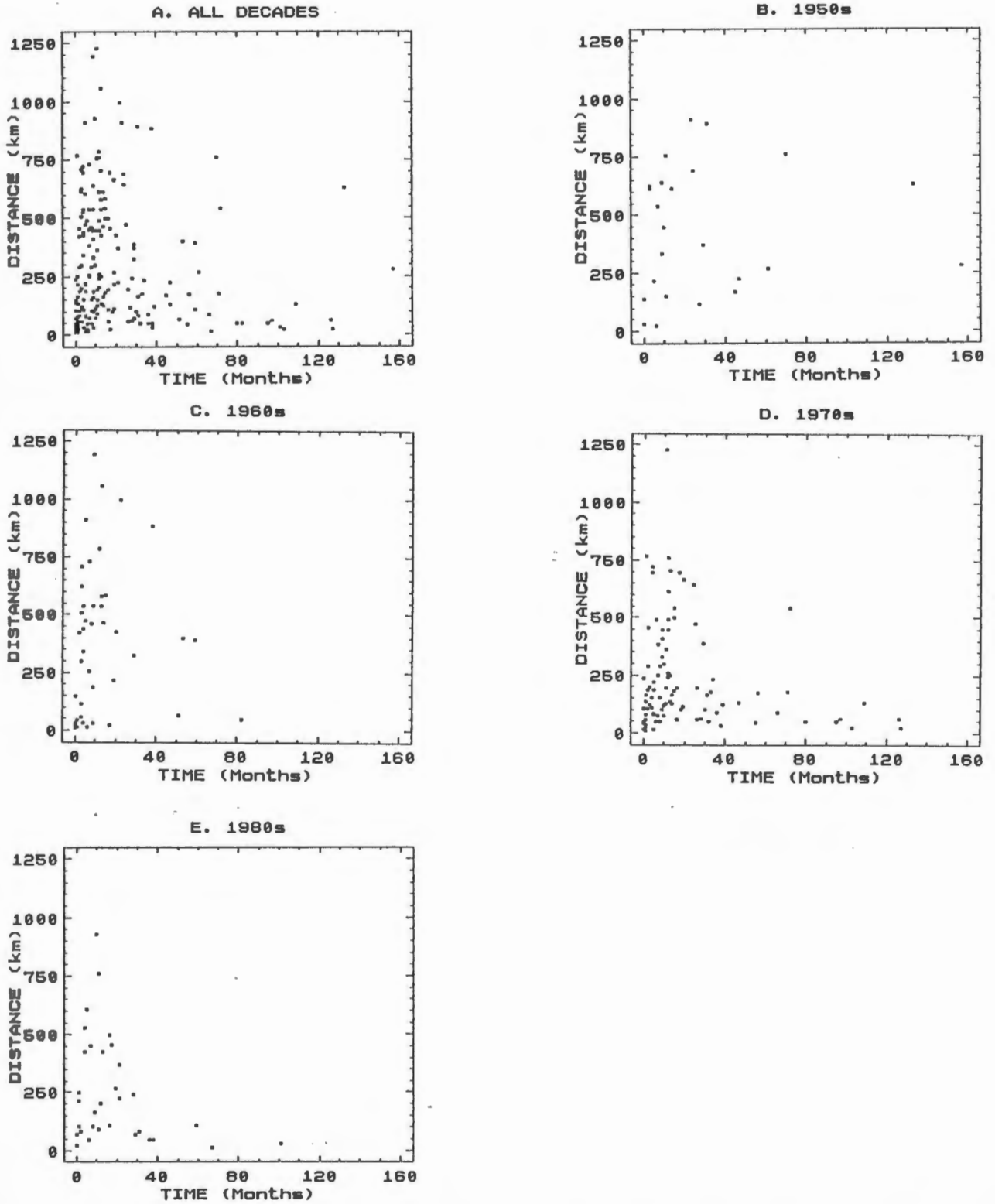


Figure 6.10 Relationship between distance (km) travelled and lifespan (months) by age class. A. All birds. B. 1950s. C. 1960s. D. 1970s. E. 1980s.

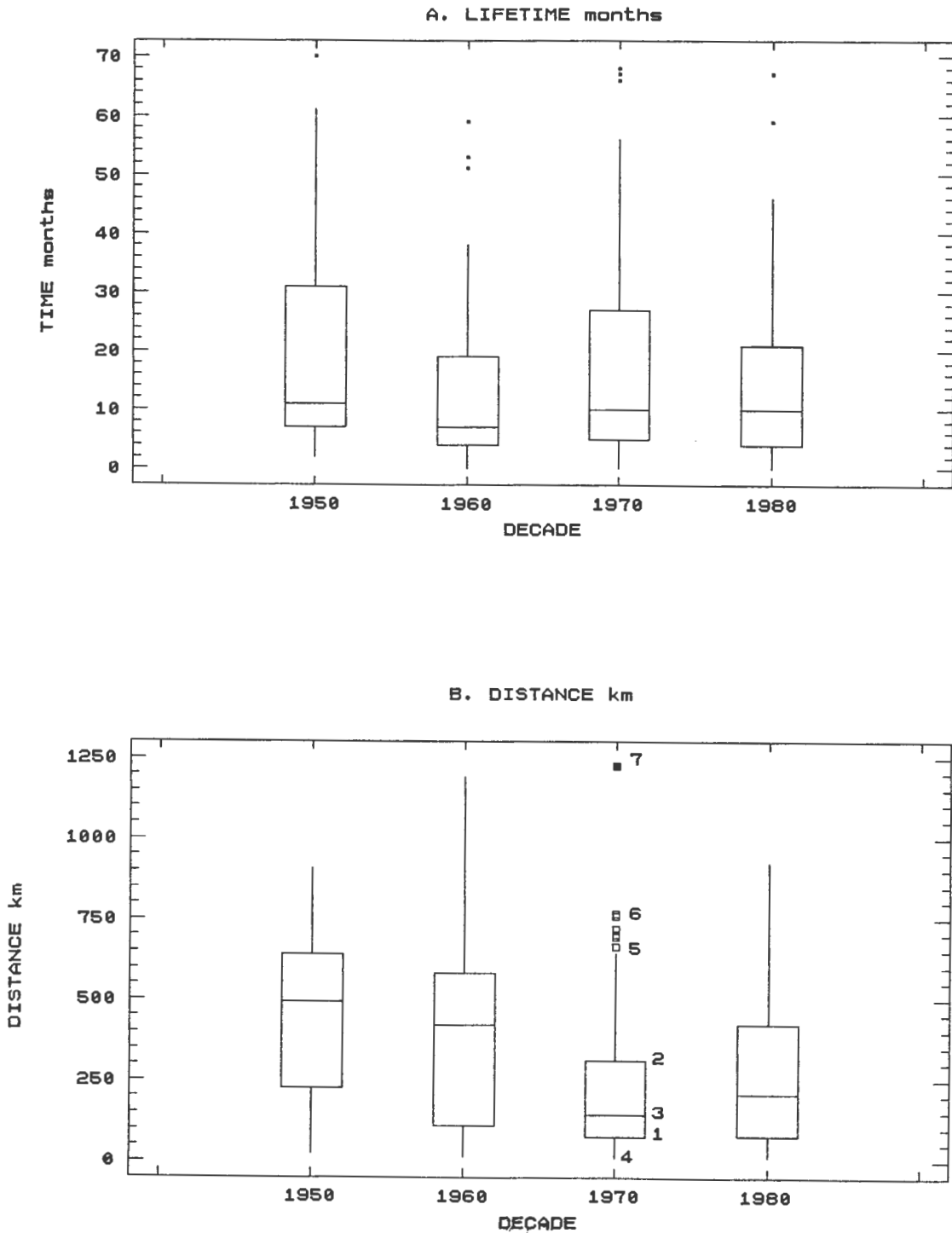


Figure 6.11 Box-and-whisker plots of survival and distance travelled summarized by decade. A. Lifetime (months) as a function of decade in which ringed. B. Distance (km) travelled as a function of decade in which ringed. Explanation of Box-and-whisker plot: the box contains 50% of observations from first quartile, i.e. 25% (1) to third quartile, i.e. 75% (2) and includes the median, i.e. 50% (3). The lower whisker which is the lesser of the minimum or median plus 1.5 times the inter-quartile range (4). The upper whisker which is the greater of the maximum and the median plus 1.5 times the inter-quartile range (5). The outliers (6) and extreme outliers are flagged (7).

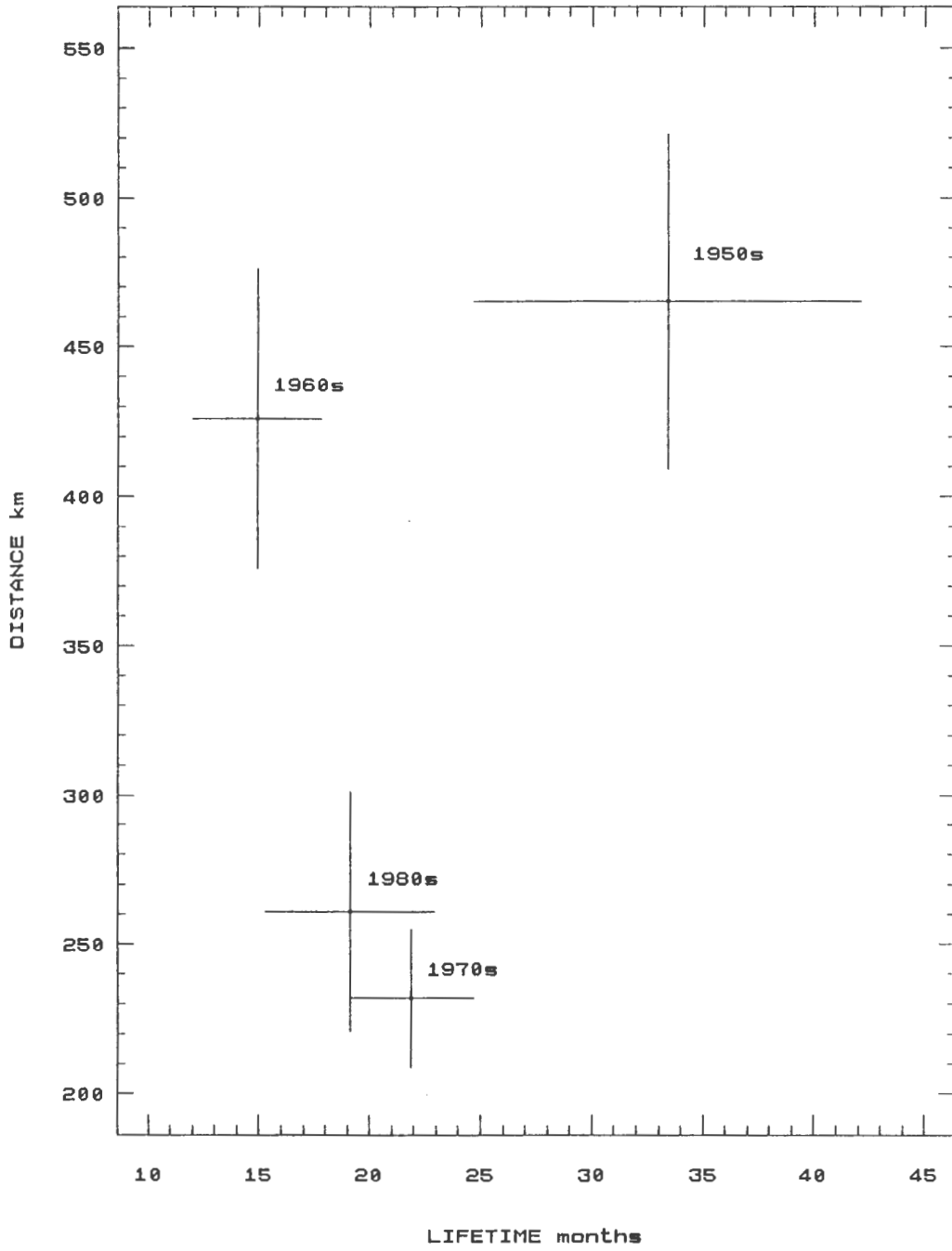


Figure 6.12 Mean distance  $\pm$  s.e. (km) traveled by all birds ringed in a given decade plotted against mean lifetime  $\pm$  s.e. (months).

Table 6.9

Proportion of recoveries from each decade found within the current Cape Vulture distribution.

Age class	Outside present range	Inside present range	Total	Proportion within range	Lower 95% limit	Upper 95% limit
1950*	15	7	22	31.8%	13.9%	54.9%
1960	29	10	39	25.6%	13.0%	42.1%
1970	42	54	96	56.3%	45.8%	66.4%
1980	10	22	32	68.8%	50.0%	83.9%
Total	96	93	189	49.2%	41.9%	56.9%

\* Includes one recovery of a bird ringed in 1948.

(Chi-squared = 18.1224, 3 df,  $p = < 0.0001$ )

The proportion of recoveries found within the species' current range was about 32% in the 1950s and dropped to 25% during the 1960s. However, it rose to more than double these levels in the 1970s and 1980s (Figure 6.13), this change being statistically significant (Table 6.9).

Plotting all the recoveries from nestlings ringed at all colonies on a decade-by-decade basis yields a complex and not particularly informative picture, from which it is difficult to see how the distribution patterns have changed with time. To elucidate the temporal changes in spatial distribution the following stratagem is employed. The recoveries from the south-central Transvaal colonies are grouped together because they have similar recovery distributions (see maps and descriptions at start of this section). These recoveries are plotted separately for each of the decades 1950 (including a recovery from a bird ringed in 1948), 1960, 1970 and 1980. The colonies chosen are Kranzberg, Roberts' Farm, Skeerpoort and Nooitgedacht. The radial-arm plot for each decade is overlain with the minimum convex hull which encloses all the recoveries and helps to delineate the recovery region. From an inspection of the resulting maps the following conclusions are drawn.

- 1950s The 22 recoveries are in a near rectangular zone running along a north-east to south-west axis with no recoveries in the east nor in Namibia (Figure 6.14 A). The convex hull peels indicate a loose core with its axis aligned along the south western Transvaal-Karoo axis.
- 1960s Of the 35 recoveries fewer are from the eastern Cape, but more are from the northern Cape with four in Namibia, a westward expansion is suggested (Figure 6.14 B). The distribution is more diffuse than in the 1950s and the core has moved slightly to the north west.

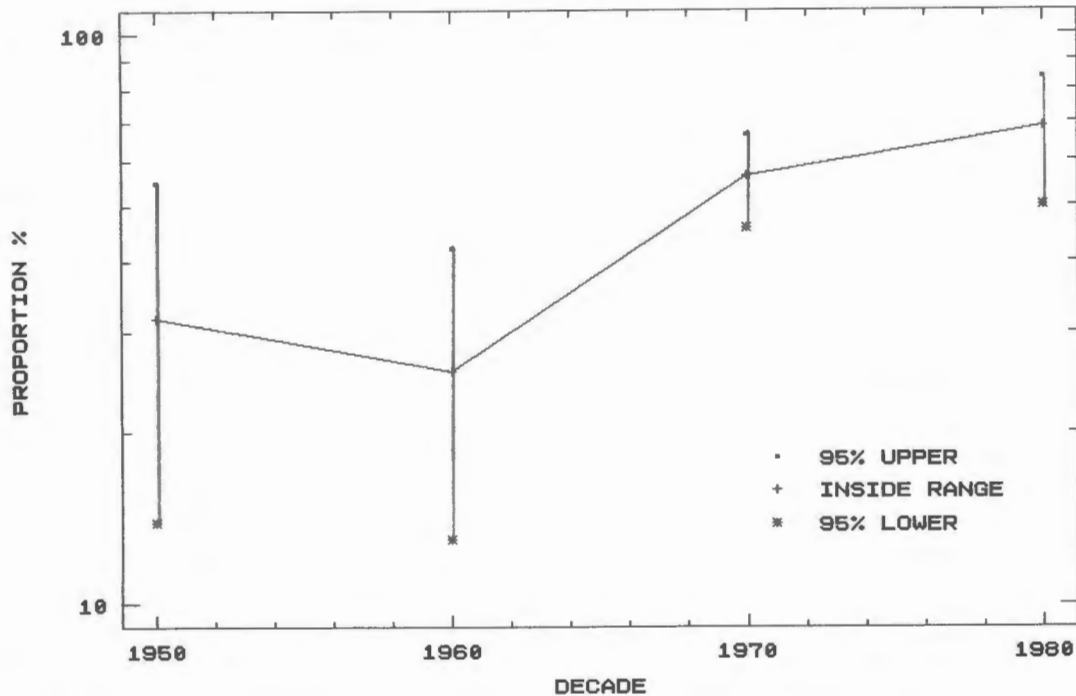


Figure 6.13 Estimated proportion of recoveries found within the species' current range as a function of decade of ringing.

- 1970s Although the number of recoveries from the south-central Transvaal increased to 74, there were fewer recoveries in the north and far west but there were many more from the western Transvaal (Figure 6.14 C). The overall range is about the same as for the 1960s except for a large internal shift northwards of the main concentration of recoveries.
- 1980s There were only 14 recoveries giving a picture for the 1980s which is one of a range collapse on all fronts (Figure 6.14 D). The core, as seen from the convex hull peels, is even tighter for the 1980s than the 1970s.

Has there been a temporal variation in age at death, as suggested above? To test this the number of recoveries in each 20-month category is compared among decades (Figure 6.15 - shown in 10-month intervals) for the south-central Transvaal. There are no significant variations (Table 6.10), which suggests that there have been no major changes in life expectancy for these colonies. This contrasts with the conclusion reached above, and suggests that the observed variations in lifespan may be caused by the variation in ringing effort at colonies outside the south central Transvaal <sup>2</sup>.

2 An examiner (Dr. A. Dhont) suggested collapsing Table 6.10 to two columns (0-19 and 20+ months) and to two rows (1950s vs 1960s & 19870s) and ignoring the recoveries from the 1980s (as they are not yet complete). This was done (Chi-squared = 5.79, 2 df,  $p \approx 6\%$ ). This result is closer to being significant; thus the above conclusion may not be correct. It was also suggested that all the chi-squared tests should be replaced by G-statistics. This is will tried when the thesis is broken down into a number of papers for publication.

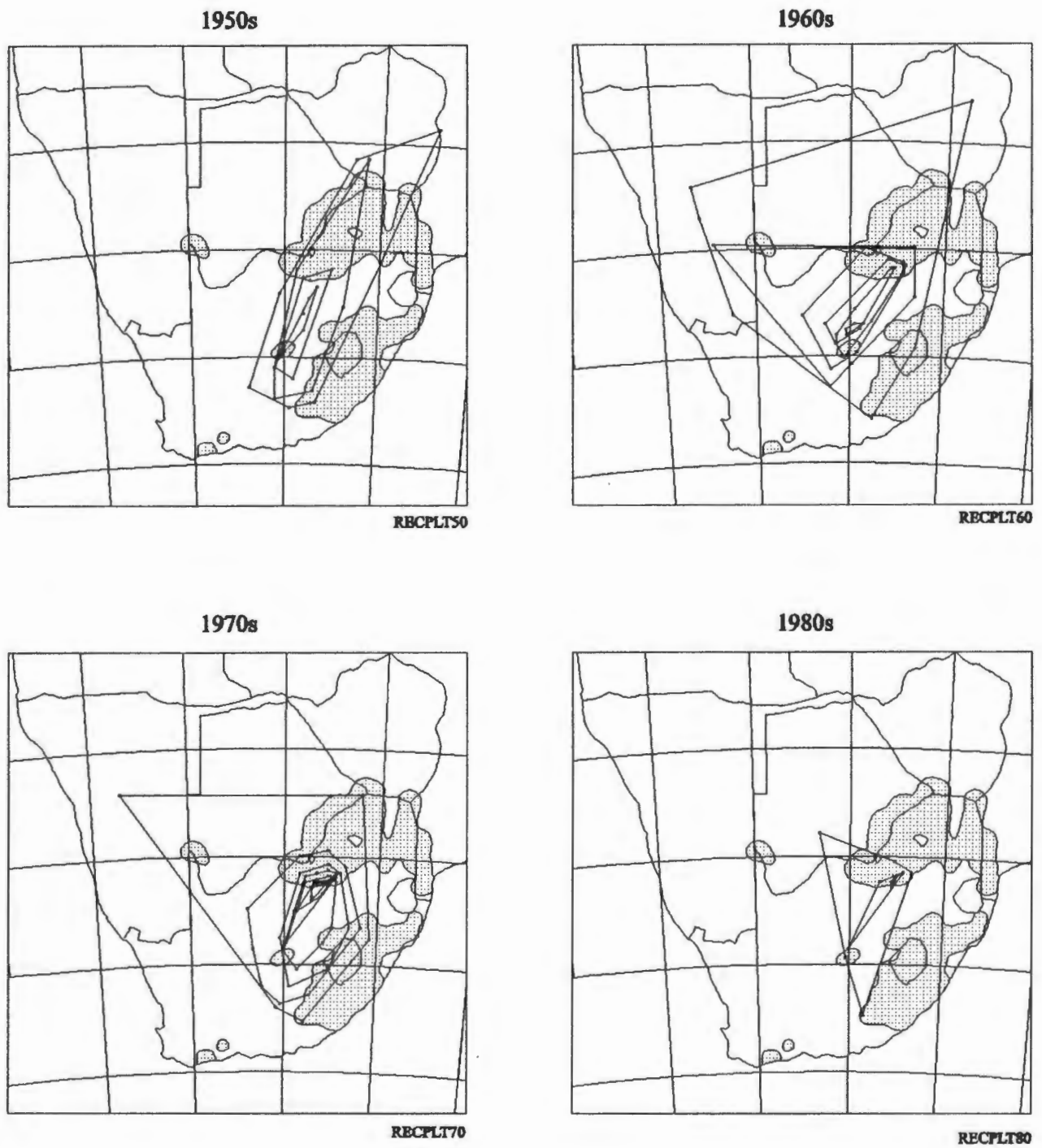


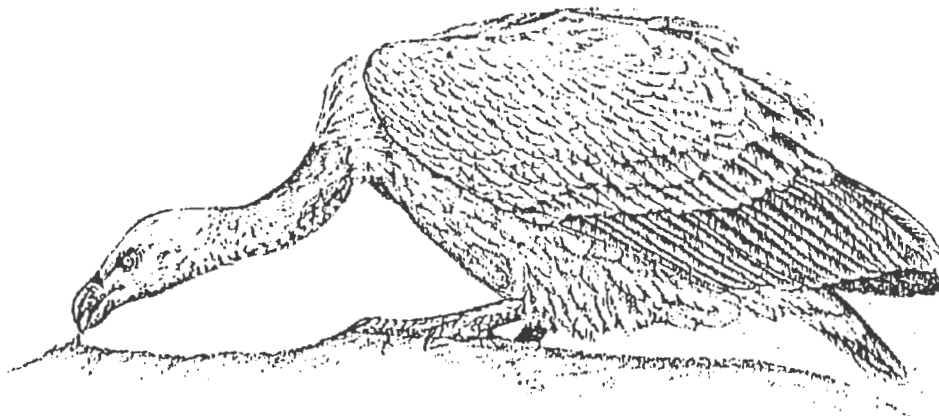
Figure 6.14 Distribution of recoveries by decade. A) 1950s, B) 1960s, C) 1970s and D) 1980s.

Table 6.10  
 Number of recoveries found in each age category with a comparison among decades.  
 (The numbers in the second line of each cell are the column percentages.)

Decade	0-19	20-39	40-59	60-79	80-99	100-119	120-139	140-159
1950	11 11%	5 23%	2 29%	2 40%	0 0%	0 0%	1 33%	1 100%
1960	28 28%	3 14%	3 43%	0 0%	1 25%	0 0%	0 0%	0 0%
1970	52 52%	11 50%	2 29%	2 40%	3 75%	2 67%	2 67%	0 0%
1980	9 9%	3 14%	0 0%	1 20%	0 0%	1 33%	0 0%	0 0%
Total	100 69.0%	22 15.2%	7 4.8%	5 3.4%	4 2.8%	3 2.1%	3 2.1%	1 0.7%

(Chi-squared = 23.1, 21 df, p > 0.1)

Comparing the spatial patterns from the above four epochs suggests that there may have been a NE-SW axis in the 1960s with a shift to a more uniform spread in the later decades. To examine this suggestion a rose diagram is constructed for each decade (Figure 6.16) and it is seen that there is indeed a *prima facie* case to be made for this hypothesis.



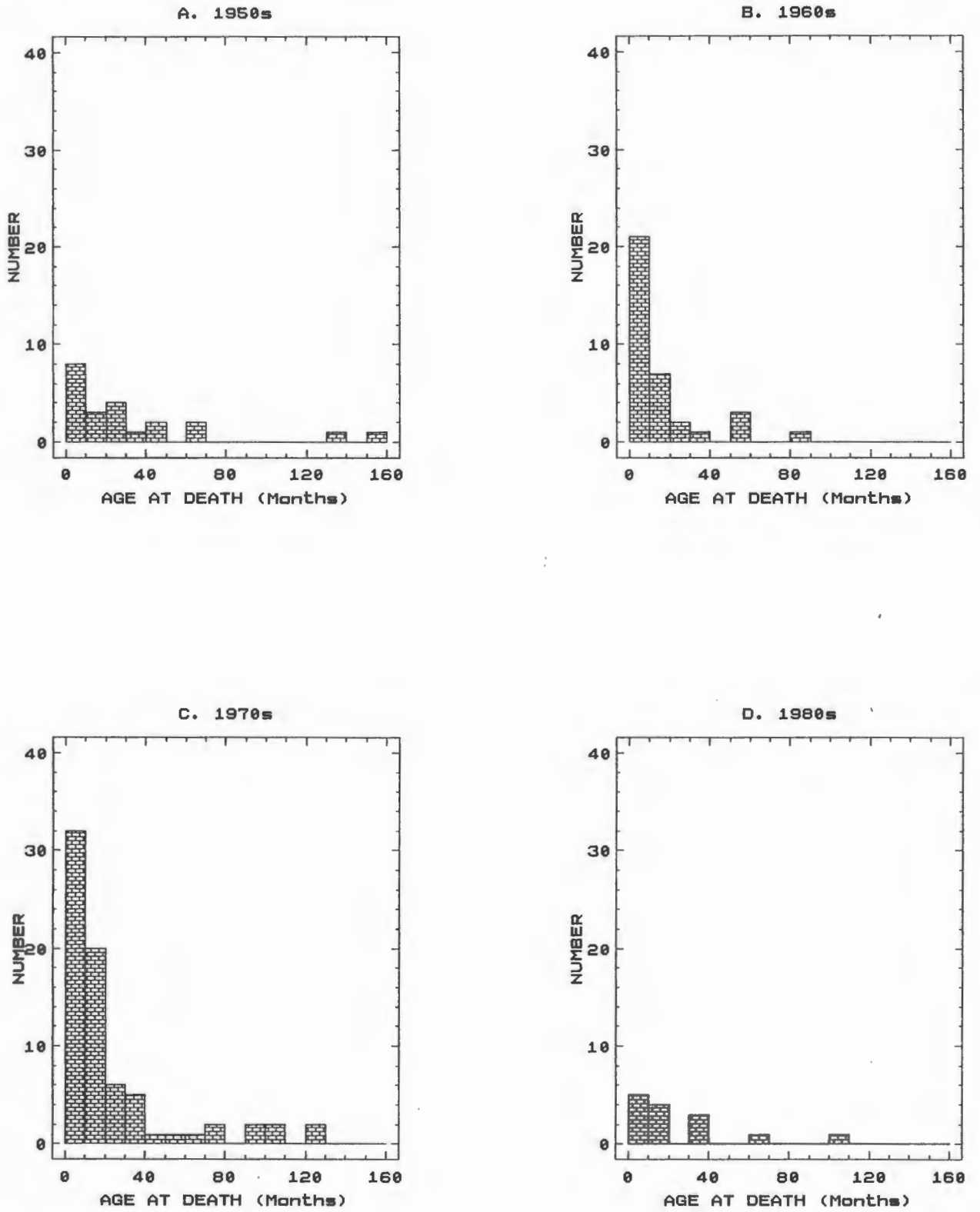


Figure 6.15 Distribution of lifespan by decade for birds-ringed in the south-central Transvaal. A. 1950s, B. 1960s, C. 1970s and D. 1980.

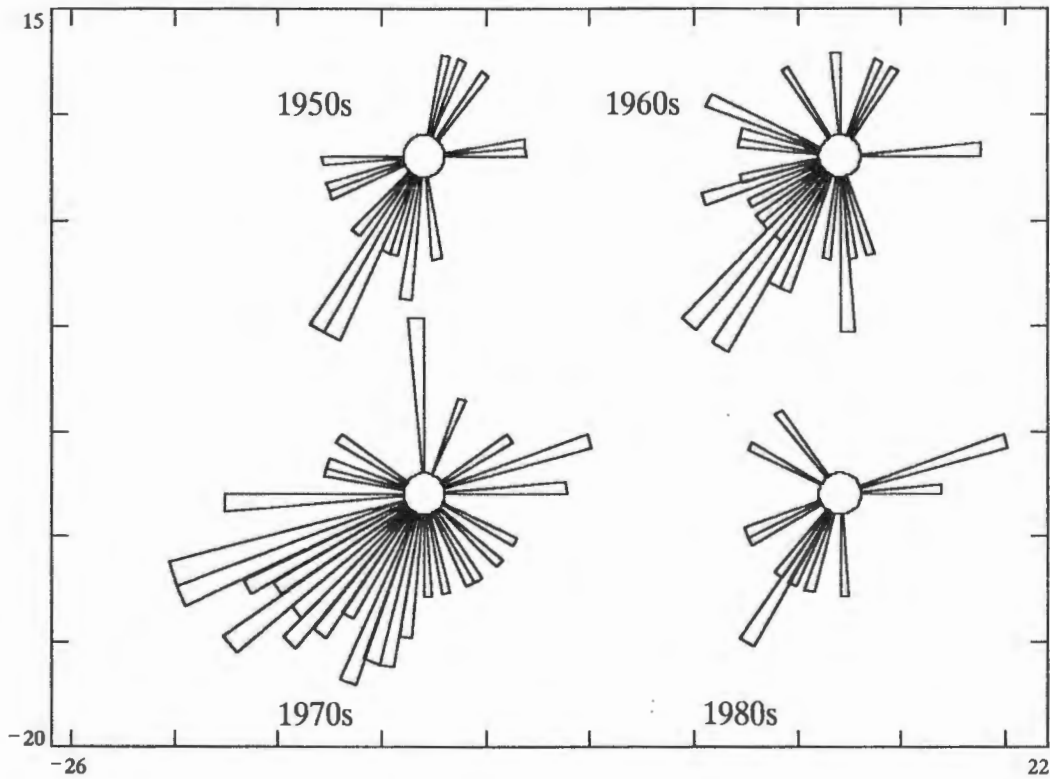


Figure 6.16 The number of recoveries at a given azimuth for recoveries from the south-central Transvaal plotted separately by decade.

It is possible to reduce these circular distributions of recovery directions using a suite of 'circular statistics' (Upton & Fingleton 1989: 207-311). As there was no suitable package available to compute these statistics a small set of routines was developed (Exhibit 6.1.1). The following quantities and terms are defined (loc. cit.).

<i>Term</i>	<i>Definition</i>
$n$	Number of recoveries.
$r_i$	A vector of unit length in the direction of the $i^{\text{th}}$ recovery, $i = 1, 2, \dots n$ .
$\Phi_i$	Direction of the $i^{\text{th}}$ recovery, $i = 1, 2, \dots n$ .
$x_i$	$= r_i \cdot \cos(\Phi_i)$ . Component of $r_i$ in the x-direction.
$y_i$	$= r_i \cdot \sin(\Phi_i)$ . Component of $r_i$ in the y-direction.
$X$	$= \sum x_i$ . Sum of the x-direction components.
$Y$	$= \sum y_i$ . Sum of the y-direction components.
$XX$	$= X \cdot X$ . Squared sum of the x-direction components.
$YY$	$= Y \cdot Y$ . Squared sum of the y-direction components.

- $R$  =  $XX + YY$ . Resultant vector sum. With  $n$  recoveries (i.e. observations), each of unit length it follows that  $0 \leq R \leq n$ . If  $R = 0$  then there is no preferred direction because the recoveries are equally spread out around the circle and so cancel out each other. If  $R = n$  then all recoveries are from the same direction and add together.
- $\Phi_{\text{bar}}$  =  $\arctan(X/Y)$ . The direction of  $R$ , i.e. the mean direction. Care must be taken to place the resultant angle in the correct quadrant.
- $R_{\text{bar}}$  =  $R/n$ . The concentration. From the above description of  $R$  it follows that  $R_{\text{bar}}=0$  implies the uniform distribution and  $R_{\text{bar}}=1$  implies perfect alignment, i.e. total concentration in one direction.
- $\text{Var}$  =  $1 - R_{\text{bar}}$ . The circular variance.
- $\text{Psi}$  =  $( [\cos(2 \cdot \Phi_{\text{bar}})] \cdot [\Sigma\{\cos(2 \cdot \Phi_i)\}] + [\sin(2 \cdot \Phi_{\text{bar}})] \cdot [\Sigma\{\sin(2 \cdot \Phi_i)\}] ) / n$ .  
An intermediate parameter.
- $W_{\text{bar}}$  =  $n \cdot (1 - \text{Psi}) / (4 \cdot R^2)$ . The circular variance of  $\Phi_{\text{bar}}$ , under the assumption that the circular distribution is unimodal.
- $u_\alpha$  The upper  $(1-\alpha)$  percentage point for the unit normal distribution. For 95% confidence limits  $u_\alpha = 1.96$ .
- $a$  =  $\arcsin(u_\alpha \cdot \{2 \cdot W_{\text{bar}}\}^{1/2})$ . A constant.  
Note that if the argument  $u_\alpha \cdot \{2 \cdot W_{\text{bar}}\}^{1/2}$  is not strictly less than unity, then the mean direction is ill-defined and it is not possible to compute a real value for  $a$ .
- $\Phi_l$  =  $\Phi_{\text{bar}} - a$ . The lower confidence limit for the mean direction.
- $\Phi_u$  =  $\Phi_{\text{bar}} + a$ . The upper confidence limit for the mean direction.

Once the descriptive statistics have been computed it is important to choose an appropriate model for the circular distribution. The first distribution to investigate is the circular uniform distribution. If the recoveries are uniformly distributed around the compass the expected value of  $R$  is:

$$E(R) = 1/2 \cdot (n \cdot \pi)^{1/2}$$

If the distribution is not uniform, then the second distribution to consider is the von Mises distribution which is the circular equivalent of the normal distribution. It is defined below.

<i>Term</i>	<i>Definition</i>
$f(\Phi)$	= $C_{\text{vm}} \cdot \exp(K \cdot \cos\{\Phi - \mu\})$ defined for $0 \leq \Phi \leq 2 \cdot \pi$ .
$C_{\text{vm}}$	= $1 / (2 \cdot \pi \cdot I_0\{K\})$ . The constant of integration.
$I_0\{x\}$	A modified Bessel function of the first kind and of order zero.
$K$	Concentration parameter.
$\mu$	Mean direction.
$A(x)$	= $I_1\{x\} / I_0\{x\}$ . Ratio of two Bessel functions needed to estimate $K$ .

The maximum likelihood estimate (MLE) of  $\mu$  is  $\Phi_{\text{bar}}$  and the MLE of  $K$  is the solution to:

$$A(K_{\text{cst } 1}) = R_{\text{bar}}$$

An 'improved' estimate is the solution to the equation:

$$n \cdot A(K_{cst2}) = R \cdot A(R \cdot K_{cst2})$$

For large values of  $R_{bar}$  an alternative estimator is:

$$K_{large} = (1-1/n)/(2 \cdot \{1-R_{bar}\}) + (R_{bar} - 1/n^2)/(4 \cdot R_{bar} \cdot \{1-1/n\})$$

In order that the distributions of recoveries may be modelled it is necessary to determine if the circular distributions are uniform, unimodal von Mises, multimodal or take some other functional form. To test if the distribution is adequately modelled by the uniform distribution, two tests are performed and these use the value of  $R$ . The following tests are performed.

$\Gamma = 2 \cdot R^2/n$ . This is the Rayleigh test with  $\Gamma$  being distributed as chi-squared with two degrees of freedom which is useful for  $n > 100$ . The 5% critical value is 5.991 and thus if the actual value of  $\Gamma \geq 5.991$ , the assumption of uniformity may be rejected.

$P_{RAY} = \exp\{[1 + 4 \cdot n + 4 \cdot (n^2 - R^2)]^{1/2} - (1 + 2 \cdot n)\}$ . This is the Wilke (1983) probability of exceeding  $R$  given a sample of size  $n$  from a uniform distribution. If  $P_{RAY} \leq 0.05$  then the assumption of uniformity may be rejected.

These two statistics test the null hypothesis that the distribution is uniform against the alternative hypothesis that the distribution is unimodal.

Is the distributions of recoveries uniform around the circle, unimodal or multimodal? To test two gap tests are described. Gap tests may be used to test for concentrations in directions. To conduct these tests the data are ordered such that they range from least to greatest angle.

$$\Phi_1 \leq \Phi_2 \leq \Phi_3 \dots \leq \Phi_n$$

Define the gaps:

$$G_i = \Phi_{i+1} - \Phi_i, \quad i = 1, 2 \dots n-1$$

The last gap is defined as:

$$G_n = 2 \cdot \pi + \Phi_1 - \Phi_n.$$

As a check note that  $\sum G_i = 2 \cdot \pi$ . Compute the maximum gap from:

$$G_{max} = \text{MAX}(G_i).$$

If the value of  $G_{max}$  is greater than the critical value (Table 9.14 in Upton & Fingleton 1989: 247) then this is evidence for one, or more clusters in the distribution of recoveries. This test is 'extremely simple to perform, but, inevitably, is of rather low power, since it takes note of the value of only one of the  $n$  gaps' (Upton & Fingleton 1989: 246). For the second gap test compute:

$$G_s = \sum |G_i - 2 \cdot \pi/n|.$$

Table 6.11  
Summary of directional (i.e. circular) statistics for the four epochs.<sup>3</sup>  
(Notation and symbols as per text and Exhibit 6.1.1)

		1950s	1960s	1970s	1980s
n	Sample size	22	37	74	15
R	Resultant vector sum	11.62	22.56	45.06	5.309
$R_{\text{bar}}$	Concentration	0.5282	0.6096	0.6089	0.354
Var	Circular variance of $R_{\text{bar}}$	0.4718	0.3904	0.3911	0.646
$\Phi_{\text{bar}}$	Mean direction	243.8°	225.5°	222.8°	243.0°
$W_{\text{bar}}$	Circular variance of $\Phi_{\text{bar}}$	0.01498	0.01029	0.004588	0.09183
$\Phi_l$	Lower 95% limit	224.0°	209.2°	211.9°	185.9°
$\Phi_u$	Upper 95% limit	263.6°	241.9°	233.6°	300.2°
$K_{\text{large}}$	von Mises distribution Concentration parameter Large sample estimate	1.273	1.503	1.515	0.9868
$K_{\text{est 1}}$	M.L.E.	1.251	1.555	1.552	0.7586
$K_{\text{est 2}}$	Improved estimator	1.187	1.518	1.534	0.6126
$\Gamma$	Rayleigh test	12.28	27.5	54.88	3.759
	Probability of uniformity	0.0022	0.0000	0.0000	0.1527
$P_{\text{RAY}}$	Wilke estimate of p	0.001554	2.812*10 <sup>-7</sup>	6.631*10 <sup>-14</sup>	0.1533
$G_{\text{max}}$	Maximum gap	100.7°	70.02°	55.01°	108.4°
	G <sub>critical</sub> value	91.0°	?	?	121.0°
	Result:	cluster	-	-	Uniform
$G_s$	Multiple gap test	378.2°	371.8°	429.2°	357.9°
	Critical value	321.0°	308.8°	?	331.5°
	Result:	1+ clusters	1+ clusters	? 1+ clusters	
$U^*$	Watson-Stephen test	0.2116	0.1385	0.2228	0.0965
	Critical value	0.08424	0.09241	0.09275	0.06835
	Accept/reject von Mises	reject	reject	reject	reject

For small values of n (i.e.  $\leq 50$ ) special tables must be consulted (Table 9.15 in Upton & Fingleton 1989: 248). As with  $G_{\text{max}}$ , a large value suggests one or more clusters of recovery directions in the data.

As a result of computing the circular statistics for the four epochs (Table 6.11), it is possible to draw the following conclusions (refer also to Figure 6.17).

- 1) During the 1950s the mean vector was slightly to the south of southeast and the concentration was 0.53. The 95% confidence intervals on the mean vector are from 224° to 264°, a range of 40°.

<sup>3</sup> Note that only the recoveries from the south-central Transvaal are used in this analysis because they form a homogeneous sample.

- 2) In the following decade (i.e. 1960s) the mean vector swung slightly anti-clockwise to face southeast while the concentration increased to 0.61. The 95% confidence intervals on the mean vector are from  $209^{\circ}$  to  $242^{\circ}$  a range of  $33^{\circ}$  which is about 17% narrower, i.e. more concentrated, than that for the 1950s.
- 3) In the 1970s the direction and concentration of the mean vector hardly changed at all when compared with the 1960s, but the 95% confidence intervals on the mean vector are from  $212^{\circ}$  to  $234^{\circ}$  a range of  $22^{\circ}$  which is even narrower. This indicates that the recoveries are spread through a more concentrated range, even though the spatial patterns of the 1960s and 1970s appear similar (Figures 6.14 B and C).
- 4) However, in the last decade (i.e. the 1980s) the mean vector swung back to its 1950s position but with a much more diffuse concentration of 0.35. When the 95% confidence intervals on the mean vector (i.e. from  $186^{\circ}$  to  $300^{\circ}$  a range of  $114^{\circ}$ ) are examined it is seen that the distribution is indeed much more diffuse. The recoveries from the 1980s are indeed more from the south (Figure 6.14 D), but only a small sample is available.

Only the 1980s data failed the Rayleigh test for uniformity. This was also true for the  $G_{\max}$  test, which found the 1980s data to be clustered. However, the multiple gaps test found the 1980s data to have more than one cluster. None of the decades could be adequately fitted by a unimodal von Mises distribution. From an examination of the rose diagrams (Figure 6.16), it is seen that these distributions tend to be bimodal with the second mode opposite (i.e. at  $180^{\circ}$ ) to the first. It is likely that it is this bimodality which causes the lack of fit with the uniform and unimodal von Mises distributions.

The mean direction at which recoveries were found during the four decades show considerable overlap (Table 6.11) and it is clear that the mean directions are not different. This suggests that while birds have had different lifespans and travelled different distances during the four decades, they were going out to approximately the same sector.

*Colony effects.* The distributions of recoveries from those eight colonies at which many Cape Vultures have been ringed are described at the start of this section. It is clear that there are great differences in the distances and directions at which dead Cape Vultures are found from their natal colonies. There are sufficient data from four colonies (i.e. more than ten useful recoveries from Colleywobbles, Mannyelanong, Roberts' Farm and Skeerpoort) to construct frequency histograms of the distribution of their recovery distances (Figure 6.18). From these diagrams it is seen that the two colonies located in 'tribal' areas (i.e. Colleywobbles in the Transkei and Mannyelanong in Botswana) have their modal recovery distance in the range 150-250 km while the others, in non-tribal areas, have their modal recovery distances at 0-50 km.

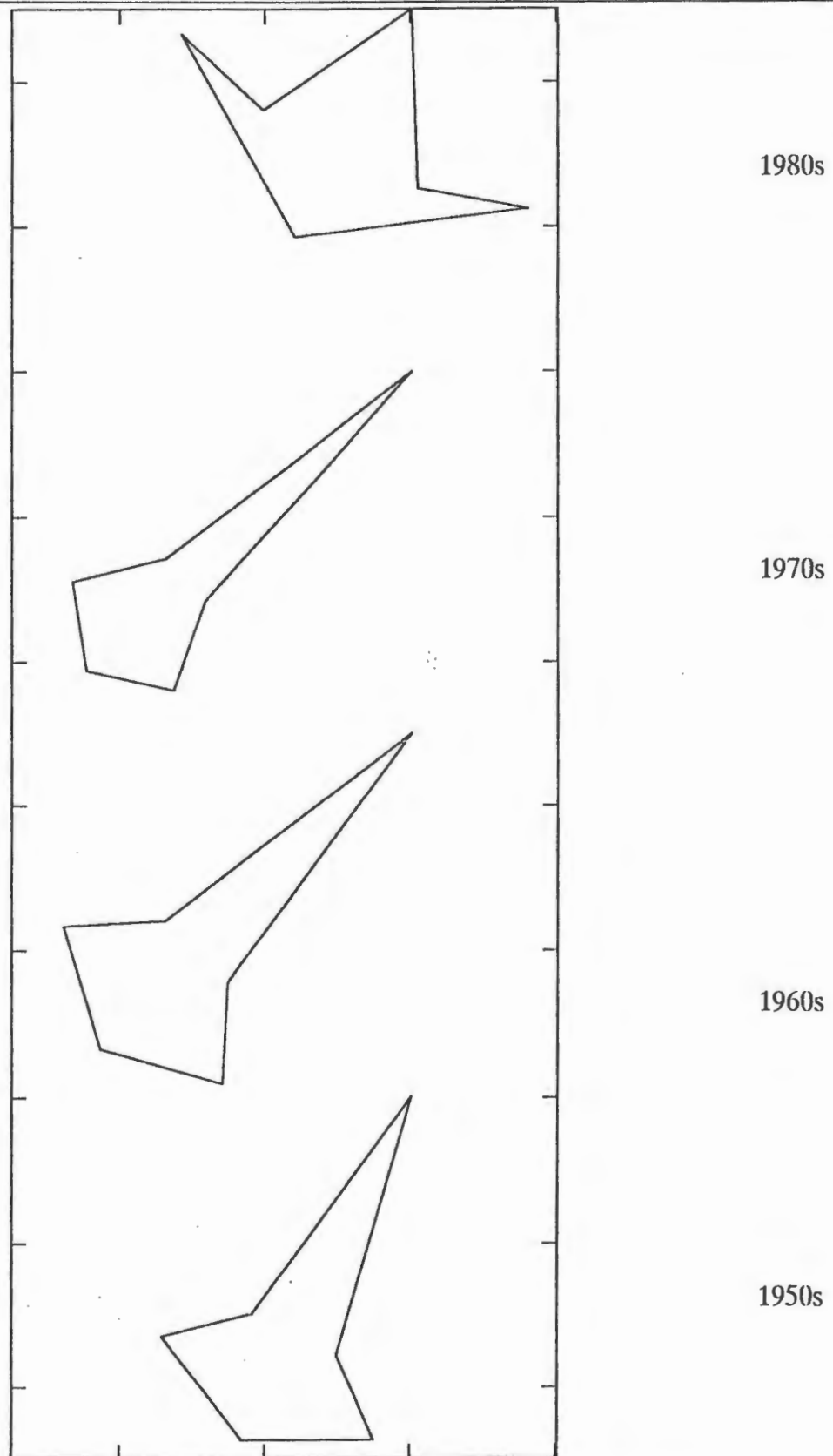


Figure 6.17 The direction, concentration and confidence limits on the mean direction vector for the decades of the 1950s, 1960s, 1970s and 1980s. The distribution of recoveries was highly concentrated in the 1950s but by the 1980s it had become more diffuse.

Table 6.12  
Number of recoveries found in each distance category comparing tribal and non-tribal colonies.

(The second figure in each block is the column proportion%)

	10–49 km	50–99 km	100–149 km	150–199 km	200–249 km	250+ km	Total
Non-tribal	34 91.9	24 92.3	18 75.0	13 65.0	5 38.5	71 85.5	165 81.3
Tribal	3 8.1	2 7.7	6 25.0	7 35.0	8 61.5	12 14.5	38 18.7
Total	37 18.2	26 12.8	24 11.8	20 9.9	13 6.4	83 40.9	203 100.0

(Chi-square = 25.6, 5 df,  $p < 0.01$ )

To see if this trend holds across all colonies, they are grouped into 'tribal' (i.e. Colleywobbles, Manyana and Mannyelanong) and non-tribal (i.e. the rest), and the distances have been grouped into 50 km categories. Comparing the two frequency distributions (Figure 6.19) it is clear that they differ markedly. Subjecting the counts to a contingency analysis (Table 6.12) reveals that the two distributions are indeed significantly different. This difference in patterns suggests that there are different ring-reporting processes operating around each type of colony. It is likely that the low return of ringed birds from tribal areas is caused by cultural and economic factors (see discussion in section 5.2.2 above).

Constructing a rose diagram (for the seven colonies with two, or more recoveries) of the directions in which recoveries are found (Figure 6.20) reveals that there are indeed great differences among the colonies. Roberts' Farm and Skeerpoort have a similar distribution pattern. Mannyelanong gives the impression that all but one of its recoveries are southwards while all those from Colleywobbles are from the west. Viewing these rose diagrams jointly with the map on which all the useful recoveries are shown (Figure 6.4 A) it is seen that most of the recoveries are to the western Transvaal, northern Cape, Karoo and the Eastern Cape, i.e. they are feeding into the putative nursery areas to be discussed below (section 6.4).

There are four colonies (i.e. Mannyelanong, Skeerpoort, Roberts' Farm and Colleywobbles) for which there are at least ten 'useful' recoveries (i.e. found at > 10 km) and these have been subjected to analysis using the circular statistics algorithm (Exhibit 6.1.1). Three of the sites show fairly high concentrations, but one (Roberts' Farm) shows a lower concentration (Table 6.13).

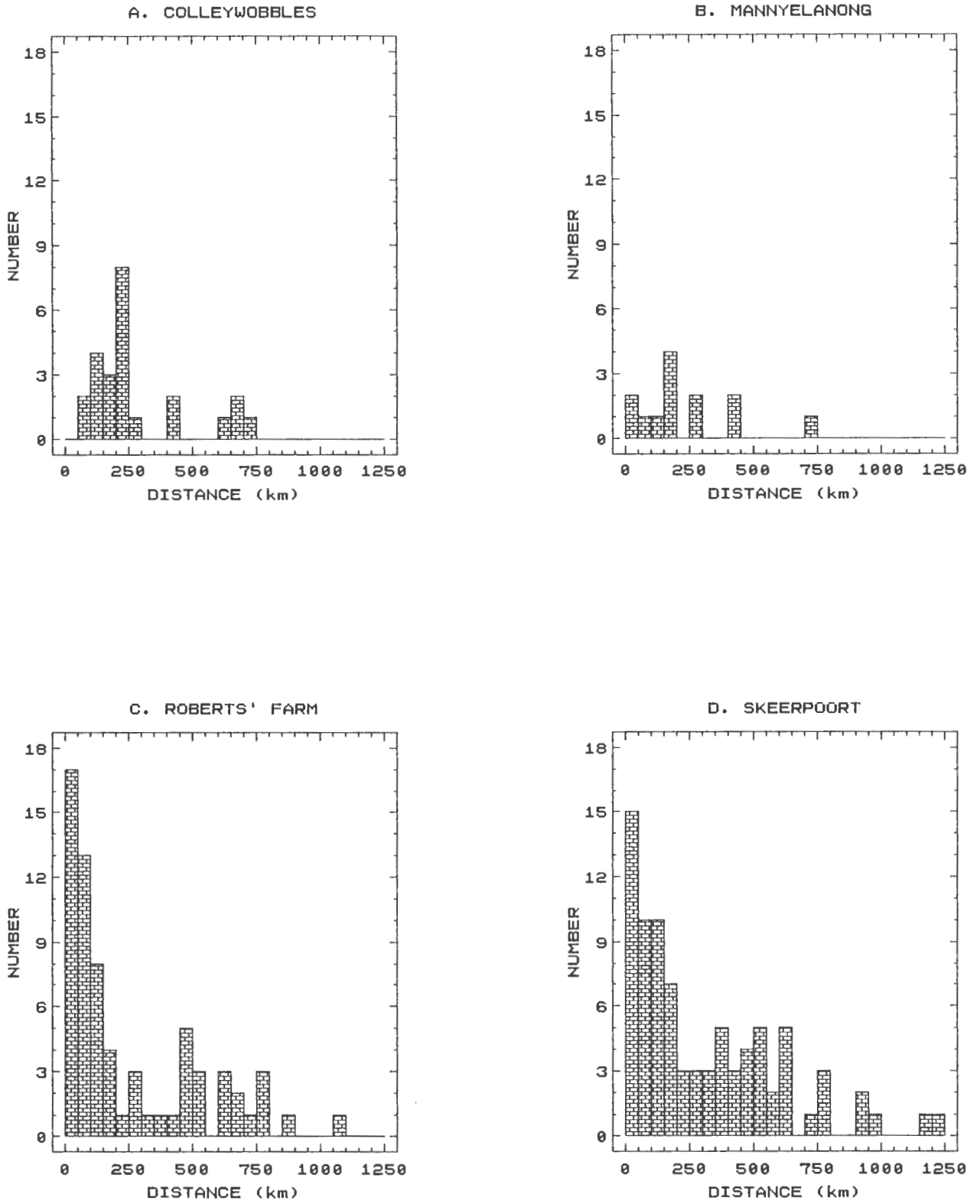


Figure 6.18 Distance travelled before being recovered by birds ringed at two 'tribal' colonies (A. Colleywobbles N=23 and B. Mannyelanong N=11) and at two 'non-tribal' colonies (C. Roberts' Farm N=64 and D. Skeerpoort N=78). Note that the 'tribal' colonies have few birds found near to the natal colony.

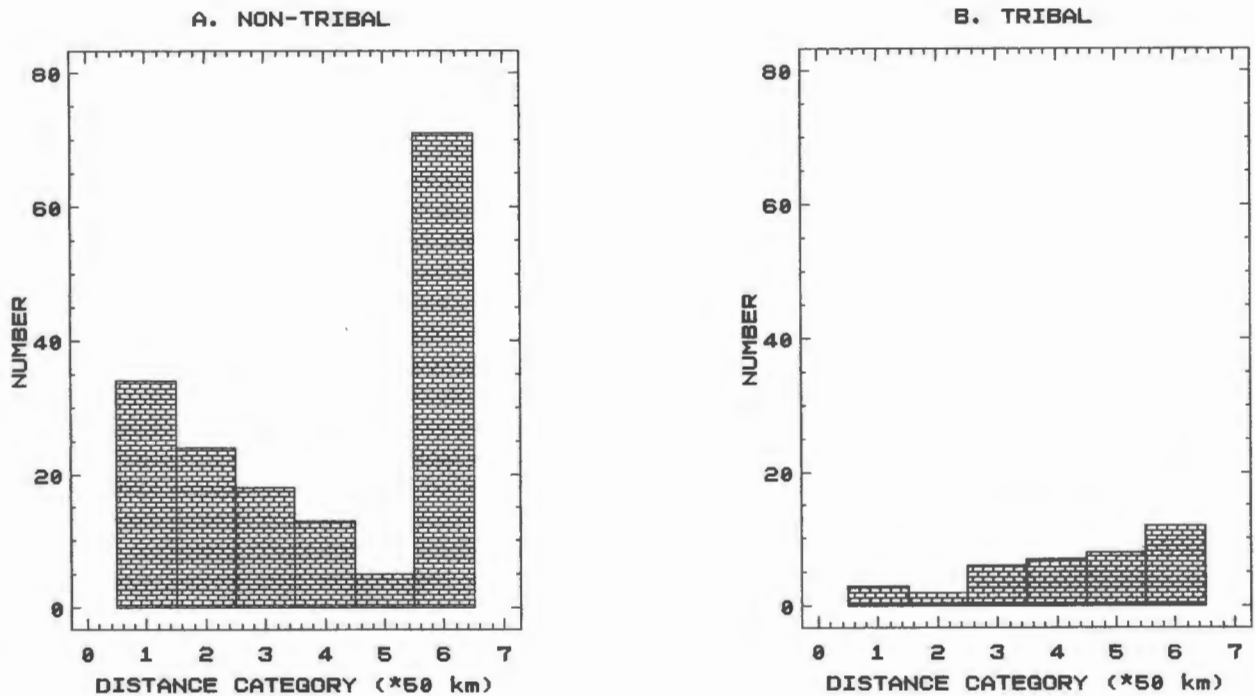


Figure 6.19 Distances travelled before being recovered. A. Birds ringed at 'non-tribal' colonies (i.e. Roberts' Farm, Skeerpoort, Kranzberg, Potberg, Manoutsa and Nooitgedacht; N=153). B. Birds ringed at 'tribal' colonies (i.e. Colleywobbles, Manyana and Mannyelanong; N=35).

There is much variation in the mean direction (Figure 6.21). The 95% confidence limits about the mean direction vary from a relatively narrow  $19^\circ$  for Skeerpoort to a slightly wider  $32^\circ$  for both Roberts' Farm and Colleywobbles while Mannyelanong has twice as wide a spread of  $67^\circ$ . None of the colonies exhibit a uniform distribution of recoveries, as measured by the Rayleigh or Wilke tests. The gap tests give a similar result, where applicable, except for  $G_s$  which indicates that Mannyelanong is uniform. This is an unexpected result as it is obvious that the Mannyelanong recoveries are concentrated in the south (Figure 6.20). It is suspected that this result may be a consequence of small sample size. The distribution of recoveries from Mannyelanong is adequately fitted by a unimodal von Mises distribution, Colleywobbles has a poor fit with  $10\% > p > 5\%$  but there is no adequate fit for Skeerpoort and Roberts' Farm. It is clear from the rose diagrams (Figure 6.20) that the distributions of recoveries from Roberts' Farm and Skeerpoort tend to be bimodal.

Table 6.13  
Summary of directional (i.e. circular) statistics for the four epochs.  
(Notation and symbols as per text and Exhibit 6.1.1)

		Mannyelanong	Skeerpoort Roberts' Farm	C/wobbles	
n	Sample size	11	81	64	23
R	Resultant vector sum	7.682	51.51	31.27	18.88
$R_{\text{bar}}$	Concentration	0.6984	0.636	0.4885	0.8207
Var	Circular variance of $R_{\text{bar}}$	0.3016	0.364	0.5115	0.1793
$\Phi_{\text{bar}}$	Mean direction	287.8	225.6	231.1	165.9
$W_{\text{bar}}$	Circular variance of $\Phi_{\text{bar}}$	0.03987	0.003681	0.009543	0.009718
$\Phi_l$	Lower 95% limit	254.2°	215.9°	215.3°	150.0°
$\Phi_u$	Lower 95% limit	321.4°	235.3°	246.8°	181.7°
$K_{\text{large}}$	von Mises distribution Concentration parameter Large sample estimate	1.779	1.61	1.216	2.928
$K_{\text{est 1}}$	M.L.E.	2.002	1.671	1.124	3.151
$K_{\text{est 2}}$	Improved estimator	1.861	1.655	1.102	3.049
$\Gamma$	Rayleigh test	10.73	65.52	30.55	30.98
	Probability of uniformity	0.004677	0.00000	0.00000	0.00000
$P_{\text{RAY}}$	Wilke estimate of p	0.002782	0.00000	0.00000	0.00000
$G_{\text{max}}$	Maximum gap	195.2°	64.44°	48.37°	248.4°
	Critical value	150.5°	?	?	88.0°
	Result:	cluster	-	-	cluster
$G_s$	Multiple gap test	329.8°	425.4°	429.7°	472.4°
	Critical value	341.0°	?	?	320.0°
	Result:	uniform	-	-	1+ clusters
U*	Watson-Stephen test	0.02858	0.1966	0.1836	0.1277
	Critical value	0.09888	0.09522	0.0819	0.1104
	Accept/reject von Mises	accept	reject	reject	reject

*Relationship of recoveries to current Cape Vulture Distribution.* The distribution of the Cape Vulture can be elucidated from the SABAP sightings data once they have been converted to a reporting rate, and simultaneously smoothed and interpolated (see section 3.2.5 above). It is interesting to relate the various classes of recovery to this smoothed reporting rate. This is done as follows. Each recovery is placed in the encompassing  $\frac{1}{4}^\circ * \frac{1}{4}^\circ$  grid cell and the smoothed (i.e. kriged) reporting rate corresponding to that cell is read out. Thus each recovery is associated with a (smoothed) reporting rate.

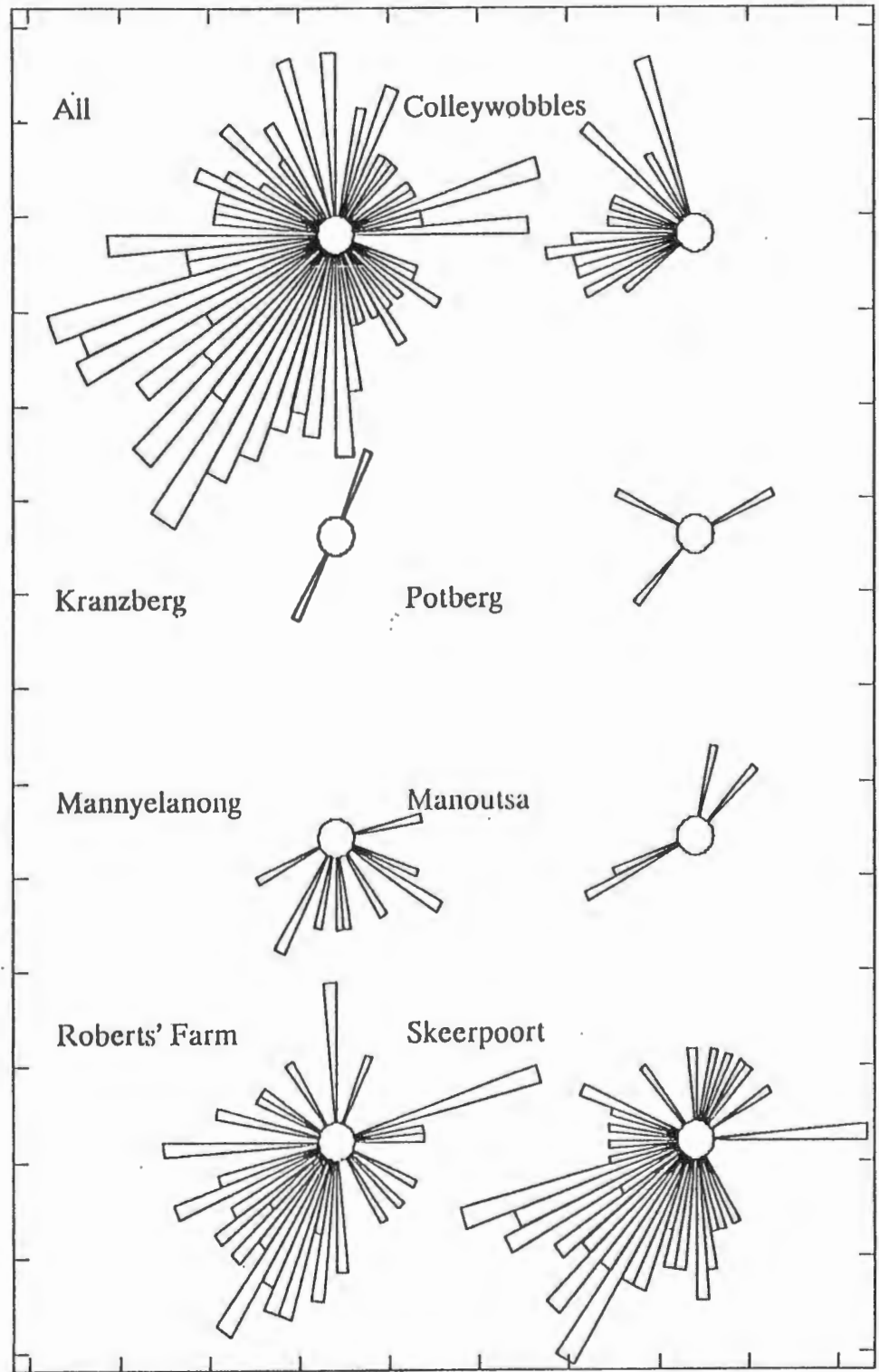


Figure 6.20 The number of recoveries at a given azimuth for all recoveries as well as for those seven colonies with two or more recoveries  $\geq 10$  km.

The smoothed SABAP reporting rates associated with the locality of each recovery may be brought together and summarized for each age-class (i.e. at death). It is seen (Figure 6.22) that the SABAP reporting rates of the regions where fledglings (age class 05) are found decrease through to the second year (age class 07) and thereafter increase strongly through the third and four+ year classes (age classes 08 and 09). This is consistent with the hypothesis that young birds drift away from their natal colonies in their first two years and then return in their third, or subsequent years. This suggests that the young birds move away from high concentrations of Cape Vultures and move outwards towards lower concentrations. Thereafter they return to those regions in which there are higher concentrations of Cape Vultures (mainly breeders).

By examining the reporting rate as a function of decade (Figure 6.23) it is seen that in the 1950s and 1960s many recoveries were from regions in which Cape Vultures are seldom seen these days (the SABAP data are from the mid-1980s). On the other hand recoveries from the 1980s are from regions with much higher reporting rates. This suggests that there has been a range contraction.<sup>4</sup>

*Number of recoveries at breeding colonies other than the natal colony.* There are a number of possible reasons for Cape Vultures to be found dead at colonies other than their natal colony.

- 1) If a bird ingests poison it may seek out the nearest colony at which to 'haul-out' and subsequently die there.
- 2) Birds may spend the years of their sub-adulthood exploring the wider environment (see section 6.4 below) and in the course of doing this die, as do other birds of similar age.
- 3) A sub-adult may have decided to settle at another colony and may then die there.

From an examination of the recoveries alone it is not possible to tease apart the above three explanations. However, it is useful to determine how many Cape Vultures have been found dead at colonies other than their natal colonies.

---

<sup>4</sup> It has been suggested (E. Danchin, pers. comm.) that this may be due low direct observation pressure in those areas where Cape Vultures are rare, and so they are overlooked. This is not so, SABAP organized many field trips to areas with poor coverage to make good gaps in observer distribution (J. Harrison, pers. comm.). In addition, D.G. Allen (pers. comm.) visited all those areas in which the Cape Vulture could be expected to be seen, on the basis of known colonies but which had poor SABAP coverage (e.g. northwestern Transvaal, Lesotho and Transkei). Thus the areas with low Cape Vulture reporting rates are in fact areas with low Cape Vulture densities.

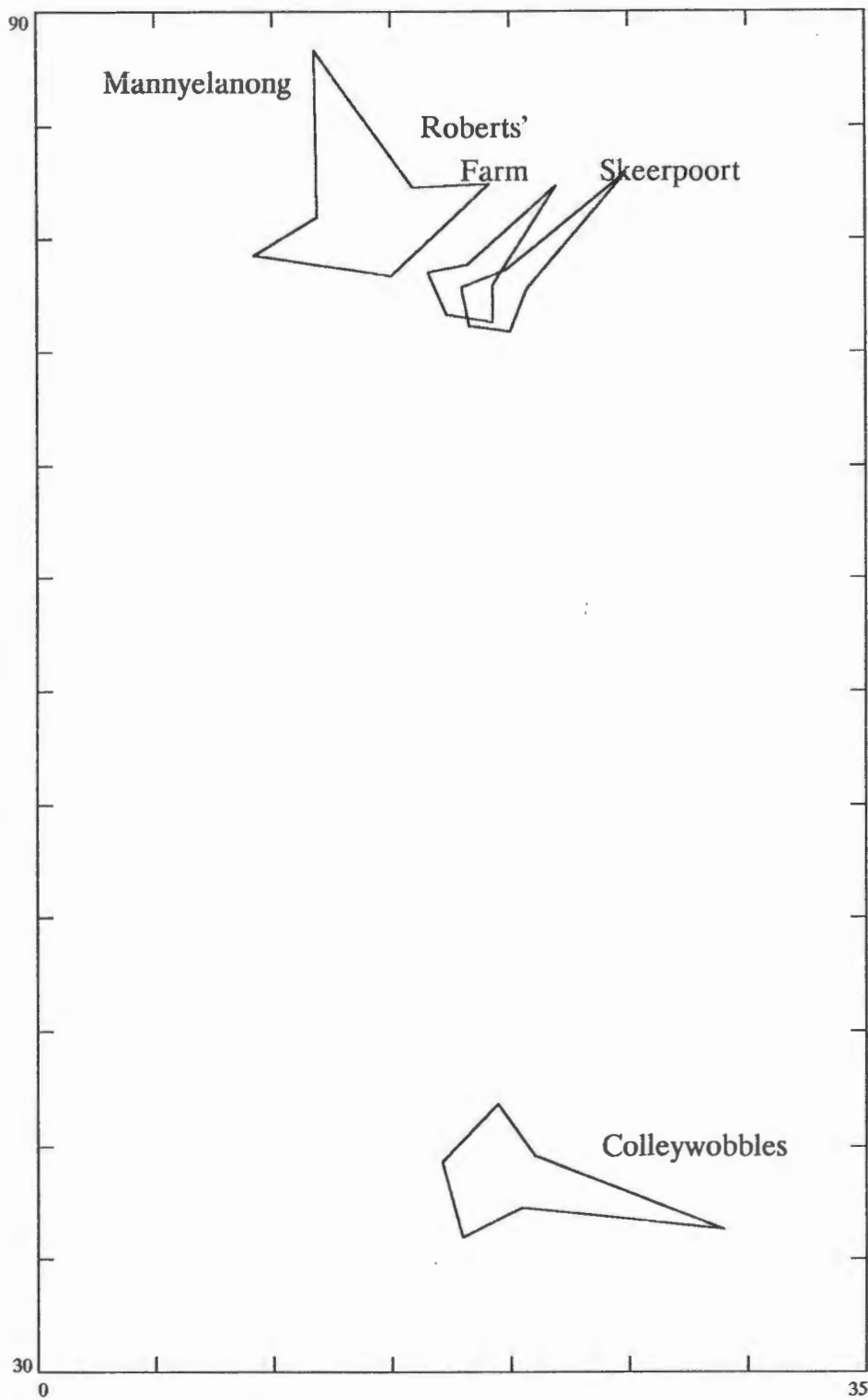


Figure 6.21 The mean vector of recoveries for each of four colonies for which there are at least 10 'useful' recoveries. The length of the mean vector indicates the concentration, the direction is the average direction of recoveries and the width of the vector head gives the 95% confidence limits of the mean angle.

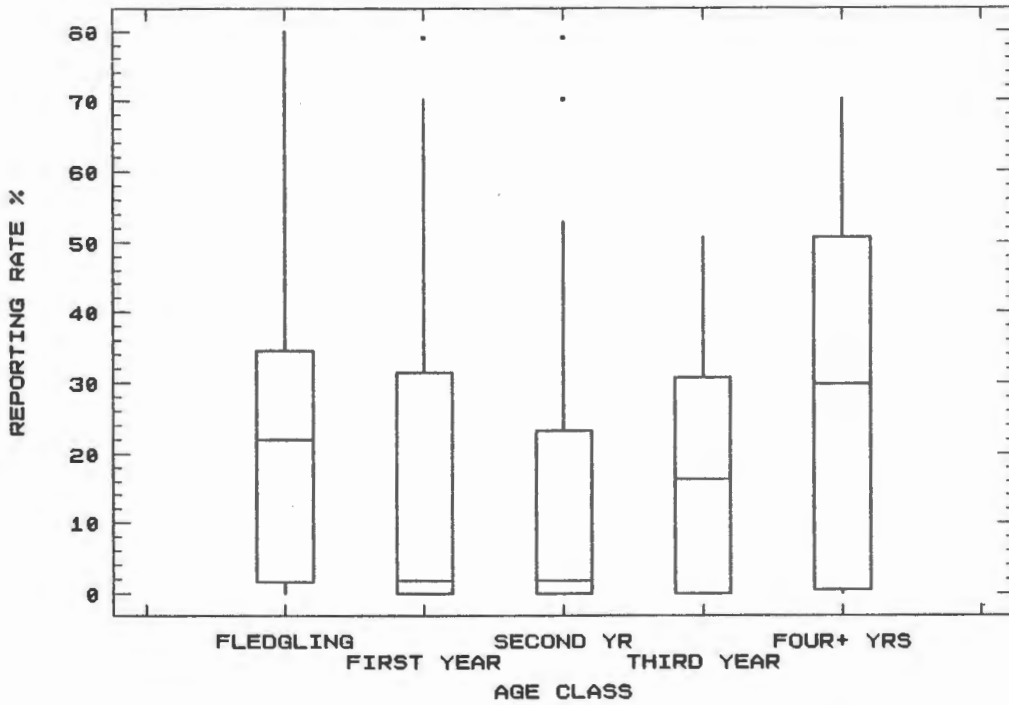


Figure 6.22 Variations in the SABAP reporting rate for each age class as portrayed by a multiple box-and-whisker plot.

Table 6.14  
 Number of birds ringed at one colony and found dead as fledglings at another colony. (Distance shown in km below No.)  
 Found dead

Natal	Avv 8	Ots 64	Rbt 72	Skr 79	Thb 83	Vmj 261
C/W 18						1 82
Pot 68	1 118					
Rbt 72		1 183		2 46		
Skr 79			1 46		1 421	

- Legend
- No. Colony Name
  - 8 Aasvogelvlei
  - 18 Colleywobbles
  - 33 Groothoek
  - 44 Mannyelanong
  - 45 Manoutsa
  - 64 Otse Hill
  - 68 Potberg
  - 72 Roberts' Farm
  - 79 Skeerpoort
  - 83 Thaba-Tseka
  - 261 Vumenjani

(Site numbers from Chapter 3)

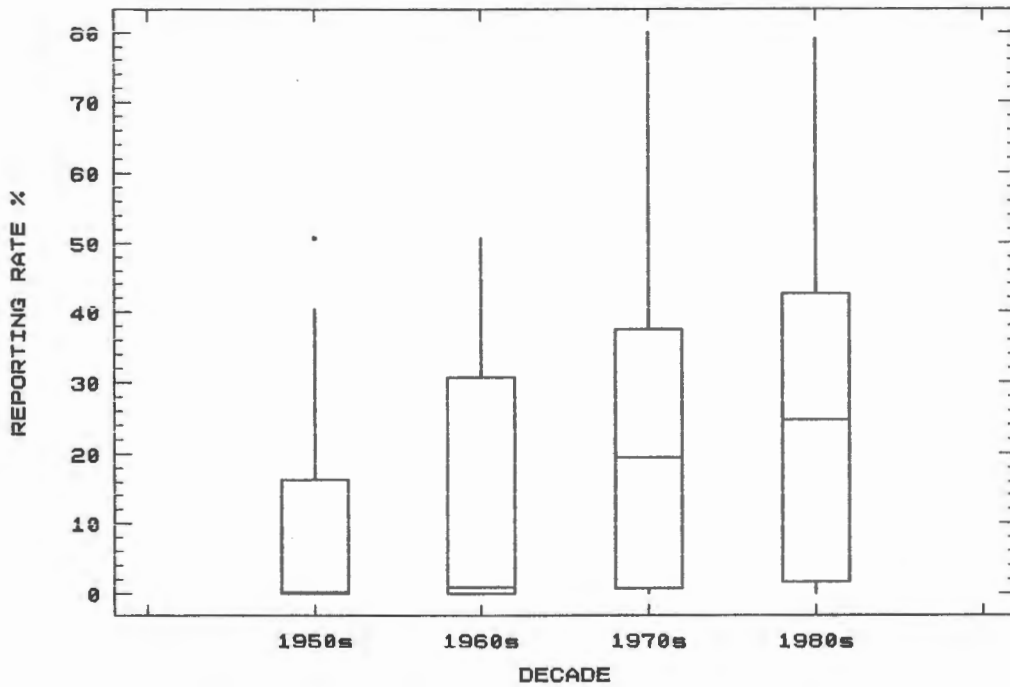


Figure 6.23 Variations in the SABAP reporting rate for each decade in which birds were ringed as portrayed by a multiple box-and-whisker plot.

Table 6.15  
Number of birds ringed at one colony and found dead as older first-years at another colony. (Distance shown in km below No.)  
Found dead

Natal	Rbt 72	Vmj 261
C/W 18		2 82
Skr 79	1 46	

Table 6.16  
Number of birds ringed at one colony and found dead as second-years at another colony. (Distance shown in km below No.)  
Found dead

Natal	Ghk 33	Mny 44
Mny 44	1 197	
Skr 79		1 213

Table 6.17

Number of birds ringed at one colony and found dead as Third-years at another colony. (Distance shown in km below No.)  
Found dead

Natal	Rbt 72	Skr 79	Vmj 261
C/W 18			1 82
Man 45	1 371		
Rbt 72		1 46	

Table 6.18

Number of birds ringed at one colony and found dead as Four+ years at another colony. (Distance shown in km below No.)  
Found dead

Natal	Rbt 72	Skr 79	Vmj 261
C/W 18			1 82
Mny 44	2 177		
Rbt 72		3 46	
Skr 79	4 46		

There were seven fledglings which died at a colony other than their natal colony (Table 6.14) and most of these had travelled a relatively short distance. Only three older first-years were recovered at another colony (Table 6.15), again having moved modest distances. Two second-years were recovered at a longer distance (Table 6.16) but this was not true for the three thirds years (Table 6.17). It is interesting to note that ten of the 4+ years old recoveries were found at non-natal colonies (Table 6.18), most of these fairly close by their natal colonies. In general terms, it appears that birds die further away from their natal colonies as time progresses during the first two to three years after fledging and thereafter die closer to their natal colonies. However, it is interesting to note that there are 10 instances of birds of breeding age (Table 6.18) found dead at colonies other than their natal colony. While this does not constitute proof of gene flow between sub-populations it does indicate that it is possible. In addition, it is noted that these birds are found at nearby colonies, only one of them is more than 100 km distant from the natal colony.

The distribution of recoveries in space and time has been shown to be a function of the age of the bird, the epoch in which it was ringed and the geographical location of its natal colony. In the next section the geographical location of various sources of unnatural mortality will be investigated.

Exhibit 6.1.1

Spatial Statistics: Directional Data

Stored as DIRECT.MCD

Defaults

ORIGIN := 1

Vectors & matrices count from 1

This material and formulae used for these analyses come from Upton, G.J.G & Fingleton, B. 1989.

Spatial data analysis by example. Wiley:Chichester

Input format of the data

Columns (1,2) = (A1,B1) = Start of the vector

Columns (3,4) = (A2,B2) = End of the vector

Sample

D := READPRN (RR09)

N := rows (D) No. of vectors

N = 23

i := 1..N Unpack matrix to vectors

A<sub>(i,1)</sub> := D<sub>(i,1)</sub> A<sub>(i,2)</sub> := D<sub>(i,3)</sub>

B<sub>(i,1)</sub> := D<sub>(i,2)</sub> B<sub>(i,2)</sub> := D<sub>(i,4)</sub>

i := 1..N Form the directional vectors

U<sub>i</sub> := A<sub>(i,2)</sub> - A<sub>(i,1)</sub> V<sub>i</sub> := B<sub>(i,2)</sub> - B<sub>(i,1)</sub>

i := 1..N Compute the length of each vector

L<sub>i</sub> :=  $\sqrt{[U_i]^2 + [V_i]^2}$

min (L) = 4.472

i := 1..N Compute the unit vectors

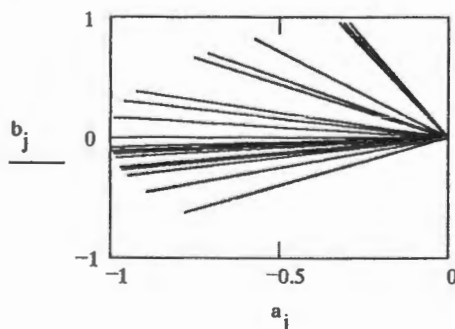
x<sub>i</sub> :=  $\frac{U_i}{L_i}$  y<sub>i</sub> :=  $\frac{V_i}{L_i}$

i := 1..N Construct the radial plot

a<sub>(2\*(i-1)+1)</sub> := 0 b<sub>(2\*(i-1)+1)</sub> := 0

j := 1..2\*N

a<sub>(2\*i)</sub> := x<sub>i</sub> b<sub>(2\*i)</sub> := y<sub>i</sub>



This is the radial-arm plot of all the vectors. Each vector is shown translated to the origin, but at its original length.

## Exhibit 6.1.1 (continued)

Spatial Statistics: Directional Data : Page 2

Summary Statistics: Mean direction

 $i := 1..N$  $X := \sum x$        $Y := \sum y$  $XX := \sum_i [x_i]^2$        $YY := \sum_i [y_i]^2$ 

U &amp; F (1989 p. 216)

 $X = -18.303$        $Y = 4.614$        $XX = 15.978$        $YY = 7.022$  $R := \sqrt{X^2 + Y^2}$ 

U &amp; F (1989 p. 218)

 $R = 18.875$ 

The length of the mean vector

 $R^2 = 356.276$ (Range is 0 = no preferred direction to  $N =$  all in same direction) $Rbar := \frac{R}{N}$ 

The concentration

 $Rbar = 0.821$  $Var := 1 - Rbar$       The circular variance $Var = 0.179$  $T := \text{angle}(X, Y)$       The direction of the mean vector  
(measured anticlockwise from the horizontal) $T = 2.895$  (in radians)       $T \cdot \frac{180}{p} = 165.851$  (in degrees)      - Relative to Horizontal $t := \text{if} \left[ T \geq \frac{p}{2}, T - \frac{p}{2}, T + 3 \cdot \frac{p}{2} \right]$  $t = 1.324$  (in radians)       $t \cdot \frac{180}{p} = 75.851$  (in degrees)      - Relative to True North $i := 1..N$  Compute the angle of each recovery       $a_i := \text{if} [L_i > 0, \text{angle} [U_i, V_i], 0]$  $G := \frac{\cos(2 \cdot T) \cdot \sum_i \cos[2 \cdot a_i] + (\sin(2 \cdot T)) \cdot \sum_i \sin[2 \cdot a_i]}{N}$  $G = 0.398$  $W := N \cdot \frac{[1 - G]}{[4 \cdot R^2]}$        $W = 0.01$       The circular variance of the angle T

Exhibit 6.1.1 (continued)

Spatial Statistics: Directional Data: Page 3

Confidence limits on the mean angle U & F (1989 p. 220)

$U_a := 1.96$  Upper limit of unit normal - 95%

$U_a \cdot \sqrt{(2 \cdot W)} = 0.273$  If this quantity is not less than unity then the mean angle is so ill-defined that it is not worth reporting!

$c := \text{asin} \left[ U_a \cdot \sqrt{(2 \cdot W)} \right]$   $c = 0.277$

$T_l := T - c$  Lower 95% limit  $T_l \cdot \frac{180}{p} = 149.993$  Relative to the horizontal  
(in radians) (in degrees)

$T_u := T + c$  Upper 95% limit  $T_u \cdot \frac{180}{p} = 181.709$  (in degrees)  
(in radians)

$u_l := \text{if} \left[ T_l \geq \frac{p}{2}, T_l - \frac{p}{2}, T_l + 3 \cdot \frac{p}{2} \right]$   $u_u := \text{if} \left[ T_u \geq \frac{p}{2}, T_u - \frac{p}{2}, T_u + 3 \cdot \frac{p}{2} \right]$

Limits relative to true north

$u_l = 1.047$  in radians Upper in degrees  $u_l \cdot \frac{180}{p} = 59.993$   
 $u_u = 1.601$  Lower in degrees  $u_u \cdot \frac{180}{p} = 91.709$

Circular Uniform Distribution U & F (1989 p. 226)

$\frac{\sqrt{N \cdot p}}{2} = 4.25$  This is the expected value of R under the assumption of a circular uniform distribution

$R = 18.875$  The actual value of R

The von Meise Circular Distribution U & F (1989 p. 229)

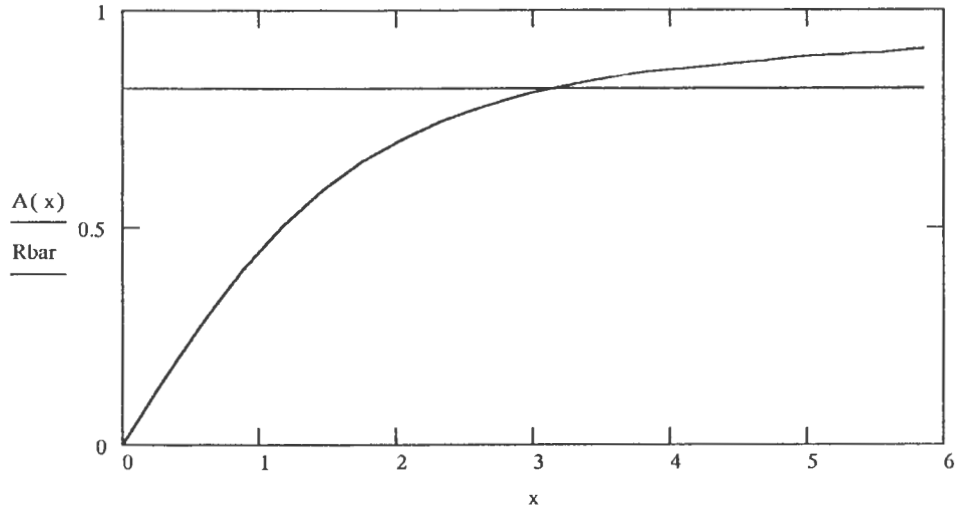
$k := \frac{\left[ 1 - \frac{1}{N} \right]}{(2 \cdot (1 - Rbar))} + \frac{\left[ Rbar - \frac{1}{N^2} \right]}{\left[ 4 \cdot Rbar \cdot \left[ 1 - \frac{1}{N} \right] \right]}$  Approximation to Kappa for large N  
 $k = 2.928$   $K1 := k$

$A[k] := \frac{I1[k]}{I0[k]}$  Ratio of two Bessel Functions

Exhibit 6.1.1 (continued)

Spatial Statistics: Directional Data: Page 4

$$x := 0, 2 \cdot \frac{k}{20} .. 2 \cdot k$$



$$k := \text{root} [ \text{Rbar} - A[k], k ] \quad k = 3.151$$

K2 := k                      Maximum likelihood estimate which may be biased

$N \cdot \text{Rbar}^2 = 15.49$                       If this quantity is < 1 then k is equal to 0

$$k := \text{root} [ N \cdot A[k] - R \cdot A[R \cdot k], k ]$$

K3 := k                      k = 3.049                      Improved estimate of k

m := T                      The mean is estimated from the preferred direction

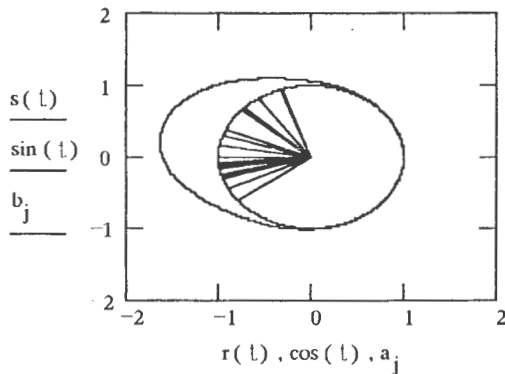
$$C_{vm} := \frac{1}{[2 \cdot p \cdot I_0[k]]} C_{vm} = 0.031 \quad \text{The constant in the distribution}$$

$$j := 1 .. 2 \cdot N$$

$$t := 0, \frac{p}{180} .. 2 \cdot p \quad f_{vm}[t] := C_{vm} \cdot \exp[ k \cdot \cos[t - m] ]$$

$$r[t] := [ f_{vm}[t] + 1 ] \cdot \cos[t]$$

$$s[t] := [ f_{vm}[t] + 1 ] \cdot \sin[t]$$



The von Mises distribution fitted to the data

Exhibit 6.1.1 (continued)

Spatial Statistics: Directional Data: Page 5

Testing for the Uniform Circular Distribution U & F (1989 p. 233)

Chi :=  $2 \cdot \frac{R^2}{N}$  Rayleigh's Chi-squared approximation with two degrees of freedom

Chi = 30.98 The 95% critical value is 5.991  
If  $X > 5.991$  then reject uniform distribution

Pray :=  $\exp \left[ \sqrt{1 + 4 \cdot N + 4 \cdot [N^2 - R^2]} - (1 + 2 \cdot N) \right]$

Pray =  $5.593 \cdot 10^{-9}$  The Wilke(1983) probability of getting a value  $> R$  from a random sample of size  $N$  from a uniform distribution

The Rayleigh test may only be used when the alternative is a unimodal distribution

Gap Test U & F (1989 p. 246)

Sort the data array  $b := \text{sort}[a]$

Compute the gaps

$i := 1 .. N - 1$

$G_i := b_{(i+1)} - b_i$  Upper value is  $G_N := b_1 - b_N + 2 \cdot p$

Check sum should be  $2 \cdot \pi$   $\sum G - 2 \cdot p = 0$

$G_m := \max(G)$   $G_m = 4.336$  in radians  $\frac{180}{p} \cdot G_m = 248.443$  in degrees

$P_4$
$P_5$
$P_6$
$P_7$
$P_8$
$P_9$
$P_{10}$
$P_{12}$
$P_{14}$
$P_{16}$
$P_{18}$
$P_{20}$
$P_{25}$
$P_{30}$

276
246
222
202
186
172
160
141
127
115
105
97
82
71

This table from U & F (1989 p. 247) gives the critical 5% values for the maximum gap. It is in degrees

Interpolate in between values 11 and 19

$j := 11, 13 .. 19$   
 $P_j := \left[ \frac{P_{(j-1)} + P_{(j+1)}}{2} \right]$

Interpolate between values 21 and 24

$j := 21 .. 24$   
 $P_j := \left[ \frac{P_{25} - P_{20}}{5} \cdot (j - 20) + P_{20} \right]$

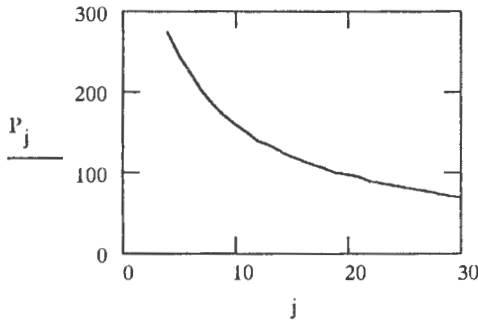
Exhibit 6.1.1 (continued)  
 Spatial Statistics: Directional Data: Page 6.

Interpolate between values 26 and 29

$$j := 26 .. 29$$

$$P_j := \left[ \frac{P_{30} - P_{25}}{5} \right] \cdot (j - 25) + P_{25}$$

$$j := 4 .. 30$$



Plot of critical value

Actual Gm is

$$G_m = 4.336 \text{ Radians}$$

$$\frac{180}{p} \cdot G_m = 248.443 \text{ degrees}$$

Critical value for N, given that  $3 < N < 31$

$$G_{crit} := \text{if} \left[ (4 \leq N) \cdot (N \leq 30), P_N, 0 \right]$$

$$G_{crit} = 88 \quad \text{in degrees}$$

$$\frac{p}{180} \cdot G_{crit} = 1.536 \quad \text{in radians}$$

To test for multiple modes use the following statistic

$$i := 1 .. N \quad G_s := \sum_i \left| G_i - 2 \cdot \frac{p}{N} \right| \quad G_s = 8.245 \text{ in radians} \quad \frac{180}{p} \cdot G_s = 472.409 \text{ in degrees}$$

$P_4$	
$P_5$	
$P_6$	
$P_7$	
$P_8$	
$P_9$	
$P_{10}$	
$P_{12}$	
$P_{14}$	
$P_{16}$	
$P_{18}$	
$P_{20}$	
$P_{25}$	
$P_{30}$	
$P_{40}$	
$P_{50}$	

This table from U & F (1989 p. 247) gives the critical 5% values for the maximum gap. It is in degrees

373
367
361
356
351
347
344
338
333
330
326
323
318
313
307
303

Interpolate in between values 11 and 19

$$j := 11, 13 .. 19$$

$$P_j := \left[ \frac{P_{(j-1)} + P_{(j+1)}}{2} \right]$$

Interpolate between values 21 and 24

$$j := 21 .. 24$$

$$P_j := \left[ \frac{P_{25} - P_{20}}{5} \right] \cdot (j - 20) + P_{20}$$

Exhibit 6.1.1 (continued)

Spatial Statistics: Directional Data: Page 7

Interpolate between values 26 and 29

$$j := 26 .. 29$$

$$P_j := \frac{P_{30} - P_{25}}{5} \cdot (j - 25) + P_{25}$$

Interpolate between values 31 and 39

$$j := 31 .. 39$$

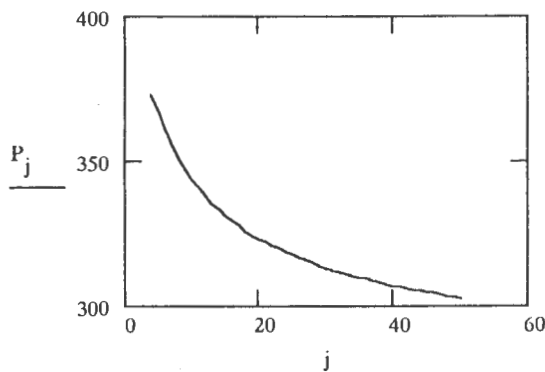
$$P_j := \frac{P_{40} - P_{30}}{10} \cdot (j - 30) + P_{30}$$

Interpolate between values 41 and 49

$$j := 41 .. 49$$

$$P_j := \frac{P_{50} - P_{40}}{10} \cdot (j - 40) + P_{40}$$

$$j := 4 .. 50$$



Plot of critical value

Actual Gs is

$$G_s = 8.245 \text{ Radians}$$

$$\frac{180}{\pi} \cdot G_s = 472.409$$

degrees

Critical value for N, given that  $3 < N < 51$

$$G_{crita} := \text{if} \left[ (4 \leq N) \cdot (N \leq 51), P_N, 0 \right] \quad G_{crita} = 320 \text{ in degrees}$$

If  $G_s > G_{crit}$  this then suggests that there is at least one cluster in the data.

Computation of the Watson-Stephens  $U^*$  test. U & F (1989 p. 260-264).

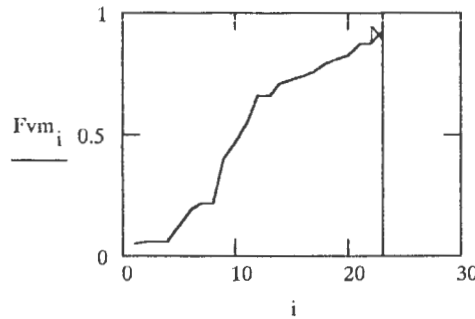
For each of the N points define the cumulative distribution as:

$$i := 1 .. N$$

$$F_{vm_i} := \int_0^{b_i} f_{vm}[t] dt$$

Exhibit 6.1.1 (continued)

Spatial Statistics: Directional Data: Page 8



Cumulative distribution of von Mises distribution for recovery data.

$$Fbar := \frac{\sum_i Fvm_i}{N} \quad Fbar = 0.51 \quad N \cdot Fbar = 11.735 \quad \text{The mean cumulative value}$$

$$Ua := \sum_i [Fvm_i]^2 \quad Ub := \frac{\sum_i [(2 \cdot i - 1) \cdot Fvm_i]}{N} \quad Uc := \left[ \frac{1}{3} - \left| Fbar - \frac{1}{2} \right|^2 \right] \cdot N$$

$$Ua = 8.196 \quad Ub = 15.732 \quad N \cdot Ub = 361.843 \quad Uc = 7.664$$

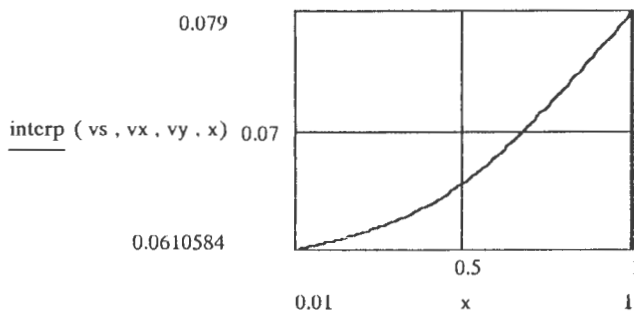
$$U2 := Ua - Ub + Uc \quad U2 = 0.128$$

$$Ustar := \left[ U2 - \frac{0.1}{N} + \frac{0.1}{N^2} \right] \cdot \left[ 1.0 + \frac{0.8}{N} \right] \quad Ustar = 0.128$$

$vx := \begin{bmatrix} 0 \\ .5 \\ 1 \\ 1.5 \\ 2 \\ 4 \\ 200 \end{bmatrix}$	$vy := \begin{bmatrix} 0.061 \\ 0.066 \\ 0.079 \\ 0.092 \\ 0.101 \\ 0.113 \\ 0.117 \end{bmatrix}$	$vs := \text{lspline}(vx, vy)$
--	---	--------------------------------

$x := 0.01, 0.02 \dots 1$

Build up the interpolation table for the 5% critical values from U & F (1989 p. 265)



Plot of 5% critical value as a function of x

$$k = 3.049$$

Critical:

$$Kcrit := \text{interp}[vs, vx, vy, k]$$

$$Kcrit = 0.11$$

If the actual value of Ustar is less than the critical value then there is no reason to reject the the von Mises distribution.

Exhibit 6.1.1 (continued)

Spatial Statistics: Directional Data: Page 9

Construction of the vector to represent the mean vector and its confidence range.

X-coordinate

Y-coordinate

$$Ar_{(1,1)} := 0$$

$$Ar_{(1,2)} := 0 \quad \text{Starting point}$$

$$Ar_{(2,1)} := 0.7 \cdot Rbar \cdot \cos \left[ \frac{(T + Tl)}{2} \right]$$

$$Ar_{(2,2)} := 0.7 \cdot Rbar \cdot \sin \left[ \frac{(T + Tl)}{2} \right]$$

$$Ar_{(3,1)} := 0.9 \cdot Rbar \cdot \cos (Tl)$$

$$Ar_{(3,2)} := 0.9 \cdot Rbar \cdot \sin (Tl)$$

$$Ar_{(4,1)} := Rbar \cdot \cos (T)$$

$$Ar_{(4,2)} := Rbar \cdot \sin (T) \text{Arrow's point}$$

$$Ar_{(5,1)} := 0.9 \cdot Rbar \cdot \cos (Tu)$$

$$Ar_{(5,2)} := 0.9 \cdot Rbar \cdot \sin (Tu)$$

$$Ar_{(6,1)} := 0.7 \cdot Rbar \cdot \cos \left[ \frac{(T + Tu)}{2} \right]$$

$$Ar_{(6,2)} := 0.7 \cdot Rbar \cdot \sin \left[ \frac{(T + Tu)}{2} \right]$$

$$Ar_{(7,1)} := 0$$

$$Ar_{(7,2)} := 0 \quad \text{Starting point}$$

i := 1..7



Output the Arrow vector

WRITEPRN (ARR09) := Ar

Exhibit 6.1.1 (continued)  
 Spatial Statistics: Directional Data: Page 10

Collect the composite results for output

Out :=	N R Rbar Var $T \cdot \frac{180}{p}$ W $Tl \cdot \frac{180}{p}$ $Tu \cdot \frac{180}{p}$ K1 K2 K3 Chi Pray $Gm \cdot \frac{180}{p}$ Gcrit $Gs \cdot \frac{180}{p}$ Gcrita Ustar Kcrit	Out =	23 18.875 0.821 0.179 165.851 0.01 149.993 181.709 2.928 3.151 3.049 30.98 $5.593 \cdot 10^{-9}$ 248.443 88 472.409 320 0.128 0.11	WRITEPRN ( SPATRR09 ) := Out
--------	---	-------	--	------------------------------

## 6.2 Location of unnatural mortality

Over twenty different proximate causes of mortality have been suggested by persons reporting the finding of a dead Cape Vulture (see section 5.3 and Table 5.15 above). The general ways in which unnatural mortality acts upon the Cape Vulture have already been discussed at some length (section 5.3 above). In my opinion, an advantage in restricting the discussion to useful recoveries (i.e. ringed birds found dead > 10 km from their natal colony and having survived to the year after ringing), as opposed to all recorded deaths, is that there will be fewer biases in the reporting of a single proximate cause. This is because the way dead birds are found at colonies is different to the ways in which dead birds are recovered by the general public (see extended discussion in section 5.2.2 above). It is known that more birds die from electrocution in the southwestern Transvaal than anywhere else (J.A. Ledger, pers. comm.). If this is indeed so then a potentially useful question to be considered here is the following.

Are there any meaningful spatial patterns to be seen in the distributions of recoveries of birds dying from different causes of unnatural mortality?

To investigate this question the causes of mortality of 189 'useful' recoveries are examined by grouping them into similar types of mortality (Table 6.19), and then plotting these out as both radial-arm plots and as point diagrams surrounded by minimum convex hulls. There are 106 recoveries (i.e. 56% of useful recoveries) which have been assessed as to their proximate cause of death. The major groupings of mortality chosen are *poison*, *electrocution*, *drowning*, *collision* and *shooting*.

It is possible to test if the spatial pattern of a given cause of death is the same as that for all useful recoveries. This has been done using the chi-squared test in the following fashion. A mesh of grid-cells is laid across the map of southern Africa and each recovery is allocated to the grid-cell into which it falls. A grid-cell with a side of 150 km is chosen as a compromise between too many recoveries per cell for a large cell and too few recoveries for a small cell. In addition, it was argued (see section 3.2.1 above) that a cell of this size (i.e. 150 km) is likely to be an adequate approximation to the daily foraging range. If there are  $p_i$  recoveries dying from poison in the  $i^{\text{th}}$  cell and  $r_i$  recoveries dying from other causes, then the total,  $t_i$  is given by  $t_i = p_i + r_i$ . If it is assumed that the spatial pattern of birds dying from poison is the same as from all other causes of death then the expected number,  $E[p_i]$  dying from poison is equal to  $t_i * (\sum p_j) / (\sum t_j)$ . The ratio  $(\sum p_j) / (\sum t_j)$  is the fraction of birds recovered poisoned and will be an estimate of the probability of poisoning in all grid-cells. The chi-squared test may be used to test the observed number poisoned in each grid-cell,  $p_i$  against the expected number,  $E[p_i]$ . In applying the chi-squared test it is important to keep the expected value above some minimum, usually taken to be 5. This is achieved by pooling classes with small expected values. If all the expected values are small then it is possible to use a lower minimum, 3 say (L.G. Underhill, pers. comm.).

Table 6.19

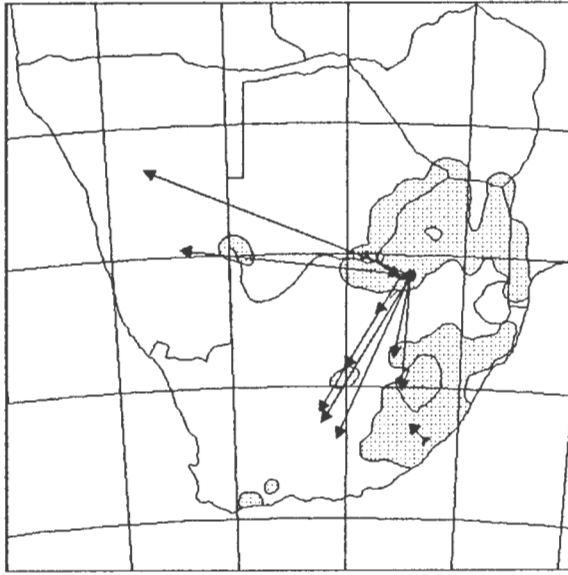
Number of 'useful' recoveries grouped by major proximate causes of mortality.

(A 'useful' recovery is a bird dying > 10km from its natal colony having survived into the year after ringing.)

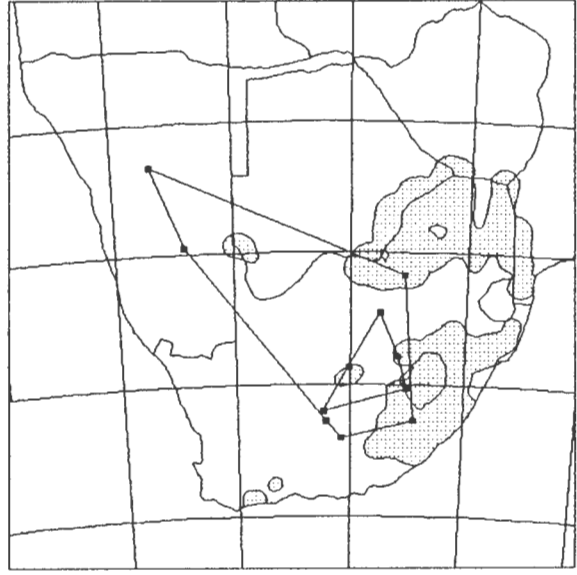
<b>Poison</b>	<i>Code</i>	<i>Meaning</i>	<i>Number</i>	
	?20	Possibly poisoned	3	
	020	Poisoned	6	
	021	Unintentionally poisoned	3	
			<i>Total</i>	<b>12</b>
<b>Electrocution</b>	<i>Code</i>	<i>Meaning</i>	<i>Number</i>	
	046	Electrocuted	36	
			<i>Total</i>	<b>36</b>
<b>Drowning</b>	<i>Code</i>	<i>Meaning</i>	<i>Number</i>	
	092	Drowned	22	
			<i>Total</i>	<b>22</b>
<b>Collision</b>	<i>Code</i>	<i>Meaning</i>	<i>Number</i>	
	061	Collided with a vehicle	1	
	067	Collided with a mast	1	
	068	Collided with a building	1	
	069	Flew into a fence	9	
			<i>Total</i>	<b>12</b>
<b>Shot</b>	<i>Code</i>	<i>Meaning</i>	<i>Number</i>	
	?09	Possibly caught and killed	1	
	009	Caught and killed	3	
	?10	Possibly shot	1	
	010	Shot	12	
	013	Shot to protect stock	3	
	043	Killed because it was ill	1	
	050	Killed by an unknown animal	2	
	052	Killed by dog	1	
			<i>Total</i>	<b>24</b>
<b>Other</b>	<i>Code</i>	<i>Meaning</i>	<i>Number</i>	
	005	Ring No. only reported	9	
	040	Illness	1	
	099	Cause unknown	72	
	753	Ring removed	1	
			<i>Total</i>	<b>83</b>

Each cause of death (i.e. *poison, electrocution, drowning, collision* and *shooting*) is investigated using two maps, the chi-squared test and is accompanied by a brief summary of observations.

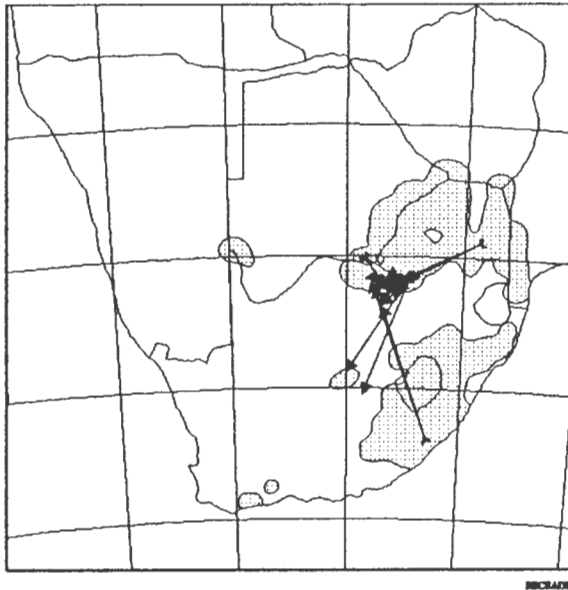
A) Poison



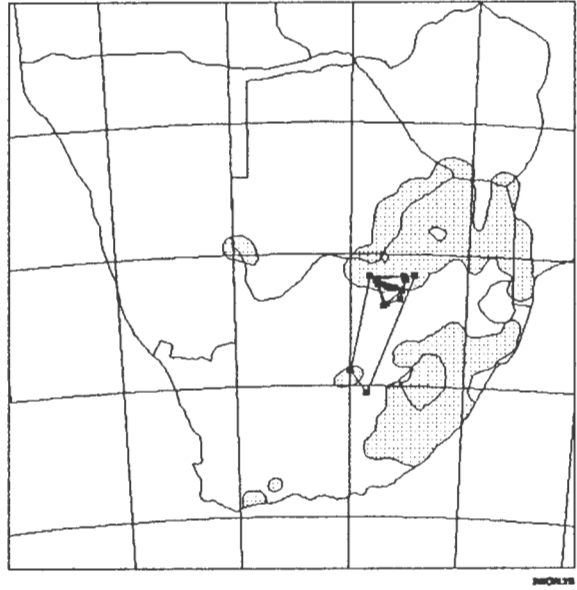
B) Poison



C) Electrocution



D) Electrocution



C\_24

Figure 6.24 Geographical distribution of recoveries where the reported cause of death is poison. A) Radial-arm display. B) Peeling of convex hulls. Geographical distribution of recoveries where the reported cause of death is electrocution. C) Radial-arm display. D) Peeling of convex hulls. The enclosed stippled region approximates the current Cape Vulture distribution.

Table 6.20

Comparison of spatial distributions by source of mortality.

<i>Cause of mortality</i>	<i>Chi-squared</i>	<i>d.f.</i>	<i>Prob.</i>	<i>Comment</i>
Poison	5.879	2	0.052	N.S. but mainly eastern Cape and Karoo
Electrocution	54.74	6	< 0.001	Highly concentrated
Drowning	15.758	4	< 0.01	More widespread
Collision	0.464	2	0.792	N.S.
Shooting	4.208	4	0.378	N.S.

## Notes:

- 1) The degrees of freedom vary between tests because of the pooling of classes necessary to ensure that the minimum expected value is  $\geq 3$ .

*Poison.* In addition to cases in which the use of poison is positively indicated, the category poison includes ‘possible poisoning’ and ‘unintentional poisoning’. The category ‘possible poisoning’ is used because poisoning is difficult to prove beyond doubt, although its signs are easily read. Most of the 12 birds poisoned (Table 6.19) came from the Magaliesberg colonies and Colleywobbles (Figure 6.24 A), with many having been poisoned far afield. Cape Vultures have been recovered after having been poisoned in the central part of their range, and also in the far west (Figure 6.24 B), but none have been found in the east. The spatial distribution of recoveries dying from poison is diffuse and largely outside the current range of the Cape Vulture but seems to be concentrated in the Karoo and eastern Cape (it is suggested that these are small-stock farming areas - P.J. Mundy, pers. comm.). The spatial distribution of poisoning is not statistically different from other causes of death, but only marginally so ( $p = 5.2\%$ , Table 6.20).

*Electrocution.* Birds can come from almost any colony to be electrocuted (Figure 6.24 C), with electrocution acting as a potential sink for the whole population. With the exception of two birds electrocuted in the Karoo, the major concentration of electrocutions (i.e. 34 birds, Table 6.19) is in the western Transvaal (Figure 6.24 D). The spatial distribution of electrocuted birds is tightly clustered, and largely within the current range of the Cape Vulture. The spatial distribution of electrocuted recoveries is very different from other causes ( $p < 0.1\%$ , Table 6.20). This tight cluster suggests that electrocution acts as a single point ‘sink’.

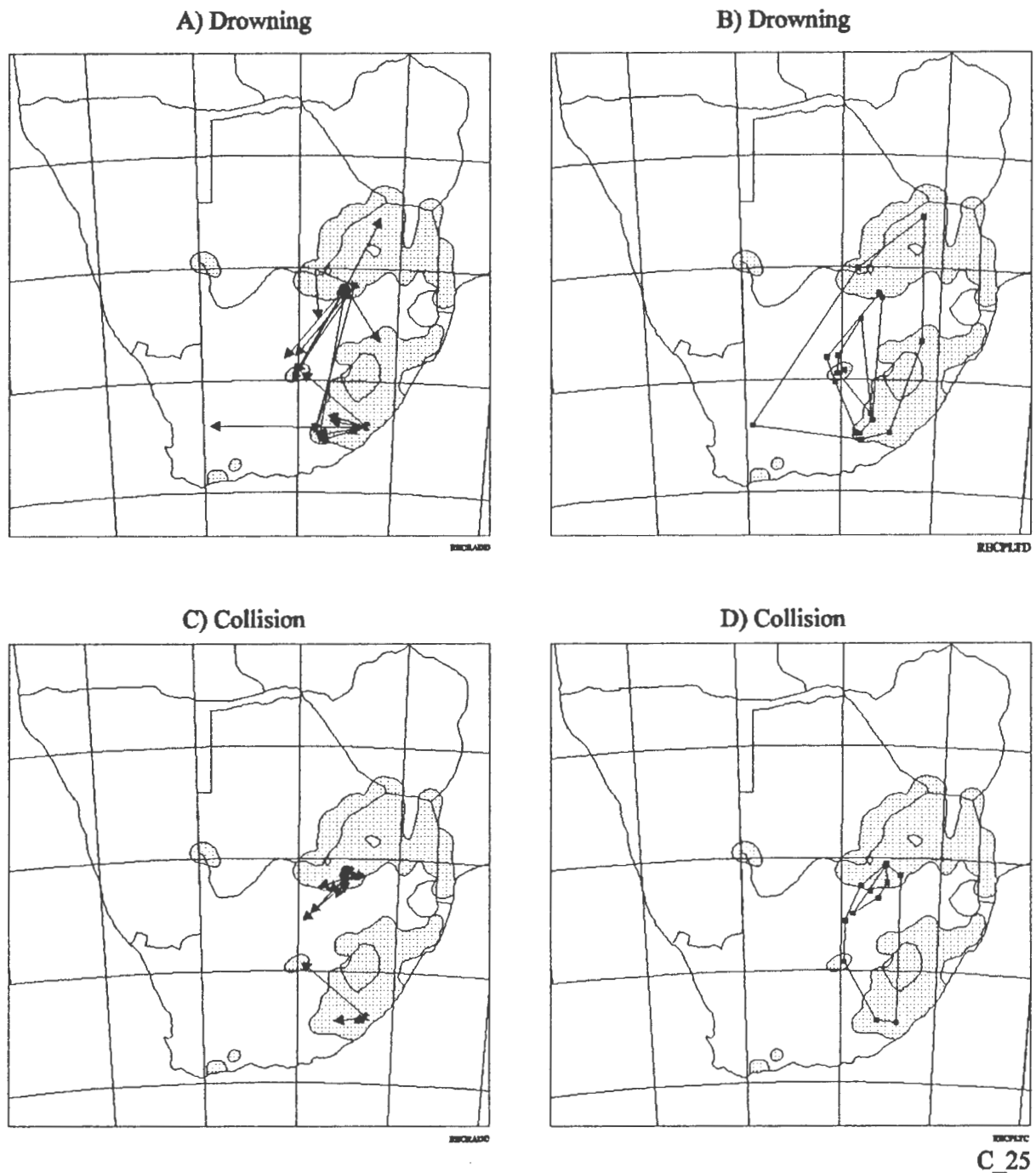


Figure 6.25 Geographical distribution of recoveries where the reported cause of death is drowning. A) Radial-arm display. B) Peeling of convex hulls. Geographical distribution of recoveries where the reported cause of death is collision. C) Radial-arm display. D) Peeling of convex hulls. The enclosed stippled region approximates the current Cape Vulture distribution.

*Drowned.* Birds can come from any colony to be drowned (Figure 6.25 A). Thus drowning is a source of mortality which may be acting as a sink on the whole population. In this respect drowning is similar to electrocution, but differs in that it occurs over almost the whole range of the species (Figure 6.25 B). Drownings tend to be concentrated in the eastern Cape, the Karoo and south-western Transvaal. The spatial distribution of recoveries reported drowned is diffuse with drownings happening at many sites spread over a wide area including many large farms devoted to livestock. This distribution differs from that of other causes ( $p < 1\%$ , Table 6.20) and appears to be 'flatter', i.e. less concentrated (compare with Figures 6.4 A and B above).

*Collision.* Four different types of collision are included in this category (Table 6.19) and it is my opinion that some informants may have confused flying into a fence, or wire with electrocution and *vice versa*. Twelve recoveries from the Magaliesberg colonies and from Colleywobbles are the only ones recorded as dying from collisions (Figure 6.25 C). The spatial distribution of collisions (Figure 6.25 D) is no different from that for other causes ( $p > 75\%$ , Table 6.20). This distribution is diffuse and collision happens at many sites.

*Shot.* The category *shot* includes all those forms of direct and indirect persecution visited upon vultures. Persecution acts in many ways and on birds that come from most of the colonies at which ringing has taken place (Figure 6.26 A). The overall spread of birds reported dead from shooting, and other forms of persecution, seems more widespread than any other cause (Figure 6.26 B) but is not different in the statistical sense ( $p > 35\%$ , Table 6.20). This great spread indicates a multiplicity of causes of unnatural mortality acting upon Cape Vultures.

Referring to the question posed at the start of this section, it is suggested that *poison* and *collision* act on a limited number of colonies while *electrocution*, *drowning* and *shooting* act on birds from all colonies. Thus these latter three sources of mortality all have the potential to be sinks into which the population's new productivity can flow. It is also noted that *electrocution* acts in a smaller region than any other cause of mortality and so may be easier to control and combat. On the other hand *drowning*, *collision* and *shooting* act over almost the species' entire range and so are likely to be harder to control. Some causes of mortality may be tackled directly, e.g. *electrocution* while other causes of unnatural mortality, e.g. *drownings* will have to be combated using indirect methods such as education.

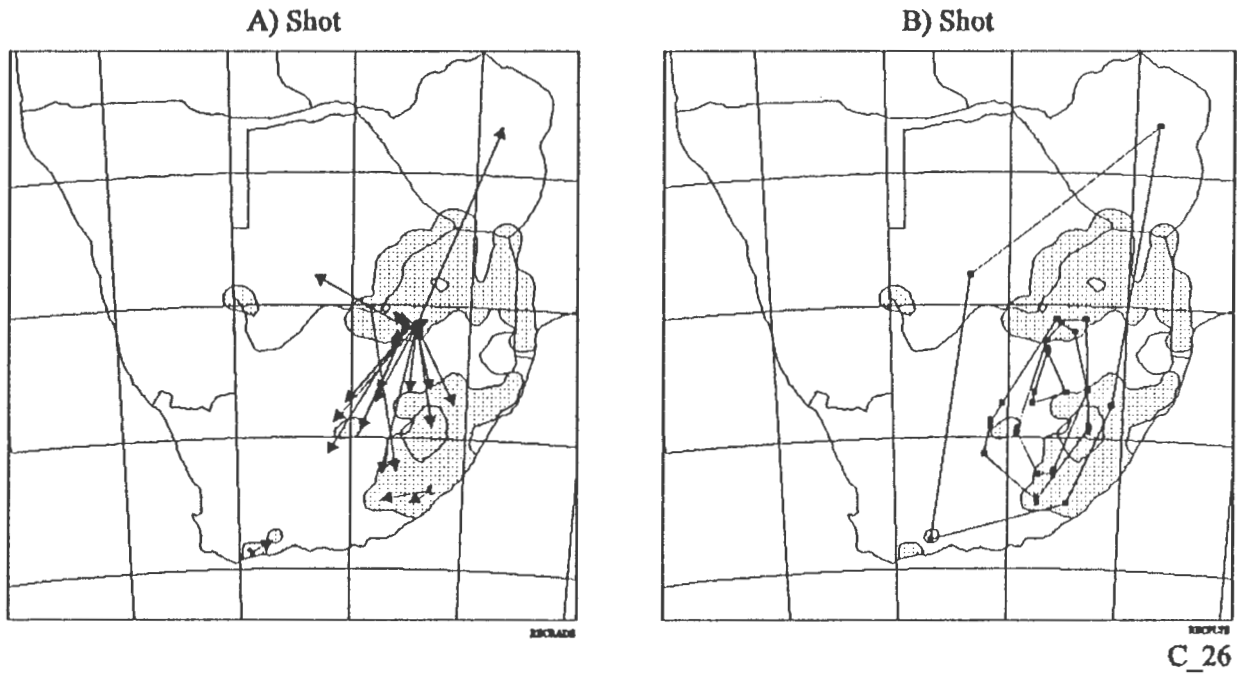
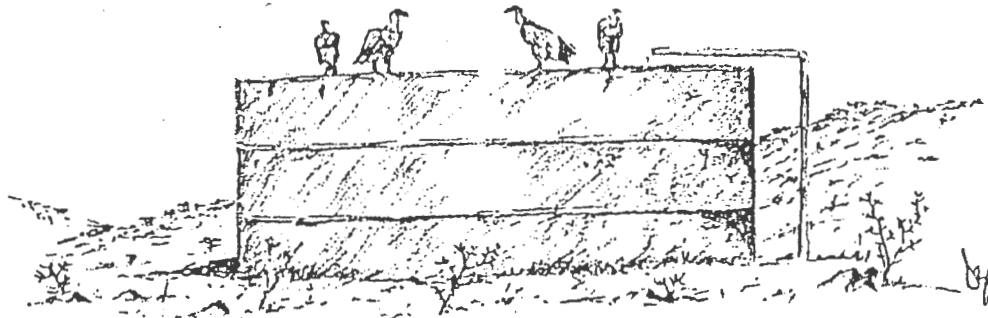


Figure 6.26 Geographical distribution of recoveries where the reported cause of death is shooting (including persecution). A) Radial-arm display. B) Peeling of convex hulls. The enclosed stippled region approximates the current Cape Vulture distribution.



### 6.3 Patterns of resightings

The resighting of a positively identifiable Cape Vulture, alive and well, contributes more information than the reporting of a dead bird (i.e. a recovery). A serious problem with a recovery (which does not apply to a resighting) is the suspicion that it died because it ventured into a region where it did not belong, so that its spatial position may not be representative of its cohort. Uniquely marked Cape Vultures have been resighted, and their positions in space and time recorded, as the result of four different processes.

- 1) *Carcass observations.* Observers have put out the carcass of a dead animal with the deliberate aim of attracting vultures, especially marked birds.
- 2) *Colony searches.* An observer repeatedly visits a colony with the primary aim of monitoring breeding activity, and incidentally records the presence of marked birds.
- 3) *Power-line searches.* As part of a wider project on electrocution, observations are made of vultures roosting on power pylons and marked birds are recorded.
- 4) *Incidental observations.* Observers are not searching for marked birds, but may notice them anyway. Examples are marked birds seen at a Lion-kill in a game reserve, and birds bathing at a water-hole overlooked by a game-viewing hide.

In most cases the colour-rings are recorded directly and the bird's identity is deduced from these. In some cases the identification is from colour photographs, or the ring number itself is read using a telescope. A grand total of 862 resightings had been collected by the end of 1990 and these yielded 678 useful records in which the species was definitely known to be Cape Vulture and the colour combination reported was sufficiently accurate to allocate the bird a ring number from a single ringing season at a single colony. Details of the original observations and the difficulties in making positive identifications are discussed elsewhere (Piper, Mundy & Mundy, in prep.). These 678 records came from 267 different individual birds who had their origins at nine colonies and two cannon-netting sessions (Table 6.21), and were resighted at 23 localities (Table 6.22).

The analysis of the resightings parallels that of the recoveries (see section 6.1 above) as far as it is relevant to do so. For those seven colonies with a reasonable number of resightings, a map is presented, with a commentary on the observed distribution of the resightings. This is followed by an examination of a radial-arm plot of all resightings and a peeling of convex-hulls of the resighting locations.

Table 6.21  
Sources of uniquely marked Cape Vultures subsequently resighted.

Coordinates south	east	Place	No. colour Ringed*	No. Resighted
		Unknown	3	2
21° 26'	32° 05'	Gonarezhou	11	2
21° 56'	29° 11'	Tuli Block	1	1
24° 26'	30° 45'	Manoutsa	363	10
24° 48'	25° 43'	Manyana	53	4
25° 00'	25° 43'	Baratani Hill	3	1
25° 03'	25° 45'	Mannyelanong	430	3
25° 03'	25° 47'	Mannyelanong (d) (included in the above)		9
25° 45'	27° 45'	Skeerpoort	1432	93
25° 51'	27° 18'	Roberts' Farm	1107	61
32° 15'	28° 36'	Colleywobbles	418	2
33° 52'	21° 40'	Aasvogelvlei	38	27
34° 22'	20° 33'	Potberg	133	52
			Total 4068	Total 267

(\* G-prefix rings only included in the total.)

*Colleywobbles.* Only two of the 418 Cape Vultures (resighting rate = 0.48%; 95% limits: 0% - 1.2%; Diem & Lentner 1970: 85-106) colour-ringed at this site have subsequently been resighted (Table 6.21). However, there is some doubt as to the validity of the identification of these two birds (Piper, Mundy & Mundy, in prep.). In addition, a colour-ringed sub-adult was seen, under poor light conditions, at the Mzikaba River colony in the mid-1980s (pers. obs.); this was probably a Colleywobbles bird. Given the wide distribution of the recoveries of Colleywobbles-ringed birds (Figure 6.1 A) it is not impossible that birds from this colony could have gone as far as is shown (Figure 6.27 A). Ringing at Colleywobbles began (see chapter 5) after the major resighting campaigns had ended in the Kimberley region (see Table 6.28 below and Figure 6.28 A). The northern Cape and Karoo is a likely place for Colleywobbles-ringed birds to be seen, based on the pattern of the recoveries (Figure 6.1 A). Thus it is possible that had the colour-ringing programme begun a decade earlier at Colleywobbles more birds from this colony would have been resighted in the Kimberley region.

*Mannyelanong.* Almost the same number of birds were ringed at Mannyelanong (i.e. 430 vs 418) as at Colleywobbles, but the number of resightings is much higher at 12 (Table 6.21); this yields a resighting rate of 2.8% (95% limits: 1.2% - 4.4%). The pattern of resightings (Figure 6.27 B) is similar to that of the recoveries (Figure 6.1 D), but not through as wide an arc.

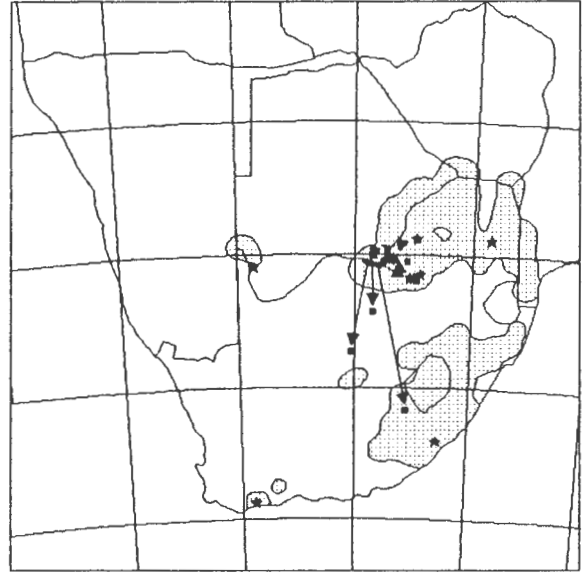
*Manyana.* There are four recoveries (Table 6.21) of the 53 birds ringed at Manyana (7.6%; 95% limits: 3.9% - 11.2%). Three of these birds were resighted in the Kimberley region while one bird was seen in the Kalahari Gemsbok National Park (Figure 6.27 C).

A) Colleywobbles



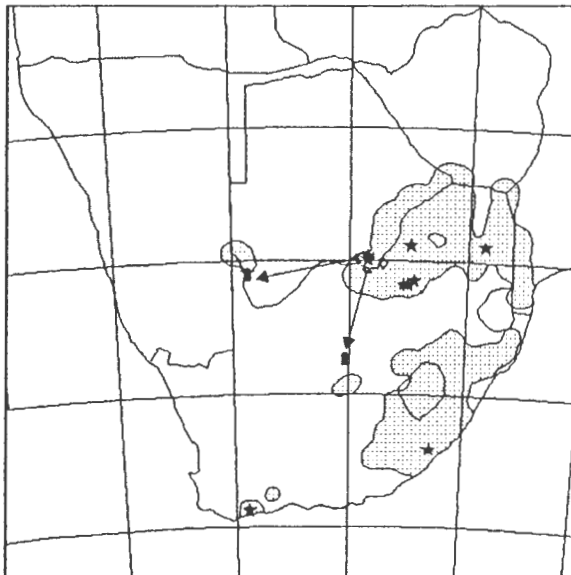
CWYRSM CDX

B) Mannyelanong



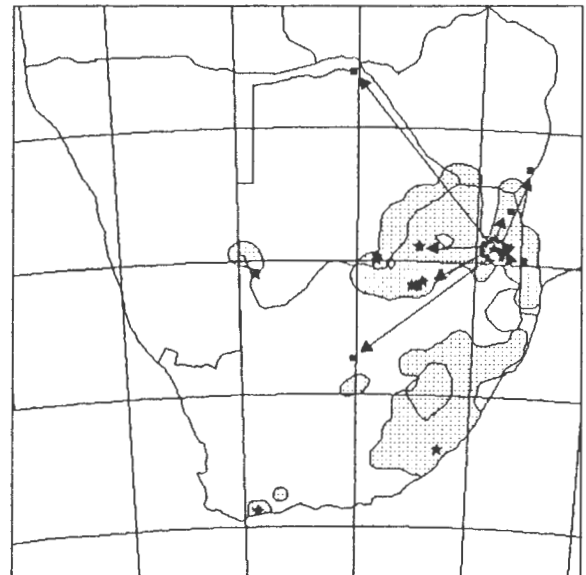
MPYRSM CDX

C) Manyana



MAPYRSM CDX

D) Manoutsa



MAPYRSM CDX

C\_27

Figure 6.27 Radial-arm display of primary resightings of birds ringed at A) Colleywobbles, B) Mannyelanong, C) Manyana and D) Manoutsa. Major ringing sites are shown as stars. The enclosed stippled region approximates the current Cape Culture distribution.

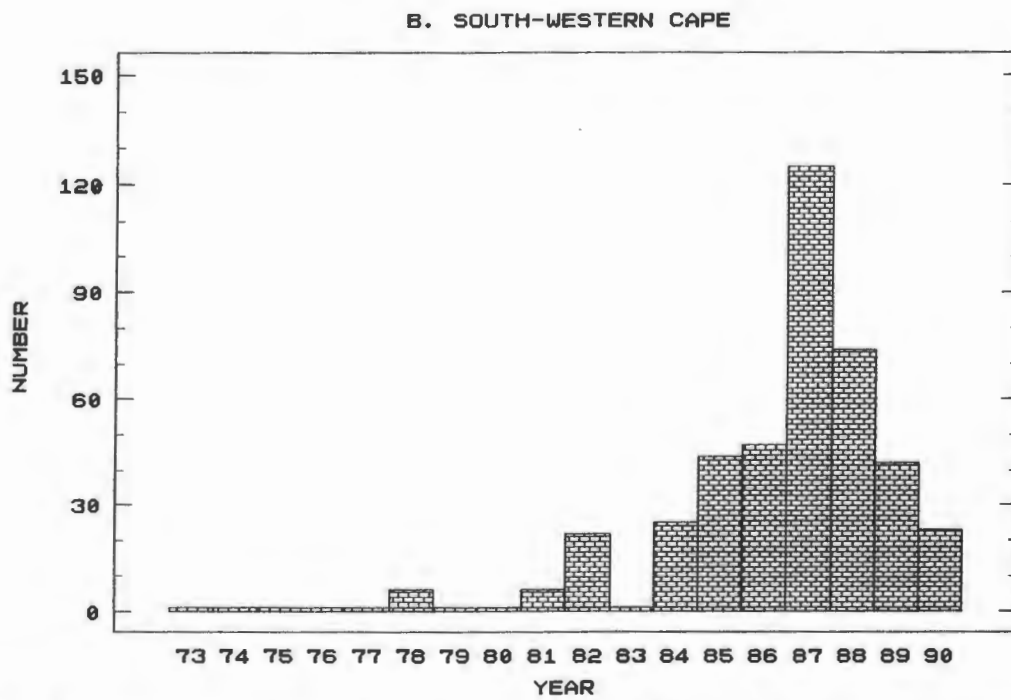
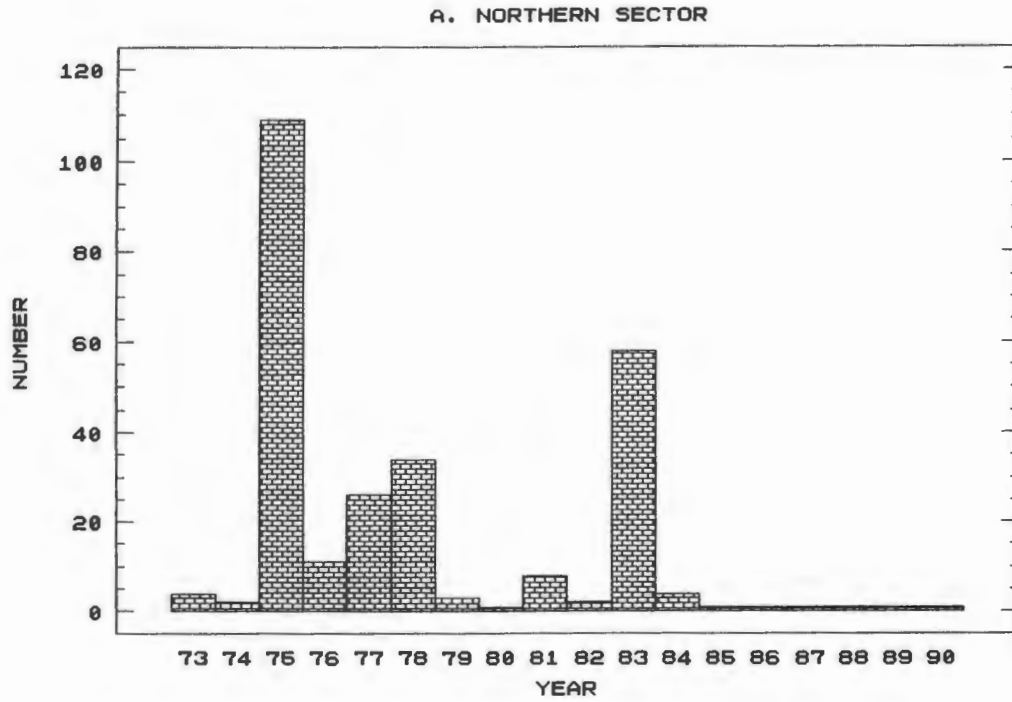


Figure 6.28 Number of resightings made in southern Africa. (A) Northern sector (including Transvaal, Botswana, Eastern Cape, OFS and Swaziland). (B) South-western Cape.

Table 6.22

Sites at which uniquely marked Cape Vultures have been resighted.

Coordinates		Place resighted	No. resighted
south	east		
17°55'	24°45'	Chobe, Ngoma Gate	1
21°26'	32°03'	Fishans, Gonarezhou	4
23°00'	31°20'	Babalala Picnic Site	1
24°20'	31°20'	Timbavati, eastern Transvaal	2
24°28'	27°36'	Kranzberg	3
24°50'	25°45'	Kannemeyer's Place	2
24°50'	32°00'	Vutome Dam.	1
25°01'	25°44'	Otse, Botswana	1
25°15'	27°11'	Pilanesberg	2
25°40'	20°40'	Kalahari, Nossob	1
25°45'	27°45'	Skeerpoort	22
25°47'	27°47'	Kommandonek Restaurant	35
25°51'	27°18'	Roberts' Farm	42
25°53'	27°18'	Roberts' Farm Restaurant	14
25°59'	27°37'	Spring Farm Restaurant	58
26°10'	31°55'	Hlane, Swaziland	1
27°10'	25°45'	Vaalbosfontein	2
28°15'	28°26'	Franshoek Farm, O.F.S.	1
28°39'	24°50'	Dronfield Ranch	50
28°41'	26°47'	Dronfield Ranch	2
28°50'	24°50'	Benfontein	19
30°51'	27°14'	Karringmelkspruit	2
33°44'	21°43'	Platrug	14
33°52'	21°40'	Aasvogelvlei	25
34°22'	20°33'	Potberg	373

Total 678

*Manoutsa.* The ten resightings from the 363 Cape Vultures (Table 6.21) ringed at Manoutsa (2.75%; 95% limits: 1.0% - 4.5%) show an exceptionally wide distribution (Figure 6.27 D), with birds being seen much wider afield than the recoveries (Figure 6.2 A). In the main, these birds were reported by ornithologically aware travellers in the game parks of the eastern Transvaal, southern Zimbabwe and northern Botswana (Piper, Mundy & Mundy, in prep.).

*Potberg and Aasvogelvlei.* Although only 133 birds have been ringed at Potberg, an exceptionally high number, 52 (39.1%; 95% limits: 34.9% - 43.3%) have been resighted (Table 6.21), all of them in the southwestern Cape (Figure 6.29 A). At Aasvogelvlei a total of 27 birds have been resighted out of 38 ringed (Table 6.21). This gives the highest resighting rate (71.1%; 95% limits: 54.1% - 86.1%) of any colony. The distribution of resightings is, like those of Potberg, confined to the southwestern Cape (Figure 6.29 A) as are the recoveries from these two colonies (Figure 6.2 C).

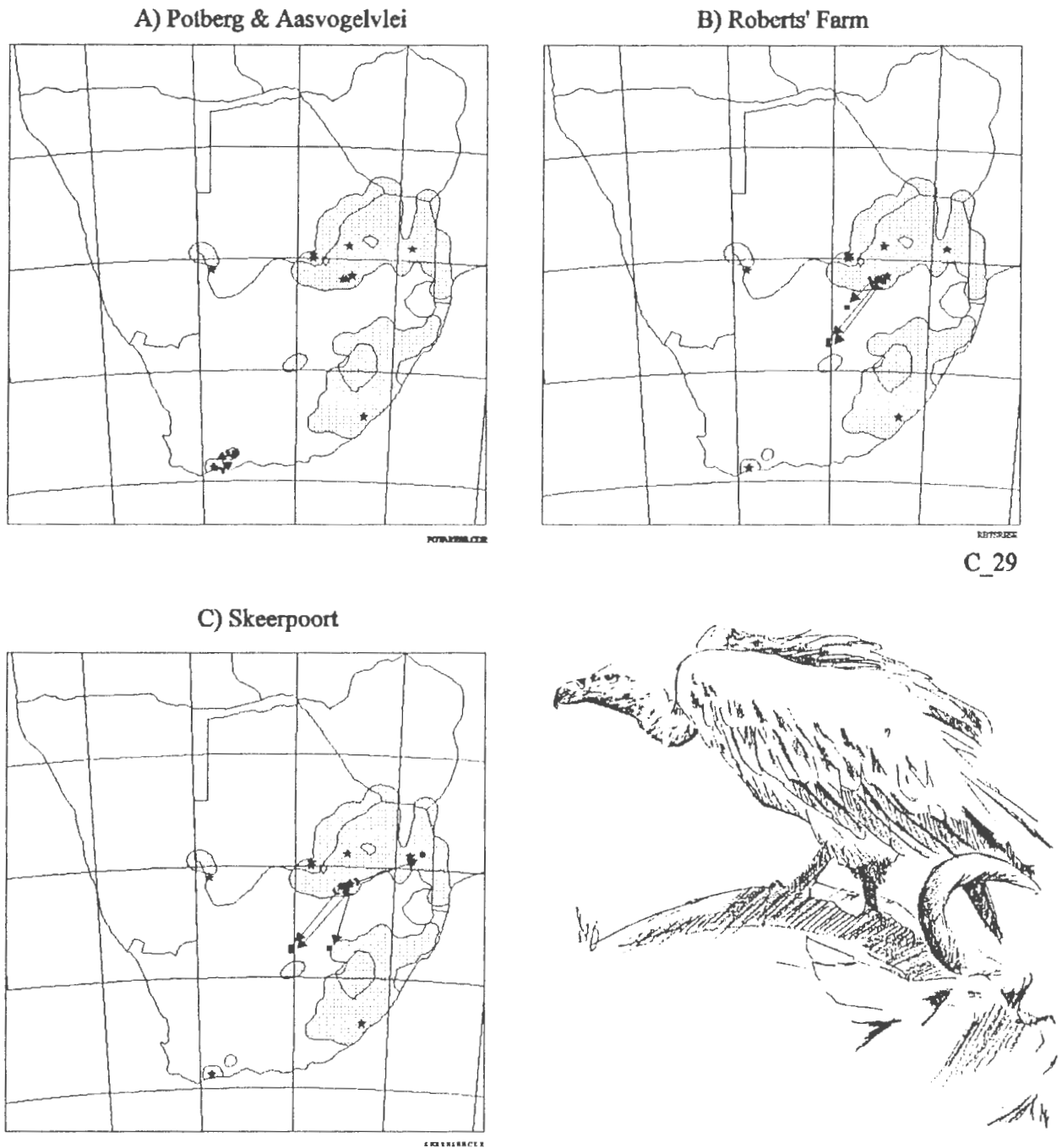


Figure 6.29 Radial-arm display of primary resightings of birds ringed at A) Potberg and Aasvogelvlei, B) Roberts' Farm and C) Skeerpoort. Major ringing sites are shown as stars. The enclosed stippled region approximates the current Cape Vulture distribution.

Table 6.23

Number of marked Cape Vultures moving from the place of ringing to that of first resighting.

From colony	Ringed		To place	First resighting	No.	
		Unknown	34°22'	20°33'	Potberg Restaurant	2
21°26'	32°05'	Gonarezhou (b)	24°50'	25°45'	Kannemeyer's Place	1
21°26'	32°05'	Gonarezhou (b)	25°59'	27°37'	Spring Farm Restaurant	1
21°56'	29°11'	Tuli Block	25°47'	27°47'	Kommandonek Restaurant	1
24°26'	30°45'	Manoutsa (b)	17°55'	24°45'	Chobe, Ngoma Gate	1
24°26'	30°45'	Manoutsa (b)	21°26'	32°03'	Gonarezhou	3
24°26'	30°45'	Manoutsa (b)	23°00'	31°20'	Babalala Picnic Site	1
24°26'	30°45'	Manoutsa (b)	24°20'	31°20'	Timbavati	1
24°26'	30°45'	Manoutsa (b)	24°28'	27°36'	Kranzberg	1
24°26'	30°45'	Manoutsa (b)	24°50'	32°00'	Vutome Dam.	1
24°26'	30°45'	Manoutsa (b)	25°59'	27°37'	Spring Farm Restaurant	1
24°26'	30°45'	Manoutsa (b)	28°39'	24°50'	Kimberley Water trough	1
24°48'	25°43'	Manyana (b)	25°40'	20°40'	Kalahari, Nossob	1
24°48'	25°43'	Manyana (b)	28°39'	24°50'	Dronfield, Pylon	2
24°48'	25°43'	Manyana (b)	28°50'	24°50'	Benfontein	1
25°00'	25°43'	Baratani Hill (b)	28°39'	24°50'	Kimberley, Pylon	1
25°03'	25°45'	Mannyelanong	25°59'	27°37'	Spring Farm Restaurant	1
25°03'	25°45'	Mannyelanong	28°39'	24°50'	Kimberley Water Trough	2
25°03'	25°47'	Mannyelanong (d)	24°28'	27°36'	Kranzberg	2
25°03'	25°47'	Mannyelanong (d)	24°50'	25°45'	Kannemeyer's Place	1
25°03'	25°47'	Mannyelanong (d)	25°01'	25°44'	Otse, Botswana	1
25°03'	25°47'	Mannyelanong (d)	25°15'	27°11'	Pilanesberg	1
25°03'	25°47'	Mannyelanong (d)	25°59'	27°37'	Spring Farm Restaurant	1
25°03'	25°47'	Mannyelanong (d)	27°10'	25°45'	Vaalbosfontein	1
25°03'	25°47'	Mannyelanong (d)	30°51'	27°14'	Karringmelkspruit	2
25°45'	27°45'	Skeerpoort	24°20'	31°20'	Timbavati	1
25°45'	27°45'	Skeerpoort	25°45'	27°45'	Skeerpoort	19
25°45'	27°45'	Skeerpoort	25°47'	27°47'	Kommandonek Restaurant	13
25°45'	27°45'	Skeerpoort	25°51'	27°18'	Roberts' Farm	1
25°45'	27°45'	Skeerpoort	25°53'	27°18'	Roberts' Farm Restaurant	10
25°45'	27°45'	Skeerpoort	25°59'	27°37'	Spring Farm Restaurant	30
25°45'	27°45'	Skeerpoort	28°39'	24°50'	Dronfield Ranch	12
25°45'	27°45'	Skeerpoort	28°41'	26°47'	Dronfield Ranch	1
25°45'	27°45'	Skeerpoort	28°50'	24°50'	Benfontein	6
25°51'	27°18'	Roberts' Farm	25°45'	27°45'	Skeerpoort	1
25°51'	27°18'	Roberts' Farm	25°47'	27°47'	Kommandonek Restaurant	10
25°51'	27°18'	Roberts' Farm	25°51'	27°18'	Roberts' Farm	24
25°51'	27°18'	Roberts' Farm	25°53'	27°18'	Roberts' Farm Restaurant	4
25°51'	27°18'	Roberts' Farm	25°59'	27°37'	Spring Farm Restaurant	4
25°51'	27°18'	Roberts' Farm	27°10'	25°45'	Vaalbosfontein	1
25°51'	27°18'	Roberts' Farm	28°39'	24°50'	Kimberley Water Trough	15
25°51'	27°18'	Roberts' Farm	28°50'	24°50'	Benfontein	1
25°51'	27°18'	Roberts' Farm	28°50'	24°50'	Benfontein	1
32°15'	28°36'	Colleywobbles (c)	21°26'	32°03'	Fishans, Gonarezhou	1
32°15'	28°36'	Colleywobbles (c)	34°22'	20°33'	Potberg	1
33°52'	21°40'	Aasvogelvlei	33°44'	21°43'	Platrug	2
33°52'	21°40'	Aasvogelvlei	33°52'	21°40'	Aasvogelvlei	10

Table 6.23 (continued)

Number of marked Cape Vultures moving from the place of ringing to that of first resighting.

From colony	Ringed	To place	First resighting	No.
33°52' 21°40'	Aasvogelvlei	34°22' 20°33'	Potberg Restaurant	15
34°22' 20°33'	Potberg	33°52' 21°40'	Aasvogelvlei	1
34°22' 20°33'	Potberg	34°22' 20°33'	Potberg	51

*Roberts' Farm.* The second-highest number of birds to be colour-ringed at any colony (i.e. 1107) were handled at Roberts' Farm (Table 6.21) and these have resulted in 61 individuals being resighted subsequently (5.51%; 95% limits 4.8% - 6.2%). The spread of places at which these resightings have occurred (Figure 6.29 B) is conspicuously narrower than those at which birds have been recovered (Figure 6.2 D).

*Skeerpoort.* A total of 1432 Cape Vultures were colour-ringed at Skeerpoort (Table 6.21), the most at any colony, and of these 93 were subsequently resighted (6.50%; limits: 5.2% - 7.8%). With the exception of one resighted at Timbavati, all those resighted (Figure 6.29 C) fall well within the range shown by the recoveries (Figure 6.3), though not as far afield.

#### *Composite primary sightings.*

All the primary resightings (i.e. the first resighting after ringing) have been summarized (Table 6.23) and have also been plotted as radial-arms on a single map (Figure 6.30 A) from which it may be seen that the spread is not as wide as that resulting from plotting the recoveries (Figure 6.4 A), especially in the eastern Cape. By enclosing all the primary resightings in a minimum convex hull and then peeling off one hull at a time (Figure 6.30 B) it is seen that the central core of primary resightings is in the south-central Transvaal, slightly to the north-west of the 'core' of the recoveries (Figure 6.4 B).

#### *Composite secondary resightings*

The secondary resightings (i.e. from the place of first, or subsequent resighting to the next resighting) have been summarized (Table 6.24) and show a much smaller range (Figure 6.30 C) than the primary resightings (Figure 6.30 A). Enclosing the secondary resightings in a convex hull (Figure 6.30 D) reveals a startlingly different pattern when compared with a similar process applied to the primary resightings (Figure 6.30 B). Because of the high number of resightings in the south-western Cape the convex hull, at all peelings, is pulled to the south-west. An interesting movement is that of a Skeerpoort bird which went to the Kimberley region and thence to Swaziland.

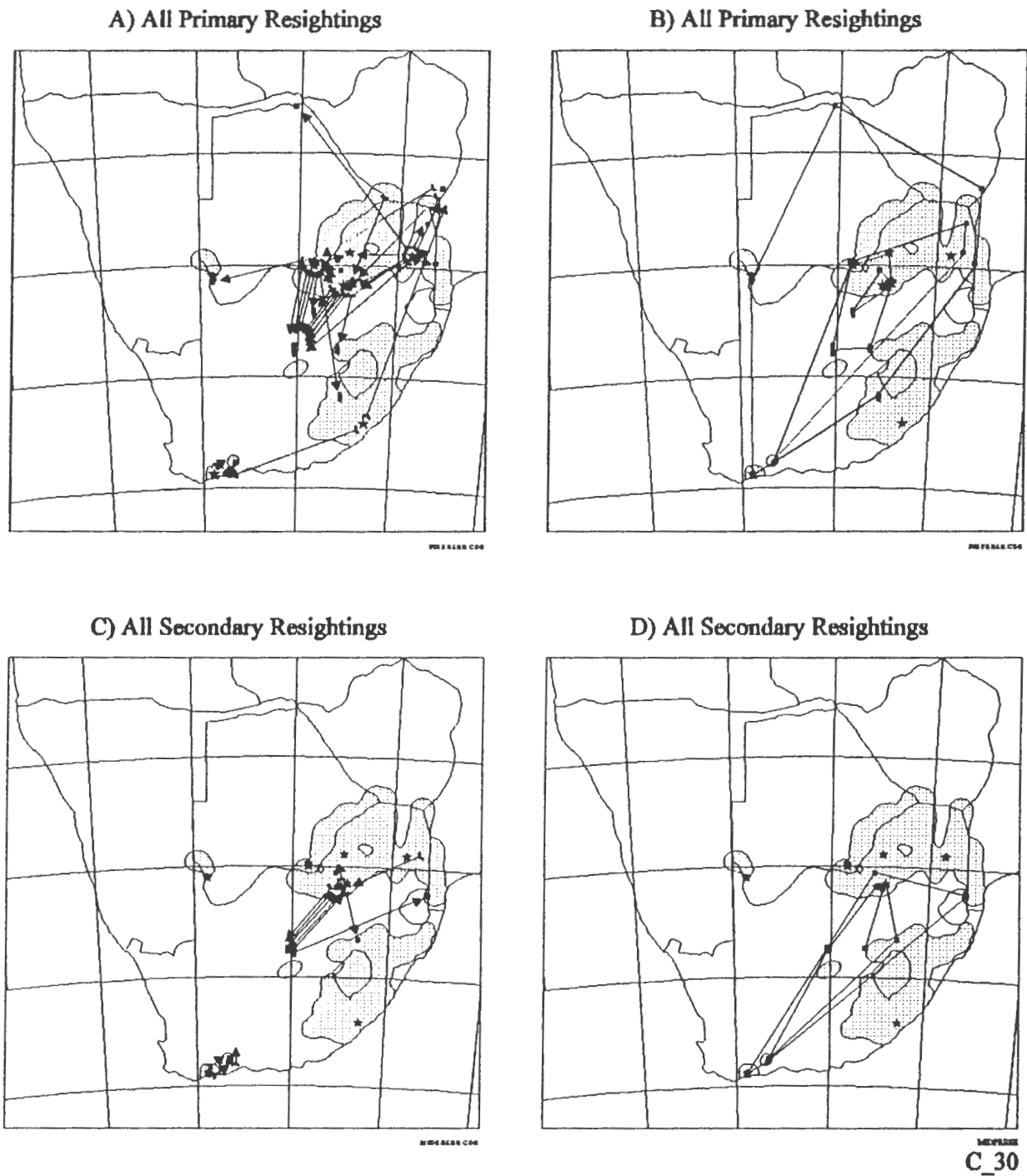


Figure 6.30 A) Radial-arm display of all primary resightings. B) Peeling of convex hulls of all primary resightings. C) Radial-arm display of all secondary resightings. D) Peeling of convex hulls of all secondary. Major ringing sites are shown as stars. The enclosed stippled region approximates the current Cape Vulture distribution.

Table 6.24

Number of marked Cape Vultures moving from the place of one resighting to a subsequent resighting.

From first Resighting		To subsequent Resighting		No.
24°20'	31°20'	Timbavati	25°47' 27°47'	Kommandonek Restarnt 1
25°45'	27°45'	Skeerpoort	25°45' 27°45'	Skeerpoort 1
25°45'	27°45'	Skeerpoort	25°59' 27°37'	Spring Farm Restaurant 4
25°47'	27°47'	Kommandonek Restaurant	25°47' 27°47'	Kommandonek Restaurant 8
25°47'	27°47'	Kommandonek Restaurant	25°59' 27°37'	Spring Farm Restaurant 2
25°51'	27°18'	Roberts' Farm	25°51' 27°18'	Roberts' Farm 16
25°51'	27°18'	Roberts' Farm	25°59' 27°37'	Spring Farm Restaurant 2
25°51'	27°18'	Roberts' Farm	28°39' 24°50'	Dronfield Ranch 2
25°53'	27°18'	Roberts' Farm Restaurant	25°47' 27°47'	Kommandonek Restaurant 2
25°59'	27°37'	Spring Farm Restaurant	25°15' 27°11'	Pilanesberg 1
25°59'	27°37'	Spring Farm Restaurant	25°59' 27°37'	Spring Farm Restaurant 9
25°59'	27°37'	Spring Farm Restaurant	28°15' 28°26'	Franshoek Farm OFS 1
28°39'	24°50'	Kimberley, Pylon	25°45' 27°45'	Skeerpoort 1
28°39'	24°50'	Kimberley, Pylon	25°51' 27°18'	Roberts' Farm 1
28°39'	24°50'	Dronfield Ranch	25°59' 27°37'	Spring Farm Restaurant 2
28°39'	24°50'	Kimberley Water Trough	26°10' 31°55'	Hlane, Swaziland 1
28°39'	24°50'	Dronfield Ranch	28°39' 24°50'	Dronfield Ranch 15
28°39'	24°50'	Kimberley, Pylon	28°50' 24°50'	Benfontein 1
28°41'	26°47'	Dronfield Ranch	28°41' 26°47'	Dronfield Ranch 1
28°50'	24°50'	Benfontein	25°59' 27°37'	Spring Farm Restaurant 1
28°50'	24°50'	Benfontein	28°50' 24°50'	Benfontein 9
33°44'	21°43'	Platrug	33°44' 21°43'	Platrug 3
33°44'	21°43'	Platrug	34°22' 20°33'	Potberg Kloof 5
33°52'	21°40'	Aasvogelvlei	33°44' 21°43'	Platrug 2
33°52'	21°40'	Aasvogelvlei	33°52' 21°40'	Aasvogelvlei 7
33°52'	21°40'	Aasvogelvlei	34°22' 20°33'	Potberg Kloof 11
34°22'	20°33'	Potberg Kloof	33°44' 21°43'	Platrug 7
34°22'	20°33'	Potberg Kloof	33°52' 21°40'	Aasvogelvlei 7
34°22'	20°33'	Potberg Colony	34°22' 20°33'	Potberg Kloof 288

'Pulling power of the restaurants'. There are three sites in the northern sector which have been used as formal restaurants and at which colour-ringed birds have been resighted: Kommandonek, Roberts' Farm and Spring Farm (Table 6.22). In addition, there is a collection of sites in the Kimberley district (i.e. Dronfield Ranch and Benfontein) where over 70 resightings were made. In the south-western Cape there are three major sites (i.e. Potberg, Aasvogelvlei and Platrug) at which observations have been made of colour-ringed birds. Each of these sites is examined to see from where it 'pulls birds in'. The location of the restaurants and the 'supplying' sites are shown in a series of sketch maps. It is to be expected that a restaurant will attract colour-ringed birds from the closest colony, or roost. The object of this examination is to discover just how many 'long-distance travellers' can be resighted at a restaurant.

Table 6.25

Summary of resightings at Kommandonek Restaurant of birds ringed as nestlings.

Colony	Ringing year	Date resighted in 1983								Totals
		06-11	08-11	08-24	08-28	08-31	09-23	09-25	09-27	
Skeerpoort	75	1	0	0	0	0	0	0	0	1
	81	1	0	1	3	1	2	3	0	11
	82	0	1	0	1	3	3	2	0	10
Roberts' Farm	77	1	0	0	1	1	0	0	0	3
	81	0	0	0	0	1	1	3	0	5
	82	1	0	2	0	0	0	0	1	4

Table 6.26

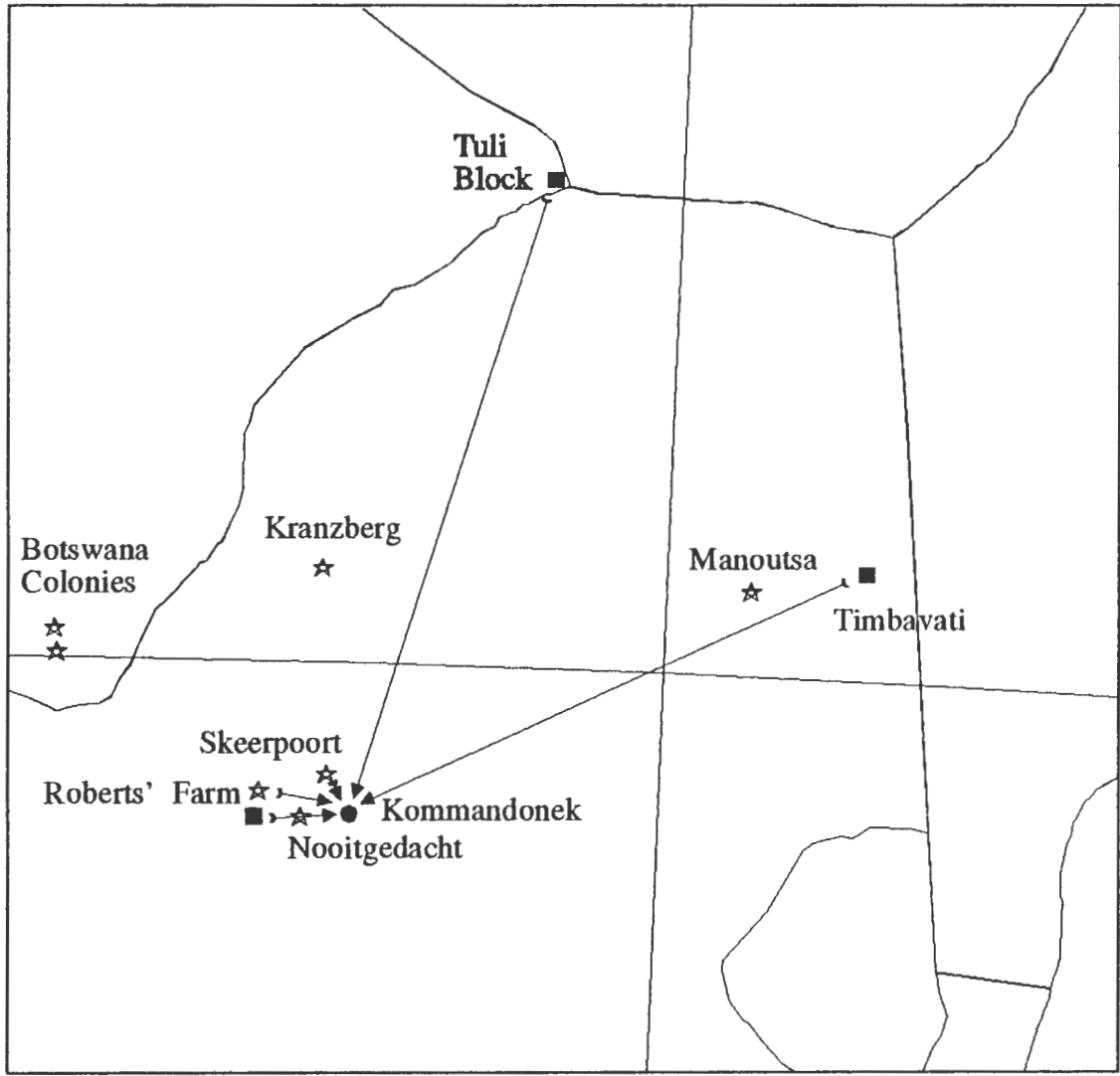
Summary of resightings at Roberts' Farm Restaurant of birds ringed as nestlings.

Colony	Ringing year	Date resighted in 1983			Totals
		08-10	08-24	09-03	
Skeerpoort	76	0	1	0	1
	81	0	0	6	6
	82	1	0	2	3
Roberts' Farm	81	0	0	1	1
	82	0	0	3	3

*Kommandonek Restaurant.* The 35 resightings at Kommandonek Restaurant came from birds originally ringed as nestlings at Skeerpoort and Roberts' Farm (Table 6.25) and one ringed in the Tuli Block. About a third (i.e. 11 of 35) were secondary resightings having been seen before at Timbavati and Roberts' Farm Restaurant as well as at the Kommandonek Restaurant itself (Figure 6.31). A bird in its seventh year, from Skeerpoort, was seen at the Kommandonek Restaurant and two fifth-year birds from Roberts' Farm were also seen there.

*Spring Farm Restaurant.* This was a wonderfully productive site, drawing in birds ringed as nestlings at Manoutsa (1), Mannyelanong (2), Skeerpoort (44) and Roberts' Farm (11); additionally, a bird ringed at Gonarezhou passed through (Table 6.27). Birds from some of these sites came to Spring Farm via sites in the Kimberley region (Figure 6.33). A bird in its eighth year, from Skeerpoort, was seen at this restaurant. On New Year's Day, 1978 and then two weeks later, there were 'spat-falls' of eight and 11 birds, respectively, which had been ringed the previous year, i.e. September 1977. The concepts of 'spat-falls' and 'age-sets' will be alluded to in the next section.

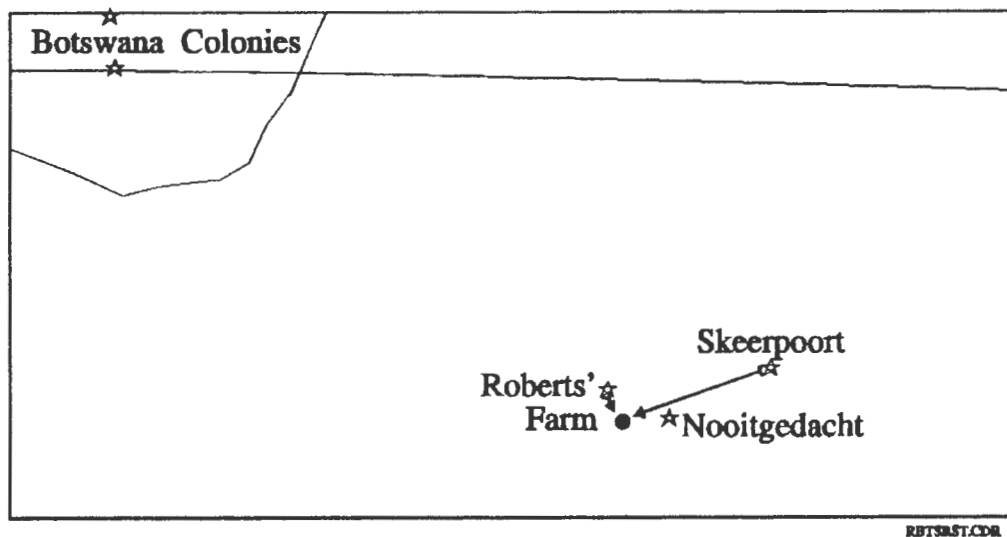
### Source of resightings at Kommandonek Restaurant



KMNRST.CDR

Figure 6.31 Colour-ringed birds seen at Kommandonek Restaurant came directly from Tuli Block (1), Skeerpoort (13) and Roberts' Farm (10) while others had previously been seen at Timbavati (1), Kommandonek Restaurant itself (8) and Roberts' Farm Restaurant (2).

### Source of resightings at Roberts' Farm Restaurant



RBTSBST.CDR

Figure 6.32 Colour-ringed birds seen at Roberts' Farm Restaurant came directly from Skeerpoort (10) and Roberts' Farm (4).

*Roberts' Farm Restaurant.* Only 14 birds were resighted at Roberts' Farm Restaurant (Table 6.26) with ten of the 14 coming, rather surprisingly, from Skeerpoort which is further away. These included a seventh-year bird. The remaining colour-ringed birds came from Roberts' Farm. No other sites 'supplied' birds to this restaurant (Figure 6.32), and there were no secondary resightings (Table 6.24).

*Kimberley Region.* Visits were made to the De Beers' Diamond Mines game farms in the Kimberley region during the period 1975 to 1977 to study African Whitebacked Vultures (P.J. Mundy pers. comm.). Incidental observations of Cape Vultures feeding at carcasses, drinking and sunbathing at water-holes, and roosting on power pylons were made. These have been summarized by month (Table 6.28) from which it is evident that these resightings originated as nestlings ringed at Manoutsa (1), Manyana (4), Baratani Hill (1), Mannyelanong (2), Skeerpoort (39) and Roberts' Farm (23) (Figure 6.34). Two possible 'age-sets' from Skeerpoort and Roberts' Farm, ringed in September, 1974, arrived in the Kimberley region about a year after ringing. The fastest arrival was of a September, 1975 ringed bird which arrived in November of the *same* year!

Table 6.27 (Part 1)

Summary of resightings at Spring Farm Restaurant of birds ringed as nestlings.

Colony	Ringing year	Date resighted in 1977						1978					Sub-total	
		07 17	07 31	08 13	08 29	09 05	09 25	10 16	01 01	01 15	04 02	06 17		07 01
Manoutsa	79	0	0	0	0	0	0	0	0	0	0	0	0	0
Mannyelanong	74	0	0	0	1	0	0	0	0	0	0	0	0	1
	76	0	0	0	0	0	0	0	0	1	0	0	0	1
Skeerpoort	74	0	1	1	0	0	3	1	2	0	0	0	0	8
	75	2	0	0	0	1	2	1	1	1	0	0	0	8
	76	0	0	0	0	1	0	0	0	0	0	0	1	2
	77	0	0	0	0	0	0	0	8	11	0	0	0	19
	81	0	0	0	0	0	0	0	0	0	0	0	0	0
	82	0	0	0	0	0	0	0	0	0	0	0	0	0
Roberts' Farm	74	0	1	0	1	0	0	0	1	0	0	2	0	5
	75	1	0	0	0	0	0	1	0	1	1	0	0	4
	81	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 6.27 (Part 2)

Summary of resightings at Spring Farm Restaurant of birds ringed as nestlings.

Colony	Ringing year	Date resighted in 1979					1983		Sub-total	Totals
		08 13	10 04	10 05	10 21	10 22				
Manoutsa	79	0	0	0	1	0			0	1
Mannyelanong	74	0	0	0	0	0			1	1
	76	0	0	0	0	0			1	1 2
Skeerpoort	74	0	0	0	1	0			1	9
	75	1	0	0	0	0			1	9
	76	1	0	0	0	0			1	3
	77	0	0	0	0	0			0	19
	81	0	2	0	1	0			3	3
	82	0	0	0	0	1			1	1 44
Roberts' Farm	74	0	0	0	0	0			0	5
	75	0	0	0	0	0			0	4
	81	0	0	1	0	0			1	1 10

*Inter-Colony Movements.* The movement of colour-ringed birds between breeding colonies has been examined and mapped. The motivation for this analysis is to see if birds ringed as nestlings at one breeding colony subsequently settle to breed at another colony. Thus all the intermediate points at which colour-ringed birds were seen have been ignored (i.e. if a bird went from Roberts' Farm to Skeerpoort via the Kimberley region then the sojourn in the Kimberley region is not plotted).

Table 6.28

Summary by month of resightings at sites near Kimberley (Dronfield Ranch, Benfontein and along power pylons) of birds ringed as nestlings.

Colony	Ringing year	Resighted in 1975					1976		1977		Totals
		06	09	10	11	12	01	09	09		
Manoutsa	75	0	0	0	0	0	0	0	1	1	
Manyana	73	0	0	0	0	1	0	0	0	1	
	74	2	0	0	0	0	1	0	0	3	4
Baratani Hill	74	0	1	0	0	0	0	0	0	1	
Mannyelanong	74	0	1	0	0	0	0	0	0	1	
	75	0	0	0	0	0	0	1	0	1	
Skeerpoort	74	1	13	10	3	3	6	0	2	38	
	75	0	0	0	0	0	0	1	0	1	39
Roberts' Farm	73	0	1	0	0	0	0	0	0	1	
	74	0	8	5	4	0	1	0	0	18	
	75	0	0	0	1	0	0	0	0	1	
	76	0	0	0	0	0	0	0	3	3	23

The movements occurring in the northern sector (Figure 6.35) show transfers to Kranzberg (i.e. one from Manoutsa and two from the Botswana colonies), to Karnmelkspruit (i.e. two from the Botswana colonies) and two each to Skeerpoort and Roberts' Farm (and vice versa). The two transfers to Skeerpoort were of adult birds of which there is good reason to suspect that they became breeding birds (Piper, Mundy & Mundy, in prep.). There is no reason to suspect that any of the other transfers in the northern sector gave rise to breeding birds at new colonies. This may be due to paucity of observations rather than a real effect.

Two of the movements between Skeerpoort and Roberts' Farm are of interest because they went via the Kimberley region. A Skeerpoort-ringed bird (i.e. G-09862) went first to Dronfield from where it travelled on to Roberts' Farm. A Roberts' Farm bird (i.e. G-10285) also went to Dronfield and then went on to Skeerpoort.

The inter-colony movements in the south-western Cape (Figure 6.36) show a considerable flux of individuals. Given that birds were ringed as nestlings at Potberg and Aasvogelvlei and that they visited Platrug as well, there are counts for all four possible movements: Potberg-ringed birds to Aasvogelvlei and Platrug as well as Aasvogelvlei-ringed birds to Platrug and Potberg. In addition, there are Aasvogelvlei and Potberg-ringed birds which went to Platrug and then moved on to Potberg (Tables 6.23 and 24).

### Source of resightings at Spring Farm Restaurant

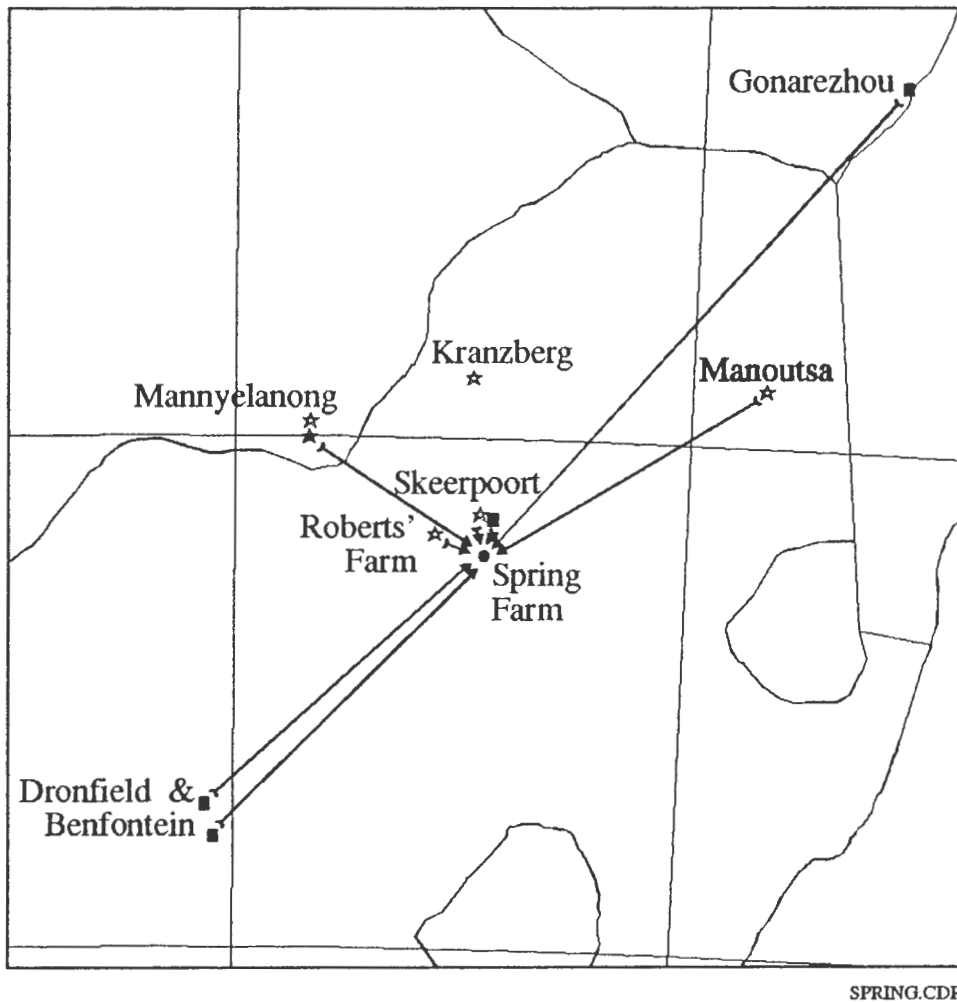
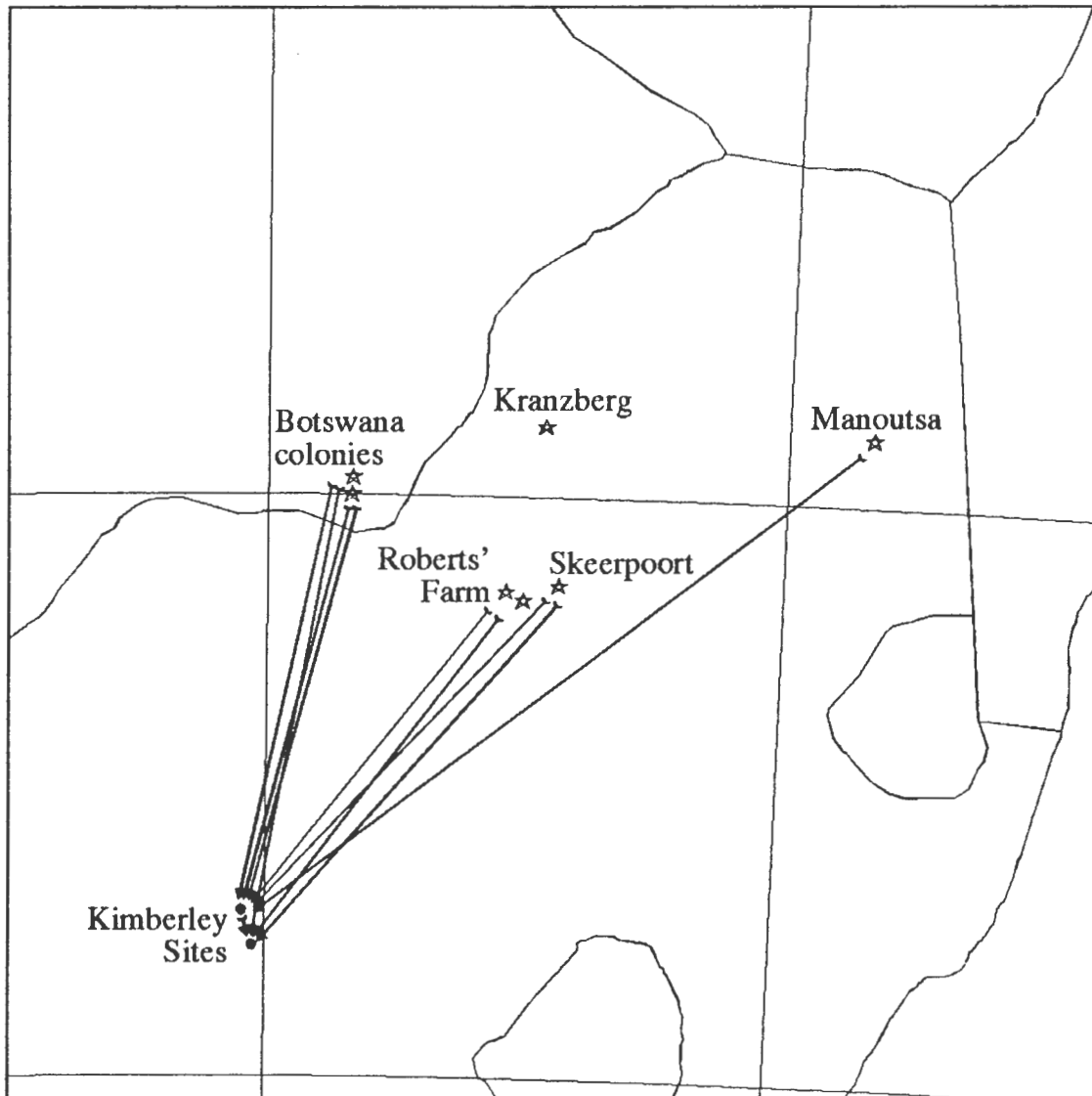


Figure 6.33 Colour-ringed birds seen at Spring Farm Restaurant came directly from Gonarezhou (1), Manoutsa (1), Mannyanong (2), Skeerpoort (30) and Roberts' Farm (4) while others had previously been seen at Kommandonek Restaurant (2), Roberts' Farm (2), Skeerpoort (4), Dronfield (3) and Spring Farm itself (9).

### Source of resightings in the Kimberley region



KIMBER.CDR

Figure 6.34 Colour-ringed birds seen in the Kimberley Region came directly from Baratani Hill (1), Manoutsa (1), Manyana (2), Mannyelanong (2), Skeerpoort (19) and Roberts' Farm (17) while others had previously been seen at Roberts' Farm (2) and in the Kimberley Region itself (26).

### Intercolony transfers in the northern region

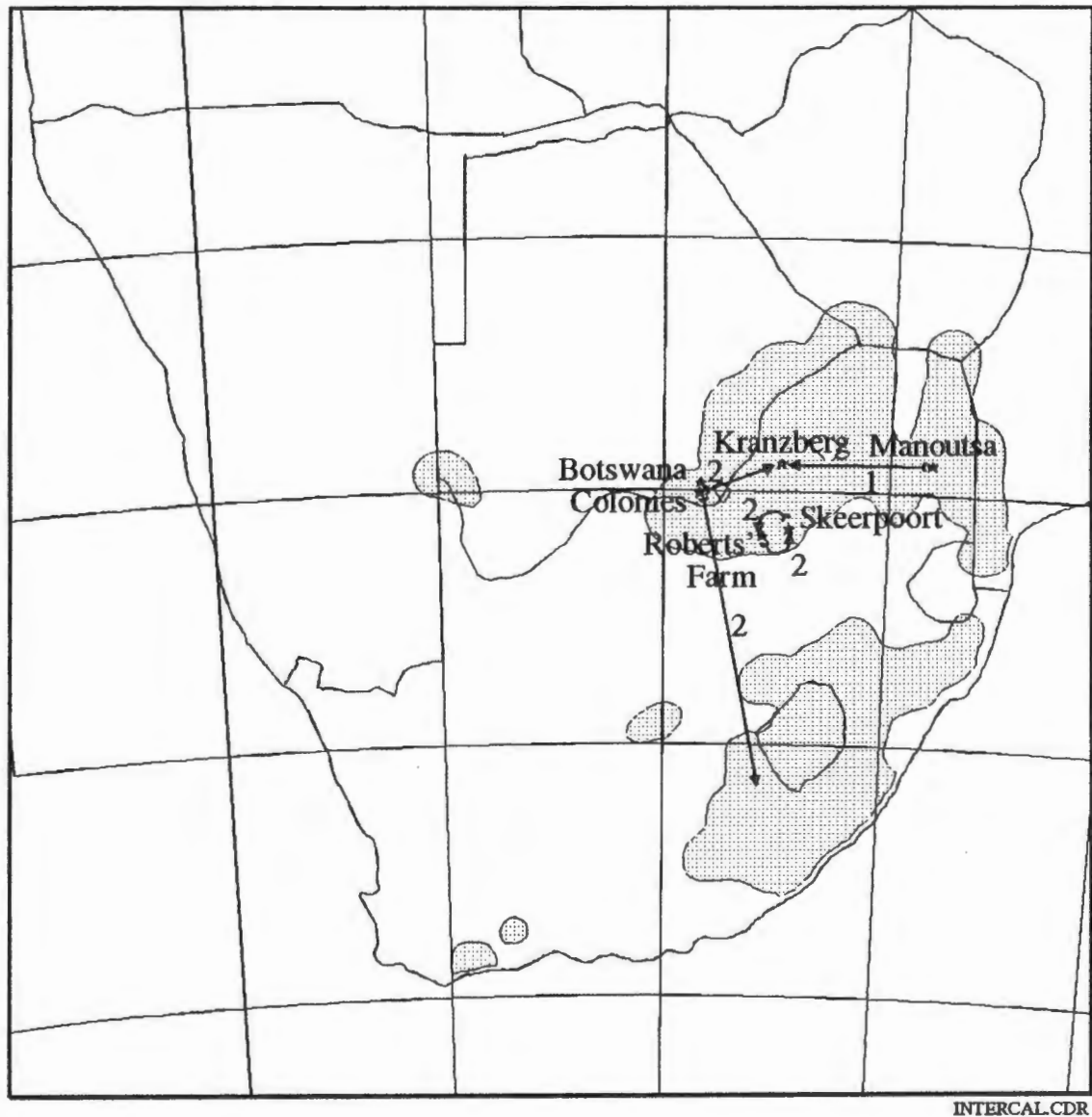
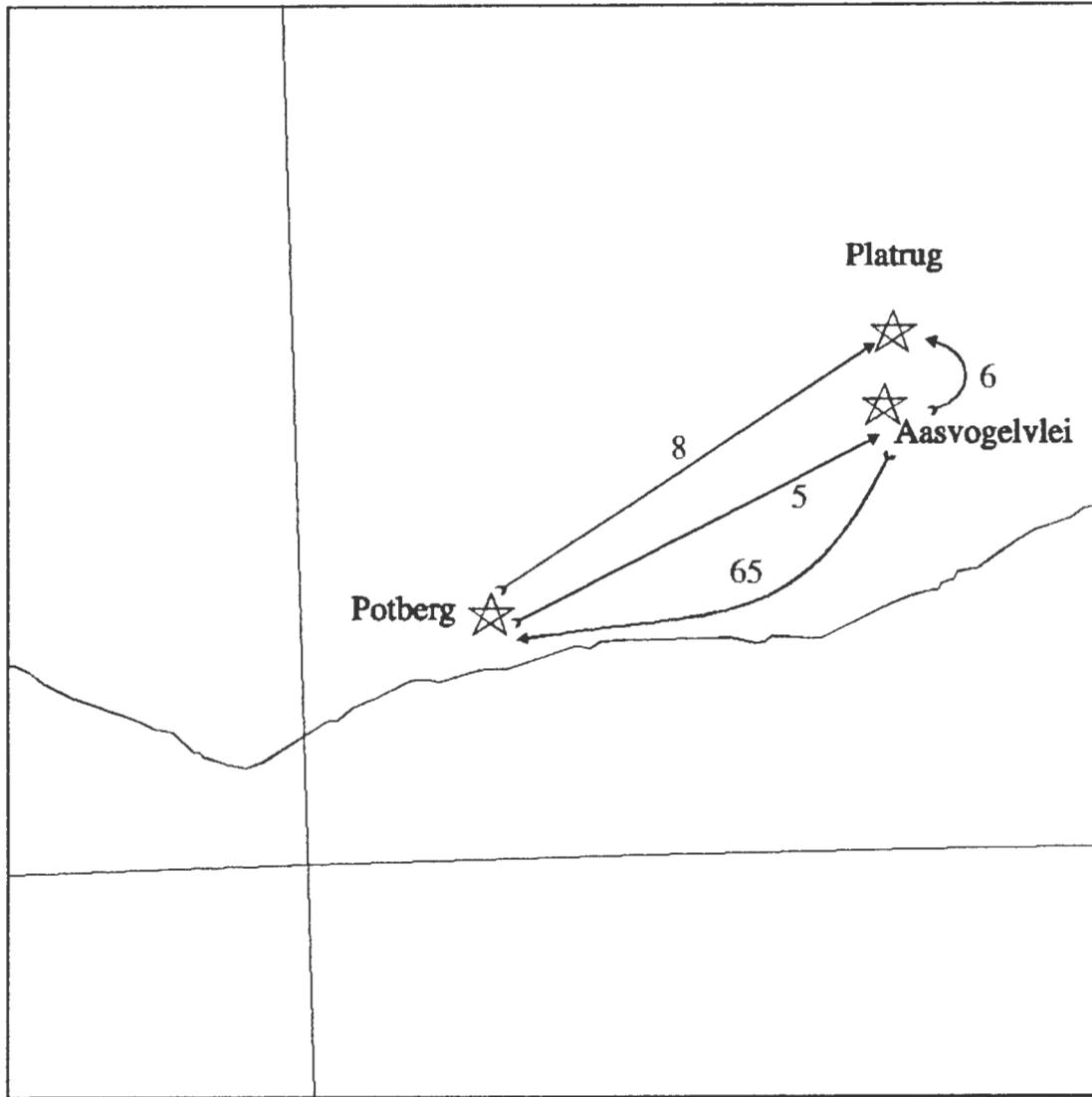


Figure 6.35 Arrows show direction and number of birds moving from the natal breeding colony to another colony in the northern region. The only evidence of breeding after transfer is of two Roberts' Farm birds breeding at Skeerpoort. The enclosed stippled region approximates the current Cape Vulture distribution.

### Intercolony transfers in the south-western Cape



INTERSWC.CDR

Figure 6.36 Arrows show direction and number of birds moving from the natal breeding colony to another colony in the south-western Cape.

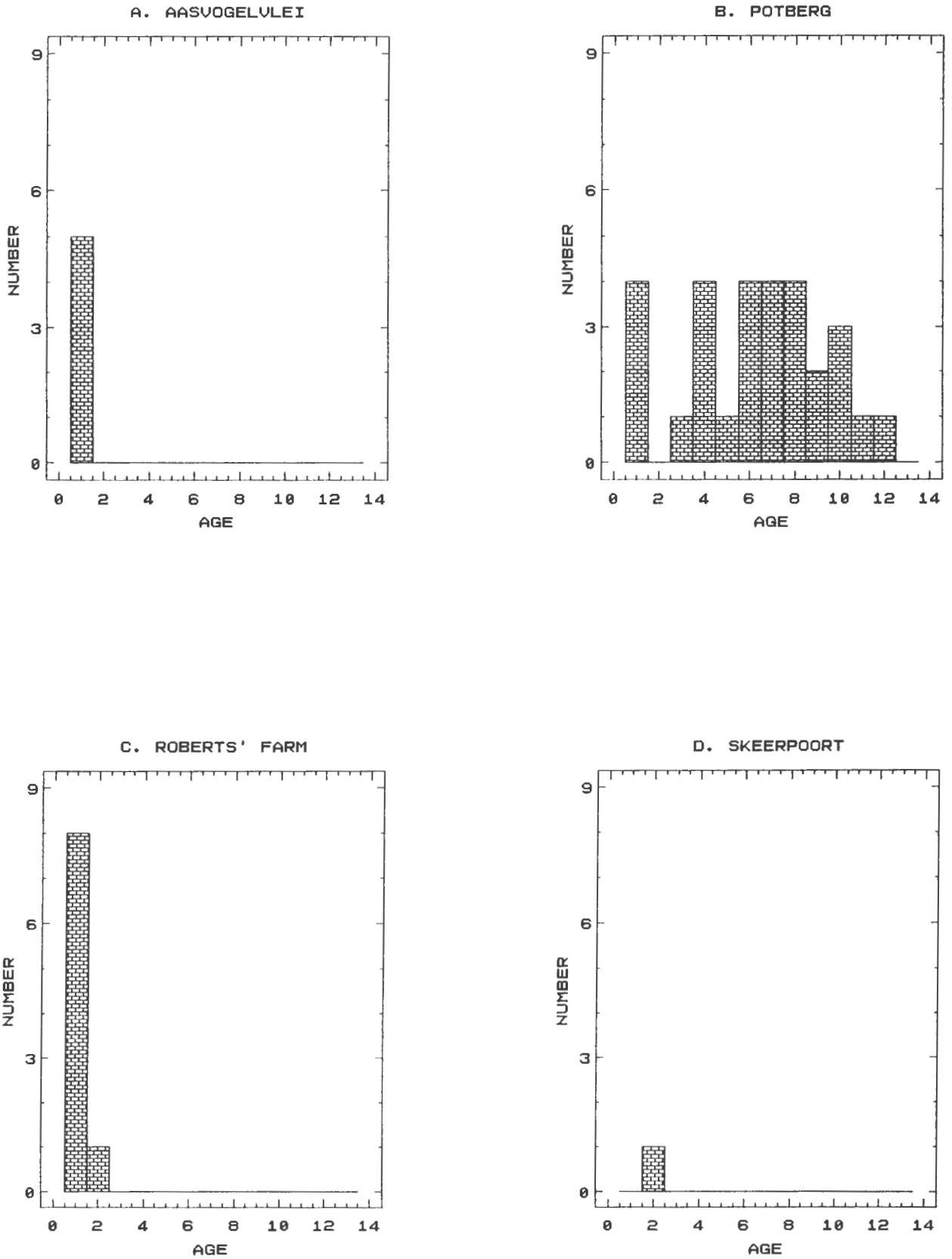


Figure 6.37 Ages at which colour-ringed birds are resighted at their natal colonies at least one year after ringing. A. Aasvogelvlei, B. Potberg, C. Roberts' Farm and D. Skeerpoort.

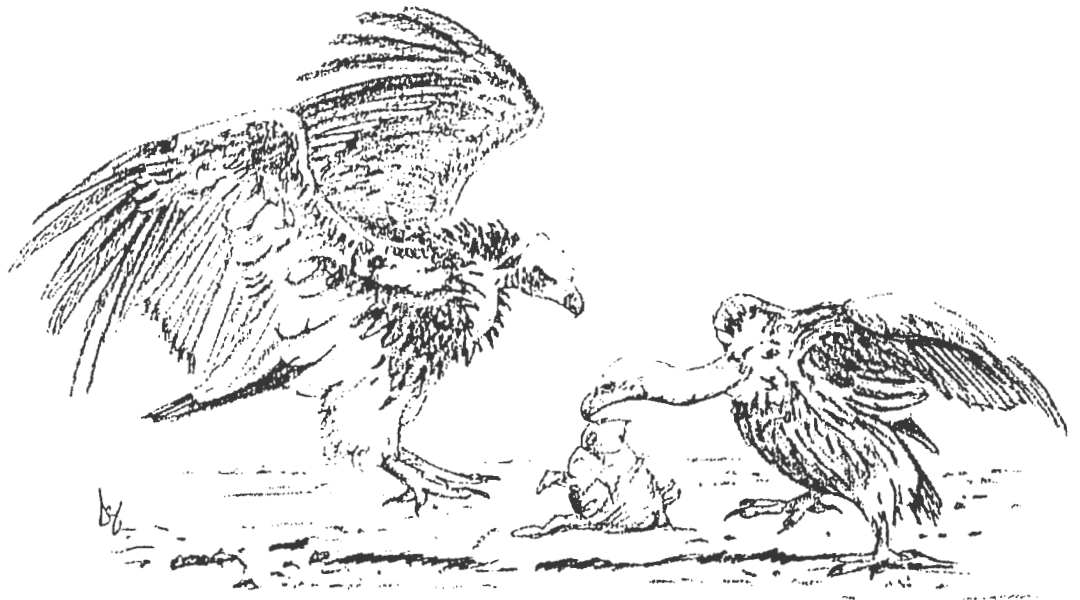
*The return of the native.* Are there birds which left their natal colony, after ringing, and wandered some distance far away, were then resighted there and eventually returned to their natal colony? The following four birds moved out from their natal colony to some distant parts and then returned to the neighbourhood of their natal colony.

- G-15480 Ringed at Skeerpoort, seen at Timbavati and returned to Kommandonek Restaurant.
- G-10284 Ringed at Roberts' Farm, seen at Dronfield Ranch and then at Spring Farm Restaurant.
- G-12023 A Skeerpoort-ringed bird seen on a pylon at Kimberley and then at Spring Farm Restaurant.
- G-09961 A Skeerpoort-ringed bird seen at Benfontein and then resighted at Spring Farm Restaurant.

The movements between the sites of the south-western Cape are over such small distances as not to be of importance in this particular analysis.

The last question to consider is how many birds were resighted at their natal colonies at least one year after having been ringed? There are 44 birds which were colour-ringed as nestlings who were later seen, at least once, at their natal colony (Figure 6.37). These resightings took place at least one year after ringing and were made at Aasvogelvlei (5), Potberg (29), Roberts' Farm (9) and Skeerpoort (1). The oldest bird was 12 years old when last resighted.

In the first three sections of this chapter a number of questions concerning movements were posed and some of them have been answered using the recovery and resightings data. In the next section a number of models of movement will be considered and investigated in the light of the answers presented above.



## 6.4 Models of movement

How far do vultures move? In their day to day comings and goings *Gyps* vultures can, and regularly do, move great distances (e.g. up to 110 to 140 km per day by African Whitebacked Vultures and Rüppell's Griffon, Pennycuick 1972; up to 150 km per day for Rüppell's Griffon, Houston 1976), so it is to be expected that the Cape Vulture will also do so. The first formal analysis of Cape Vulture recovery data (Houston 1974) confirmed that young Cape Vultures do wander far and wide across the sub-continent. At the other extreme, 25 resightings of a dozen marked Cape Vultures in the Natal and Lesotho Drakensberg showed maximum movements of about 35 km, and it was predicted that a likely maximum foraging distance would be about 54 km (Brown & Piper 1988: 130). In a study of Cape Vultures from the Potberg colony in the southwestern Cape, using radio-tracking equipment, it was found that most birds foraged within a 35 km radius of the colony (Boshoff, Robertson & Norton 1984: 75).

Given that Cape Vultures have been recovered at over 1000 km from their natal colonies, it is likely they will need to make important decisions about their use of space and time. Indeed, this is a problem for all animals, for as Baker (1982: 2-3) has argued:

One of the problems that faces all animals is where to live. Individuals have little control over where or at what stage of development they first appear. Parents decide these things according to their own best interests. Thereafter, the individual has to wend its way through time and space until it dies. The most successful individuals in terms of the number and quality of offspring they produce (i.e. *reproductive success*), will be those with a path that exploits the environment to the full, minimizing costs, maximizing benefits, always seeking the best trade-off between the two. The path that an animal produces is its *lifetime track*, the outward manifestation of the individual's solution to spatial and temporal problems, the playing off of inherited predispositions and acquired experience against the environmental backcloth, running the gauntlet of natural selection for yet another generation. (Author's italics.)

In the previous three sections, the data resulting from the recovery and resighting of marked Cape Vultures have been subjected to a detailed, but purely exploratory, statistical analysis to see what spatial patterns they revealed. In the following sections consideration will be given to current theoretical models of movement, and the available data on the Cape Vulture will be analyzed in the light of these models. Unfortunately, the whole arena of space-time utilization is bedevilled with a complex terminology which is in a state of flux and is subject to much misuse (see section 6.4.1 below). Thus, to 'clear the decks' consideration is first given to a summary of the theoretical framework, and a clear definition of the terminology as it is to be used here. This is then followed with models of drift, dispersal and exploration (section 6.4.2), a definition and analysis of nursery areas (section 6.4.3), nomadism, irruption, vagrancy and colonization (section 6.4.4), migration (section 6.4.5), natal fidelity and philopatry (section 6.4.6) and lastly home range and foraging (section 6.4.7).

### 6.4.1 Theoretical framework and terminology.

Many, if not the majority of studies of population dynamics of birds and mammals have been undertaken by scientists from the northern hemisphere and usually in temperate climates. This means that many of the species studied have been relatively short-lived and *r*-selected (MacArthur & Wilson 1967). In turn, this implies that the 'mental model' for most of the studied species assumes that an individual is born one spring, spends the summer learning about its environment and then leaves for its winter quarters in the autumn. In the next spring it returns to set up a breeding territory and thereafter the cycle repeats itself. In this 'model' the important concepts connected with movement (i.e. the use of space and time) are dispersion, dispersal, exploration, migration, nomadism, irruption, vagrancy, colonization and philopatry. These terms are presented and defined. Topics concerned with the mechanisms of movement, especially *navigation*, *sense of direction* and *sense of location*, will not be discussed because there are no relevant data for the Cape Vulture.

The daily foraging range of vultures can be up to 110-140 km (see above) and this is a reasonable fraction of the distance (from their 'regular' colony or roost) at which many birds are found dead (see section 6.1 above). This has two implications for the analysis of movement. First, it is necessary to examine the home range and foraging distance of the Cape Vulture, and secondly it is important to separate out these daily movements from permanent displacements in the Cape Vulture.

From the beginning of modern studies of vultures in southern Africa (i.e. in the 1970s), it was clear that the larger vultures are long-lived and take many years to reach their adult plumage (e.g. Lappetfaced Vulture, Mundy 1982: 40 and Cape Vulture, loc. cit.: 44). During this time there may be an age-specific segregation, with sub-adults using areas different from those used by their parents and other adults (e.g. Bearded Vulture, Brown 1990: 48). To this end the concept of a 'nursery area' is introduced.

*Dispersion.* The simplest definition is 'The distribution of individuals, pairs or groups through an area' (Weaver 1981: 38). A more complex, and possibly more realistic view is from Newton (1979: 38):

By dispersion, I mean the pattern in which birds distribute themselves over the landscape in relation to food and resources ... Dispersion is thus concerned with the spacing between nests and colonies, with the size and density of colonies, and with the day-to-day movements of individual birds.

The dispersion of the Cape Vulture, as well as ways to estimate it, have been discussed at some length (see Chapter Three above) where the emphasis was on documenting the location and size of breeding colonies and roosts. In order to understand how Cape Vultures spread

themselves out over the countryside in their daily foraging forays, use was made of the sightings data collected by SABAP. These sightings data were used to compute a visibility index (i.e. as a reporting rate). The way in which estimates of the daily foraging range interact with the elucidation of permanent displacements will be discussed below.

*Dispersal.* The standard definition (Weaver 1981: 38) is:

An outward movement from the breeding place at the end of the breeding season, when territory is abandoned and birds disperse, either in a definite direction or apparently at random. This movement takes place before true migration begins.

This definition is quite specifically based on an unstated 'temperate climates' model and is too restrictive for use in these analyses. A wider usage has been advocated (Baker 1982: 6):

the behaviour of young mammals when they abandon the area in which they are born and settle down elsewhere ... the movement of birds just after fledging ... change in breeding site which often also involves a scattering of previous breeding groups.

This term has attracted so many different shades of meaning that it is difficult to know which to use. For the purposes of this analysis it will be used in the most literal sense to mean 'to disperse', or 'to scatter' (loc. cit.), with the explicit understanding that it describes an essentially random process. The term 'dispersal' will not be used to describe the process of leaving the natal colony to settle at another colony. As the age at first breeding is somewhere between the fourth and sixth year (see section 4.1.3. above) and as few immature birds are seen at colonies (see section 3.1.3 above), Cape Vultures must spend some three to five years away from their natal colonies before returning to breed. This time period is so long that the notion of dispersal as a short and direct movement from natal site to site of breeding is not useful. To the contrary, it is likely that in the three to six years between leaving the nest and commencing breeding there may be a variety of movement patterns including exploration, random displacements and other interesting movements. The term 'dispersal' will be used sparingly in these researches.

*Exploration.* The central thesis of the works of R. Robin Baker (e.g. Baker 1982) is that young animals do not 'disperse' (using the word in the sense of Weaver 1981: 38) in one, or more random directions when they leave their parents domain; rather they explore the environment around the natal area. Exploration is defined (loc. cit.: 48-49) as having three components.

- 1) Exploratory movements into unfamiliar regions, but with the aim of returning to a familiar domain.
- 2) Habitat assessment of new regions visited, and ranking them and their resources against areas previously visited.
- 3) Return to a previously known region.

Baker goes so far as to suggest that 'exploration is an all-pervading behavioural element in animals that have a sense of location and that move short distances' (Baker 1982: 3).

*Migration.* The term 'migration' is generally taken to be (Weaver 1981: 71):

A regular seasonal movement of the whole or part of a population with an outward journey followed, some time later, by a return journey. Although most migratory movements involve travelling between breeding grounds and winter quarters at some distance, there are other types, including altitudinal migration and moult migration. An irruption or weather movement, because of its irregular nature, is not a true migration.

The concept of 'migration' may seem so well understood as to seem not in need of definition. Not so. Baker (1982) has summarized the way in which this term, like dispersal, has been misused and has suggested new meanings for it. Unfortunately, there is considerable disagreement on Baker's use of this term, for example (Sinclair 1984: 240-241):

There are some difficulties with definitions, however. Baker includes all forms of movement (apart from trivial ones) under the name of 'migration' to the extent that a boulder moving downhill performs migration.

The term migration will only be used here in the context of a '*return migration*', i.e. to mean a seasonal movement from the natal colony (or some other fixed point) to some other place and the subsequent return at a later date to that original place (Baker 1982: 15).

*Nomadism.* A useful description of nomadism is provided by Newton (1979: 181):

nomadism, in which birds drift from one area to another, residing for a time wherever food is temporarily plentiful. The areas successively occupied may lie in various directions from one another, and no one area is necessarily used each year.

For environments which show an unpredictability of resources in time and space it is to be expected that (Sinclair 1984: 251):

[natural] selection would favour those [individuals] that adopted a nomadic existence, moving in unpredictable ways rather than following a prescribed regular migration from nonbreeding range to breeding area and back.

An individual which leaves its natal area, but never settles, forever following spatially variable and favourable resources where it may from time to time and place to place breed is said to be nomadic (Baker 1982: 19).

*Vagrancy.* A vagrant is described by Weaver (1981 : 121):

A bird which wanders to a particular area if its orientation is at fault or adverse winds drive it off course but in normal circumstances would not be found there at all.

In my opinion, this definition is too tied to the 'temperate migration' model. A better definition for a widespread and wide-ranging endemic would be one in which vagrancy is seen as a rare and random excursion beyond the limits of the species' normal distribution. Conversely, in defining the distribution of an endemic species, it is important to eliminate those spatial records which result from the sighting of such vagrants (J.A. Harrison, pers. comm.). To this end, in the interpretation of the SABAP data, it has been suggested that using a cut-off reporting rate of 3% will eliminate these vagrants while leaving the basic pattern clearly defined (see section 3.2.5 above). (The term 'vagrancy' is also used, but in a different sense, as the opposite of philopatric - see below.)

**Irruption.** A useful working definition (Weaver 1981: 64) is:

An irregular movement involving large numbers of birds which takes them into areas where they are not found every year in such numbers. An irruption differs from true migration because it is essentially irregular and does not have a return movement matching the outward movement.

A slightly different view is provided by Newton (1979: 181):

invasion migrations (or irruptions), in which the proportion of birds leaving the breeding range, and the distance they travel, varies greatly from year to year (the directions are the same). Noted mainly in northern regions, such movements occur in response to annual, as well as to seasonal fluctuations in food.

**Colonization.** A simple definition is provided by Weaver (1981: 32):

Extension of the breeding distribution of a species by natural means (rather than by introduction). A rapid colonization of an area is called an invasion.

It will be seen below (see section 6.4.4) that there is some anecdotal evidence to show that Cape Vultures can suddenly appear in an area in which there is a sudden or temporary abundance of food. It is clear that these movements are to be looked upon as vagrancy or nomadic unless the population stays and breeds, in which case colonization has occurred.

**Philopatry.** How far do the young of the new generation (= propagules, in the following quotation) go before they start to breed themselves? If they do not go very far, then they may be said to exhibit philopatry (Shields 1984: 134):

The word philopatry was originally used to describe an absence of dispersal, that is, if propagules remained at their birthplace (e.g. Mayr 1963). I [Shields] define it more broadly as relatively localized dispersal, with propagules either remaining at their birthplace, or as near to it as local ecological conditions will permit ... with a median effective dispersal less than ten units [one unit = diameter of home-range] in magnitude ... Vagrancy, in turn, is characterized by median effective dispersal greater than ten units in magnitude.

**Nursery Area.** Where do young raptors go after they have left their natal areas? A general summary has been provided (Newton 1979: 173-4) in which:

young birds ... may summer in areas partly different from the breeding adults of the population. So far several such traits have emerged: (a) the immatures may remain all summer in 'winter quarters', e.g. some first-year Steppe Buzzards; (b) they may migrate north later and spend less time on the breeding areas than adults, e.g. some Broad-winged Hawks; or (c) they may migrate north but stop short of the breeding areas, e.g. some second-year Ospreys ... Moreover, different populations of a species may behave in different ways, as may different age-groups among the non-breeders of a single population.

This definition is too specific to raptors which migrate, and does not describe the situation that applies to fledgling Cape Vultures. In the late 1970s and early 1980s the phrase 'nursery area' crept into the vocabulary of southern African biologists studying vultures (pers. obs.). In the first use of the term 'nursery area' (Ledger & Mundy 1976: 7), no definition or explanation of the concept was provided. The term was employed in the sense of an area used, in the main, by recently fledged birds, immatures and perhaps a few nonbreeding adults. Although the term 'nursery area' had been current for a number of years, awaited a first rough definition in 1982 (Mundy 1982: 101):

Because so many first-year Cape Vultures were seen at Kimberley, the area was dubbed a "nursery area" (A.J. Anthony pers. comm.) ... First-year birds in particular, suffer in competition with older birds at carcasses ... and those that survive move out of the adults' foraging ranges into distant regions, where food may be available. Zululand, northern Botswana, and the Kalahari Gemsbok National Park could, for example, be present-day nursery areas for young Cape Vultures.

In addition to these areas, the Eastern Cape, in the opinion of Vernon (1984: 21), is 'a foraging ground for dispersive birds from the Transkei and Lesotho'. A concise summary of the concept of nursery areas, as applied to the Cape Vulture, was supplied by Ledger (1982: 7):

These young birds move into the so-called "nursery areas" where they exploit a food resource not available to breeding adults, which are tied to their cliff-face breeding colonies around which they forage. The young birds consequently avoid competing with adults by moving large distances to their "nurseries", and we have found that these assemblages of Cape Vultures comprise a mixture of birds from many different breeding colonies.

The characteristics of Dronfield Ranch, in respect of its use as a nursery area have been defined (Mundy 1983: 62):

[Dronfield Ranch] is 400 km from the Magaliesberg and Botswana colonies, and the distance is too great for breeding adults to travel. In addition, the Kimberley area specializes in springbok (*Antidorcas marsupialis*) game ranching, and the hunting season is June and July. The great distance from breeding colonies and a plentiful food supply combine to make this part of the subcontinent a good "nursery area" for young vultures.

Is it likely that this phenomenon may be exhibited by other sedentary raptors? In a study of California Condors *Gymnogyps californianus* (including two birds fitted with radio-tracking devices) it was found that there was 'an isolated wintering ground utilized by immatures' (Ogden, Barbour, Bloom, Grantham & Riopelle 1983). Similarly, for the Bearded Vulture it was found (Brown 1977: 52) that:

In Ethiopia high mountain areas with sparse or moderately dense populations of peasant farmers and grazers are mainly occupied by adult Lammergeiers, whereas immatures and subadults tend to congregate around village and town rubbish dumps.

An interesting variant on this theme is provided by Newton (1979: 183).

The Bald Eagles of Florida show another unexpected pattern: the young are raised in winter, then move northwards and northwest for up to 2,200 km spending from May to September in the northern United States and Canada ... They therefore travel north in spring and south in autumn with the conventional migrants but, unlike them, they have been reared in the south before doing so. Most of the adults also leave Florida for a time, but it is not clear from ringing whether they make the same journey as the juveniles.

Because the juvenile Bald Eagles from the south spend their summer months in regions also occupied by conspecific adults (Bent 1961: 332-333), they are not using a 'nursery area' as defined above. From a study of radio-tagged Grey Herons *Ardea cinerea*, it was possible to show that first-year birds showed further movements than adults (Draulans & van Vessem 1985).

*Home range and foraging.* How do raptors spread themselves out over the countryside? An appropriate pattern has been described (Newton 1979: 48):

*Pairs nest in dense colonies and forage gregariously.* This system is shown ... by the large griffon vultures (*Gyps*). In these species, the pairs typically nest closer together ... and in larger aggregations ... They also feed communally ... in the case of vultures, spread out in the air, but crowd around carcasses. The feeding flocks are not stable, but change continually in size and composition, as birds join or leave. [Author's italics.]

Why should this particular spatial pattern have arisen? It is likely that this social system is a response to the nature of the food supply which is highly clumped in space and time and comes in relatively large parcels (loc. cit.: 49-50). Thus it is to be expected that Cape Vultures will, in their daily foraging forays, spread themselves out over the countryside. The sum of these daily forays by all members of a colony make up its home range, which is defined as (Weaver 1981: 59) 'area over which an individual pair or group moves during the year'.

#### 6.4.2 Drift and exploration.

In what way, and for what reasons, does a Cape Vulture fledgling leave the region surrounding its natal colony? To address this, a number of specific questions have been formulated.

- 1) How far do fledglings go?
- 2) In which directions do they go?
- 3) Where do they go to?
- 4) What proof is there that fledglings may eventually return to the regions around their natal colonies?
- 5) At what rate do they go out and then return?
- 6) Do they go out once only, or do they go out and return on a regular or irregular basis?

In answering these questions consideration is given, where appropriate, to another question.

- 7) How do their movements vary from one colony to the next and from one epoch to the next?

Yet another question is asked: 'why do fledglings choose a particular direction when they leave their natal colony?' In arriving at the answers to these questions it is hoped that insights will be gained into the ways Cape Vultures leave their natal colonies. The ultimate aim of this enquiry is to decide if these movements can be described as *dispersal* or *exploration*. Is there a difference between exploration and 'dispersal'? The difference is real, for according to Baker (1982: 51-2):

The crucial difference between the two is that, as it travels, the explorer is continually making comparisons between present and previous locations, rejecting some, ranking others. A 'disperser' on the other hand, responds only to the habitat of the moment and settles as soon as one is encountered that is above the threshold.

### *How far do fledglings go?*

The mean distance travelled by all fledglings (i.e. 0 - 6 months) is 260 km and this increases to 424 km for second-years but decreases thereafter to 213 km for those four+ years old (Table 6.3, Figures 6.7 & 6.8 A). Not only do the mean distances travelled increase and then decrease (Figure 6.8 A) but the nature of the distributions also changes (Figure 6.7) with both fledglings and four+ year-old birds exhibiting 'inverted J-shaped' distributions while the intermediate age classes have nearly 'flat' or uniform distributions. This is apparent from the fitted gamma distributions. The maximum distances travelled by birds of each age class lie in the range 890 to 1226 km. The proportion of fledglings dying at their natal colonies (but known to have definitely fledged) is 45%, while the proportion of older free-flying birds expiring at their natal colonies is 24% (Table 6.5). This suggests that after fledging, young birds do stay around their natal colony for a little time before wandering ever further away until their third year, when they begin to return. Similar patterns have been observed, but on a smaller scale, for a population of Black Vultures *Coragyps atratus* in North America (Parker Rabenold 1985, 1986).

The mean distance travelled before death declined slightly from the 1950s to the 1960s, but thereafter there was a massive decrease in recovery distances during the 1970s. In the 1980s the recovery distances increased slightly (Table 6.7, Figure 6.11). Probable causes for this phenomenon are discussed below.

### *In which directions do fledglings go?*

Birds ringed at the south-central Transvaal colonies (i.e. Skeerpoort, Roberts' Farm, Nooitgedacht and Kranzberg) have been recovered, in the main, along a southwest to northeast axis, but with some birds found far and wide (Figures 6.3, 6.2 D, 6.2 B and 6.1 C respectively). The tendency to be found along this axis was first noted in 1959 (Anon. 1959) and later confirmed (Houston 1974). The Botswana-ringed birds (i.e. Mannyelanong and Manyana) have been recovered in 180° fan-shaped arc facing southeast (Figure 6.1 D). The birds from Manoutsa have travelled in two general directions: south-southwest and north (Figure 6.2 A). The directions travelled by birds ringed at Colleywobbles (Figure 6.1 A) have ranged from southwest to northwest in complete contrast to the other colonies (Figure 6.20)

The directions from natal colony to place of recovery for birds ringed in the south-central Transvaal have been summarized, by decade, in direction roses (Figure 6.16). These direction roses show that the recoveries in the 1950s were along a southwest to northeast axis, but mainly to the southwest. But the range of directions increased steadily during the 1960s and 1970s. There are insufficient data to make any statement about the 1980s pattern. This trend suggests that a wider range of sites was used.

*Where do fledglings go?*

From an examination of a peeling of a convex hull of all the recoveries (Figure 6.4 B) it is readily appreciated that there are recoveries from all over southern Africa (except Mozambique), but there is a tight core lying along a chord joining the southwestern Transvaal and the northern Cape. The same pattern also hold for recoveries of fledglings, but over a more restricted range (Figure 6.4 D). Older first-years show the same pattern, but slightly expanded (Figure 6.5 B) while second-years show an even wider pattern (Figure 6.5 D). However, third-years and four+ years show successively smaller ranges (Figures 6.6 B and 6.6 D), although there are nevertheless a few far-flung recoveries among four+ years. The patterns of resightings tend to be more restrictive than those resulting from recoveries (see sections 6.1 and 6.3 above), with two exceptions. Colleywobbles has two long-distance resightings (Figure 6.27 A) and Manoutsa has ten resightings spread over a much wider area than the recoveries (Figure 6.27 D). It is likely that the available resightings data do not indicate the full range of sites to which Cape Vultures travelled for there is one record of a resighting in Namibia during 1964 (Sauer 1973) and another two sightings in Namibia during October 1978 (Clinning 1980: 10). The origins of these ringed birds can no longer be established, but it is likely that they could only have come from the Transvaal or southeast Botswana, over 1000 km away (because these were the only sites at which ringing had taken place).

These patterns, together with the above examination of distances travelled, lend credence to the hypothesis that fledglings move out from their natal colonies for the first two to three years and then start to return.

There are some interesting changes with time among the recoveries. Taking only the recoveries of the birds ringed at the south-central Transvaal colonies (i.e. Skeerpoort, Roberts' Farm, Nooitgedacht and Kranzberg) and plotting their recoveries with time, it is apparent that in the 1950s the recoveries fell in an elongated rectangle lying along a southwest to northeast diagonal (Figure 6.14 A) but that this pattern became more elliptical with a far west Namibian arm during the 1960s (Figure 6.14 B) and then shrunk back during the 1970s and 1980s (Figures 6.14 C and 6.14 D). These changes are also reflected in the direction roses (Figure 6.16) which show the increasing angles through which recoveries were found, from the 1950s to 1970s and then there was a seeming reduction in the 1980s. This suggests that there has been a range contraction and expansion.

*What proof is there that fledglings may eventually return to the regions around their natal colonies?*

The fact that recoveries are found further afield for the first two years, and then closer to their natal colonies during the subsequent years, does not prove that they are returning. While this is probably true it may just be that as they get older they do not go as far. There are two colour-ringed birds each from Roberts' Farm and Skeerpoort which travelled far afield (three to the Kimberley district and one to Timbavati) where they were resighted. They then returned to the Magaliesberg where they were again resighted some years later (see section 6.3 above). This confirms that a bird which leaves its natal colony can indeed go far away and return. Weaker evidence comes from the resighting of 44 colour-ringed birds at their natal colonies at least a year after ringing (section 6.3 above, Figure 6.37). But this does not prove that they ever left their natal colony for any time. The observations of the birds in the southwestern Cape have not been included because they move over relatively small distances and they seem to constitute a single population visiting the roosts and colonies in the region.

*At what rate do fledglings move away from their natal colonies and then return?*

If it is assumed that birds dying are a random selection from their cohort, then the patterns of their deaths should reveal the patterns of the survivors from the same cohorts, at the same time. Based upon this assumption, a model is constructed of the rate at which young birds move away from their natal colonies (see below). However, it is likely that this assumption might not be completely satisfied by some cohorts (see discussion in section 5.2.2 above). It must be emphasized here that it is necessary for the reporting rate to be constant within a cohort and within a year only. Variations between age-classes and years are of no concern because the relative proportion of deaths in each age- or year-class are not examined, only the distance from the natal colony, at death, is modelled.

To construct a model of the rate at which fledgling Cape Vultures move out from their natal colonies and then return the following assumptions are made.

- 1) The distances travelled are isotropic (i.e. the same in all directions).
- 2) The relationship between distance travelled until death is a smooth function of elapsed time since fledging, and of epoch.
- 3) The colony effects, if any, are additive in a logarithmic model.
- 4) The impact of unnatural causes of mortality is assumed to act through longevity, not distance travelled, i.e. unnatural mortality may truncate the life of a bird and so influence how far from the colony the bird was when it died.

Table 6.29

Model parameters for  $Y = \text{Ln}(\text{Dist})$  as a critical exponential function of  $X = \text{Time}$  estimated using the GENSTAT 5.1 function FITCURVE. Elapsed distances (i.e. Dist) are measured in km and Time in months. A separate model is simultaneously fitted for each decade.

	Parameter	Estimate	s.e.
	U	0.9389	0.0112

Decade	Parameter	Estimate
1950s	b	-0.317057
	c	0.0290854
	a	5.90012
1960s	b	-0.340318
	c	0.251448
	a	4.73071
1970s	b	0.219674
	c	0.220421
	a	4.05861
1980s	b	1.76973
	c	0.306094
	a	3.07769

- 5) The reporting rate and probability of death is assumed to be the same for all individuals of a given age- and year-class, but may vary between calendar years and cohorts.

As some causes of unnatural mortality may have varied with time, but remained under-reported, it is possible that epoch may act as a surrogate variable for such factors.

The model is built in a two step process. First, the distance travelled is modelled as a non-linear function of time elapsed and then the residuals are used to test for the effects of other factors. This is the procedure suggested in the GENSTAT 5.1 package (Anon. 1988: 375). From an inspection of the data it is clear that the distance increases rapidly in the first year, or two, and then declines slowly. The initial increase is almost linear while the subsequent decline is approximately exponential. Consequently, the critical exponential function was chosen as an appropriate model (Anon. 1988: 366).

Because the various effects are thought to act in a multiplicative way the distances are transformed using a logarithmic function. It is also clear that the relationship between distance travelled and time elapsed is different in the four decades and so four models are fitted simultaneously, one for each decade.

$$Y = \text{Ln}(\text{Dist}) = a + (b + c \cdot \text{Time}) \cdot U^{\text{Time}}$$

(see parameter estimates in Table 6.29)

### Distance travelled vs elapsed time by decade

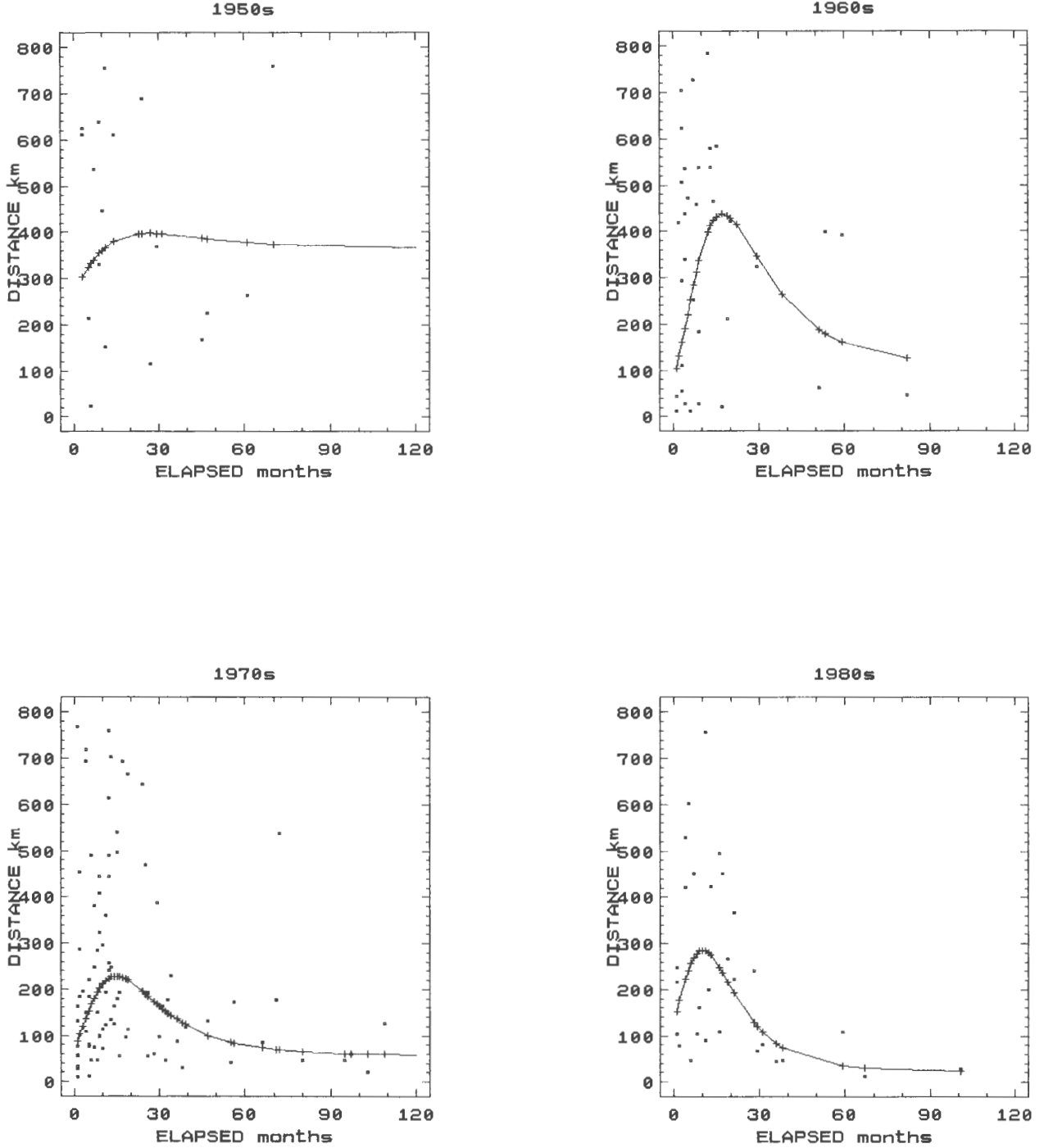


Figure 6.38 The distance travelled plotted against the time elapsed for ringed Cape Vultures found dead (i.e. recovered). Decades plotted separately. (One of the examiners felt that these models were a poor description of the data (BTJ Morgan, pers. comm.). These critical exponential functions are fitted to provide a general ‘picture’ of elapsed distance with time so as to illustrate the way in which young Cape Vultures move away from their natal colonies and then return some years later.)

### Comparison of critical exponential functions by decade

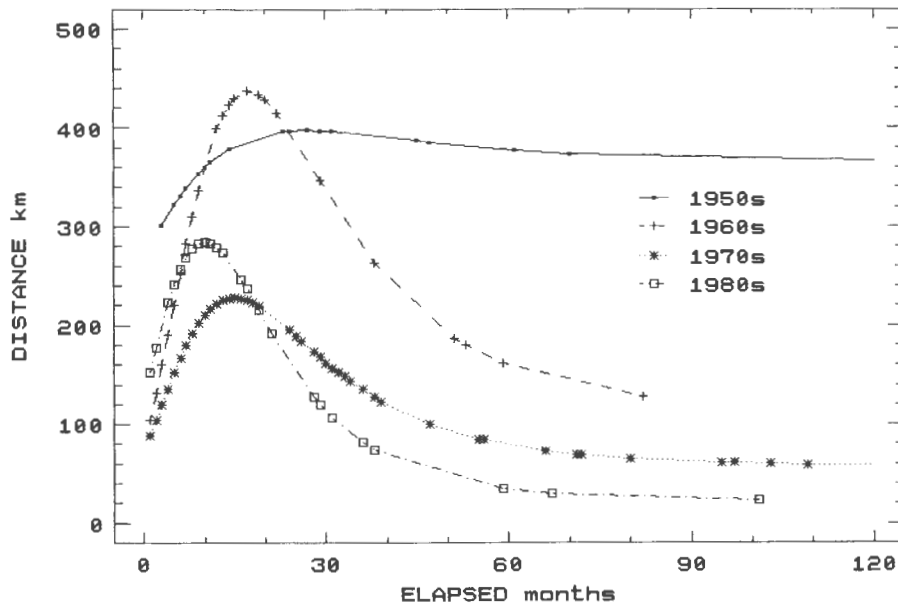


Figure 6.39 Models of distance travelled as a function of time elapsed for the four decades.

A comparison of the actual distances travelled plotted against time elapsed, for each of the four decades shows two interesting patterns (Figure 6.38).

- 1) There is still much variation about the models, even though they show the general trend. The models fitted achieve an overall reduction in variance of just over 20% and this suggests that the overall fit is probably not adequate.
- 2) The models for each decade are very different (Figure 6.39). The general shape of the curves for the 1960s, 1970s and 1980s are similar but with decreasing peak heights indicating that birds were not travelling out as far. This could imply that the species' range was contracting. It is likely that the rather 'flat' nature of the 1950s curve is due to the paucity of recoveries over five years during that decade and this may in turn be a function of the poor quality rings used (i.e. none lasted beyond 70 months). In addition, there is an outlier at (770 km, 70 months).

The residuals were computed from the following equation.

$$\text{Resid} = \text{Ln}(\text{Dist}) - \text{Ln}(\text{Fitted})$$

Variations in the residuals as a function of age at death, colony of ringing, tribal vs non-tribal colony of ringing and cause of death were investigated using one-way analysis of variance (ANOVA). It was found that there was no significant variation with any of these variables ( $p > 0.05$ ). In considering variations with cause of death the category 'cause unknown' was omitted. Colony of ringing as a source of variation was investigated after removing those colonies for which there was only one recovery. The residuals were also subject to a multivariate analysis of variance (MANOVA), but no significant effects or interactions were found ( $p > 0.05$ ).

Thus the variations in distance from natal colony, at death, can be explained in terms of elapsed time only with one model for each decade. The implications of this will be discussed below.

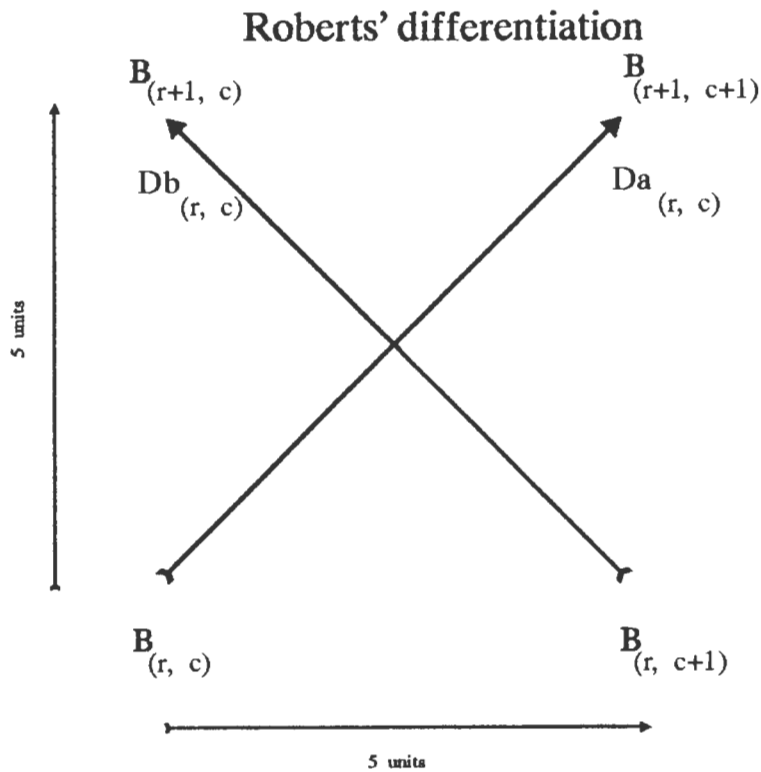
*Do fledglings leave their natal colony once only or do they depart and return many times on a regular, or irregular basis?*

To answer this question it would be necessary to have resightings of birds near the natal colony and far away from it. If they did in fact return then this could be elucidated from multiple resightings. This is not possible with the current data-set. All that can be said, given the constraints of the current data-set, is that Cape Vulture fledglings are capable of leaving their natal colonies and returning. Unfortunately the observational data of colour-ringed birds from the southwestern Cape cannot be used in this regard because the birds at the colonies and roosts in the sub-region behave as a single population (A.F. Boshoff pers. comm.).

*Why do fledglings choose a particular direction when they leave their natal colony?*

The key to finding an answer to this question is the observation (Mundy 1982: 101) that 'First-year birds in particular, suffer in competition with older birds at carcasses'. If this is an important 'push factor' which causes them to leave their natal colonies, or more specifically areas of high concentrations of adult birds, then it should be possible to illustrate this.

To this end a density map of breeding birds has been constructed using the known numbers of breeding pairs at the extant 83 breeding colonies (Figure 3.8), and then 'spreading out' these birds over the countryside using an exponential density function (see section 3.2.1 for a fuller description and motivation). The computation for mapping these point concentrations over the plane using an exponential probability density function are shown section 3.2.11. The resultant map (Figure 3.51 A) gives the density of breeding pairs. From this density map it is possible to compute gradient vector at each point using the Roberts' four-point function (Ganzalez & Wintz 1977: 157). This done in the following fashion.



**Figure 6.40** Mathematical conventions used in computing the gradient and its azimuth.

Construct a rectangular grid of side  $\delta$ . Let the number of breeding pairs at the intersection of the  $r^{\text{th}}$  row and  $c^{\text{th}}$  column be  $B_{(r,c)}$ . Consider the 'a' direction to run from the  $(r,c)$  to the  $(r+1, c+1)$  intersection. The 'b' direction runs from the  $(r, c+1)$  to  $(r+1, c)$  intersections. These two directions will be orthogonal because the grid has equal intervals in  $r$  and  $c$ .

Define the two differences

$$Da_{(r,c)} = (B_{(r+1,c+1)} - B_{(r,c)})/\sqrt{2\delta}$$

$$Db_{(r,c)} = (B_{(r+1,c)} - B_{(r,c+1)})/\sqrt{2\delta}$$

These are the components of the gradient. The magnitude of the gradient is:

$$D^2 = ((Da_{(r,c)})^2 + Db_{(r,c)}^2)$$

The angle of the gradient vector is computed from the arctan function taking into account the quadrants of the two vectors  $Da$  and  $Db$  (Exhibit 6.4.1).

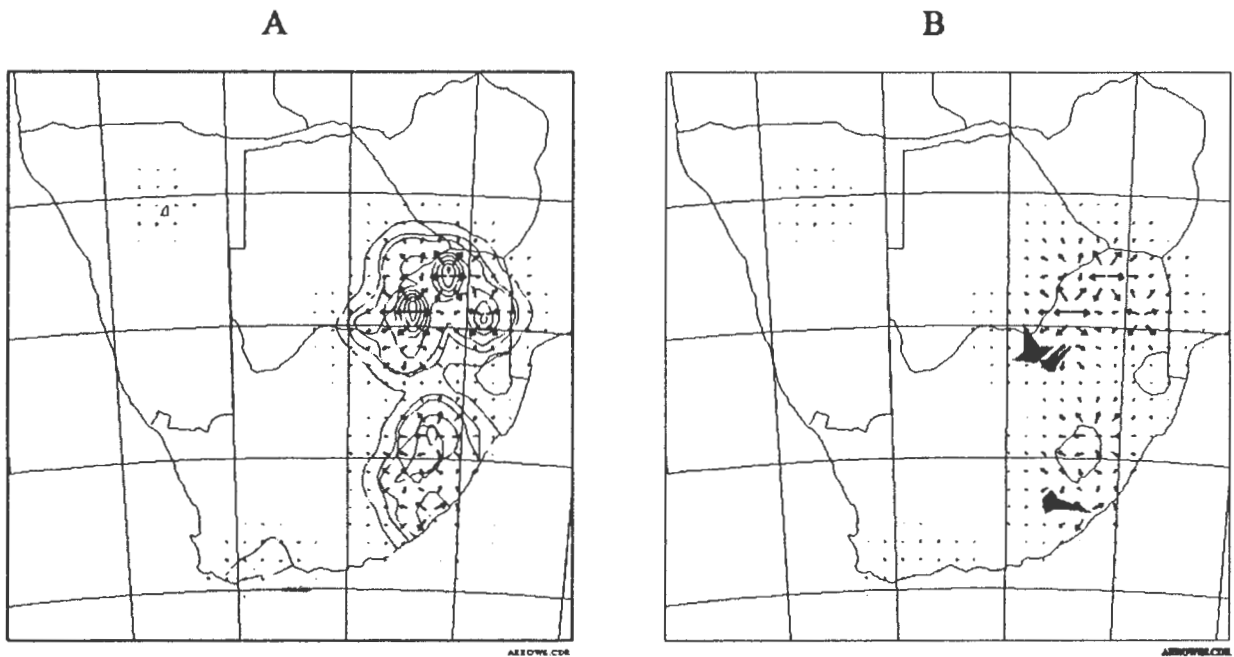


Figure 6.41 A) The gradient vector is shown superimposed on the contour map of the breeding pair density. Vectors are shown as arrows pointing 'down hill' with their lengths proportional to the magnitude of the slope. B) The mean directions in which the recoveries from four colonies (in clockwise order: Mannyelanong, Roberts' Farm, Skeerpoort and Colleywobbles) are found.

These computations, as well as those necessary to compute the magnitude and direction of the gradient (see Figure 6.40 for a sketch of the mathematical conventions) are illustrated in Exhibit 6.4.1. The gradient is shown on a map (Figure 6.41 A) with length proportional to magnitude. The direction is shown at  $180^\circ$  to the direction of maximum gradient - this is to indicate 'water-like flow' from high to low densities. Overlaying the direction roses of recoveries from four major colonies clearly illustrates the tendency for young Cape Vultures to 'drift down the gradient' (Figure 6.41 B). In other words, fledglings have difficulty in competing with the breeding birds at their natal colony and so tend to wander away in search of food in regions where the competition is less fierce. In so doing, it is suggested that they naturally tend to flow 'down gradient', moving from a region of a high concentration to one in which the concentration of adults is much lower and where the young birds can find food more freely.

### 6.4.3 Nursery areas.

The idea of a 'nursery area' for Cape Vultures has been suggested (see section 6.4.1 above) by a number of authors and these are brought together to formulate a working definition of the 'nursery area' concept.

A nursery area is a region to which recently fledged birds go. It is so far from the nearest breeding colonies that adults are only found there in low numbers and in small proportions. It should be populated by other Cape Vultures (because vultures do not forage on their own) and should also have a good food supply for at least part of the year (otherwise it not be reused).

Areas suggested as nursery areas, by a number of observers, are as follows.

- 1) Eastern Cape, Vernon (1984: 21).
- 2) Northern Natal, 'Whether Zululand is a "nursery area" for young Cape Vultures remains to be seen', Mundy, Ledger & Friedman (1980). See also Mundy (1982: 101).
- 3) The Orange Free State, Colahan (1988: 5, 1989: 2)
- 4) Northern Cape and Kimberley region, Brown (1987), Ledger & Mundy (1976: 7) and Mundy (1982: 101, 1983: 62).
- 5) Northern Botswana, Mundy (1982: 101).
- 6) Kalahari Gemsbok National Park, Mundy (1982: 101).

Possible additional nursery areas are motivated on the basis of existing information.

- 1) Southern and western Zimbabwe. It has been known for some time that there is a population consisting mainly of immatures in the region, many roosting at Wabai Hill (Mundy & Steyn 1977).
- 2) Northwestern and southwestern Botswana. It is clear from the extensive survey of the Cape Vulture in Botswana (Borello 1987) that the sightings in the southwest and northwest are of birds too far from the breeding colonies to be residents. Thus it would seem reasonable to expect them to be non-breeders. Given the wide distribution of African Whitebacked Vultures also found in these regions it is possible that the Cape Vultures are 'riding piggyback', so as to speak, on their 'sister' griffons (i.e. the African Whitebacked Vultures form a stable foraging-net in a region and the itinerant Cape Vultures then use this network to find food). If this is so then it is possible that these two 'horns' of distribution (Borello 1987) could be feeding Cape Vultures through to the Kalahari Gemsbok National Park in the south and to Namibia in the north.

What evidence is there for nursery areas?

- 1) A necessary condition for an area to be a nursery area is that there should be few adults there to compete with the young and less experienced birds. It is not possible to provide a map showing age composition (see section 3.1 above), but it is possible to show that

there are areas in which non-breeding birds predominate (section 3.1.3 above). Taking as a cutoff an arbitrary proportion of 70%, there are three such areas: eastern Cape, O.F.S. and northern Natal and Zimbabwe (Figure 3.17 B).

- 2) It is clear from the spatial analysis of recoveries that there are certain areas in which many birds die (see section 6.1 above). Some of these areas are the same as those where the proportion of non-breeding birds is high, or adjacent to those areas (e.g. compare Figure 6.3 with Figure 3.17 B).
- 3) The resighting of young birds from a number of different colonies in the same places as each other indicates that these places are used by the young from those colonies as nursery areas (see Figures 6.30 A and 6.34).
- 4) The fact that birds seen at these nursery areas return to their natal colonies indicates that these regions are used for a short time only (see Figure 6.30 C).

When using the ratio of non-breeders to breeders (from counts at roosts and colonies) to predict the proportion of young birds, a difficulty arises in those regions used by young birds where the birds roost in trees or on electricity pylons. The census of roosts and colonies misses these birds.

From the above, it is suggested that a region is likely to be a stable nursery area if it satisfies the following conditions.

- 1) The region is seldom used for foraging by adult birds, i.e. it is more than a given distance from the nearest breeding colony, probably 150 km.
- 2) The ratio of pre-breeders to adults is in excess of 50% for much of the year.
- 3) Young birds consistently visit the region and stay there to forage.
- 4) There are few sites in the region at which adults could breed.
- 5) If there are suitable sites for breeding, then the food supply will be seasonal, sporadic or unpredictable.

#### 6.4.4 Nomadism, vagrancy, irruptions and colonization.

*Nomadism.* From the analysis of 'secondary resightings' (i.e. marked birds seen at least twice) there is some evidence to suggest that once birds have left their natal colony they can visit other places in the sub-continent, moving from place to place (Figure 6.30 C).

*Vagrancy.* It is clear from the recovery data (see section 6.1 above) and the SABAP sightings (see section 3.2.5 above) that individuals do turn up in ones and twos at 'out-of-the-way' places. Given that Cape Vultures can move across country at about 45 km/hr for four to five

hours a day, it is not surprising that they can get to almost any part of the subcontinent. It has been suggested that there were 'vagrants at the extreme south of the range' (Snow 1978). As yet, no analysis has been undertaken of the extent of vagrancy in the Cape Vulture. In an attempt to use the SABAP data to construct a distribution map for the Cape Vulture, it was decided to exclude all those areas for which the reporting rate, of the smoothed data (i.e. using the kriging algorithm) was less than 3% (see section 3.2.5 above). This cut-off level was seen to eliminate the more obvious errors in the SABAP data and to provide a smooth distribution. The SABAP team are suggesting a cut-off of 1 - 2% for the raw data to eliminate identification (of vulture species) errors and vagrants (J.A. Harrison pers. comm.).

*Irruption and colonization.* Since the beginning of this century it has been known that the Cape Vulture can arrive in fair numbers in a region where there is a sudden and unpredicted increase in food. Six examples of such arrivals are presented.

- 1) An increase in Cape Vultures in the Transvaal just after the turn of the century was ascribed to 'Rinderpest and the South African War which led to a northwards movement of Cape Vultures' and 'Many dead horses, mules and cattle during and afterwards led to a population increase' (Anon. 1907).
- 2) 'About 80-90 Cape Vultures took up residence on E.K. Moorcroft's farm Clifton 60 km north of Adelaide, Cape during July, 1979.' (Bands 1979).
- 3) 'Graaff Reinet. The drought in the Karoo has brought ... vultures .. 150 of the huge birds ... vultures ... seldom seen near Graaff Reinet.' (E.P. Herald 1973).
- 4) At a farm on the way to Kei Mouth on 19 December 1982 a farmer was overstocked and suffering high sheep mortality. The Cape Vultures appeared there for the first time in seven years (Vernon 1983).
- 5) There was a strong Cape Vulture colony at Bawa Falls in the Transkei during the 1930s and 1940s, but it was deserted by about 1945. In 1967 birds were seen at the colony by an observer in a low-flying aircraft (Quickelberge 1989: 39). In 1979 it was said to have been reoccupied, while in May 1981 an estimate of about 300 birds was made (Vernon 1982). The actual number of nests found in June 1981 was 49 of which 51% were successful by September of that year. The colony is no longer active (C.J. Vernon pers. comm.).
- 6) "This source of food [10 000 culled African Elephants in May to August each year] ... resulted in an influx of Cape Vultures ... between 1982 and 1984", in the Hwange National Park, Zimbabwe (Hustler & Howells 1990).

These anecdotes lend credence to the 'conventional wisdom' that provided an area is not too far from an existing population, it is possible for that area to be colonized should there be a

supply of food there. It is likely that should the food supply persist the birds will remain and breed there so long as it lasts.

In the above it is not clear where the dividing lines between nomadism, vagrancy and irruption should be drawn<sup>1</sup>.

#### 6.4.5 Migration.

The Cape Vulture population is made up of two components: breeding (or paired) and nonbreeding. Consideration needs to be given to these sub-populations to determine if either is migratory. Before doing so, it is important to note that immatures not yet in full adult plumage may breed, and adults may not yet be breeding or may have skipped a year and refrained from breeding.

Breeding birds are tied to their breeding colonies from the start of nest building until the end of the post fledgling dependence period. At Colleywobbles, this lasts from early April through to late November or early December, i.e. a period of about eight to nine months (pers. obs.). This leaves the successful breeding birds less than four months in which to migrate. Observations at a number of sites indicate that there is considerable variation in Cape Vulture numbers during a given year. There are few birds at Colleywobbles during the height of summer, and it has been suggested that these breeding birds may have moved into the nearby Drakensberg Mountains (C.J. Vernon pers. comm.). At vulture restaurants along the high Drakensberg of Natal it has been noted that few vultures come to feed during the summer months October to March (D. Yuni, Giant's Castle and L. Tungay, Dragon Peaks pers. comm.). On the other hand, at the Estcourt vulture restaurant most birds come during the summer months (D. Wang pers. comm.). The Estcourt site is about 50 km from the Drakensberg, but is in open country. It is likely that breeding birds, during the summer when freed from their colonies, wander. There is no evidence yet to suggest that they migrate to any other area, but there is no contrary evidence to prove that they stay at their breeding sites.

In an earlier chapter (see section 3.2.4 above) a number of  $\frac{1}{4}^{\circ} * \frac{1}{4}^{\circ}$  grid cells were investigated for seasonal variations in the occurrence of Cape Vultures in the SABAP bird checklist data, but none showed any statistically significant temporal variations. This suggests that there is no migration. Unfortunately, there were few  $\frac{1}{4}^{\circ} * \frac{1}{4}^{\circ}$  grid cells with enough data to be tested. In an earlier assessment of Cape Vulture recoveries (Benson 1982, quoting Ledger & Mundy 1978), it was stated 'these [recoveries] indicate wide dispersal (up to 1000 km or more) but no regular migration'.

---

<sup>1</sup> D.S. Butterworth (*in litt.*) asks: "Would there ever be the data to test this? Are they not all elements along a continuum?"

Other vulture species show migratory movements. Alexander (1898) reported that the Egyptian Vulture showed local movements on the Cape Verde Islands. In an extensive survey of raptors in West Africa, it was found that Palmnut Vultures underwent considerable movements (Thiollay 1975, 1977). There are some vulture species in West Africa which show various levels of migration (Elgood, Fry & Dowsett 1973: 16): the Egyptian Vulture is fully migratory, while the Hooded and Lappetfaced Vultures are not migratory, there is little evidence for migration in the scarce Whiteheaded Vulture or in the common African Whitebacked Vulture. The movements noted in Rüppell's Griffon are explained as 'dispersal'.

#### 6.4.6 Natal fidelity and philopatry.

To determine the extent of philopatry it is necessary to consider the following questions.

- 1) Do Cape Vultures which left their natal colonies as fledglings return exclusively to their natal colonies to breed?
- 2) Do adults who have bred at least once at one colony ever move to another colony to breed?

To answer these questions a summary is provided of earlier results.

A number of birds have been ringed at one colony and then recovered (i.e. found dead) at another, different colony (see section 6.1). It is not possible to say if these were indeed inter-colony transfers, or just that the bird happened to die there. It is clear that birds which died in their first three years at another colony were unlikely to have begun breeding there. There were seven fledglings, three older first-years, two second-years and three third-years which died at other colonies (Tables 6.14 to .18). The potentially interesting movements are of ten birds of four+ years of age having moved from Colleywobbles to Vumenjani (1), Mannyelanong to Roberts' Farm (2), Roberts' Farm to Skeerpoort (3) and Skeerpoort to Roberts' Farm (4) (Table 6.18).

There are nine records of birds which were ringed at one colony having been seen alive at other sites (Figure 6.35), but for only two of these was there any reason to believe that they may have bred at the new colony (see section 6.3 above); these two birds moved from Roberts' Farm to Skeerpoort.

There are four records of birds which left their natal colonies to be seen some distance away, and later returned to their natal colony (section 6.3). In addition there were 44 birds which were ringed as nestlings, and then seen alive at their natal colony more than one year later (section 6.3 and Figure 6.37).

Cape Vultures from a given colony can, and do return to breed at their natal colony, but also may move to other colonies to breed. As yet, there are insufficient data to make any quantitative assessments concerning natal fidelity and philopatry.

#### 6.4.7 Home range and foraging.

What home range might be expected for the Cape Vulture? From a comparison of home range and body weight data from over 20 large raptors, the likely area needed per pair has been estimated to be about 50 km<sup>2</sup> (Newton 1979: 63). However, a foraging area of 13 to 27 km<sup>2</sup>/pair was estimated for Rüppell's Griffon (Pennycuik 1983: 182) - but they were feeding on large herbivores living at high densities. Using these estimates it is possible to devise a rough home range radius vs colony size relationship (Table 6.30). However, the estimate of 50 km<sup>2</sup> (Newton 1979: 63) per breeding pair is based on a set of assumptions which are directly applicable to solitary raptors. Thus, this analysis should be treated with caution. Notwithstanding, this comparison does indicate that there is a reasonable correspondence with observed inter-colony distances. This then suggests that the foraging radius of birds will increase as colony size increases. Given that these are realistic estimates then it follows that adult Cape Vultures may regularly need to forage at distance of about 100 to 125 km from their breeding colonies, given that they come from large colonies. This implies that it will be difficult to decide if a recovery at 100+ km from its natal colony was in fact a breeding bird, or was a bird still wandering about the sub-continent looking for a site or mate. Furthermore, given that some breeding colonies are well within 75 to 100 km of each other it is possible that a breeding bird could die closer to a neighbouring colony while foraging from its own colony. Thus the location of recoveries may yield less information than the resighting of a uniquely marked bird actually seen to be breeding.

Given that the maximum recorded colony size for the Cape Vulture is about 900 to 1000 pairs (Benson, Tarboton, Allan & Dobbs 1990), this suggests that the maximum foraging radius is likely to be about 125 km. This distance is well within the daily travel distances observed for *Gyps* vultures in east Africa (see start of this section).

Lastly, it should be borne in mind that 'the behaviour involved in regulating the size of colonies and the spacing between them has not been studied' (Newton 1979: 292).

Table 6.30

Comparison of actual intercolony distances with predicted colony foraging range from estimate of 50 km<sup>2</sup> per breeding pair (Newton 1979: 63).

No. of breed. pairs	Approx. area km <sup>2</sup>	Foraging radius km*	Inter-colony distance km*	Examples
30	1500	22	44	Potberg. Actual area = 1940 km <sup>2</sup> , forage within 40 km, Robertson & Boshoff (1986)
40	2000	25	50	It is suggested that birds from the high Drakensberg forage at distances of up to 54 km (Brown & Piper 1988 : 130)
350	17 500	75	150	The distance from Colleywobbles to the nearest big colony (Mtentu and Mtzikaba) is about 155 km.
875	43 750	118	236	Blouberg (825 pairs) and Kransberg (925 pairs) have an inter-colony distance of 200 km (Benson, Tarboton, Allan & Dobbs 1990: 136-137).

\* Distances are rounded to the nearest km after computation. Area is calculated at 50 km<sup>2</sup> per pair, foraging radius is  $\sqrt{(\text{Area}/\pi)}$  and inter-colony distance is twice foraging radius.

#### 6.4.8 Age-sets and spat-falls.

Most Cape Vulture nestlings fledge at about the same time because breeding is synchronized, so that most of the fledglings will be starting their lives as free-flying birds within a few weeks of each other. Consequently it is to be expected that they will experience the same 'push-factors' at about the same time, and will tend to move away from their natal colony together. It is also possible that they will move off in similar directions (see Figure 6.41 B) and so give the impression of being an 'age-set'. If this hypothesis is true then it is to be expected that groups of fledglings from the same natal colony and cohort should tend to turn up together at places about the sub-continent.

At Spring Farm Restaurant on New Year's Day 1978, a group of eight fledglings arrived from Skeerpoort, having been ringed there the previous year. Two weeks later, on 15 January 1978, 11 fledglings were seen (Table 6.27). It is possible that these fledglings had moved out as a group from their natal colony that morning. Three years previously, at Kimberley in the northeast Cape, fledglings were seen from both Skeerpoort (13, 10 and 3 birds) and Roberts' Farm (8, 5 and 4 birds) in September, October and November 1978 - they had been ringed the previous year. This suggests that they took at least nine months to reach this area. However, it does not prove that they all moved away from their natal colonies together.

**Exhibit 6.4.1**

Stored as E:\MCAD\CVFLOWP.MCD

Given a grid on which the number of breeding pairs is defined compute for the centre of each cell the magnitude and direction of the derivative

**Defaults**

ORIGIN := 1                      All vectors and matrices start at unity  
 Nr := 28                         Number of rows  
 Nc := 32                         Number of columns

**Zero data matrices**

r := 1..Nr  
     c := 1..Nc  
         D<sub>(r,c)</sub> := 0            A<sub>(r,c)</sub> := 0

Read in the count data for the number of breeding birds at each 5 mm by 5 mm grid intersection

Data are in a linear array N of length 896

N := READPRN(CVRADIAL)            rows(N) = 896

The rectangular array of count data is called P (for breeding Pairs)

There are 32 columns - from -90 mm to +65 mm in steps of 5 mm

There are 28 rows - from 10 mm to 145 mm in steps of 5

r := 1..Nr                              Cycle through the rows

c := 1..Nc                              Within each row cycle through the columns

$$P_{(r,c)} := N_{((r-1) \cdot 32 + c)}$$

**Compute the Roberts' Derivatives**

r := 1..Nr - 1            c := 1..Nc - 1

$$Da_{(r,c)} := \frac{P_{(r+1,c+1)} - P_{(r,c)}}{\sqrt{10}} \quad \text{The derivative at 45}$$

$$Db_{(r,c)} := \frac{P_{(r+1,c)} - P_{(r,c+1)}}{\sqrt{10}} \quad \text{The derivative at 135}$$

$$D_{(r,c)} := \sqrt{[Da_{(r,c)}]^2 + [Db_{(r,c)}]^2} \quad \text{Magnitude of the derivative}$$

$$A_{(r,c)} := \left[ \text{if} \left[ \left[ |D_{(r,c)}| + |D_{(r,c)}| \right] > 0, \left[ \text{angle} \left[ Da_{(r,c)}, Db_{(r,c)} \right] \cdot \frac{180}{\pi} + 135 \right], 0 \right] \right]$$

$$A_{(r,c)} := \text{if} \left[ A_{(r,c)} > 360, A_{(r,c)} - 360, A_{(r,c)} \right] \quad \text{Its direction; in degrees}$$

## Exhibit 6.4.1 (Continued)

It is now necessary to convert the D and A matrices into vectors so that they can be imported into SURFER's routine called TOPO

Convert the D matrix into the vector Dv

Convert the A matrix into the vector Av

r := 1..Nr

c := 1..Nc

Dv<sub>((r-1)·Nc+c)</sub> := D<sub>(r,c)</sub>

Av<sub>((r-1)·Nc+c)</sub> := A<sub>(r,c)</sub>

In order to plot these quantities using SURFER's routine TOPO it is also necessary to have the X and Y coordinates of the centre of the grid-cell

r := 1..Nr

c := 1..Nc

X<sub>((r-1)·Nc+c)</sub> := -90 + 2.5 + 5·(c - 1)

Y<sub>((r-1)·Nc+c)</sub> := 10 + 2.5 + 5·(r - 1)

Create an augmented vector called Derive to be written out as an ASCII file

WRITEPRN(DERIVEP) := augment(X, augment(Y, augment(Dv, Av)))

rows(X) = 896

rows(Y) = 896

rows(Dv) = 896

rows(Av) = 896

## 6.5 Summary

A 'word-model' of Cape Vulture movements from fledging to the time they start to breed many years later is presented below. This 'story' is pieced together from the evidence given above, but it also draws on studies of other long-lived species (e.g. Baker 1982: 55-56).

- 1) Fledglings are only fed at their nest during the post-fledging dependence period. Any other food they require must be found without their parents' assistance. Fledglings are consistently out-competed by adults at carcasses in the region of the natal colony.
- 2) It is likely that parents become increasingly unwilling to feed their fledgling at the nest as the summer progresses, so that the fledgling must find more food on its own. As it cannot compete adequately with adults it is likely that it will move away from its natal colony, avoiding areas with high numbers of adults. Thus it will wander 'down-gradient' from areas of high adult densities. This is likely to take place from January onwards in the summer rainfall areas.
- 3) Because many birds fledge from a colony at about the same time, they tend to drift away together as an age-set and so to turn up at new localities in a 'spat-fall' like fashion.
- 4) As they drift away from their natal colony, they are attracted to other vultures they see circling in the sky and towards evening they are pulled towards roosts where there are proportionally more young birds.
- 5) Fledglings will tend to gravitate to non-breeding roosts.
- 6) Fledglings, and first-years, will continue drifting away from their natal colony until they are in nursery areas.
- 7) Once in a nursery area they wander, nomad-like, exploring and evaluating vast tracks of country for about four to five years. During this time they will perfect their foraging, aerial and social skills.
- 8) From time-to-time they visit breeding colonies, possibly even their natal colony, evaluating their potential for acquiring a mate and a nest site.
- 9) Because they are not yet tied to any particular breeding colony, sub-adults will easily gravitate to new sources of food.
- 10) If a new source of food turns out to be long-lasting, a new breeding colony may form or a deserted breeding colony may be recolonized.
- 11) Of those birds that survive until their fourth or fifth year, some will return to their natal colony, or to another breeding colony, and will attempt to pair and breed.
- 12) Once a bird becomes a breeding adult at a colony it will embark upon a (daily) *return migrant cycle* (RMC). This RMC may be undertaken every one, two or three days while the pair is incubating an egg or every second day when they are feeding a nestling. At other times of the year, they may only go out when hungry. The frequency of foraging will be influenced by weather conditions, especially rain, thick mist and the absence of wind or thermals. On occasions a bird may spend one or more nights away from the colony if it is 'caught-short' by environmental conditions.

- 13) From the time the fledgling has departed until the start of the next breeding season (e.g. January to March at Colleywobbles), the breeding adults may wander in a nomadic fashion.

To place this model on a firm footing four types of experimental technique are required.

- 1) Nestlings and adults need to be fitted with unique combinations of colour-rings so that attendance at their breeding colonies can be monitored.
- 2) Fledglings and other sub-adults need to be fitted with radios so that their daily movements can be followed using conventional radio-tracking equipment.
- 3) A sample of birds from each age group needs to be fitted with high-powered radios so that they can be followed from a satellite-based system as they wander across southern Africa.
- 4) Young birds need to be caught and colour-ringed at sites known to be nursery areas. These birds are a good risk having survived the first year, or two, of life and are more likely to make it to adulthood. In addition their return to a breeding colony will yield useful information on recruitment to the adult population (Mundy and Steyn 1977).

This chapter has been about a peculiar class of behaviour - movements, rather than about some specific aspect of population dynamics. From this analysis it is clear that movements impact on the spatio-temporal aspects of demography in a number of ways.

- 1) Fledglings leave the vicinity of their natal colony before the start of the subsequent breeding season and so do not contribute to their parent population during the next time cycle.
- 2) Fledglings move to nursery areas where they are immigrants, supplementing the local population in fashion which may be density-independent.
- 3) Sub-adults may wander nomad-like about the sub-continent leaving and joining different spatial sub-populations.
- 4) Fledglings are only recruited into the parent population after a delay of some four to seven years.
- 5) Recruitment may be to a breeding colony other than the natal colony.
- 6) The fundamental spatial unit, or deme, may be greater than a single colony. Breeding birds from a group of colonies (e.g. the southwestern Cape) may act as a single unit.

Lastly, it is noted that a fledgling Cape Vulture from any given colony can wander to just about any part of southern Africa - and be killed there by some unnatural cause of mortality (e.g. electrocution). This has profound implications for conservation for it means that it is not sufficient to set aside a specific Cape Vulture nature reserve. The spatial domain of the Cape Vulture is the whole of southern Africa and if this species is to be conserved at all it has to be conserved everywhere.



# Demographic Models

## Contents

7.1	Leslie-Matrix and Life-Table models .....	392
7.1.1	Formulation .....	393
7.1.2	Most-likely projections .....	396
7.1.3	Sensitivity analyses .....	399
7.1.3.1	Age of first breeding .....	401
7.1.3.2	Variations in breeding success with age .....	402
7.1.3.3	Proportion of adults which breed .....	403
7.1.3.4	Sub-adult survival & recruitment .....	405
7.1.3.5	Adult survival .....	406
7.1.3.6	Interaction of sub-adult and adult survival .....	407
7.1.3.6	Maximum age of breeding .....	409
7.1.4	Recommendations for research and conservation .....	411
7.2	Model of Cape Vulture population in Southwestern Cape .....	414
7.2.1	Model construction .....	422
7.2.2	Model evaluation .....	425
7.2.3	Summary .....	428
7.3	Stochastic models .....	433
7.3.1	Environmental stochasticity .....	433
7.3.2	Demographic stochasticity and extinction .....	442
7.3.4	Minimum viable population .....	450
7.4	Spatial-compartment models: Meta-population analysis .....	452
7.4.1	Model formulation .....	454
7.4.2	Environmental stochasticity .....	461
7.4.3	Demographic stochasticity and migration .....	466
7.4.4	Summary .....	468
7.5	Summary .....	470

## Abstract

A Leslie-matrix model is constructed of the Cape Vulture population using the best estimates of fecundity and survival. From a sensitivity analysis, recommendations for a colour-ringing programme are devised which could provide adequate demographic parameter estimates. A model of the southwestern Cape sub-population reveals that the adult survival rate could be in excess of 90% p.a. Stochastic models are then used to show that the central core population is likely to be stable in the long-term, provided current conditions persist. Peripheral sub-populations may go extinct as a result of demographic stochasticity, but they could be stabilized by permanent immigrants.

# Demographic Models

A 'Grand Question' is asked in this thesis.

*What is the probability that the Cape Vulture will survive well into the twenty-first century as a free-flying bird?*

To answer this 'Grand Question' consideration has been given in earlier chapters to the subsidiary questions.

- 1) How many Cape Vultures are there? (section 3.1.1).
- 2) Where are they? (section 3.2).
- 3) How fast are they increasing or decreasing at each colony and roost? (section 3.3).
- 4) At what rate can new individuals be added to the population? (Chapter Four).
- 5) At what rate are individuals lost from the population? (Chapter Five).
- 6) At what rate are individuals transferred between the spatially disjoint sub-populations? (Chapter Six).

In response to questions posed in earlier chapters, data have been collected and analyzed. The results of these analyses are estimates of various population parameters and variables as well as some insight into the nature of the population dynamics of this species. To answer the 'Grand Question' posed above a subsidiary question is asked.

*What is the stability of the population in space, time and age-structure?*

Answers to these questions will be generated in a number of ways. The first approach will be to use a 'bottom-up' approach by building a Leslie-matrix model based upon the life-table. The data for the life-table are in the form of age-specific breeding productivity and survival rates. Initially the Leslie-matrix approach assumes that the population is spatially homogeneous and that the various age-specific population parameters are the same for all individuals of that age. Consideration is given to the sensitivity of the population growth-rate to each of the major population parameters and variables by means of Leslie-matrix models. From this sensitivity analysis will be drawn a number of conclusions concerning the need for further data collection, research and analysis. In particular, recommendations will be made as to the way the philosophy of conserving the Cape Vulture should change.

Both birth and death are probabilistic processes, and while deterministic models are adequate for modelling large populations, it is necessary to use stochastic models for small isolated populations, such as those in Namibia and the southwestern Cape. Consideration will be given to estimating the minimum viable population size by employing a stochastic model.

A 'top-down' approach will be used to model the observed population dynamics of the Cape Vulture in the southwestern Cape, where the total numbers have been counted most years between 1974 and 1990, and where the number of large nestlings produced each year is known exactly for the same time period.

It is clear, from the discussions of earlier chapters, that the Cape Vulture population is spatially heterogeneous in terms of its density, productivity and losses. To model this a spatial-compartmental model will be developed.

### 7.1 Leslie-matrix and Life-Table models

It has been shown, in earlier chapters, that the Cape Vulture population is age-structured with young birds having much lower survival rates than old birds, and young birds not breeding until their fourth to seventh year. Thus it is important to choose, as the simplest mathematical model one which acknowledges this age-structure. If it may be assumed that all the population processes are a function of *age only*, and independent of all other density and environmental effects then an appropriate model (Caswell 1989: 5 ff.) is that known as the Leslie-matrix model.

Initially a simple, augmented, Leslie-matrix model will be developed. It will be shown that if the population has reached a stable age distribution (i.e. the *proportion* of individuals in each age class does not change from one epoch to the next) then the population size ( $N_{t+1}$ ) at time ( $t + 1$ ) is related to the size at  $t$  ( $N_t$ ) by the equation:

$$N_{t+1} = N_t e^r$$

or its equivalent:

$$N_{t+1} = N_t \Gamma$$

(Note that my word processor does not have the lambda used conventionally so I am using  $\Gamma$  instead.)

The factor  $\Gamma = e^r$  is known as the *finite rate of natural increase* and  $r = \ln(\Gamma)$  is known as the *intrinsic rate of natural increase* (Pielou 1969: 43). This corresponds to showing that when the population has reached a stable age distribution it then grows (or declines) at a constant (exponential) rate.

This simple model is to be used to compute the growth rates corresponding to the various demographic parameter estimates which were derived in earlier chapters (section 7.1.2 below). This will be followed by a series of seven sensitivity analyses in which the change in the intrinsic rate of natural increase ( $r$ ) in response to a change in each of the demographic parameters is investigated (sections 7.1.3.1 through to 7.1.3.7 below). From an examination of these sensitivity analyses, a set of recommendations will be presented for managers wishing to refine their conservation action programmes.

The matrix method named after Patrick Holt Leslie (known to his friends as George<sup>1</sup>) was developed independently by Bernardelli (1941), Lewis (1942) and Leslie (1945, 1948). The emphasis of Bernardelli (1941) is on the ‘population waves’ that can develop from the application of a simple projection matrix. The formulation of Lewis (1942) is more compact than that of Leslie (1945) and the primacy of Lewis’ development was subsequently acknowledged by Leslie (1948). Later it was shown that the life-table methods (e.g. Lotka 1924) are functionally similar to the Leslie-matrix methods (Leslie and Park 1949).

### 7.1.1 Formulation

In formulating the Leslie-matrix model a number of assumptions and conventions are adhered to; unless stated otherwise this derivation follows Caswell (1989: 5-15).

- 1) The population is divided into a finite number of discrete age classes of equal duration. This ‘age class duration’ is taken to be equal to the time-step through which the model is iterated and both are scaled to unity. If  $x$  is the age of a member of the population then the age classes are defined as follows.

$0 \leq x < 1$ . This is age class 1.

$1 \leq x < 2$ . This is age class 2.

$2 \leq x < 3$ . This is age class 3.

This continues until the last two age classes are reached:

---

1 For a more extensive review of the historical development of the topic see Caswell (1989 p. 24-26), from which the material for this paragraph is drawn.

$$(A-1) \leq x < A$$

$A \leq x$ . This is termed the 'adult' age class.<sup>2</sup>

- 2) The time-step, or population projection interval, is scaled to unity.
- 3) The quantity  $n_i(t)$  is defined as the number of females in the  $i^{\text{th}}$  age class (i.e. aged  $(i-1) \leq x < i$ ) at time  $t$ .
- 4) If the population is closed with no immigrants, or all permanent emigrants are counted as losses, then the number of females in age class  $i$  at time  $(t+1)$  will be:  

$$n_i(t+1) = S_{i-1}(t) * n_{i-1}(t) \quad \text{for } i=2,3, \dots A-1.$$

Where  $S_{i-1}(t)$  is the survival rate for those females in the age class  $(i-1)$  during the period  $t \rightarrow t+1$ , i.e. the probability of surviving from the  $(i-1)^{\text{th}}$  to  $i^{\text{th}}$  age classes.

- 4) For the adult age class:  

$$n_A(t+1) = S_{A-1}(t) * n_{A-1}(t) + S_A(t) * n_A(t)$$
 where the second term represents 'adult retention', i.e. the number of adults who survive from one year to the next, and are thus 'retained' in the population.

- 5) The number of large fledglings produced each year is:  

$$n_1(t+1) = F_1(t) * n_1(t) + F_2(t) * n_2(t) + \dots + F_A(t) * n_A(t)$$
 Where  $F_i$  is the fecundity of the  $i^{\text{th}}$  age class during the period  $t \rightarrow t+1$ . This is defined as the average number of large, female fledglings produced each year per adult female physiologically capable of breeding in that year (see definition of first age class below).

These finite difference equations may be written as a set of linear equations (taking age class six and above as adult for the case under investigation):

$$\begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \\ n_6 \\ n_7 \end{bmatrix} (t+1) = \begin{bmatrix} 0 & 0 & 0 & 0 & F_5(t) & F_6(t) & F_7(t) \\ S_1(t) & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_2(t) & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_3(t) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_4(t) & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_5(t) & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S_A(t) & S_A(t) \end{bmatrix} * \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \\ n_6 \\ n_7 \end{bmatrix} (t)$$

This may be written in the more compact matrix notation as follows.

$$n(t+1) = B(t) * n(t)$$

---

2 It is of little consequence that the numbering of the age classes begin at one rather than at zero (see Caswell 1989: 7)

Where  $n(t)$  is the population size vector (i.e. the number of individuals in each age class) at time  $t$ ,  $n(t+1)$  is the population at time  $t+1$  and  $B(t)$  is the *augmented* population projection matrix at time  $t$ . If  $B(t)$  lacks the adult retention term (i.e. the lowest rightmost) and does not vary with time then the matrix will be:

$$\begin{bmatrix} 0 & 0 & 0 & 0 & F_5 & F_6 & F_7 \\ S_1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_4 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S_A & 0 \end{bmatrix}$$

This is the population projection matrix of the standard Leslie-matrix theory (Caswell 1989: 8).

The augmented Leslie-matrix model, as formulated here, differs in two minor respects from the standard. First, it has the adult retention term which augments the population projection matrix. Secondly, the matrix projection cycle is assumed to run from the start of one calendar year to the next. This puts the definition of the first age class slightly at variance with the other age classes. The age classes are defined in the following manner.

- Age Class 1. The number of large female nestlings in the population at the time of ringing. This can be between early September for the Transvaal colonies through to late December for the southwestern Cape colonies. Consider an individual ringed on 12 September 1986. It will be in its first year until the 31 December 1987.
- Age Class 2. The number of individuals which have survived at least one full *calendar* year since fledging. Thus the fledgling ringed on 12 September 1986 will be in its second year, and in age class 2 from 1 January 1988 through to 31 December 1988.

This ageing convention is best illustrated graphically (Figure 7.1). The reason for this slightly awkward convention is purely pragmatic. It is possible to count the number of large nestlings with some ease, and so it is possible to provide accurate estimates of fecundity. The losses at fledging have not been estimated independently, and are subsumed into the first year survival rate which is estimated from ringing (see Chapter Five).

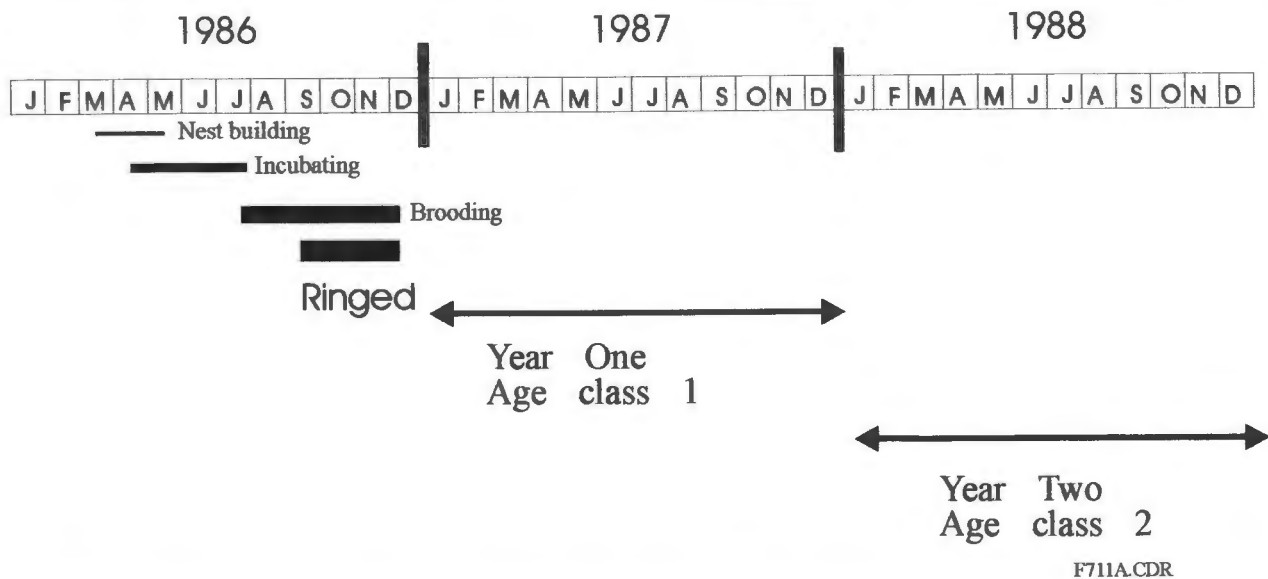


Figure 7.1 Relationship between age-class and calendar year for a large nestling ringed in late 1986.

Using arbitrary, but reasonable, values for the survival probabilities a typical simulation is performed (Figure 7.2) from which it may be seen that population stabilizes after some 8-10 years. The way in which the population varies from any given starting point to the stable age distribution will be considered in more detail below (see section 7.2).

### 7.1.2 "Most-likely" projections<sup>3</sup>

From chapters Four and Five it is possible to extract estimates of fecundity and survival. These estimates are summarized here and where two or more estimates exist for the same parameter, an explanation is provided as to why one in particular should be chosen. The estimate of fecundity made for the population at Colleywobbles during the decade 1980-1989 is the best made so far, because it is based on the biggest data-set and has been collected in the most consistent manner (pers. obs.). The estimates of survival are not as reliable and three different sets will be used: Piper, Mundy & Ledger (1981), the estimates based on the ring-recovery data-set (from section 5.2.3 above), and the estimates based on the ring-resighting data-set of the southwestern Cape (from section 5.2.4 above). For each data-set, the intrinsic rate of natural increase will be computed along with stable age distribution. The time-to-extinction will also be calculated.

3 All Leslie-matrix computations were written as routines in Mathcad 3.0 and copies can be supplied to interested readers.

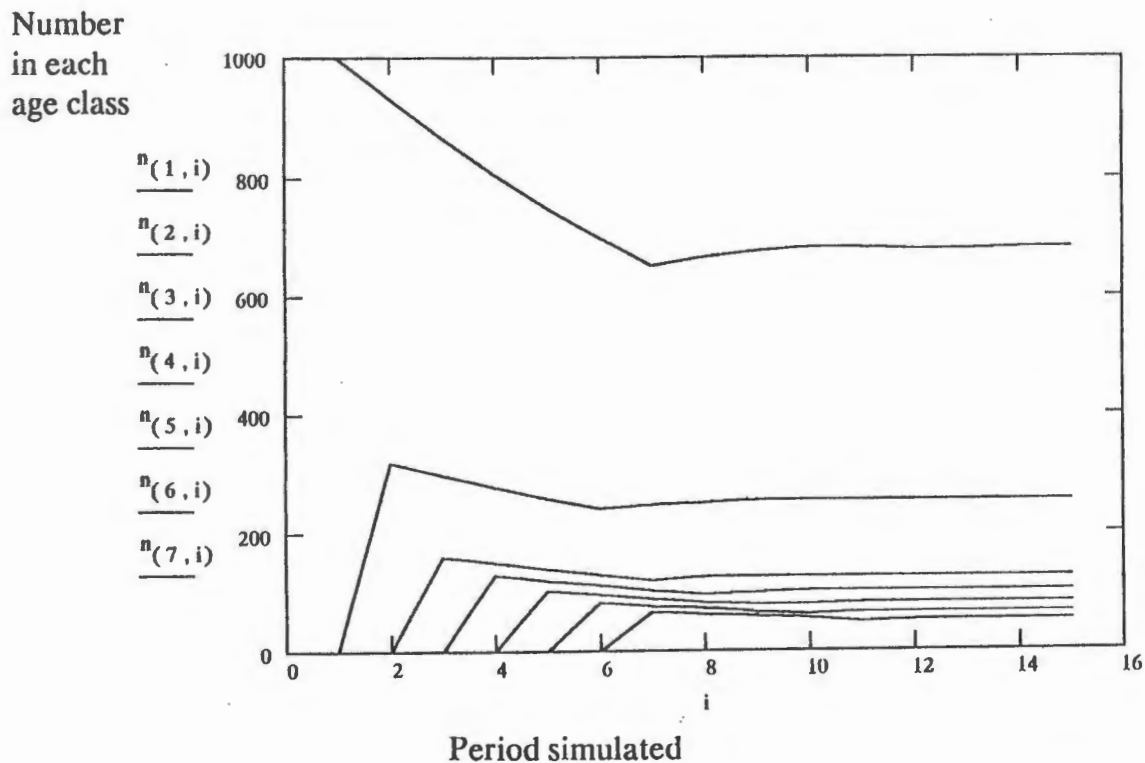


Figure 7.2 Variation in age-structure with time. The age-distribution tends to the stable age-distribution in about eight to ten cycles for this particular initial age-distribution.

*Fecundity*

The maximum proportion of adult pairs which breed is 85% and their maximum breeding success is 75% (see Chapter Four). Thus they can, at most bring forth  $(0.85) \cdot (0.75) / 2 = 0.31875$  (i.e. 0.32) large female fledglings p.a. (assuming that the proportion of female offspring is  $\frac{1}{2}$ ). It will be assumed that females can begin to breed in their fifth year and do so at the maximum rate possible.

*Survival estimates from Piper, Mundy & Ledger (1981) <sup>4</sup>*

These estimates are based on 118 recoveries from 3708 ringed birds. Independent estimates are provided for the first two age classes and thereafter the estimates for all older age-classes are lumped.

Age Estimate	Lower	Upper
1	17%	49%
2	61%	72%
3+	74%	92%

(Survival estimates all as % surviving p.a.)

<sup>4</sup> No confidence is placed in these estimates, they are used for illustrative purposes only.

The finite rate of natural increase,  $\Gamma = 0.79$  and this is equivalent to a decrease of 23.9% p.a. It is predicted that the adults will constitute some 54% of the population and it is projected that the current population of 12 000 birds (see Chapter Three) could decline to one bird in about 39 years. If this model were true, then the population should have declined to about 8% of its size since the time these survival estimates were first published over a decade ago. Clearly it has not.

*Survival estimates from ring-recovery data (section 5.2.3)*

This data-set is essentially the same as that of Piper, Mundy & Ledger (1981), but is based on two and a half times as many recoveries (i.e. 295 vs 118). The data yield much higher estimates for the early age classes.

Age Estimate	Lower	Upper
1	42%	49%
2	61%	70%
3	64%	75%
4	65%	78%
5+	70%	79%

(Survival estimates all as % surviving p.a.)

The finite rate of natural increase,  $\Gamma = 0.79$  and this is equivalent to a decrease of 23.3% p.a. The adults constitute some 41% of the population and it is predicted that the current population of 12 000 birds could decline to one bird in 40 years. This model does not give an appreciably lower estimate of population decline than the previous model. Initially this seems somewhat surprising as the first year survival rate is much higher, however, this is counterbalanced by an estimate of adult survival which is lower.

*Survival estimates from ring-resighting data from the S.W. Cape (section 5.2.4).*

These are probably the most believable estimates as they are based on direct observation.

Age Estimate	Lower	Upper
1	53%	62%
2	84%	92%
3	78%	88%
4+	70%	81%

(Survival estimates all as % surviving p.a.)

The finite rate of natural increase,  $\Gamma = 0.85$  and this is equivalent to a decrease of 16.2% p.a. The adults constitute some 41% of the population and it is projected that the current population of 12 000 birds could decline to one bird in 58 years. Of the three models, this projection gives the highest finite rate of natural increase, but it is still not close enough to unity to permit stability.

These analyses all suggest that the Cape Vulture population is declining at a high rate. While it is possible that the population could indeed be declining (see Chapter Three) there are no reports from observers in the field to suggest that it is decreasing at the rate predicted by these models. So what is wrong? The fecundity term cannot be made much higher (Chapter Four) and the first year survival estimate is probably at its upper limit (Chapter Five). On the other hand, the estimate of adult survival is not reliable (*loc. cit.*). Thus it is likely that the estimate of adult survival is too low. From the comparative data reviewed in Chapter Five it is probable that the Cape Vulture should have a higher survival rate for adult birds.

### 7.1.3 Sensitivity analyses

Although the Cape Vulture is the most-studied Old World vulture (Mundy, Butchart, Ledger & Piper 1992: 72), no thought has been given to planning systematic experiments to estimate its demographic parameters. The sensitivity analyses to be presented below have been designed to answer three broad groups of questions.

- 1) Within what realistic and feasible limits must the demographic parameters lie to ensure that population will be stable?
- 2) By how much will the intrinsic rate of natural increase change when a single demographic parameter, or a group of demographic parameters, is changed?
- 3) Given that a demographic parameter is estimated with an error of  $\pm e$  what will be the concomitant error in the estimate of the intrinsic rate of natural increase?

The sensitivity of the intrinsic rate of natural increase will be computed with respect to the following seven parameters, or groups of parameters.

- 1) Age-at-first breeding.
- 2) Variation in breeding success with age.
- 3) Proportion of adults which breed.
- 4) Sub-adult survival (i.e. varying in consort, as a group).
- 5) Adult survival.
- 6) The joint interaction of sub-adult with adult survival.
- 7) The maximum age of breeding.

While the intrinsic rate of natural increase has been chosen as the target for sensitivity analyses it has been suggested that attention could also be directed at the generation time,  $T_0$  (Lebreton & Clobert 1991: 110).

All the sensitivity analyses will be computed directly, not analytically. Many authorities have recommended direct computation (see list of references in Caswell 1989: 119-120). The main reason for doing so here is that some of the sensitivities (e.g. with respect to age-at-first-breeding) cannot be computed directly using the standard analytical methods which use some form of  $\delta R / \delta a_{ij}$  (where  $\delta$ =curly d means partial differentiation and  $a_{ij}$  is an element of the Leslie-matrix). However, a variety of analytical results have been derived for sensitivity analyses (e.g. Caswell 1989: 120 ff.) and these will be used where appropriate.

The starting point for some of the analyses used below is the characteristic equation.

$$\det(\mathbf{B} - R \cdot \mathbf{I}) = 0$$

where  $\mathbf{B}$  is the augmented Leslie-matrix,  $R$  the leading eigenvalue and  $\mathbf{I}$  an identity matrix. It is sometimes possible to expand this equation explicitly and estimate the sensitivity of  $r$  with respect to the parameter of interest directly. This is the method used to determine an approximate minimum value for the maximum age of breeding.

For these sensitivity analyses, a population projection matrix which exhibits zero population growth (ZPG) is used as the baseline from which changes are measured. The ZPG population projection matrix is used for two reasons.

- 1) The Cape Vulture population is nearly constant in size. Two arguments are advanced for this. In Chapter Three it was shown that some peripheral roosts and colonies are decreasing while some core colonies are increasing. It has been independently suggested that the Transvaal sub-population was constant for the first five years of the 1980s (Benson, Tarboton, Allan & Dobbs 1990). This is an important observation because about 60% of the breeding population is contained within the Transvaal (Chapter Three).
- 2) Given that the ZPG population projection matrix is used as the baseline means that the finite rate of natural increase will be unity so that any sensitivities are measured relative to unity and do not need to be scaled.

In the previous section, it was shown that all three "most-likely" projections yielded values of  $\Gamma$  which were much less than 1, implying that the populations were nowhere near equilibrium. The population projection matrices had all parameters at near their maximum values, except for adult survival which was poorly estimated, and probably also negatively biased (Chapter Five). To achieve ZPG, an adult survival of nearly 90% is needed, such an adult survival rate is feasible, by comparison with other griffons (Chapter Five).

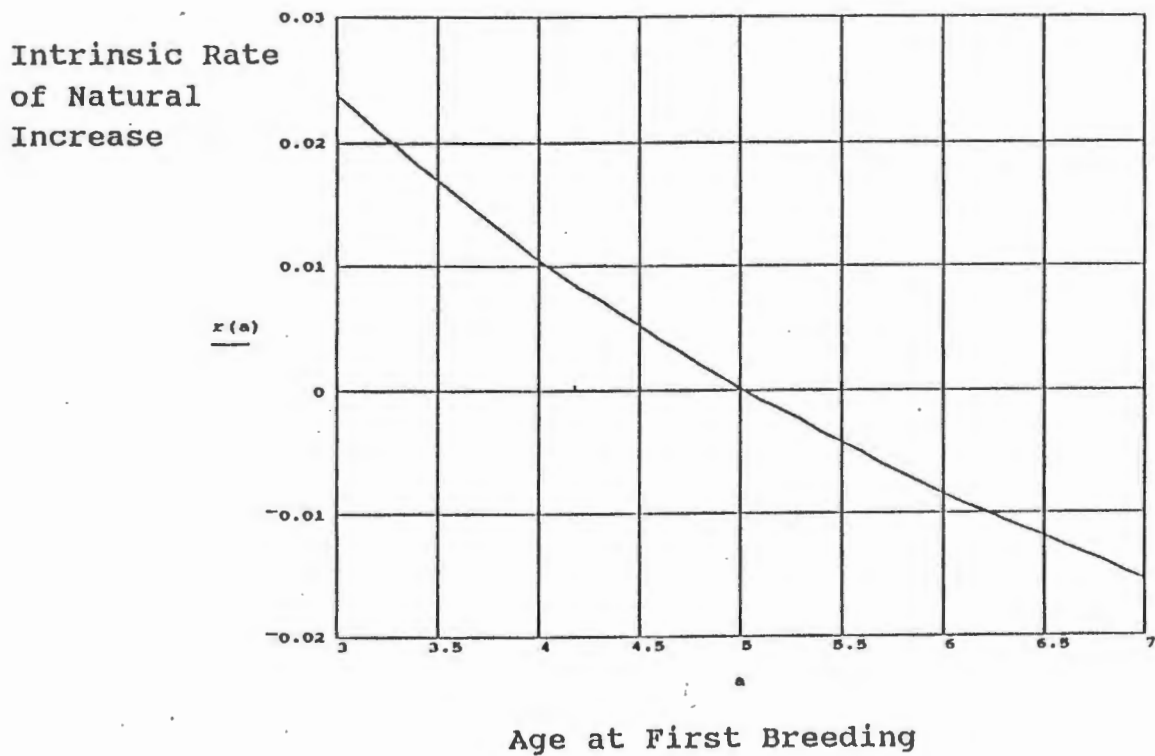


Figure 7.3 Variation of intrinsic rate of natural increase with age at first breeding.

### 7.1.3.1 Age of first breeding

It has been suggested that the age at first breeding is likely to be an important factor in the population dynamics of a species (Clobert & Lebreton 1991: 78-9 & references therein):

Age at first breeding is a potentially important factor in population regulation as well as in life history theory.

By how much can the age at which Cape Vultures first breed vary? From the observations of colour-marked birds at Potberg (Robertson 1983), it is known that birds can make their first breeding attempt in their fourth year, but this is not true for all birds. At the other extreme, a bird may begin breeding only once in adult plumage, i.e. when it is at least six years old (Piper, Mundy & Vernon 1989). It is known that there are birds in full adult plumage which are not breeding. These adult non-breeders may be seen, during the breeding season, at breeding colonies standing at nests not used (C.J. Vernon pers. comm.), or they may be seen at roosts which are so far from breeding colonies that they cannot be breeding (e.g. Dronfield Ranch, near Kimberley and Wabai Hill in Zimbabwe, P.J. Mundy

pers. comm.). Thus, to include all possibilities, the age at first breeding is allowed to vary through the range 3 to 7 years. It is likely that even though some birds are capable of breeding in their sub-adult plumage, not all will be able to breed then. To allow for this the proportion that are able to breed is allowed to run through the range 0 to 100% for each age class in succession.

The sensitivity analysis (Figure 7.3) reveals that allowing the age of first breeding to vary from the start of the third year to the end of the sixth year causes the intrinsic rate of natural increase to vary from about +2% down to just under -1%. Contrary to the expectation expressed above (i.e. Clobert & Lebreton 1991: 78-9) this is a negligible amount. Why is this so? It is suspected that the opinion of Clobert & Lebreton (1991) is based on studies of short-lived species where deferring breeding for a single year is equivalent to between a quarter and half a lifetime (see Newton 1989 and the discussion therein on lifetime reproductive success). Thus, provided that the average age at which all birds start to breed is confined to the range three to six years then the variation in intrinsic rate of natural increase will be within the range  $\pm 2\%$ . This variation will be seen to less than with some other parameters.

### 7.1.3.2 Variations in breeding success with age

There is considerable evidence to suggest that with experience breeding pairs get better at bringing forth new young. As time progresses, they show greater breeding frequency and breeding success. This has been shown for the Great Tit *Parus major*, Arctic Tern *Sterna paradisaea* and Eurasian Sparrowhawk *Accipiter nisus* (see review in Partridge 1989).

There are absolutely no data to test this hypothesis in the case of the Cape Vulture. It is, however, possible to get some idea of the potential limits of age-specific variation by examining the breeding success data from Colleywobblers (Chapter Four). For nests laid in twice only out of a possible maximum of ten years, the breeding success was about 60%. At the other extreme, nests laid in ten times out of ten yielded a breeding success of 80%. This is equivalent to assuming that pairs which fail most often, *when they do breed*, will in turn breed less often. Assuming that adults breed, on average, in 85% of years and that the sex ratio is 50:50 then this represents fecundities of  $(0.85) \cdot (0.60) \cdot (0.50) = 0.255$  through to  $(0.85) \cdot (0.80) \cdot (0.50) = 0.34$ . By way of exploring this phenomenon the fecundity of birds in their fifth year was put at 0.25 and that of adults in their seventh and subsequent years was allowed to be 0.34.

---

 Intrinsic Rate of Natural Increase
 

---

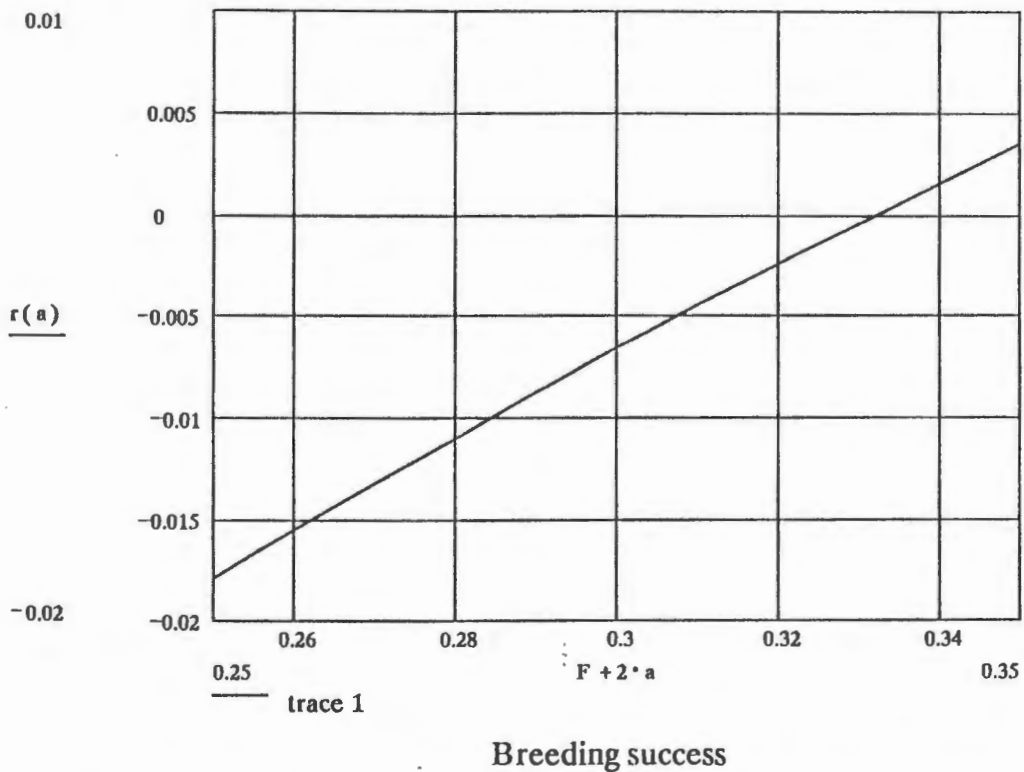


Figure 7.4 Variation of intrinsic rate of natural increase with increase in breeding success.

From a sensitivity analysis (Figure 7.4) it may be concluded that the maximum change in the intrinsic rate of natural increase is likely to be in the range  $\pm 0.5\%$ . Thus this effect is likely to be small in the Cape Vulture. This is largely due to the fact that with a clutch size of one there is little potential for large variations in fecundity.

### 7.1.3.3 Proportion of adults which breed

It is known from the Colleywobbles data that there has been considerable variation in the proportion of Cape Vultures which breed each year (Chapter Four). At Colleywobbles, the proportion of pairs which breed each year is estimated from the proportion of nest sites tenanted at the start of the breeding season and in which eggs are subsequently laid in. (A tenanted nest site is one which has a pair of birds standing assiduously at the nest site, or building a nest.) Unfortunately, there are few colour-ringed birds, at Colleywobbles so that estimating the breeding proportion from nests tenancy will underestimate the true ratio because some non-breeders may not return to their nest site during a 'year out'.

### Intrinsic Rate of Natural Increase

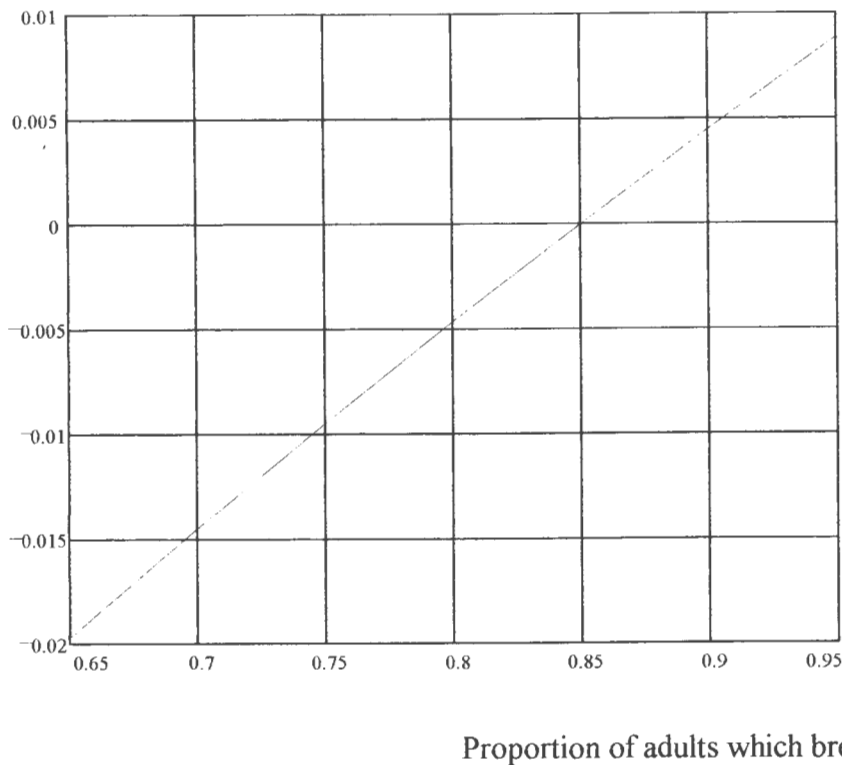


Figure 7.5 Variation of intrinsic rate of natural increase with the proportion of adults which breed.

It is known for a number of other large species that some birds, or pairs, ‘take a year out’, especially after having bred successfully the previous year (e.g. Rothery & Prince 1990 for Blackbrowed Albatross *Diomedea chrysostoma*). From the Colleywobbles data, it is estimated that the proportion that breed each year is about 85% and this ratio varies from 68% to 92%, though this variation is not statistically significant ( $p > 0.2$ ; Chapter Four). For the purposes of the simulation the limits are set at 0.65 to 0.95.

From a sensitivity analysis (Figure 7.5) it is seen that increasing the attendance from the Colleywobbles nominal value of 85 through to 95% causes the intrinsic rate of natural increase to vary upwards by about 0.75%. However, lowering the proportion which breeds to 65% causes a decrease of nearly 2% in the intrinsic rate of natural increase.

The variation of intrinsic rate of natural increase with the proportion of adults which breed is nearly linear and so it is easy to make approximate predictions for values outside the range used above (Figure 7.5); in particular, it has been suggested that the proportion of pairs which breed could be even lower than the minimum of 0.65 suggested above (E. Danchin, pers. comm.).

## Intrinsic Rate of Natural Increase

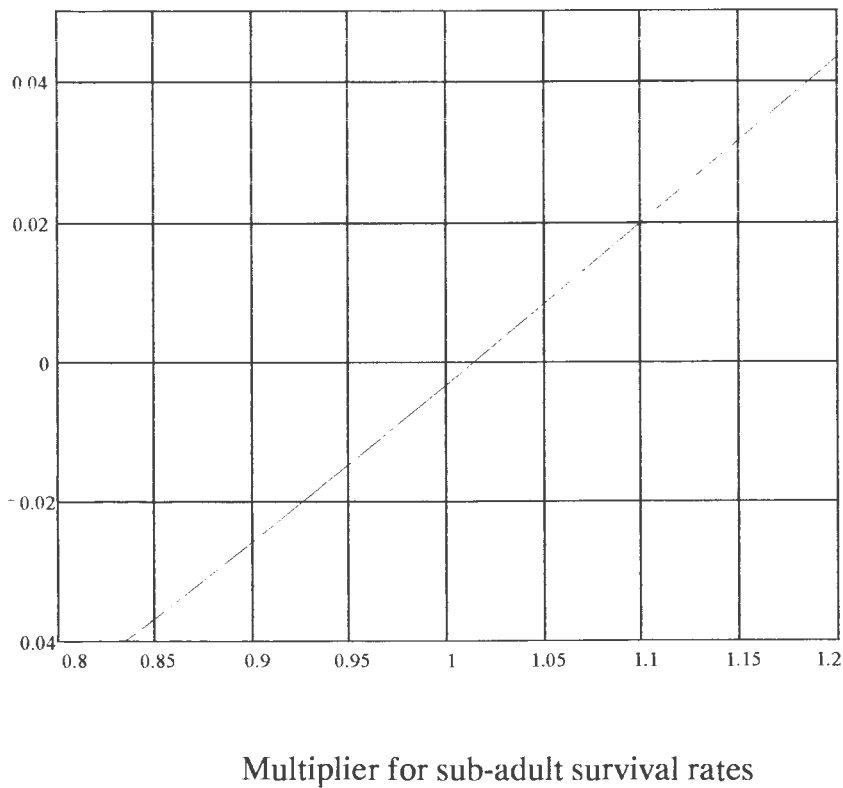


Figure 7.6 Variation of intrinsic rate of natural increase with sub-adult survival rates.

#### 7.1.3.4 Sub-adult survival and recruitment.

The best estimates of survival of the immature age-classes come from observations of colour-ringed Cape Vultures in the southwestern Cape. The estimated survival rates for the immature age-classes had 95% confidence limits of about  $\pm 20\%$  of the estimate (section 5.2.4 above). It is known that when estimating survival rates the estimates tend to be correlated (see Lakhani & Newton 1983, Anderson, Burnham and White 1985). Thus a sensitivity analysis was set up in which the survival rates of sub-adults were allowed to vary *jointly* through a range of  $\pm 20\%$ . Recruitment is defined as the proportion of large nestlings which reach age of first breeding. From the estimates presented above it is likely that recruitment will be about 25% and could range from about 20% to 35%.

It was found that depressing sub-adult survival by 20% causes the intrinsic rate of natural increase to drop by nearly 4% while increasing all the sub-adult survival rates by 20% increases  $r$  by just over 4% (Figure 7.6). This is a fairly large effect and shows that it is important to estimate these parameters with finer precision. If, as will be argued below, an error of  $\pm 2\%$  in estimating  $r$  is the maximum tolerable error, then the sub-adult survival rates need to be estimated to better than  $\pm 10\%$ .

## Intrinsic Rate of Natural Increase

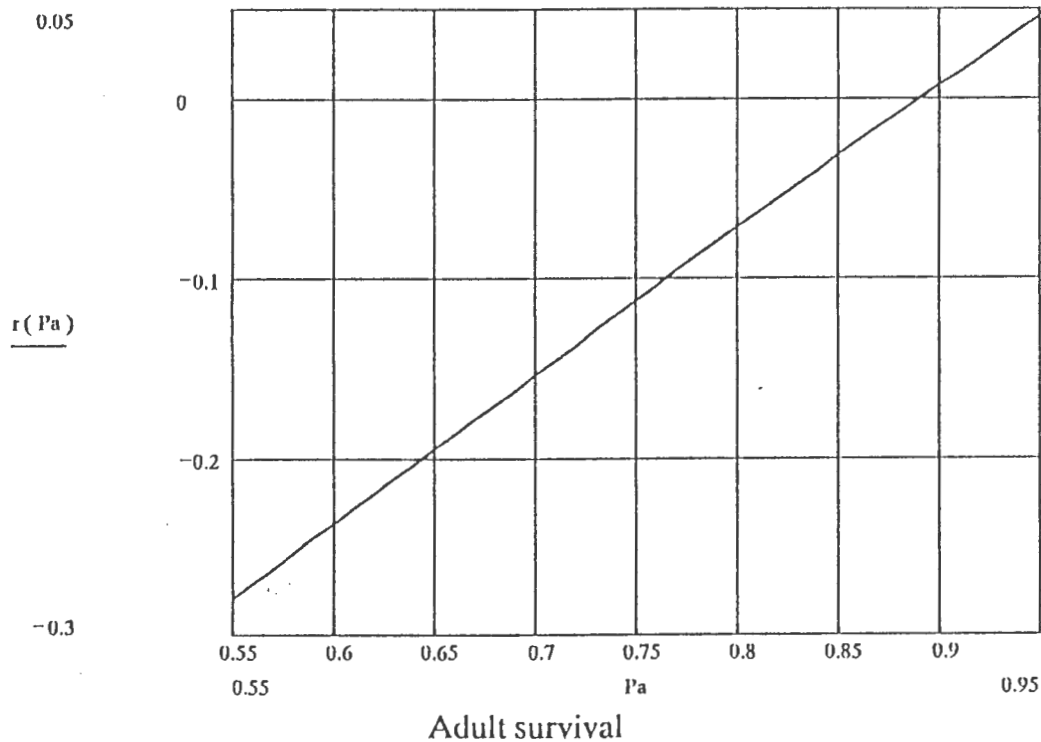


Figure 7.7 Variation of intrinsic rate of natural increase with adult survival.

### 7.1.3.5 Adult survival

There are no adequate estimates of survival for adult Cape Vultures (Chapter Five). From a comparison with other large scavengers (*loc. cit.*) it is suggested that a likely upper limit on adult survival in the Cape Vulture will be 95% p.a. Using the lowest 95% confidence limit of 55% p.a. (see section 5.2.3 above, from ring-recovery data) it is thus possible to set feasible bounds within which adult survival might lie.

Adult survival was allowed to vary between 55% and 95% (Figure 7.7) and it was found that the intrinsic rate of natural increase dropped by nearly 30% for an adult survival rate of 55% and rose to about +4% for an adult survival of 95%. This has two interesting consequences. First, the correct estimate of adult survival is vital to providing an accurate estimate of the rate of increase or decrease of the population as a whole. Secondly, all the demographic estimates used in this 'base-model' are at their maxima and thus this is a highly optimistic model. As a consequence, the maximum value of  $r$  produced by this model is likely to be the maximum achievable in the 'real-world', given that these estimates are

reasonable. This means that whenever a population increase of more than 4% is observed in a real Cape Vulture sub-population it is likely that there is immigration into that population. The Leslie-matrix model is much more sensitive to this demographic parameter than any other. Thus, the provision of a good estimate for adult survival is the most important requirement for the construction of a realistic model.

#### 7.1.3.6 Interaction of sub-adult and adult survival

There are two reasons for wanting to investigate variations in the intrinsic rate of natural increase as a joint function of both sub-adult and adult survival rates.

- 1) To model the effects of estimation errors.
- 2) To determine the effects of those unnatural mortality factors which may depress both adult and sub-adult survival.

*The nature of estimation errors.* Estimates of survival are subject to many sources of error. First among these is the stochastic nature of death. When two samples of birds of equal size are observed, the dates at which they die will vary from one sample to another, even when all else is constant. However, the larger the sample size, and the more samples observed, the less the influence of this effect. The second source of error comes from the way in which survival is estimated. If survival is estimated from ring recoveries then it is commonly found that recoveries of young birds are positively biased while recoveries of adults are negatively biased (Chapter Five). This causes the estimate of sub-adult survival to be negatively biased while the estimate of the survival rate of adults is positively biased. If survival is estimated from the sighting of marked birds in a supposedly closed population then the estimates of both sub-adult and adult survival rates will be negatively biased as a result of permanent emigration.

*The effects of unnatural causes of mortality.* There are a number of unnatural causes of mortality currently acting on the Cape Vulture population: poisons, persecution, disturbance, drowning and electrocution (Chapter Five). While it is probable that these factors act to different degrees on different components of the population, it is likely that they depress the survival of both sub-adults and adults.

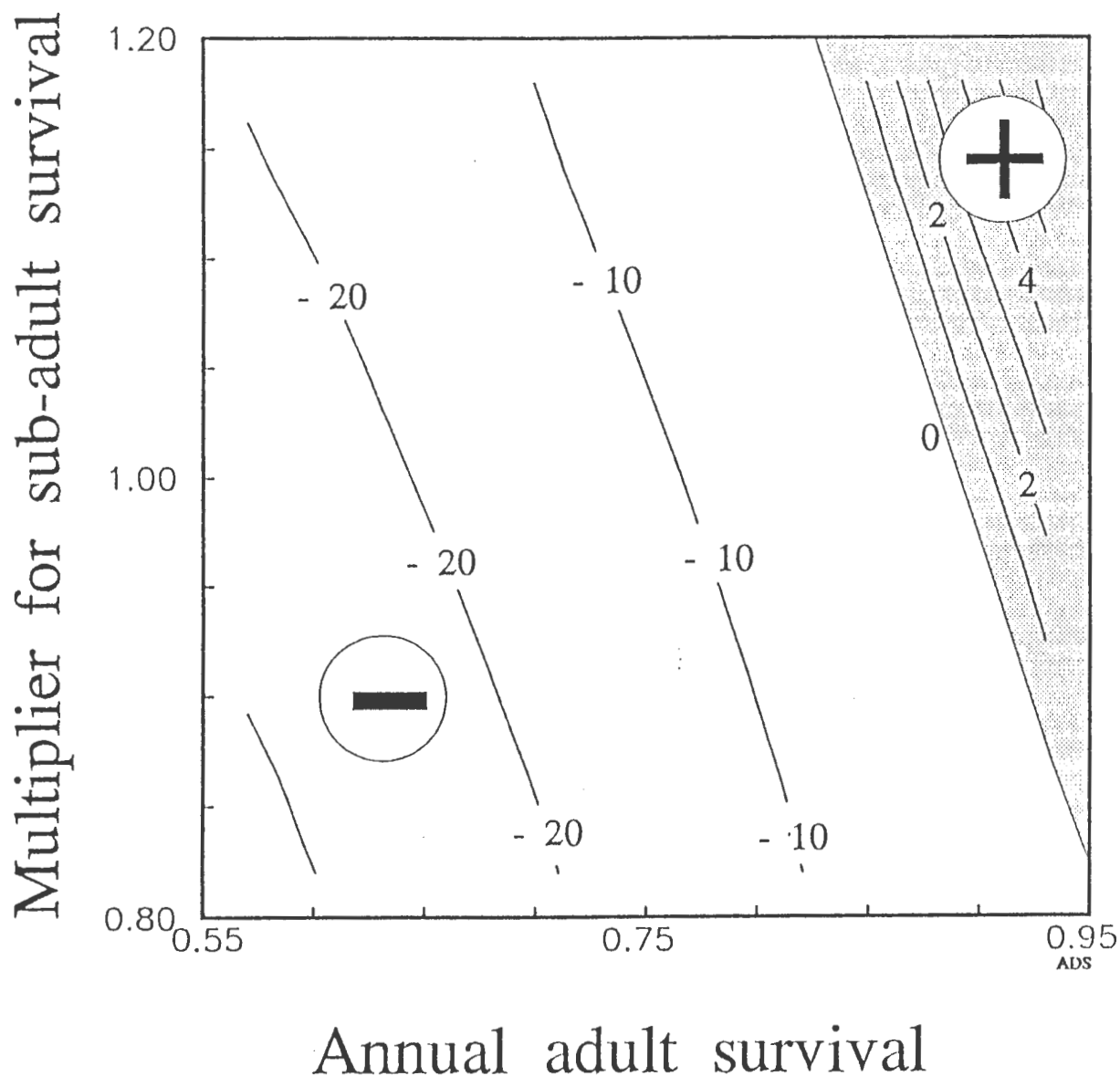


Figure 7.8 Response of the intrinsic rate of natural increase to variations in sub-adult and adult survival rates. Contours as % change p.a.

To provide a tool which will be useful for investigating variations in both sub-adult and adult survival, a response surface has been constructed in two ways. In the first adult survival is allowed to vary through the range 55% to 95% p.a. while sub-adult survival rates are allowed to vary by up to  $\pm 20\%$  of their nominal values (Figure 7.8).

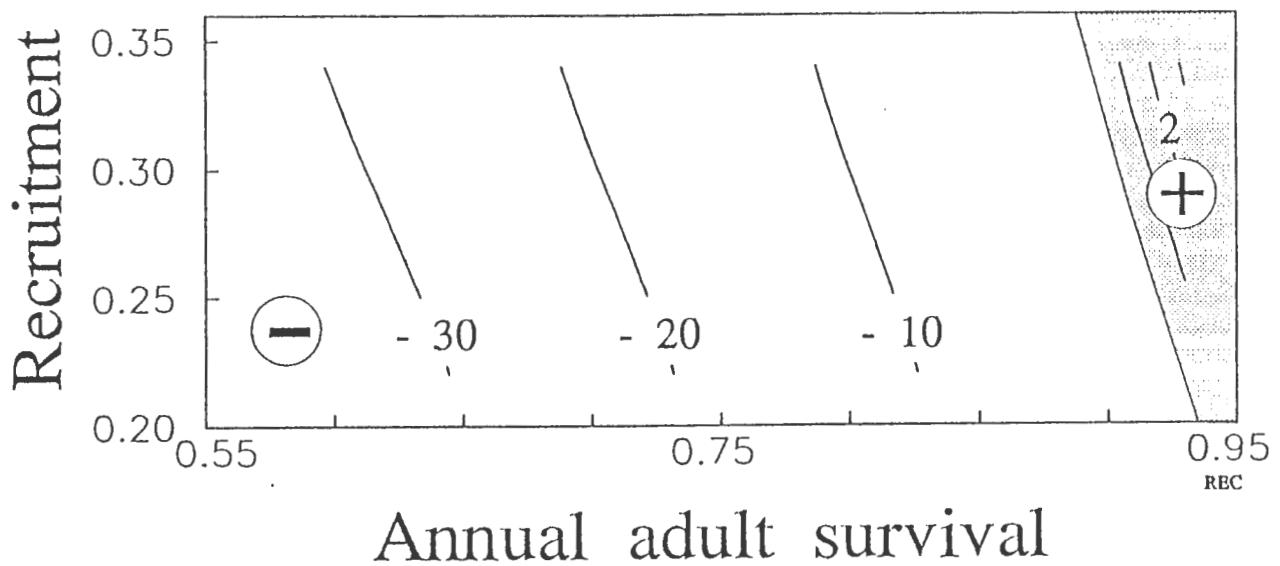


Figure 7.9 Response of the intrinsic rate of natural increase to variations in recruitment and adult survival. Contours as % change p.a.

In the second, the sub-adult survival rates are combined to form a single number, the recruitment to the adult population. Recruitment is allowed to vary between 20% and 35% when constructing the response surface (Figure 7.9).

From both of these responses it is immediately clear that the intrinsic rate of natural increase,  $r$  is much more sensitive to adult survival than to sub-adult survival or recruitment. It is also clear that the 'feasible region' within which the population is at equilibrium, or is increasing, is small and it is necessary for adult survival to be high, approximately 90%, to achieve this.

#### 7.1.3.7 Maximum age of breeding

The augmented Leslie population projection matrix is constructed on the assumption that adult survival is constant after a certain age (see section 7.1.1 above). This is unlikely, since it is probable that most females will cease breeding after a certain age and few adults will survive beyond a certain maximum age, even in captivity (see Wooller, Bradley, Skira & Serventy 1989: 416 for a description of the Shorttailed Shearwater *Puffinus tenuirostris*; Partridge 1989: 433-4 for descriptions of the Fulmar *Fulmarus glacialis*, Great Tit and Blackcapped Chickadee *Parus atricapillus* and Newton 1989: 458 for a general summary). The questions to be asked are listed below.

Adult survival rate

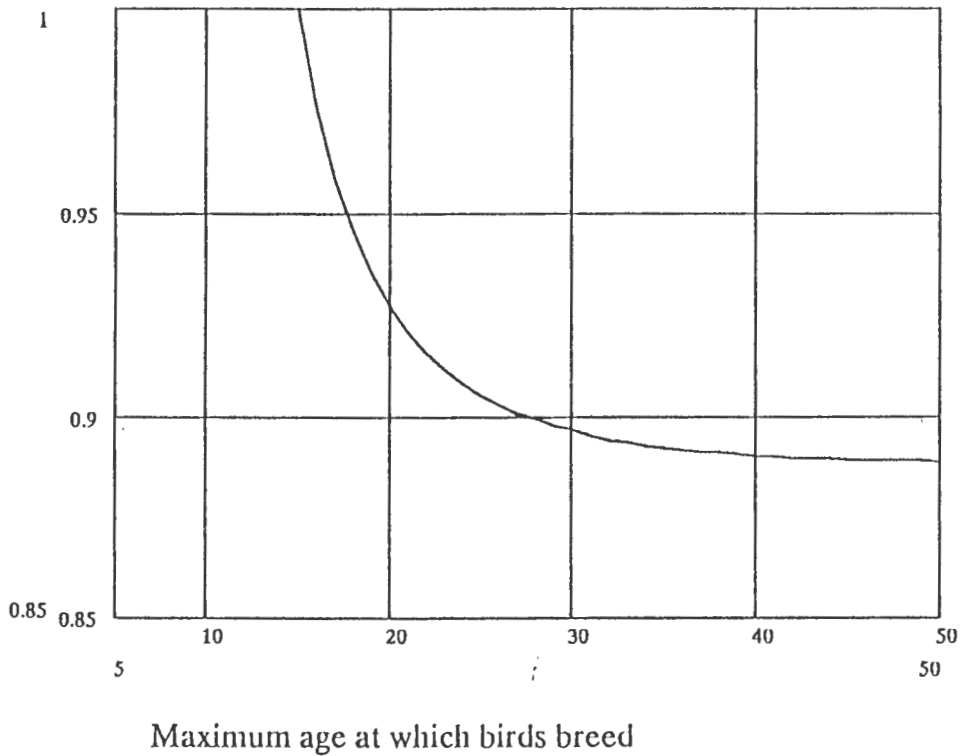


Figure 7.10 Variation in adult survival rate with maximum age of cessation in breeding for a population at equilibrium.

- 1) For how long must a Cape Vulture keep breeding in order to replace itself?
- 2) How does this value compare with the postulated maximum longevity?

To answer this question consider a Leslie population projection matrix, **B** of the form:

$$B = \begin{bmatrix} 0 & F & F & F & F & F & F \\ C_0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & Sa & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & Sa & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & Sa & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & Sa & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & Sa & 0 \end{bmatrix}$$

Where  $C_0$  is the recruitment to the adult population,  $F$  the fecundity and  $Sa$  adult survival (see section 7.1.1 above for definitions). It is assumed that adults breed from the start of their sixth year, i.e. when they have just turned five and recruitment,  $C_0$  is defined as the product  $S_1 \cdot S_2 \cdot S_3 \cdot S_4 \cdot S_5$ . Given a Leslie population projection matrix of the form shown above, it is possible to show that the characteristic equation resulting from evaluating the determinant  $\det(A-I)$ , at equilibrium, i.e.  $R = 1$  is given by:

$$(-1)^j + (-1)^{(j+1)} \cdot R \cdot F \cdot (1 - S_a^{(j-1)}) / (1 - S_a)$$

where  $j$  is the number of rows of the matrix.

If birds take five years before they start breeding then the maximum age at which they cease is  $j+5$ . The above equation was solved for  $S_a$  for each value of  $j$  in the range 5 to 45 (i.e. corresponding to maximum ages of breeding of 10 to 50 years) given  $F=0.31875$  and  $C_0=0.35$ . The plot of survival against maximum age of ceasing breeding (Figure 7.10) shows that survival must be very high, over 95% p.a. if Cape Vultures live to at most 18 years only. On the other hand, given the predicted longevity of about 24 to 25 years (Chapter Five) it is possible for the population to be stable with an adult survival rate of about 91% p.a. This is certainly feasible, when compared to survival rates computed for other species of similar weights and lifestyles (Chapter 5).

#### 7.1.4 Recommendations for research and conservation

The Leslie-matrix model has been formulated as a tool useful to investigate two problems: first, to evaluate the consequences of the current estimates of the population parameters, and secondly to conduct a sensitivity analysis around each parameter. The sensitivity analyses conducted will be used to formulate a strategy for Cape Vulture research and conservation. Naturally, these sensitivity analyses are based upon the ‘best’ estimates of the parameters used in the models. Should it be found that the ‘true’ values are different from these then it is possible that the recommendations could change. This is no bad thing. The sensitivity analyses are easy to perform, thus it is hoped that they will be rerun many times as the estimates of the demographic parameters are improved. As stated earlier in this Chapter, there has been no well thought out or consistent research programme to estimate the various population parameters. To produce such a design, it is necessary to have a reasonably clear idea of what criterion to use in deciding upon the accuracy with which parameter estimates need to be known.

It is proposed that a simple criterion on which to base an experimental design is to assume that all parameters should be estimated with sufficient precision such that the resulting error in estimating the intrinsic rate of natural increase,  $r$  is within the range  $\pm 2\%$ . The following reasons are advanced in support of this.

- 1) Populations of K-selected organisms, such as the Cape Vulture, are unlikely to be able to grow at more than 2% p.a. (see arguments below in sections 7.2 to 7.4). Thus to detect a real growth greater than +4% p.a. the error must be constrained within the limits  $\pm 2\%$  p.a.

- 2) At a decline of 2% p.a. the current population of about 12 000 birds (Chapter Three) will decline to extinction (ignoring stochastic effects) in just under 500 years. This, it is suggested, is sufficiently close to equilibrium for the population to be regarded, for all practical purposes, as stable.

Consideration will now be given to each of the parameter estimates and a decision made as to how much effort, if any, needs to be devoted to providing a better estimate.

*Age at first breeding.* From the studies of Robertson (see Chapter Four), and by comparison with the Eurasian Griffon (F. Sarrazin pers. comm.), it is likely that birds will begin to breed somewhere between their fourth and sixth years. This causes  $r$  to vary by about  $\pm 1\%$ . Thus no additional effort needs to be devoted to providing a better estimate. However, if more nestlings are colour-ringed, then it should be possible to improve the estimate of this parameter while monitoring breeding, recruitment and adult survival, i.e. without any additional experimental effort. Notwithstanding, this parameter is of interest as a possible indicator of density dependent effects in breeding. It has been suggested that as the number of adults declines at a colony, or the food-base increases, more sub-adults should attempt to breed (C.J. Vernon, pers. comm.). Also it is to be expected that as new colonies are formed, or deserted colonies are reoccupied, sub-adults would seize these new, and possibly easier opportunities.

*Variation in breeding success with age.* Initial estimates, based on hypothetical data, suggest that this effect is likely to cause  $r$  to vary between  $-1.5\%$  p.a. and  $+0.5\%$  p.a. This parameter can only be estimated from known-age birds, and it is suggested that consideration should only be given to investigating these potential variations when the proposed ringing programme for the 1990s (Vulture Study Group pers. comm.) has been running for at least another three years (i.e. from 1995). It should be noted that breeding success is also likely to vary from one year to the next and from one region to the next (A. Dhont, pers. comm.). These additional sources of variation also need to be measured and monitored.

*Proportion of adults which breed.* The estimate of the proportion of adults which breed is not well known, and until the population of individually marked adults increases to somewhere in the range 100 to 200, it will not be possible to provide a better estimate. Using rough estimates of its likely variation it is possible to say that  $r$  is likely to vary between  $-2\%$  p.a. and  $+1\%$  p.a. Thus there is no immediate need to devote effort and energy to improving the estimate of this parameter.

*Sub-adult survival.* In order that  $r$  varies by no more than 2% it is necessary to have the estimates of sub-adult survival accurate to  $\pm 10\%$ . Survival is estimated from a binomial distribution which has standard deviation of  $(S \cdot [1-S]/n)^{1/2}$ . This is a maximum for  $S=0.5$ . For 95% confidence limits to be within 10% of  $S$  means that  $1.96 \cdot (S \cdot [1-S]/n)^{1/2} = 0.05$  and this yields  $n=384$ . Thus the sample size for the smallest sub-adult age class should be about 384 and given that recruitment is about 35% this implies that about 1097 nestlings should be ringed so that the number of four-year old colour-ringed birds is about 384. As these estimates tend to be on the conservative side, it will probably be sufficient to ring 1000 nestlings. It is to be emphasized that this experimental design is based upon the assumption that there will be an intensive campaign to resight colour-ringed birds. To rely on recoveries (i.e. birds found dead) is just not feasible (see arguments in Chapter Five).

*Adult survival.* For  $r$  to lie in the range  $\pm 2\%$  it is necessary that adult survival lie in the approximate range 0.865 to 0.915, i.e. an average of 0.89 with an error of  $\pm 2.5\%$ . To achieve this means that the sample size  $n$  must satisfy  $1.96 \cdot (S_A \cdot [1-S_A]/n)^{1/2} = 0.05$  with  $S_A=0.89$ . This means that about 600 bird-years must be observed. There are two ways in which this can be achieved. First, if 1000 nestlings are colour-ringed with long-lasting rings then these will generate about 200 adults (assuming recruitment at 20%) and if these are observed for three years the required adult survival estimates will be generated. There are two draw-backs to this proposal. The first is that it is likely to take some five to ten years to have all the nestlings ringed, and this means that it will take seven to twelve years to collect the data needed. A faster method is needed. It is thus recommended that 50 adults be caught and ringed each year for five years. This will speed the data-collection process. These adults will have to be actively sought out and their colour-rings sighted.

*Maximum age at which adults can still breed.* From the sensitivity analyses it is likely that Cape Vultures will continue to breed in their early twenties otherwise the population could not be at equilibrium. If that is indeed the case, then it is imperative that we start marking nestlings straightaway so that we can estimate this parameter in our lifetime!

*Summary.* It is clear that the parameters which are in greatest need of improved estimates are those relating to survival. It is also clear that it is imperative that a sound colour-ringing and resighting programme be instituted immediately. It has been stressed that ringing is not enough, it is important to "monitor marked birds more efficiently and systematically" (E. Danchin, pers. comm.).

## 7.2 Model of Cape Vulture population in the southwest Cape

The Cape Vulture population centered on the Potberg breeding colony has been monitored, on an annual basis since 1974, by the Cape Nature Conservation Department. It has been the subject of a Master's dissertation (Robertson 1984), and a number of scientific papers and reports (see Boshoff 1987; Boshoff & Scott 1990; Robertson 1986 and references therein). This population is of interest for a number of reasons.

- 1) The population, centered on Potberg but also visiting sites in the nearby Little Karoo, is thought to be 'closed' and 'isolated' from the rest of the Cape Vulture population (A.F. Boshoff pers. comm.).
- 2) All breeding at Potberg, and some breeding at sites in the Little Karoo, has been monitored every year from 1974 to 1990, both years inclusive. This means that a near-complete record of productivity exists.
- 3) Most of the Potberg nestlings were fitted with unique combinations of colour-rings during the period 1974 to 1988, both years inclusive.
- 4) Much effort has been devoted to observing colour-ringed birds and sufficient data have been collected to provide good age-specific estimates of survival for the first-, second- and third-year classes.
- 5) Counts have been made of the total number of free-flying birds, at the most important sites, in most years.

Each of the important demographic aspects of this population are discussed first before the model is built (section 7.2.1), evaluated (section 7.2.2) and summarized (section 7.2.3).

*Closed Population.* It is commonly held that the southwestern Cape population of Cape Vultures is closed, with all losses being permanent and no influx of foreign birds (A.F. Boshoff pers. comm.). This perception is based on the observation that few ringed birds from the colony have ever been recovered far away, most of the colour-ringed birds have been resighted locally subsequent to fledging (and for some years later), and few foreign-ringed Cape Vultures have been found dead in the region or have been resighted there. However, the following anomalies need to be noted.

- 1) An 'atypical' Cape Vulture was seen at Potberg from 25 August 1989 to 12 March 1991. It was atypical in that its plumage bore similarities to a Rüppell's Griffon. It was likely that this bird came from outside the southwestern Cape (Scott 1991).
- 2) Two colour-ringed birds were resighted near Potberg during 1985 with partial colour-combinations (i.e. not all colour-rings seen) which did not correspond to combinations fitted in the southwestern Cape - the birds were thought to have come from Kimberley and Colleywobbles respectively (Boshoff 1987: 38-40).
- 3) A possible influx of outside birds into the southwestern Cape was suggested as a reason for the high totals counted during 1988 (Boshoff & Scott 1990: 39).

Table 7.1

Numbers of Cape Vulture nestlings produced at southwestern Cape colonies during the period 1974 to 1990 inclusive.

Year	<i>Potberg</i>												Grand total	
	Rng	NRng	Dd	Tot	Rng	NRng	Dd	Tot	Rng	NRng	Dd	Tot		
1974	22	0	0	22									22	
1975	15	8	0	23									23	
1976	11	5	0	16									16	
1977	13	2	0	15									15	
1978	7	2	0	9									9	
1979	9	1	0	10									10	
1980	6	2	0	8	<i>Aasvogelvlei</i>								8	
1981	7	0	0	7	Rng	NRng	Dd	Tot					13	
1982	10	0	4	6	6	0	0	6					11	
1983	5	2	0	7	5	0	0	5					12	
1984	6	0	0	6	4	1	0	5					9	
1985	6	0	0	6	4	0	1	3					12	
1986	6	0	0	6	6	0	0	6					15	
1987	6	1	0	7	8	0	0	8	<i>Platterug</i>				15	
1988	5	3	0	8	4	3	0	7	NRng	Dd	Tot	<i>Perdeberg</i>	15	
1989	0	8	0	8	<i>Boschberg</i>				9	0	9	NRng	Dd	Tot
1990	0	11	0	11	Rng	NRng	Dd	Tot				2	0	2
	0	13	0	13	0	1	0	1						14

Notes:

Rng = No. of nestlings ringed

NRng = No. of nestlings not ringed

Dd = No. nestlings dying before fledging

Tot = Sub-total for colony-year

Aasvogelvlei was re-activated in 1981 and then abandoned after the 1987 breeding season.

Breeding then took place in the Little Karoo at Platterug during 1988, at Perdeberg during 1989 and at Boschberg during 1990.

Breeding and ringing data are from Boshoff &amp; Scott 1990 and references therein.

Total 234

- 4) In 1991 a sick Cape Vulture was found near Potberg, rehabilitated, colour-ringed and released. It was found sick near Vryburg in the Northern Cape two months later, having moved 922 km. Again the bird was rehabilitated and released near Kimberley in October of the same year. It was next found at Riviersonderend in the southwestern Cape five weeks later. Yet again the bird was rehabilitated and released in Potberg where it has since been seen (Scott 1991; H.A. Scott pers. comm.). This indicates that a Cape Vulture from the southwestern Cape has the potential to move far away (i.e. out of the region) and then return sometime later.

Table 7.2

Numbers of free-flying Cape Vultures seen at each site in the southwestern Cape during the period 1974 to 1990 inclusive.

Year	Potberg	AVV	Platte- rug	Perde- burg	Bosch- berg	"A"	Totals "B"	Simultaneous Counts
1974	<u>87</u>	-	-	-	-	87	-	-
1975	-	-	-	-	-	-	-	-
1976	-	-	-	-	-	-	-	-
1977	50	-	-	-	-	-	-	-
1978	45	14	-	-	3	62	-	-
1979	45	-	-	-	-	-	-	-
1980	51	-	-	-	-	-	-	-
1981	62	25	-	-	-	87	79	<u>82</u>
1982	62	18	-	-	-	80	79	<u>74</u>
1983	50	20	-	28	-	98	<u>65</u>	-
1984	52	27	-	12	-	91	<u>71</u>	-
1985	57	29	-	0	-	86	<u>69</u>	-
1986	48	35	-	-	-	83	73	<u>73</u>
1987	52	34	-	0	-	86	70	<u>66</u>
1988	52	2	38	-	-	92	85	<u>84</u>
1989	59	0	0	10	-	69	<u>66</u>	-
1990	66	0	0	0	9	75	61	<u>62</u>

## Notes:

- 1) The numbers entered under the columns Potberg to Boschberg inclusive represent the maximum numbers of free-flying birds counted in that calendar year.
- 2) "A" Total is the sum of the maxima.
- 3) "B" Total is the sum of the maximum number counted during the breeding season at all colonies, data from Table 4 Boshoff & Scott (1991: 35).
- 4) The simultaneous counts were at Potberg and the current active site in the Little Karoo.
- 5) All data are from Boshoff & Scott (1990) and references therein.
- 6) Data used to evaluate the model are underlined (see Figure 7.13)

5) During early 1986, an unringed first-year was sighted at Potberg. Another unringed juvenile was captured at Porterville in early 1987. All known southwestern Cape nestlings had been colour-ringed the previous two years. Thus these birds may have come from undiscovered colonies in the area, or may have been immigrants.

Griffon vultures can and do move great distances, often into regions where there are no other members of their own species, or even other vultures. Examples are the sighting of a possible Cape Vulture in Kenya (A.F. Boshoff, pers. comm.), the confirmed sighting of a Rüppell's Griffon at the Wabai Hill roost in Zimbabwe (P.J. Mundy, pers. comm.), and the movement of a Eurasian Griffon which escaped from an aviary in Cévennes during 1980. This bird was next seen in Brittany 700-800 km away and then returned three years later to breed at the re-introduction site; where it was still in 1991 (Piper 1992). This southwestern Cape population may indeed be closed; but the assumption needs to be treated with caution.

*Location of colonies and roosts.* The site at Potberg has been known to have been a nucleus breeding colony for at least 40 years (Ledger & Mundy 1978). However, it was only in the 1970s and 1980s that it was realized that there were other sites in the Little Karoo, that the Cape Vultures from Potberg visited these sites and that some nestlings from these sites subsequently moved to Potberg (Boshoff 1987). The sites in the Little Karoo are Aasvogelvlei, Platterug, Perdeberg and Boschberg (Figure 7.11).

### Location of southwestern Cape Colonies

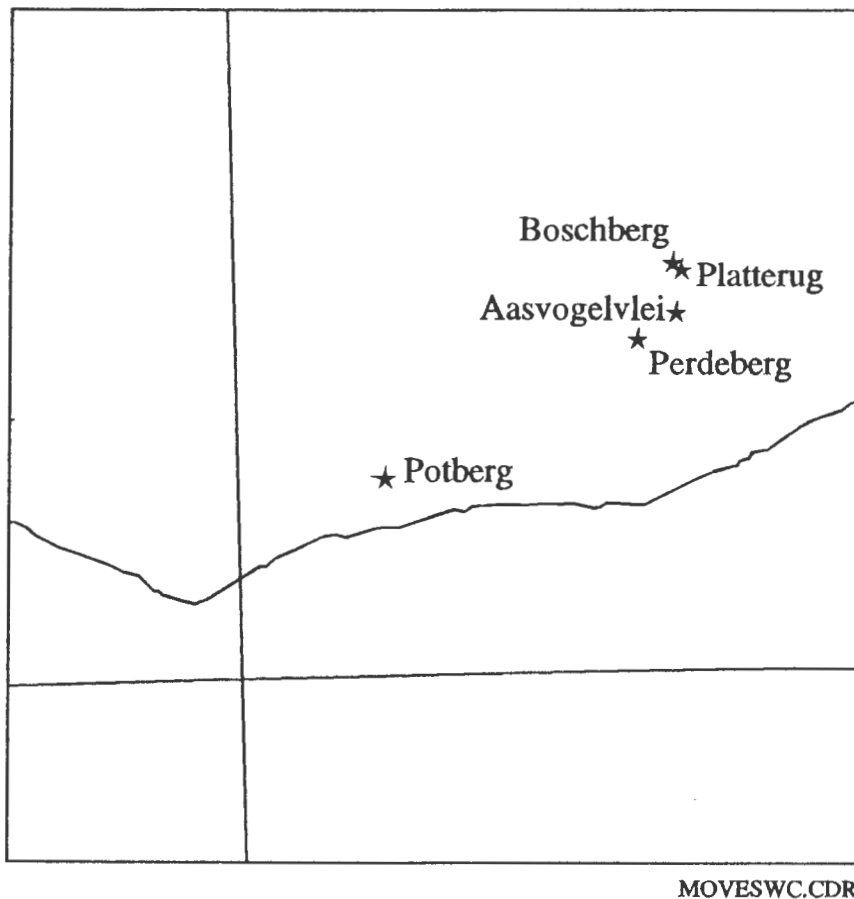


Figure 7.11 Location of Cape Vulture colonies mentioned in the text. Note that the location of the Boschberg colony has been shifted slightly northwest of its true position to distinguish it, spatially, from Platterug.



Figure 7.12 Number of large nestlings produced during each calendar year in the southwestern Cape. Nestlings dying before fledging are excluded.

*Productivity.* The numbers of large nestlings produced, the number ringed and the number dying before fledging are fairly well known for Potberg, but not as well known for the other sites (Table 7.1). It is likely that some of the smaller sites may have been missed in some years, especially before 1980. Thus, this is a minimum estimate of productivity (as measured by large nestlings) for the years 1974 to 1990, both inclusive (Figure 7.12). A minimum of 234 nestlings were produced in 17 years, i.e. an average of 13.76 p.a. There is no evidence that productivity declined during this period (both linear and exponential models gave  $p > 0.05$ ).

*Colour-ringed birds.* Of the 186 large nestlings produced at Potberg during the period 1974 to 1990, both years inclusive, 69% were colour-ringed; 93% of the 40 nestlings at Aasvogelvlei were also colour-ringed. A total of 165 of the 234 large nestlings were ringed (i.e. 71%). Nestlings from the other sites were not ringed. A few adults were also ringed, generally when they were found sick and immobile.

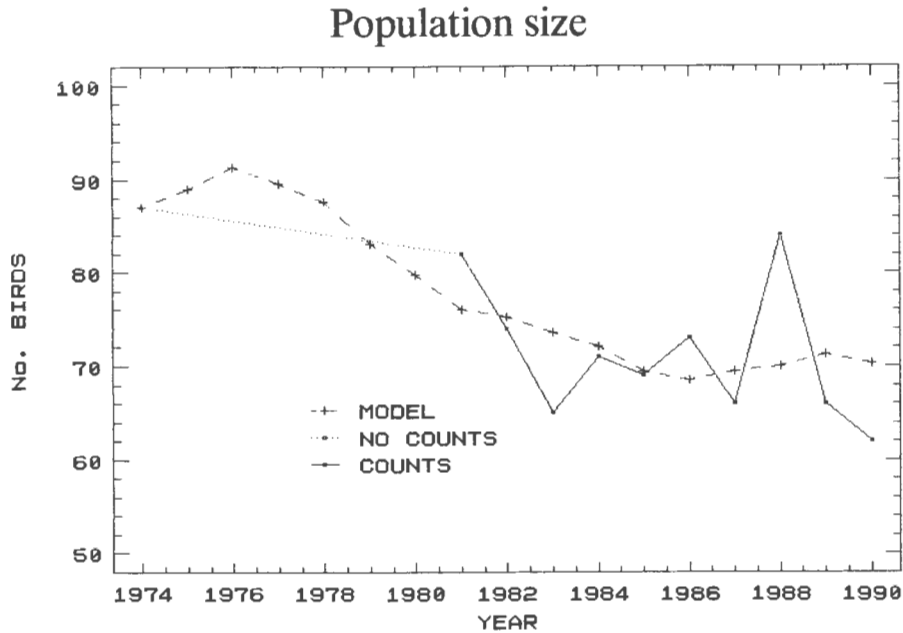


Figure 7.13 Estimated number of birds at all sites during the breeding season.

*Estimates of age-specific Survival.* There were so many colour-ringed birds seen at the colonies, roosts and vulture restaurants that it has been possible to construct good estimates of age-specific survival for the first three age-classes (see sections 5.2.4 and 7.1.2 above). However, it should be noted that the 95% confidence interval for each estimate increases with age, a consequence of smaller samples of older birds (the following summary comes from page 244).

Age Estimate	Lower	Upper	Interval
1	53%	62%	20%
2	84%	92%	20%
3	78%	88%	25%
4+	70%	81%	23%

(These age-specific survival estimates are quoted as % surviving p.a. The confidence interval is the difference between the upper and lower 95% confidence limits)

*Population estimates.* From time-to-time counts were made of all the free-flying birds at a colony or roost. Sometimes counts were made simultaneously at Potberg and at the active site in the Little Karoo (Boshoff & Scott 1990). Particularly useful were those counts made during the breeding season, as they tend to reveal adults tied to their breeding colonies. These counts have been summarized and compared (Table 7.2). To be conservative, the simultaneous counts have used, when available, while the sum of the maximum breeding season counts have been used otherwise. No reliable counts exist for the years 1975 to 1980, inclusive, so they are omitted (Figure 7.13). The population is decreasing at about -1.18 birds p.a. (linear model,  $p < 0.05$ ) with an intrinsic rate of natural increase of -0.016, i.e. -1.6% p.a. (exponential model,  $p < 0.05$ ).

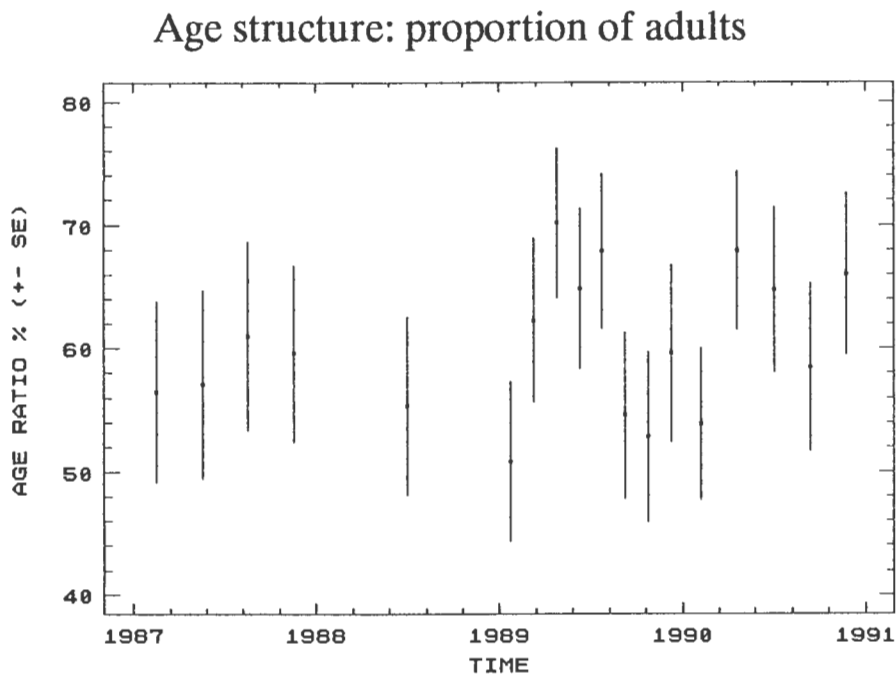


Figure 7.14 Proportion of adults estimated from counts at Potberg (data from Boshoff & Scott 1990).

*Age-structure.* The total number of birds in the age-categories first-year, second-year, immature and adult were counted at Potberg 18 times during the years 1987 to 1990 inclusive (Boshoff & Scott 1990: 37). The non-adult classes have been grouped together and the proportion of adults computed (Table 7.3). The standard error of each proportion has been estimated using the normal distribution approximation (i.e.  $se = \sqrt{p \cdot \{1-p\}/N}$ , where  $p$  is the proportion and  $N$  is the total number counted; Feller 1969: 186). There is considerable year-to-year variation, but no obvious trend (Figure 7.14).

*Proportion of breeding birds.* The proportion of breeding birds was estimated for the six years 1985 to 1990, both years inclusive, at Potberg, and for 1988 at Platterug (Boshoff & Scott 1990: 35). The breeding proportion shows no trend (Table 7.4; Figure 7.15) but it is clear that the proportion was low in 1986 and high in 1991. No explanation was offered for this (A.F. Boshoff pers. comm.).

Table 7.3

Age ratio estimated from counts at Potberg

Year	Count	Adults	Total	Ratio	se
1987	1	26	46	56.5%	7.3%
1987	2	24	42	57.1%	7.6%
1987	3	25	41	60.9%	7.6%
1987	4	28	47	59.6%	7.2%
1988	1	26	47	55.3%	7.3%
1989	1	30	59	50.9%	6.5%
1989	2	33	53	62.3%	6.7%
1989	3	40	57	70.2%	6.1%
1989	4	35	54	64.8%	6.5%
1989	5	38	56	67.9%	6.2%
1989	6	30	55	54.6%	6.7%
1989	7	28	53	52.8%	6.9%
1989	8	28	47	59.6%	7.2%
1990	1	35	65	53.9%	6.2%
1990	2	36	53	67.9%	6.4%
1990	3	33	51	64.7%	6.7%
1990	4	31	53	58.5%	6.8%
1990	5	35	53	66.0%	6.5%

Notes:

Counts were made sporadically during the year, the 'Count' number does not imply a particular month.  
Data are from Boshoff & Scott (1990)

Table 7.4

Proportion of birds breeding

Year	Count	Bred	Total	Ratio	se
1985	1	32	44	72.7%	6.7%
1986	1	22	45	48.9%	7.5%
1987	1	32	41	78.1%	6.5%
1988	1	34	45	75.6%	6.4%
1988	2	26	37	70.3%	7.5%
1989	1	38	53	71.7%	6.2%
1990	1	48	54	88.9%	4.3%

Notes:

Data are from Boshoff & Scott (1990)  
All counts were made at Potberg, except for Count 2 which was made at Platterug.

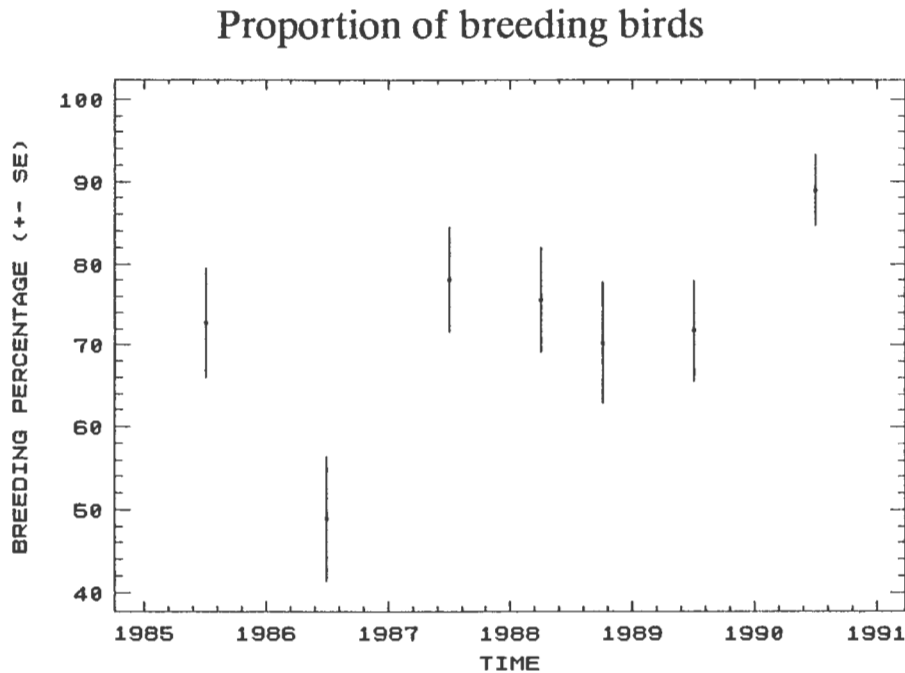


Figure 7.15 Proportion of birds breeding estimated from six counts at Potberg and one at Platterug (data from Boshoff & Scott 1990).

### 7.2.1 Model construction

It is clear from the analysis of the data from the southwestern Cape population that it has a definite age-structure, both in terms of survival (section 5.2.4) and age at first breeding (hence fecundity also) (Robertson 1983). Thus any model of this population must take cognizance of this. An obvious choice for a model of an age-structured population is the Leslie-matrix model (Caswell 1989: 24). Before being tempted to use the Leslie-matrix model in its standard form, it is important to note that productivity (as measured in terms of large nestlings) is known exactly (Table 7.1) and the age-specific survival rates for the first three age-classes have been estimated independently (see section 5.2.4).

*Model structure.* An alternative approach is to write out the Leslie-matrix as a set of finite-difference equations.

$$\begin{aligned}
 N_j &= \text{No. Nestlings - read out of a look-up table} \\
 O_{j+1} &= b_j \cdot N_j && = \text{No. of older First-years} \\
 S_{j+1} &= c_j \cdot O_j && = \text{No. of Second-years} \\
 T_{j+1} &= d_j \cdot S_j && = \text{No. of Third-years} \\
 F_{j+1} &= f_j \cdot T_j && = \text{No. of Fourth-years} \\
 A_{j+1} &= g_j \cdot (F_j \cdot T_j) && = \text{No. of Adults} \\
 M_{j+1} &= O_j + S_j + T_j + F_j + A_j && = \text{Number of free-flying birds}
 \end{aligned}$$

The parameters used above are defined as follows.

- $b_j$  = Survival from large nestling to end of first-year
- $c_j$  = Second-year survival rate
- $d_j$  = Third-year survival rate
- $f_j$  = Fourth-year survival rate
- $g_j$  = Adult survival rate

Both the numbers of individuals in each age-class and the age-specific survival rates are defined as a function of the calendar year,  $j$  even though some of them (especially the first three survival rates) will be kept fixed.

*Initial population size.* The maximum count of Cape Vultures at Potberg 1974 was 87 during mid-February. It is possible that this includes some of the 19 nestlings from the 1973 breeding season. The breeding season counts for 1972 and 1973 were 111 and 79 respectively, i.e. comparable numbers. Bearing in mind that no sites in the Little Karoo were counted in 1974, it would seem that the estimate of 87 free-flying birds is not unreasonable for 1974.

*Initial age-distribution.* The only Potberg age-structure data available are from the late 1980s (Table 7.3). In addition, only the division between adults and non-adults is considered reliable (see above). As a starting point, the initial age-distribution is approximated by the stable age distribution from the zero population growth (ZPG) model used for the sensitivity analyses (see section 7.1.3); also, five other initial distributions were constructed to test the widest range of starting conditions (Table 7.5).

Table 7.5

Age-class	Initial age-structure used in model				
	ZPG	B	C	D	E
First	0.117326	0.15	0.2	0.50	0.00
Second	0.099726	0.15	0.2	0.25	0.00
Third	0.088459	0.10	0.2	0.10	0.00
Forth	0.078464	0.10	0.2	0.10	0.00
Adult	0.616025	0.50	0.2	0.05	1.00
	1.000000	1.00	1.0	1.00	1.00

*Productivity.* The number of nestlings produced each year,  $N_j$  has been conservatively estimated (Table 7.1) and these estimates will be used directly in the model.

*Observed number of free-flying birds.* As a basis for evaluating the model, use is to be made of the numbers of free-flying birds counted,  $\text{Count}_j$  (Table 7.2; Figure 7.13), even though there are a number of years with missing counts (viz. 6 out of 17 = 35%).

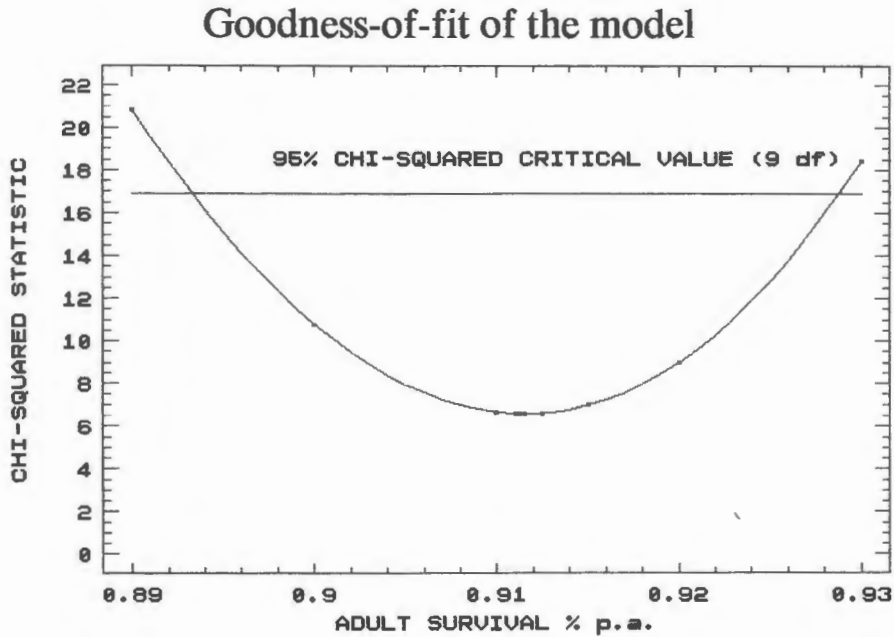


Figure 7.16 The goodness-of-fit of the model is measured using the chi-squared statistic which computes the agreement between the observed number of free-flying birds in the region with the number predicted from the model. Points are at evaluations of the model, the curve was fitted using cubic splines.

*Age-specific survival rates.* The estimates for the first three age-classes are used directly (see section 5.2.4, page 244). A single figure will be used for the fourth, and higher age-classes. This will be varied so as get the model to fit the data.

Age-class	Parameter	Estimate
1	$b_j$	52.6%
2	$c_j$	84.3%
3	$d_j$	78.1%

*Measure of agreement.* The model will be 'tuned' so that the number of free-flying birds,  $M_j$  closely matches the observed number,  $\text{Count}_j$ . It is possible to measure the agreement between observed number,  $\text{Count}_j$  and predicted number,  $M_j$  using functions of the form  $|\text{Count}_j - M_j|$  - the absolute operator, or  $(\text{Count}_j - M_j)^2$  - the sum-of-squares. However, given that the 'unit' of measure is a count, then appropriate measure of association is the Chi-squared statistic (Feller 1969: 148).

$$\text{Chi-squared} = \sum_j ((\text{Count}_j - M_j)^2 / \text{Count}_j)$$

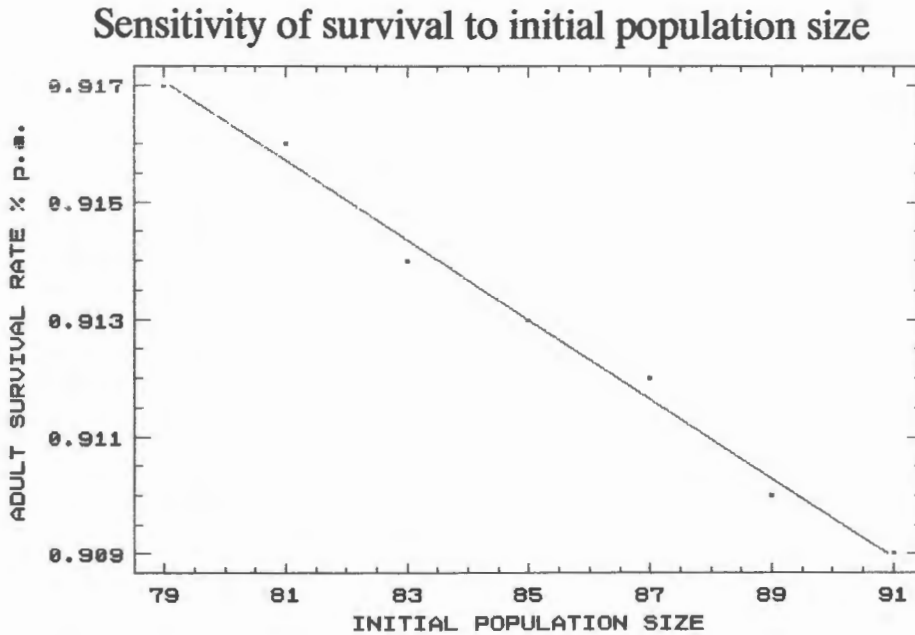


Figure 7.17 The initial population size is varied from 79 to 91 and the adult survival rate re-estimated to give the best goodness-of-fit of the model.

In computing the Chi-squared statistic those years without counts are ignored because it is not possible to match the model to the data. The degrees of freedom are computed in the following manner.

Degrees of freedom = Number of years for which there are valid counts

- 1 (because the initial population size is estimated from the data)
- 1 (because the adult survival is estimated from the model).

*Fitting the model.* The model has one parameter, a survival rate. This rate may be varied and the way in which the goodness-of-fit statistic responds may be used to find that value of survival which yields the best fit. The model is written in Mathcad 3.0 and will be supplied on request to the interested reader.

### 7.2.2 Model evaluation

The adult survival rate was varied from 0.85 to 0.95% p.a. and the best fit was found at 0.912 where chi-squared was 6.56 ( $p > 0.1$ ; Figure 7.16). This is an excellent fit and suggests that total numbers of individuals in the population are well modelled (Figure 7.13). All values of adult survival in the range 0.893 to 0.929 gave chi-squared values of less than 16.9, and with 9 degrees of freedom this is equivalent to  $p > 0.05$ , i.e. an adequate fit. Thus the 95% confidence limits on the survival rate estimate are 0.893 to 0.929. This is a variation of -2.1% to +1.9% of the estimate.

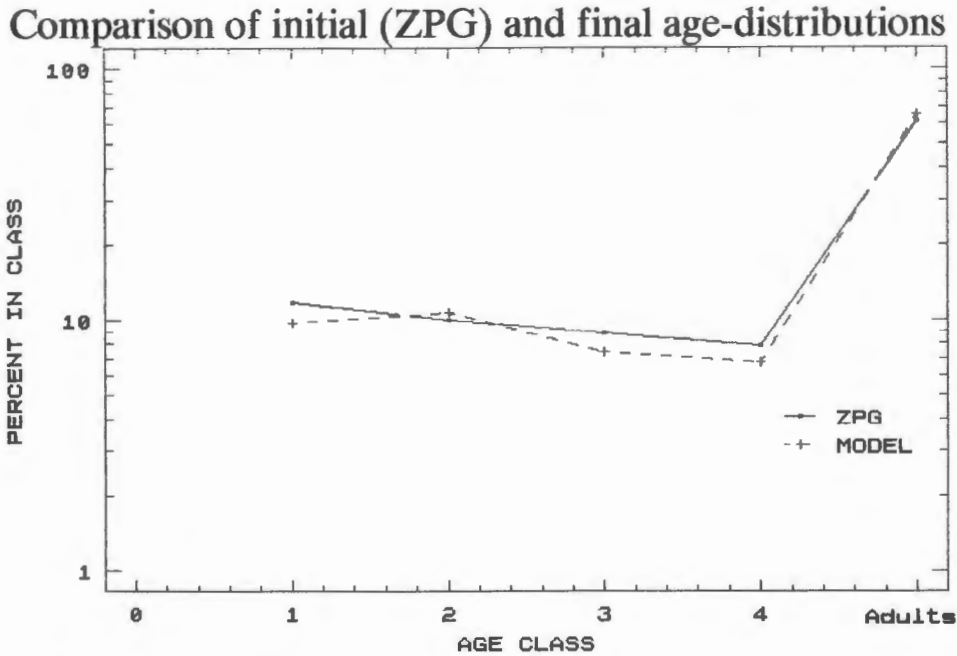


Figure 7.18 The initial age-distribution was from the ZPG-sensitivity model and it is compared with the age-distribution at the end of the simulation.<sup>1</sup>

In constructing the model, the initial population size was chosen to be 87, but with some doubt as to its correct magnitude (see previous section). To test the sensitivity of the model to errors in estimating this parameter, the initial population size was varied from 79 through to 91 and for each value an estimate of adult survival was made, using the model. It was found that the optimal estimate of adult survival responded in a negative linear fashion. (Figure 7.17). A 13.8% variation in initial population size caused the adult survival rate to vary by less than 1%.

There was no known age-distribution to initiate the model, so the ZPG age-distribution was used. The age-distribution at the end of the model was almost identical to that at the start (Figure 7.18), which suggests that using the actual number of large nestlings produced each year (i.e. not using the Leslie-matrix estimates) does not have a major effect. To test the effect of initial age-distribution, four other initial age-distributions were used (Table 7.5 above). It was found that the optimal estimate of adult survival did not vary by more than  $\pm 1\%$  and the goodness-of-fit (as measured by chi-squared) still gave  $p > > 0.1$ , i.e. excellent fits (Table 7.6).

The variation in the proportion of adults shows a rather 'humpbacked whale' (Figure 7.19) shape with proportions of over 65% for much of the early- to mid-1980s. This is probably due to the high number of nestlings from the mid-1970s being recruited in the adult population during the early 1980s. The proportion of adults at the end of the 1980s is similar to that observed in the population.

1 It has been argued that these two curves should be identical because the model used here is the same as the Leslie-matrix model and the ZPG age-distribution is the asymptotic age-distribution (E. Danchin, pers. comm.). This is not so because the number of large nestlings added to the population are not estimated from the Leslie-matrix model, rather the actual observed numbers are used.

### Comparison of observed with predicted age-ratios

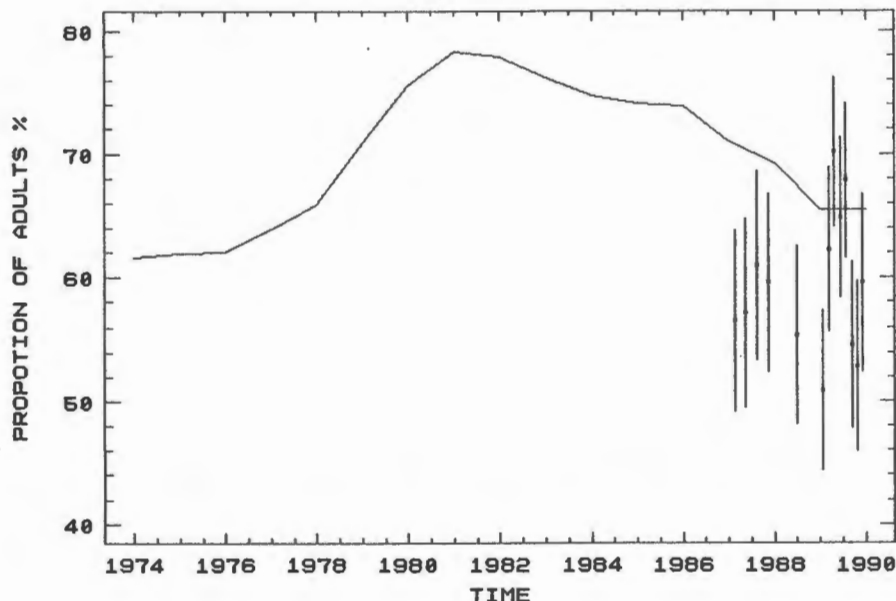


Figure 7.19 There are a number of estimates of the proportion of adults in the population from observations in the late 1980s. These are compared with the age-ratio computed from the model.

Table 7.6

Effects of using different initial age-structures in model

Parameter	ZPG	B	C	D	E
Adult survival	0.912	0.912	0.914	0.919	0.909
Chi-squared	6.56	6.59	6.63	6.94	6.54

With 9 degrees of freedom  $p > 0.1$  for all estimates

The number of nestlings produced (known from the field observations) is compared with the total population size (estimated from the model) and this suggests that there is a negative linear trend (Figure 7.20). Although this is not statistically significant ( $p > 0.2$ ), there are two potential outliers, i.e. the first two years (1974 and 1975). Removing these two years yields a significant negative linear relationship ( $p < 0.05$ ).

Plotting the number of nestlings produced per adult as a function of time (Figure 7.21) produces a very different picture. The production of nestlings per adult decreases strongly from a high of about 0.42 in 1974 through to a low of 0.13 in 1980, whence it rises steadily through to 1990.

### Relationship between numbers of adults and nestlings produced

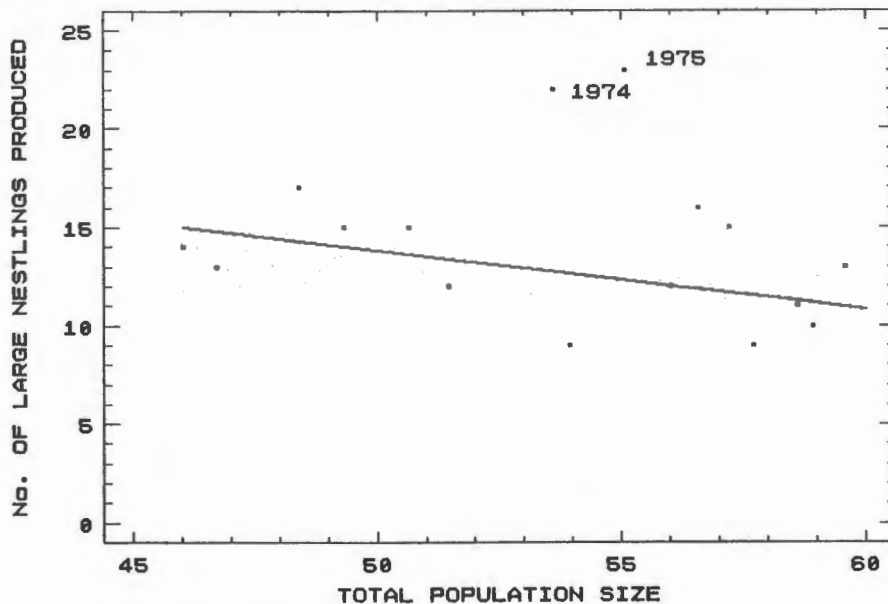


Figure 7.20 The number of large nestlings produced vs number of adults in the population. The negative relationship is significant only if two possible outliers (i.e. 1974 and 1975) are excluded.

#### 7.2.3 Summary

The fit between the estimated number of free-flying birds in the population and the number counted is excellent and statistically significant. A number of factors contribute to this.

- 1) The minimum number of nestlings is known exactly from direct observation. Thus the input to the model is well-known, assuming no immigration.
- 2) Over 70% of the nestlings were fitted with unique sets of colour-rings. This was coupled with an aggressive re-sighting programme leading to good estimates of age-specific survival, for the first three-year classes at least. As a consequence, given an adequate estimate of survival for those birds four years and older, it is possible to estimate the number of individuals in the population who have 'accumulated' from the known nestlings produced since 1974 (Figure 7.22). These will form about half the population in 1980 and will predominate thereafter. Thus the initial population size will not have much effect on the population trajectory.
- 3) Irrespective of the (unknown) initial age-distribution in 1974 all those birds will be adult by 1980 (adult plumage is assumed at about age six; Piper, Mundy & Vernon 1989). This is true for the two 'extreme' initial age-distributions (all sub-adults: model E & all-adults: model F - see Table 7.5) both of which yield similar total population sizes from about 1980 onwards (Figure 7.22). Thus the initial age-distribution will have little effect after the first six years.

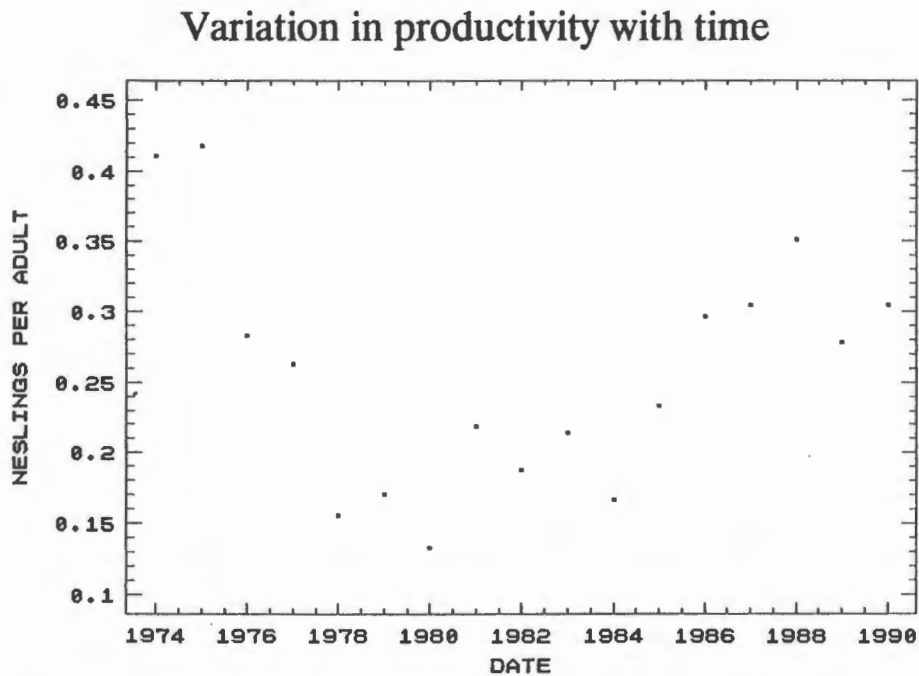
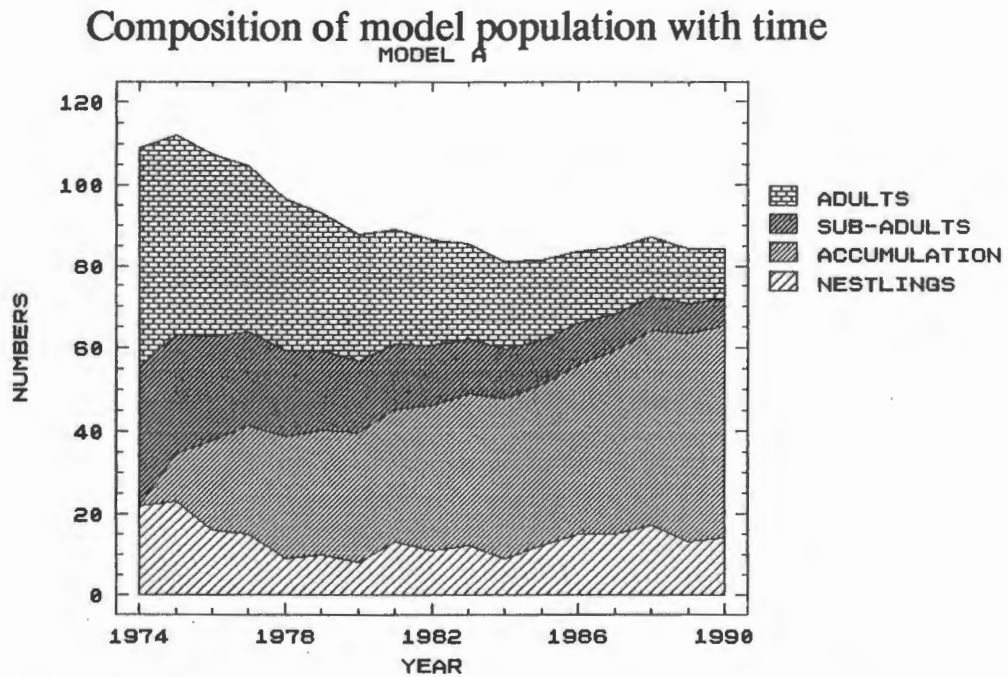


Figure 7.21 The number of large nestlings produced per adult as a function of time.

The most important parameter in the model is adult survival which is estimated at about 91% p.a. This is both feasible and consistent with estimates obtained for similar species (see Chapter Five). The estimated confidence limits on adult survival are about  $\pm 2\%$ .

Total population size is not the only characteristic of the population to be modelled. Consideration needs to be given to age-structure. The proportion of adults in the population, using the estimates from the model, rises from about 62% in 1974 to about 78% in 1980 and drops to 64% at the end. The proportion of adults in the model is generally much higher than that observed at the colonies (Figure 7.19). But it is consistent with the proportion of breeders (Figure 7.14). Given the discrepancy between the proportion of adults and proportion of breeders it has been suggested that "some adult birds may have been classified as 'immatures'. On the other hand, some sub-adult birds may breed" (Boshoff & Scott 1990: 39). Thus the fault may lie in either the model or the original field observations.

An alternative explanation may be that there is an influx of young birds from undiscovered colonies in the region, or from outside the southwestern Cape. If this indeed the case, then this would imply that the proportion of adults in the population could be lower while still maintaining the same total population size. Also, the adult survival rate would also be lower because fewer of the locally-reared birds would need to be recruited to the adult population.



Notes: Adults: The number of adults in the initial population (i.e. in 1974) and the number that survive year-by-year.

Sub-adults: The number of sub-adults in the initial population and the number which survive.

Accumulation: The number of nestlings which become first-years and join the population of free-flying birds.

Nestlings. The number of nestlings produced each year.

Total population includes nestlings and so is not directly comparable with population trajectory (Figures 7.13) unless nestlings are removed.

**Figure 7.22** The number of large nestlings produced per adult as a function of time.

The population is declining slowly at about -1.6% p.a. (see p. 419 above). What is the cause? A comparison of the survival rates used here with those used in the ZPG model shows that they are similar. In fact, when inserted therein they suggest that the population should increase at +0.90% p.a. There are two other possible causes for this decline: age at first breeding could be higher and fecundity could be lower.

From the sensitivity analyses investigated above it was seen that population growth is insensitive to this parameter. In addition, sub-adults are known to breed in the Potberg (Robertson 1983). Productivity is a function of the product of the proportion of birds which attempt to breed and their subsequent breeding success (see Chapter Four above).

### Composition of model population with time

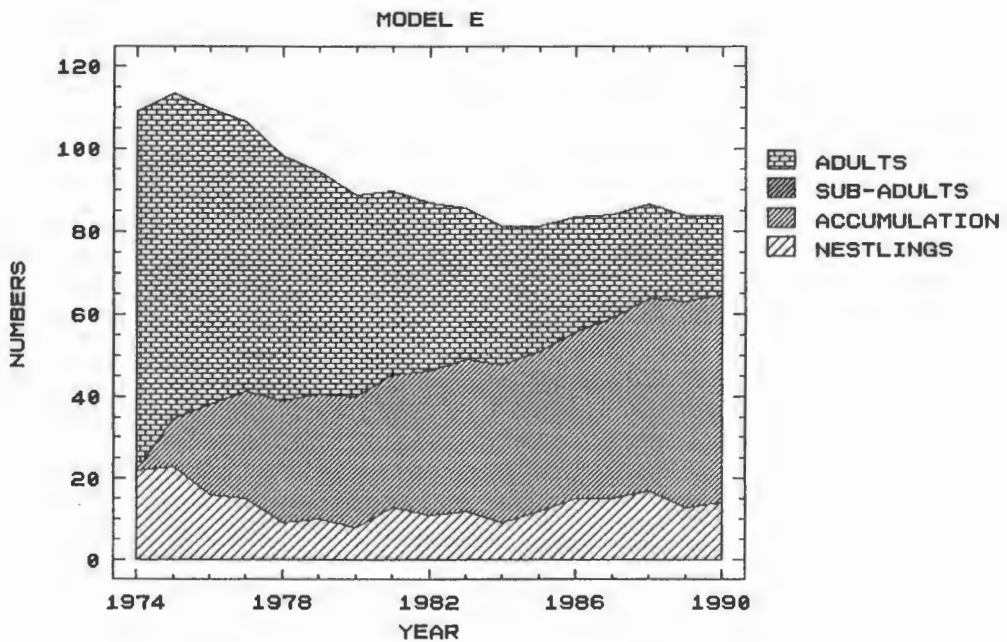
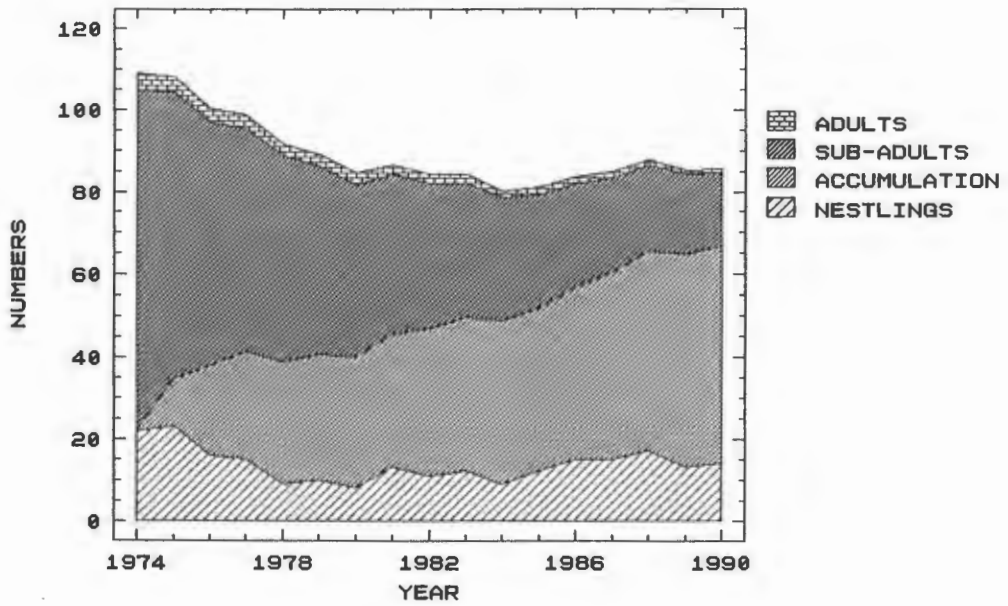
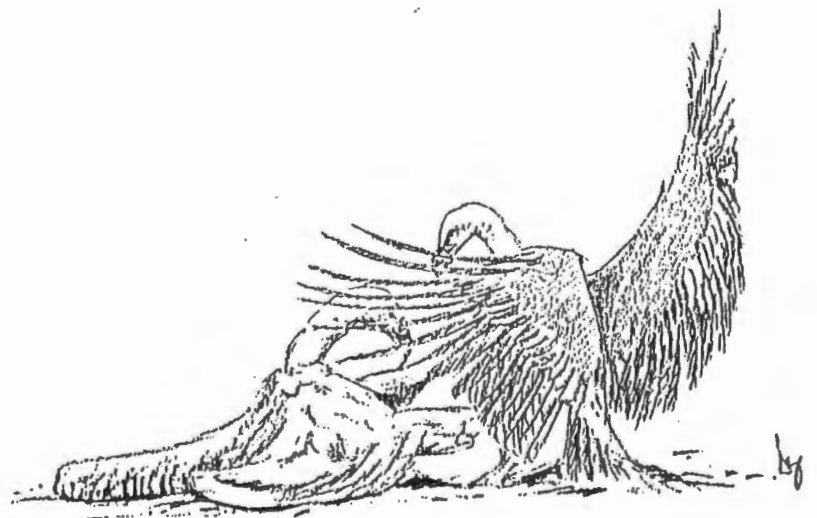


Figure 7.22 (Continued).

The proportion of birds that breed in the southwestern Cape varies from 70% to 80%, in the main, with two values outside that range (Table 7.4). This is slightly lower than that at Colleywobbles. The productivity at Potberg for the years 1986 to 1990, both years inclusive, was 69% (i.e. 40/58). During the same period breeding success was higher at the Little Karoo colonies: 79% (i.e. 15/19) and it is claimed that this difference continued an earlier trend for Little Karoo colonies to be more successful than Potberg (Boshoff & Scott 1990: 36). However these differences are not statistically significant (Fisher's exact test,  $p > 0.1$ ). The overall success of 71.4% is lower than the 75% recorded for Colleywobbles. If breeding has ceased at the Little Karoo colonies, and the population has to rely on Potberg, then the productivity may be even lower.

Thus, while the proportion that breeds and the breeding success are lower (but not much) than at Colleywobbles, the population will continue to decline slowly. It is thus crucial to investigate ways of increasing productivity.



### 7.3 Stochastic models

Life for the Cape Vulture is not deterministic. To give an example, on a cold clear spring morning, at Colleywobbles in the Transkei, the wind blew strongly from the southeast creating so many slope drafts and standing waves in the Mbashe valley that most of the non-incubating birds were away at first light and far into the interior by sunrise. By mid-morning, birds started drifting back to the colony, all with full crops. That afternoon the south-easter turned into a cold front bringing non-stop rain for three days. Almost none of the vultures were able to go out to forage. For vultures feast alternates with famine. Some days, seasons and years are good while others are bad.

To investigate this obvious randomness in the vultures' lives two models are considered: environmental stochasticity and demographic stochasticity. In the model for environmental stochasticity, the vital rates (i.e. age-specific survival and fecundity) are allowed to vary randomly. The relationship between the extent of the variability in each of the vital rates and the resultant variability in the population is investigated. In the model for demographic stochasticity, consideration is given to simulating small populations where random variations could drive a population to extinction even though the mean rate of recruitment to the adult population, averaged over a long time, equals the average losses of breeding adults over the same time. Analytic models were not contemplated (Bartlett 1960: 27):

While in general we have to reckon with such complications as varying age-structure in any actual populations, the complexity of the corresponding stochastic models may preclude such complete specifications ...

The use of stochastic models may be seen as part of a development of more realistic modelling paradigms (Simberloff 1980). The approach to understanding these two stochastic effects (i.e. environmental and demographic) is to use simulation, rather than analytic models. The complexity of analytic stochastic models is such that solution, in closed form, is not easy. However, 'brute force' simulations are relatively straight forward using *Monte Carlo* simulations (Bartlett 1960: 33), especially with modern computer packages designed for use on personal computers (Ferson & Akçakaya 1991: 13 ff.).

#### 7.3.1 Environmental stochasticity

It is likely that as the environment varies, so will the ability of individuals to reproduce and to survive. For the Cape Vulture, it is not yet possible to relate variations in vital rates to environmental variations. As a substitute, random variations in the vital rates are simulated, and the resultant changes in the total population are studied.

The starting point for simulating the Cape Vulture population under environmental stochasticity is via the generalized and augmented Leslie population projection matrix (see section 7.1.1 above).

$$\begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \\ n_6 \\ n_7 \end{bmatrix} (t+1) = \begin{bmatrix} 0 & 0 & 0 & 0 & F_5(t) & F_6(t) & F_7(t) \\ S_1(t) & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_2(t) & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_3(t) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_4(t) & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_5(t) & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S_A(t) & S_A(t) \end{bmatrix} * \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \\ n_6 \\ n_7 \end{bmatrix} (t)$$

The way demographic parameters vary with time determines the manner in which the population responds. It is assumed that all the demographic parameters are statistically stationary, i.e. if  $S_3(t) \equiv F_3(\mu, \sigma^2)$ , where  $F_3$  is a random variate which follows some statistical probability distribution function with parameters  $\mu$  and  $\sigma$ , then these parameters do not vary with time. These parameters are required to be stationary (in the statistical sense), because the interest is in the variability about the mean; temporal trends are not of interest here (but see section 7.1 above).

*Nature of the probability distributions.* When simulating variable survival rates and variable fecundities, it is necessary to know from what statistical distribution to draw. Are the rates uniformly distributed across some range, or do they follow some other statistical distribution? The observed variance in a demographic parameter is a function of two components: estimation errors and real-world variability. Both survival and fecundity rates are estimated from ratios, i.e.  $n$  out of  $N$  birds of a given age-class survive and  $m$  out of  $M$  pairs produce a large fledgling (see chapters four and five above). This means that these rates are distributed as the binomial distribution. It is known, for large sample sizes, that the binomial distribution tends to the normal distribution with mean,  $\mu = p$  and variance,  $\sigma^2 = p(1-p)/N$  (Patel, Kapadia & Owen 1976: 180 ff.) where  $p = n/N$  (i.e.  $n$  individuals of  $N$  survive one further year). Thus it is reasonable to approximate the sampling variations by means of a normal distribution.

Unfortunately, there is no information for the Cape Vulture as to how the demographic parameters vary in the real world. Thus, by default, all vital rates are simulated using random normal variates.

Table 7.7

Mean values of demographic parameters used in simulation model

Age class	Stable age distribution	Fecundity	Survival
First	181.2	0.0	0.53
Second	96.1	0.0	0.85
Third	81.7	0.0	0.89
Fourth	72.4	0.0	0.89
Fifth	64.2	0.32	0.89
Sixth	57.0	0.32	0.89
Seventh	447.4	0.32	0.89
Total	1000.0		

*Mean values of the demographic parameters.* For reasons advanced above (section 7.1), the mean value used for each demographic parameter is taken to be equal to that in the Zero Population Growth (ZPG) model used to estimate sensitivity (see section 7.1.3 above). Only the females are modelled, which involves no loss of generality provided the sex ratio is assumed to be unity.

*Coefficients of variation.* Having decided to use the normal distribution from which to draw the random variates it is necessary to estimate the mean (Table 7.7) and variance of each vital rate. The variance, and hence coefficient of variation ( $CV = \sigma/\mu =$  ratio of standard deviation to mean), for each group of parameters is estimated in the following manner.

- First-years.** From the estimate of first-year survival, and the associated confidence limits (see section 7.1.2 above - based on data from section 5.2.4) it is possible to estimate the coefficient of variation at 0.10.
- Older age classes.** In the same way it is possible to estimate the coefficient of variation of survival for the two+ year age-classes as 0.075.
- Fecundity.** The coefficient of variation in fecundity at Colleywobbles, from one year to the next, over nine years was found to be 0.15 (from section 7.1.3.3 based on data in Table 17 of Vernon & Piper 1991). This data-set, from a single breeding colony, is taken to be representative of the population as a whole, only because of a lack of other observations.

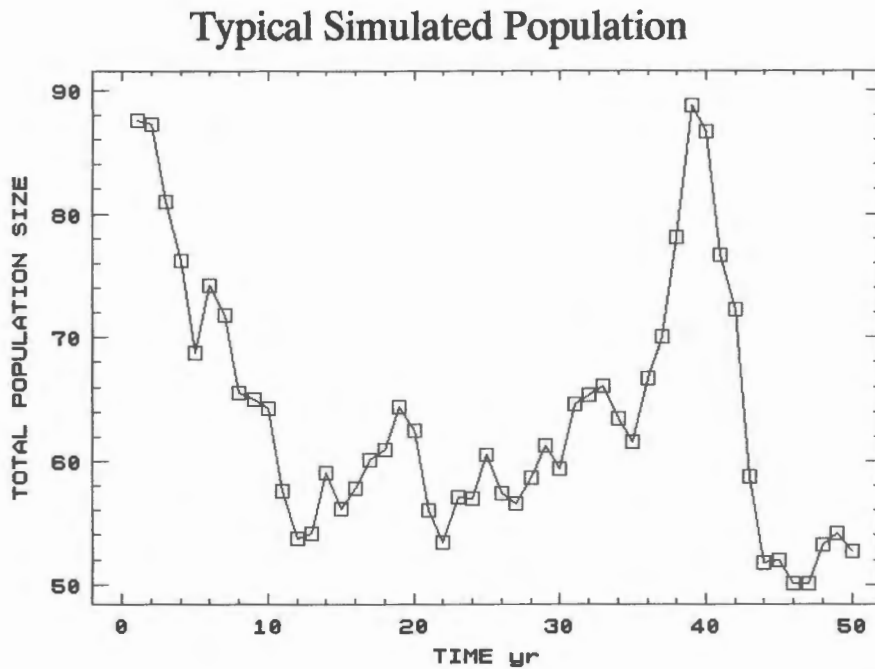


Figure 7.22. An example of simulating the Cape Vulture population under environmental stochasticity using the 'standard parameters' (i.e. Table 7.7).

*Correlations between population parameter estimates.* It is likely in the real world that there will be correlations between the parameter estimates of the vital rates. This is a consequence of the way estimates are computed (Anderson, Burnham & White 1985: 233) and also it is likely that those environmental factors which depress first-year survival (e.g. reduced foraging as a result of long periods of inclement weather) are likely also to depress the survival of older individuals as well as reduce breeding success. However, no data exist on the nature of these correlations and so they are set to zero for the calculations that follow.

*Simulation Package.* The simulations were conducted using the RAMAS/age package (Ferson & Akçakaya 1991). The simulations are set up in four phases.

- 1) A description of the species to be simulated is provided for documentation purposes.
- 2) The average values, which correspond to the estimates, are entered for the vital rates.
- 3) The probability distributions best describing the variations in the vital rates are chosen.
- 4) The duration of the simulation (i.e. number of years) and number of replicates are specified.

The simulations are carried out using the generalized and augmented Leslie-matrix described above. The mean value for each vital rate (Table 7.7), coefficient of variation and sampling distribution are those described on the previous three pages.

### Summary of 100 Replicated Simulated Populations

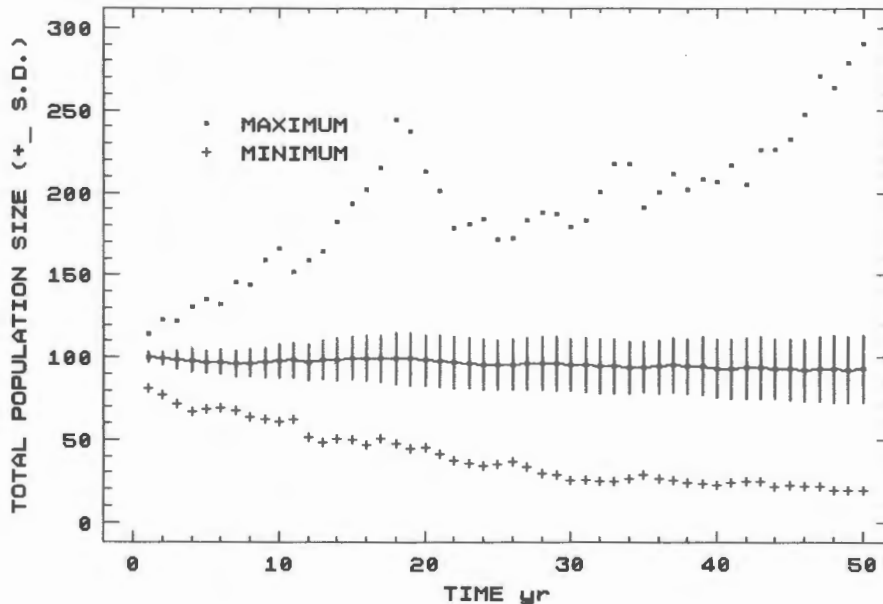


Figure 7.23. Summarizing the results of simulating the Cape Vulture population 100 times under environmental stochasticity using the 'standard parameters' (i.e. Table 7.7).

If a simulation is run just once then it is possible to trace the population variation with time (Figure 7.22). Plotting, on the same graph, the trace of more than one simulation results in a picture reminiscent of boiling spaghetti and so it is necessary to produce one or more summaries. To summarize two, or more, simulations a plot is produced with four components (Figure 7.23).

- 1) The mean population size for each year.
- 2) The 95% confidence limits about the mean, for that year.
- 3) Minimum value recorded for each year.
- 4) Maximum value recorded for each year.

By adjusting any one parameter (e.g. mean, coefficient of variation, probability distribution or covariance matrix), it is possible to see how the population will vary with time.

*Quasi-extinction risk curve.* At least ten different summarization procedures are provided by the RAMAS/age package. The one most useful here is the quasi-extinction risk curve (Ferson, Ginzberg & Silvers 1989). At the end of the simulation (i.e. after  $t=T$  periods) with  $N$  replicates, it is possible to order the final population sizes from smallest to largest and compute the proportion of simulations yielding a population size less than some specified maximum value.

### Risk Analysis: an Example

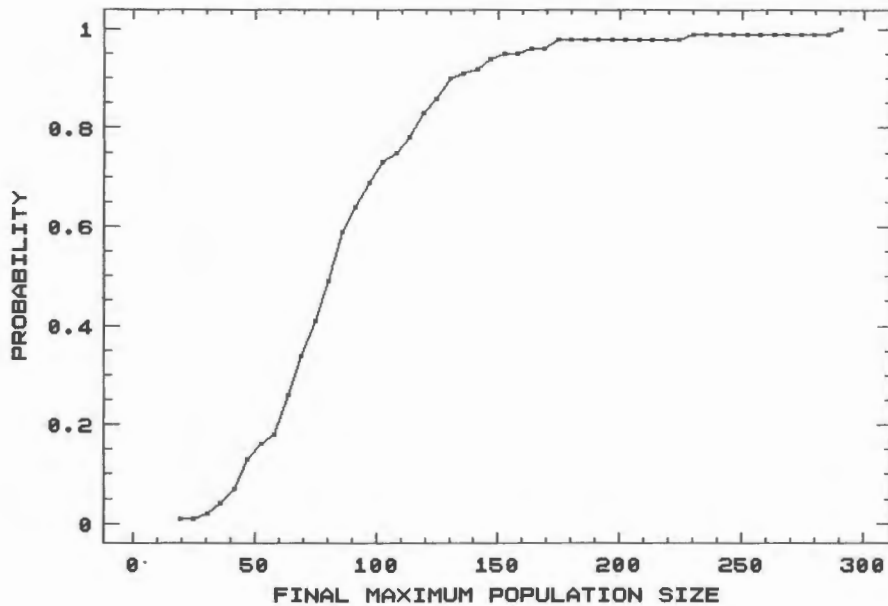


Figure 7.24. The risk curve. The proportion of simulations yielding a final population size less than or equal to a given maximum value. Simulation of Cape Vulture population 100 times under environmental stochasticity using the 'standard parameters' (i.e. Table 7.7).

An example is given (Figure 7.24) of the results from 100 replicates of simulating a Cape Vulture population under 'standard conditions' (i.e. Table 7.7). This cumulative distribution of the final population size (Figure 7.24) is an approximation to the cumulative probability of having a final population size less than a given maximum. The steeper this curve the less variable the population at the end of the simulation. For these 100 replicates of the simulation it is seen that the final population lay between 18 and 297. If the minimum had been zero then the population would have gone extinct during at least one replicate.

*Replicates.* In order to determine the probability of extinction, it is necessary to run the model a number of times and count the proportion of times the population goes to extinction, i.e. the probability of extinction is estimated from a binomial proportion. It is well known when estimating the population proportion,  $P$  from an unbiased sample proportion  $p = n/N$  that  $p \rightarrow P$  as  $N \rightarrow \infty$  (Kendall & Stuart 1969: 223). Thus the larger the number of replicates the better. However, high numbers of replicates take a long time to run and this reduces the total number of different simulations which can be run in a given time. To illustrate this problem, a population of 100 individuals was subjected to a simulation using the standard parameters (i.e. Table 7.7) described above over a period of 50 years (i.e. 50 time cycles).

### Number of Replicates Needed

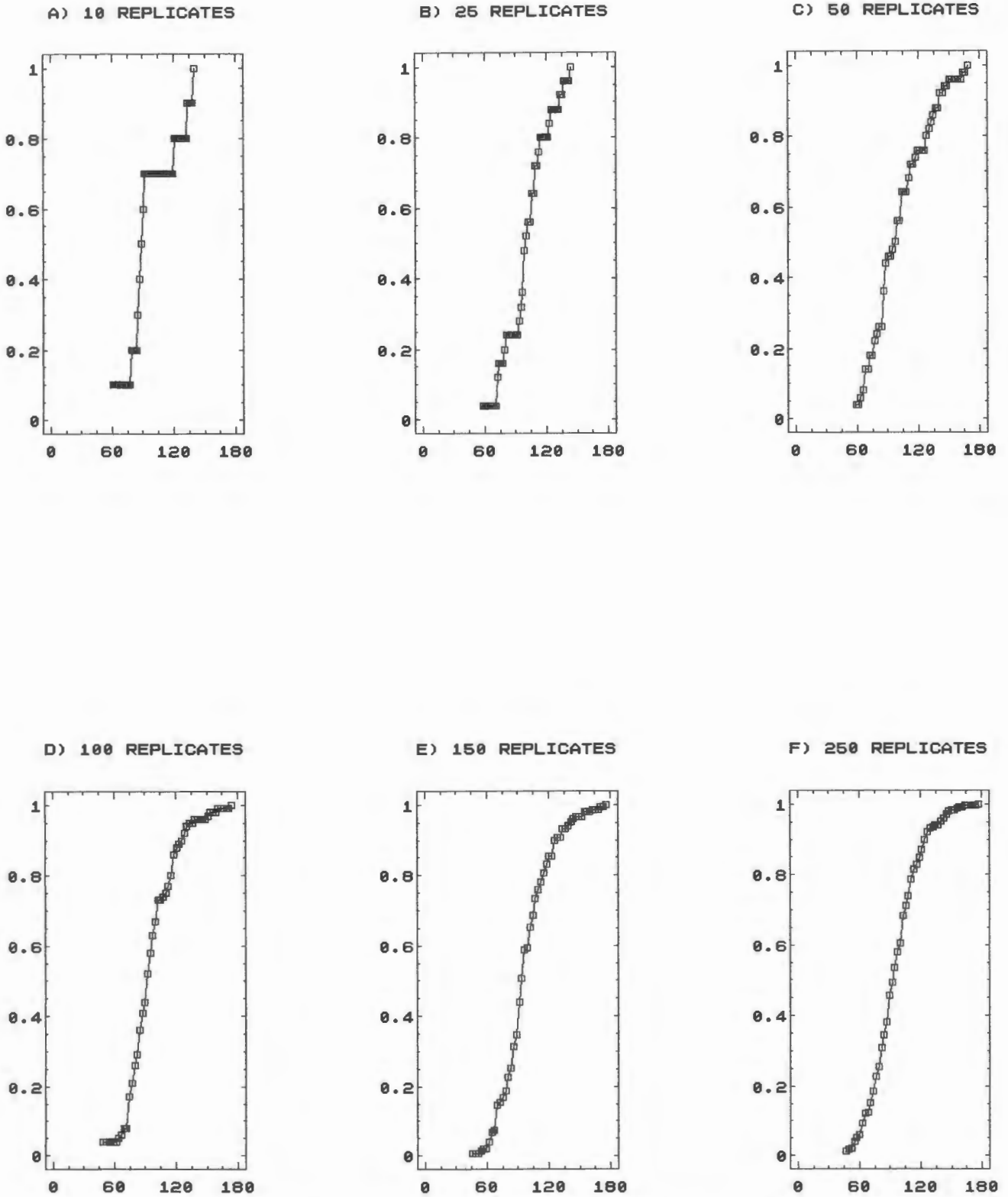


Figure 7.25. Estimating the number of replicates required. Comparison of risk curves estimated from 10, 25, 50, 100, 150 and 250 replicates. Final population size is plotted along the horizontal axis and cumulative probability along the vertical. Simulations of Cape Vulture population under environmental stochasticity using the 'standard parameters' (i.e. Table 7.7).

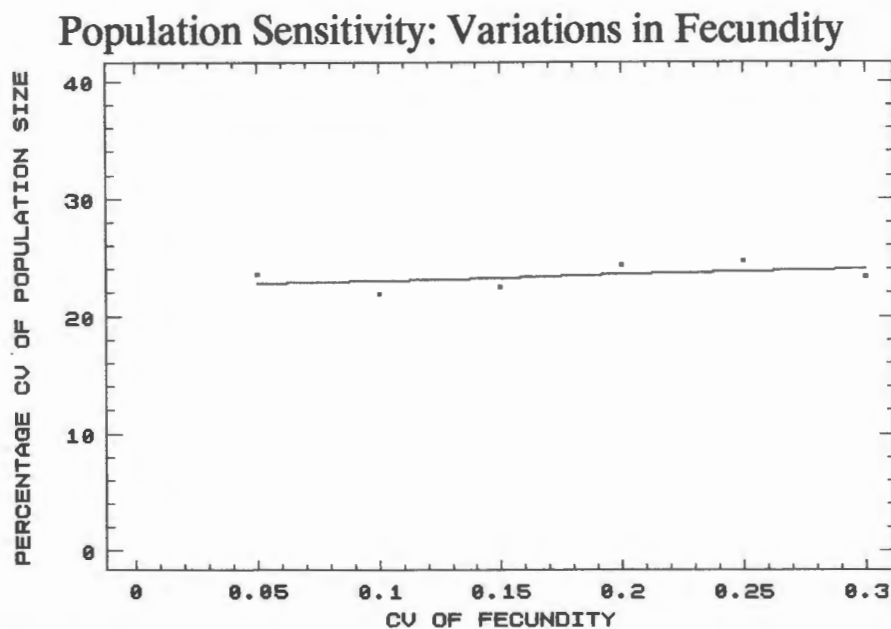


Figure 7.26. Population sensitivity to variations in fecundity. Population response is measured as the coefficient of variation (as a percent). Straight line to show trend only - regression not significant ( $p=0.36$ ). Simulation of Cape Vulture population 100 times under environmental stochasticity using the 'standard parameters' (i.e. Table 7.7).

The simulations were replicated 10, 25, 50, 100, 150, 200 and 250 times. For each set of replicates the cumulative maximum population size curve (i.e. the quasi-extinction risk curve) was plotted (Figure 7.25). It is seen that for few replicates (e.g. 10, 25 and 50) that the distribution has many 'steps' and 'jaggies', while for many replicates (i.e. 100 and above) the curve is smooth and there are few differences between the distributions. Thus 100 replicates were run of each simulation.

*Population response variations in the vital rates.* It is clear from the example presented above (i.e. Figure 7.23) that the variability of the population size increases with time. The 95% confidence limits slowly increase outwards like the cone of a trumpet as the time,  $t$ , increases. The maximum variation is thus likely to be at the last year,  $t=T$ . To measure this terminal variability the following approximation is used.

$$\text{S.D.} = [(\text{Upper 95\% limit}) - (\text{Lower 95\% limit})]/4$$

This is based on the following assumptions.

- 1) The distribution of final population sizes will be approximately normal.
- 2) For  $N = 100$  replicates Student's  $t$ -value is just under 2.

### Population Sensitivity: Variations in First-year Survival

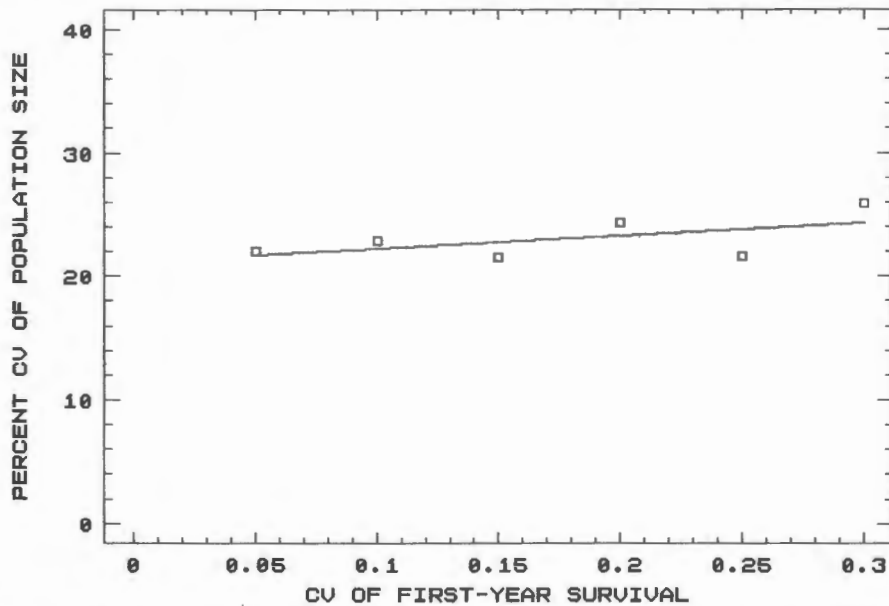


Figure 7.27 Population sensitivity to variations in first-year survival. Population response is measured as the coefficient of variation (as a percent). Straight line to show trend only - regression not significant ( $p=0.24$ ). Simulation of Cape Vulture population 100 times under environmental stochasticity using the 'standard parameters' (i.e. Table 7.7).

The terminal variation is presented as the coefficient of variation (CV) using the S.D. (as defined above) and the mean population size (measured as the mean of the 100 values of the terminal population size). The population response is investigated for three classes of parameter: fecundity, first-year survival and survival of older Cape Vultures.

*Variations with Fecundity.* The CV of the fecundity terms was allowed to take on the values 0.05, 0.10, 0.15, 0.20, 0.25 and 0.30 with 100 simulations performed for each value. The CV (as a percent) of the final population size is plotted against the CV of fecundity (Figure 7.3.1.G). There is a slight increase in population variability with increasing variability in fecundity, but it is not statistically significant ( $p=0.36$ ). In other words, the increase in population variability, even if it were real, is less than the simulation noise.

*Variation with First-Year survival.* The CV of first-year survival was varied through the values 0.05, 0.075, 0.10, 0.125, 0.15, 0.175 and 0.20 with 100 simulations performed for each value. The CV (as a percent) of the final population size is plotted against the CV of first-year survival (Figure 7.27). As with fecundity, there is no detectable linear relationship ( $p=0.24$ ).

### Population Sensitivity: Variations in Survival of Two+ year-olds

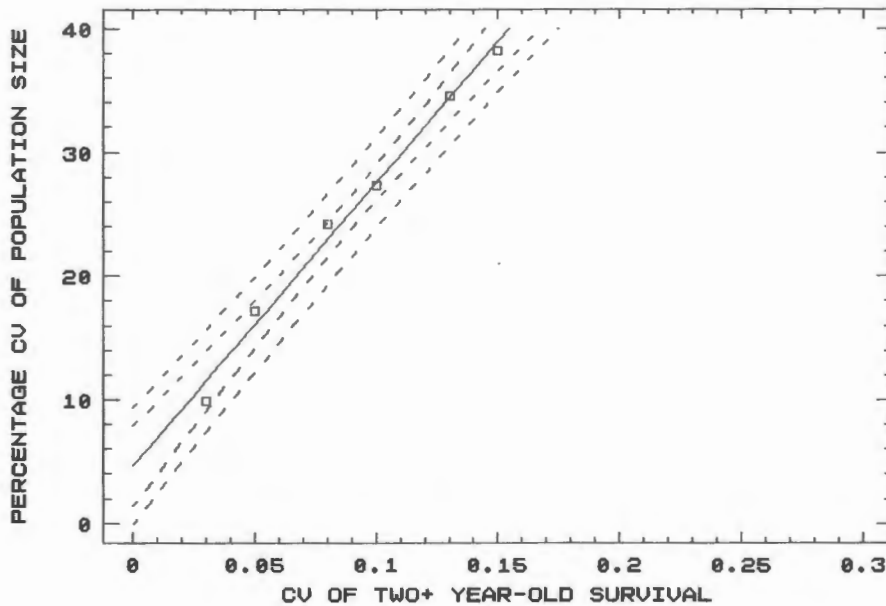


Figure 7.28. Population sensitivity to variations in the survival of birds two+ years old. Population response is measured as the coefficient of variation (as a percent). Regression significant ( $p < 0.01$ ; 95% confidence limits for regression line and predictions shown as dotted lines). Simulation of Cape Vulture population 100 times under environmental stochasticity using the 'standard parameters' (i.e. Table 7.7).

*Variation with survival of birds two+ years-old.* The CV of the survival of those Cape Vultures two+ years-old was allowed to take on the values: 0.025, 0.05, 0.075, 0.1, 0.125 and 0.15 with 100 simulations being performed for each value. The CV (as a percent) of the final population size was found to increase strongly with increasing variability in post-juvenile survival (Figure 7.3.1.I;  $p < 0.01$ ).

#### 7.3.2 Demographic stochasticity and extinction

For a small Cape Vulture population, a single chance event such as a helicopter flight through the breeding colony or a period of inclement weather which is longer than usual can result in the deaths of both nestlings and breeding adults (Boshoff & Scott 1990: 36). A similar proportional loss in a much larger population is less serious because the remaining birds can, over time, make good the losses. An area of concern in managing small populations is that of demographic stochasticity and the probability of extinction. It has been suggested that demographic stochasticity is an important factor when considering the conservation of rare species (Goodman 1987).

Simulations for demographic stochasticity differ from those for environmental stochasticity in one important respect. Because the population is small, the estimated numbers of survivors and recruits must be whole numbers. Thus, it is not possible to have 2.2 offspring. To achieve this, fecundity is simulated using a Poisson random number generator which returns an integer number of births 0, 1, 2, ... (Ferson & Akçakaya 1991: 97). For survival, a binomial random number generator is used.

Given a population with vital rates that are stationary (in the statistical sense), it is likely that from an initial population size of  $M$  individuals, say, the final population after  $t=T$  years will be more variable the larger the initial population and the longer the simulation period. To test this for the Cape Vulture population, initial population sizes of 10, 20, 30, ... 100 were taken and simulated for  $t=T$  years using 100 replicates. For each set of replicates, a risk curve was generated and these were brought together and used to create a contoured map (e.g. Figure 7.3.2.A) showing the probability of getting a final population size less than or equal to a given maximum value. Each figure shows the probability vs initial population size for a given number of years. The number of years was allowed to vary from 10 (Figure 7.29) through to 50 years in steps of 10 years (Figure 7.30 through to 7.33). It is clearly seen that the final population size is more variable the longer the simulation period and the larger the initial population size and this establishes the pattern.

Of crucial importance in this study is the answer to the question: "What is the probability that the population will go extinct?" While it is possible to read these off each of the above contours (i.e. Figures 7.29 to 7.33) it is not easy to do so. To answer this specific question 100 simulations were run of 250 replicates each for all combinations of initial population sizes of 5, 10, ... 50 and years  $t=T$  of 5, 10, ... 50 years. The risk curve for each simulation was examined and the proportion of times that the final population was zero (i.e. extinct) was computed. These values were then used to compute a contour map (Figure 7.34) in which the probability of extinction is shown as a function of initial population size and number of years since the start of the simulation.

To construct this figure, a certain amount of smoothing was used in drawing the contours. This was necessary because when simulating the probability of a rare event there is a certain amount of noise from the simulation process itself, even with 250 replicates. All those simulations with at least one extinction are shown as solid squares, while those with none are shown as small crosses (Figure 7.34). It can be seen that the boundary between the crosses and squares is not smooth.

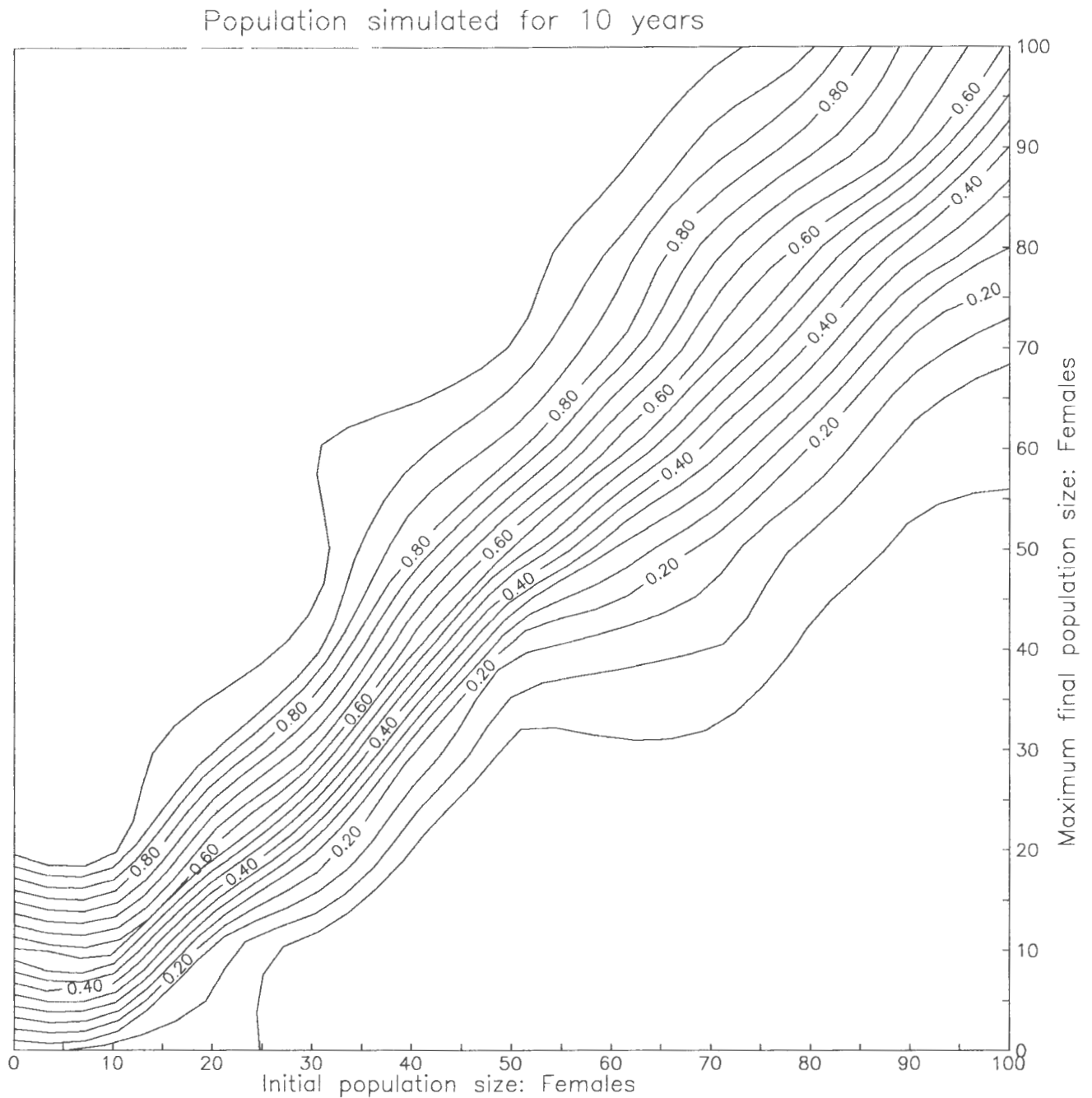


Figure 7.29. Contour map of risk probability of final population being less than or equal to a maximum value given the initial population size. Population simulated for 10 years. Results from simulating the Cape Vulture population 100 times for initial female population sizes of 10, 20, ... 100 under demographic stochasticity using the 'standard parameters' (i.e. Table 7.7). (Note. These contours represent cumulative probabilities and the population size on the vertical axis is also cumulative. Thus, for an initial population of 30 females the probability that the final population size will be 40 or fewer females is 0.90.)

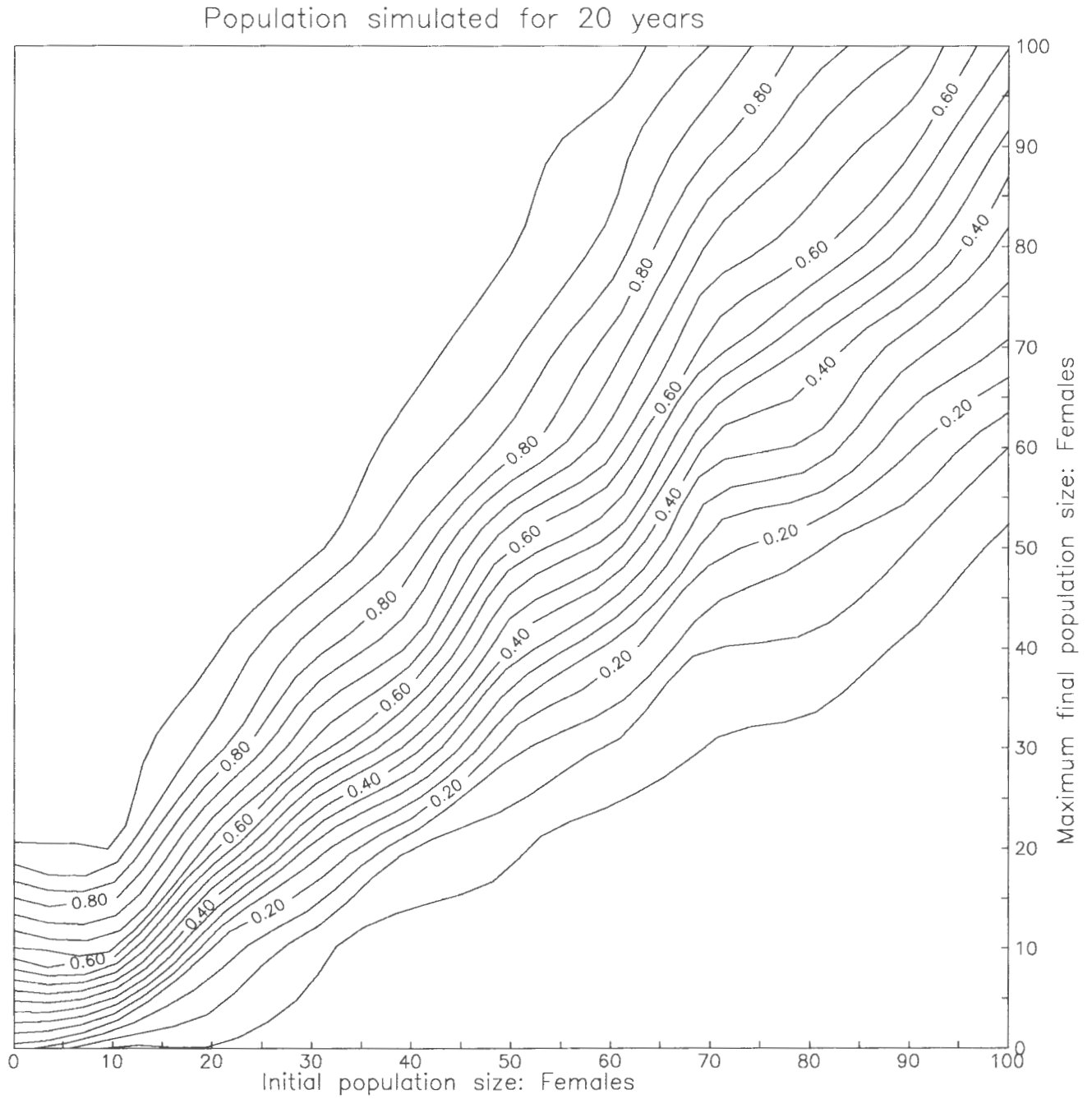


Figure 7.30. Contour map of risk probability of final population being less than or equal to a maximum value given the initial population size. Population simulated for 20 years. Results from simulating the Cape Vulture population 100 times for initial female population sizes of 10, 20, ... 100 under demographic stochasticity using the 'standard parameters' (i.e. Table 7.7).

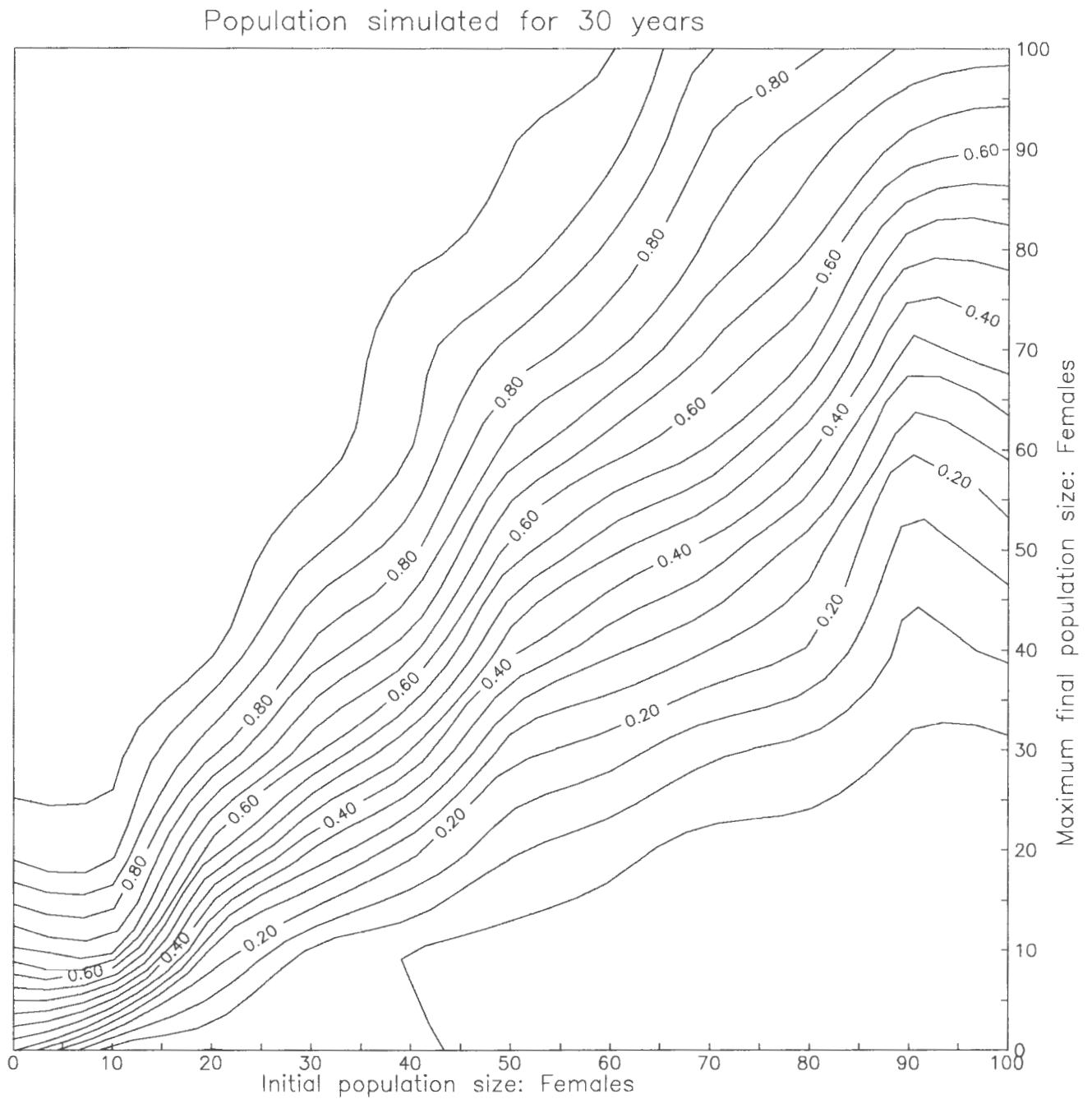


Figure 7.31. Contour map of risk probability of final population being less than or equal to a maximum value given the initial population size. Population simulated for 30 years. Results from simulating the Cape Vulture population 100 times for initial female population sizes of 10, 20, ... 100 under demographic stochasticity using the 'standard parameters' (i.e. Table 7.7).

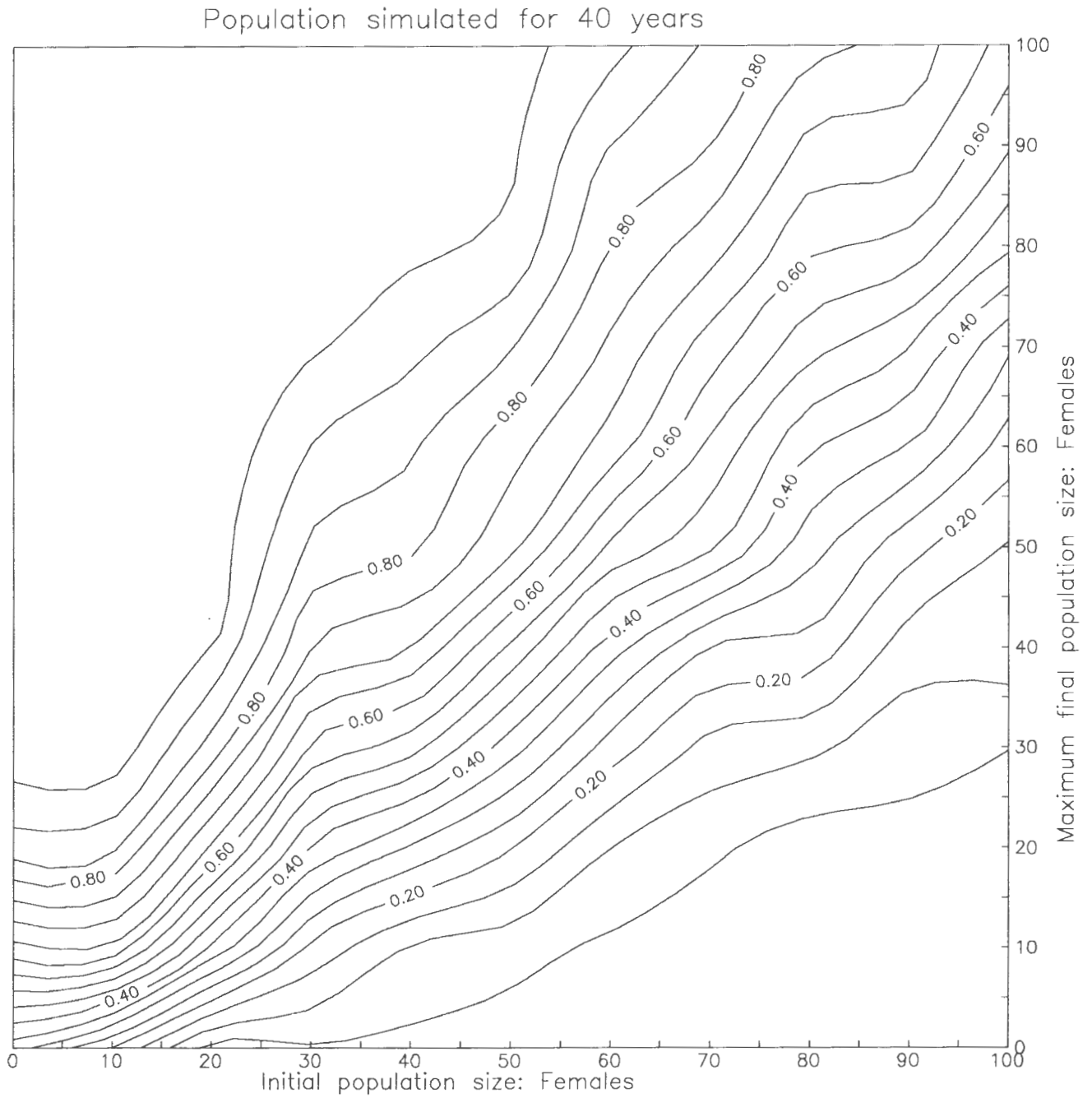


Figure 7.32. Contour map of risk probability of final population being less than or equal to a maximum value given the initial population size. Population simulated for 40 years. Results from simulating the Cape Vulture population 100 times for initial female population sizes of 10, 20, ... 100 under demographic stochasticity using the 'standard parameters' (i.e. Table 7.7).

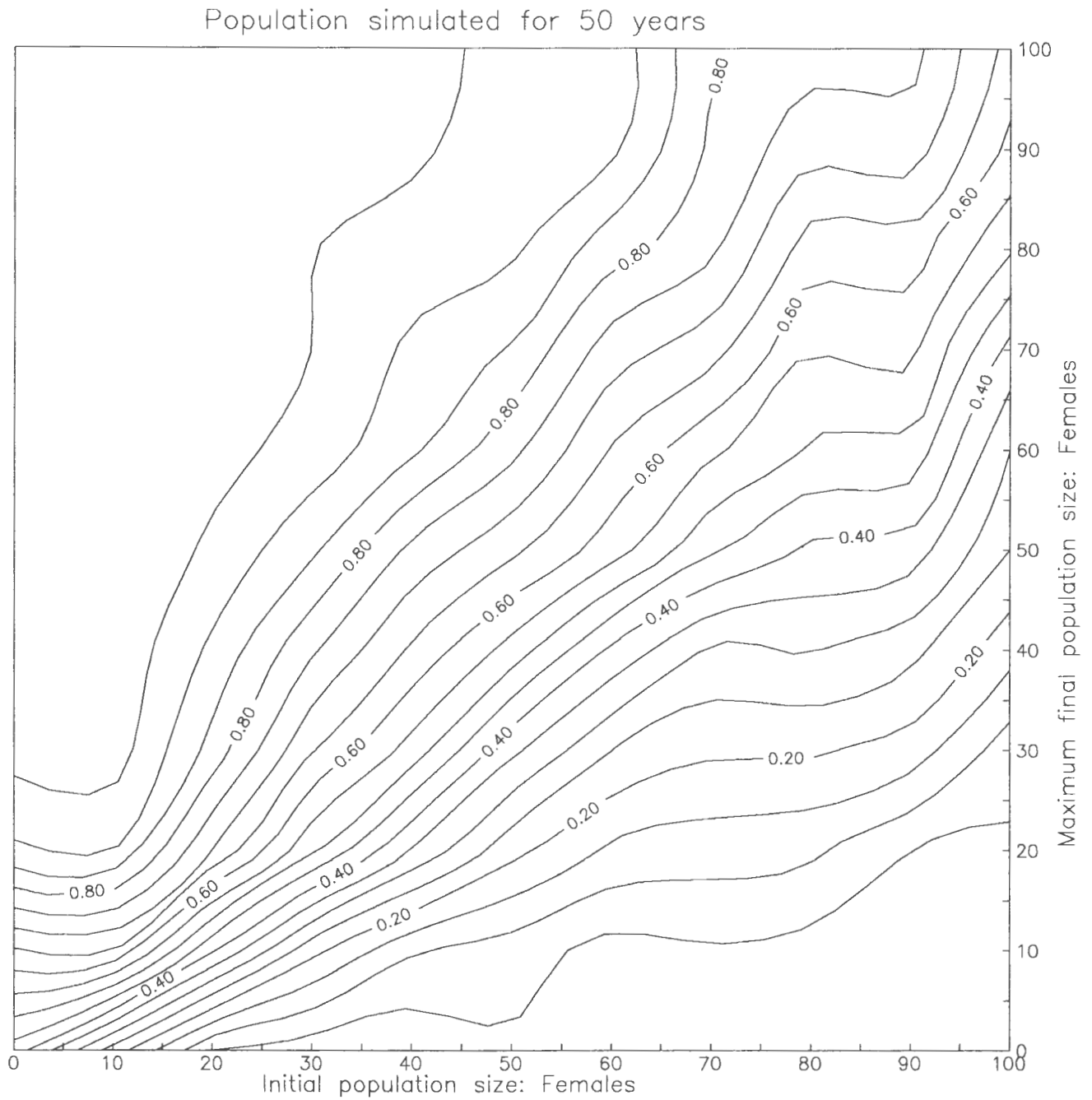


Figure 7.33. Contour map of risk probability of final population being less than or equal to a maximum value given the initial population size. Population simulated for 50 years. Results from simulating the Cape Vulture population 100 times for initial female population sizes of 10, 20, ... 100 under demographic stochasticity using the 'standard parameters' (i.e. Table 7.7).

## Extinction Probability

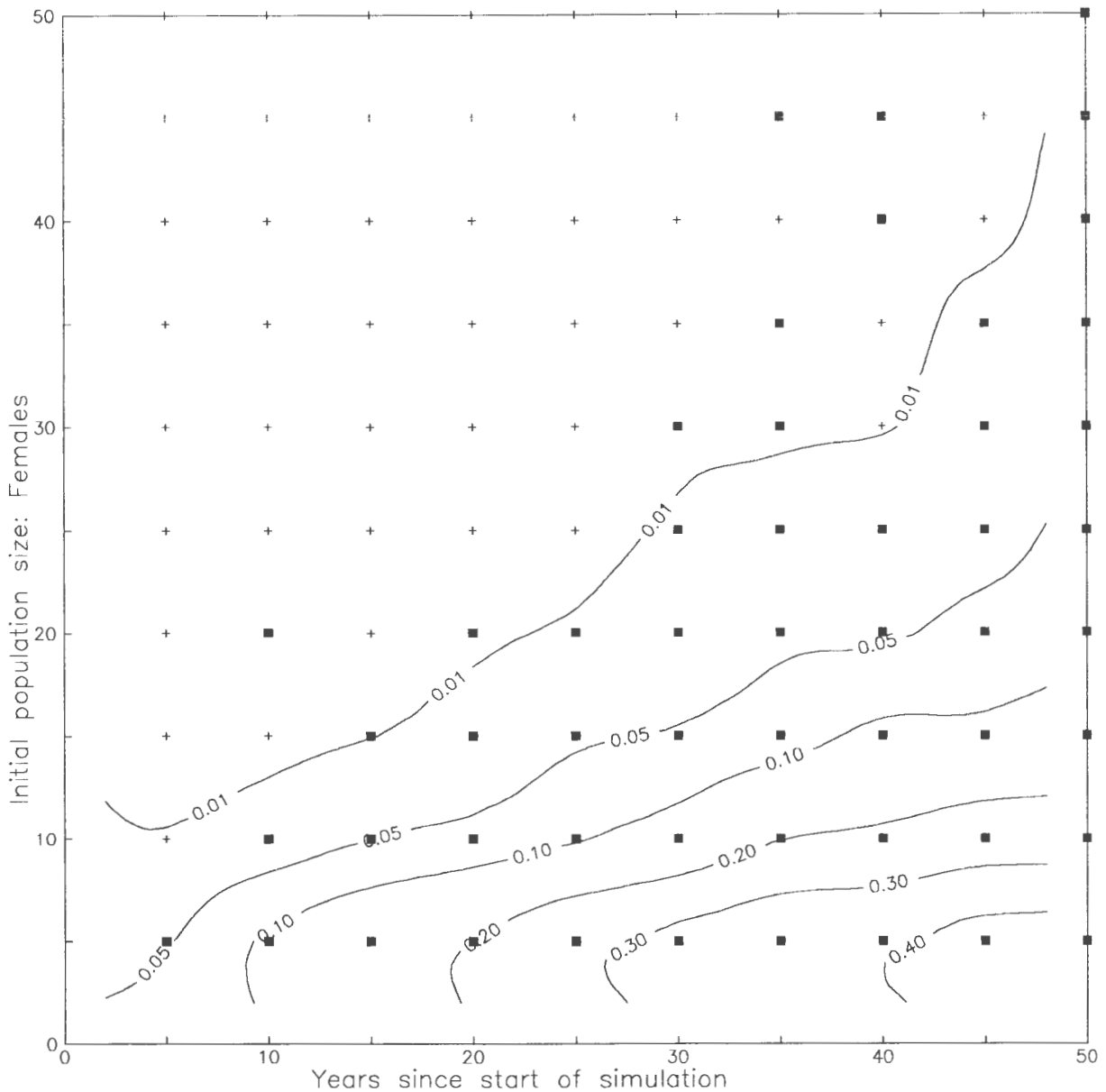


Figure 7.34. The probability that a Cape Vulture population will have a final size of zero after  $t=T$  years with a starting number of  $N$  females. Results from 100 simulations, each of 250 replicates under demographic stochasticity using the 'standard parameters' (i.e. Table 7.7). This figure is derived from the previous five figures. The probability of extinction, as a function of initial population size was noted for each (and hence for number of years simulated). These data were then used to construct the contours shown here.

From this analysis, using the standard parameters (i.e. Table 7.7), it is clear that an initial population of at least 50 females (i.e. a total of 100 males and females) has a less than 1% probability of going extinct in any period of about 50 years, or less.

### 7.3.3 Minimum viable population.

The minimum viable population (MVP) is defined (Soulé & Kohm 1989: 37) as:

... the population size which provides a given probability of persistence of the population for a given amount of time ...

Those extrinsic factors which are likely to influence a population's ability to survive are environmental uncertainty and natural disasters while the intrinsic factors are demographic and genetic uncertainty (*ibid.*).

In the simulations of the previous sections, consideration was given to the effects of environmental and demographic stochasticity. It was seen that for a population of about 100 birds the probability of extinction in 50 years was less than 1%. These simulations were carried out on the assumption that there was no density dependence, because there were no data upon which to choose an appropriate model or estimate its parameters. Stochastic models without density dependence are likely to be *conservative* estimators of extinction probabilities (Ginzberg, Ferson & Akçakaya 1990). It has been suggested that density dependence does have a small 'self-correcting' tendency (Ferson & Akçakaya 1990: 52). Thus it would be tempting to conclude that this estimate of 100 individuals was the MVP. Unfortunately, two additional factors need to be considered: genetic variation and natural disaster.

Currently there is no information available on the degree to which Cape Vultures can tolerate the deleterious effects of inbreeding, though some research is currently being planned (G.H. Verdoorn pers. comm.). (The conventional wisdom that inbreeding is universally deleterious may be incorrect, and there may, in fact, be an optimal level of inbreeding coupled with philopatry; Shields 1984<sup>1</sup>.) There are two small Cape Vulture populations which are so far away from the main concentration of the species that it might be thought that they could be genetically isolated: the Waterberg colony in Namibia and the roosts and colonies in the southwestern Cape. Although these sites are over 500 km from the nearest colonies, there is

---

1 P.J. Mundy (*in litt.*) comments: "For long-lived birds and animals, particularly colonial ones such as the griffons where offspring are able to breed with parents (and certainly with kin) in due time, then the genetic system is *resistant* to inbreeding depression. Genetic variation is likely to be low in such a population. The Whooping Crane *Grus americana* and California Condor are ready-made examples."

reason to believe that they do attract 'foreign' birds (southwestern Cape, see section 7.2 above; Namibia, C.J. Brown pers. comm.). It has been suggested that the acquisition of a single new breeding bird once every 100 generations may be sufficient to prevent genetic drift (M.E. Gilpin, pers. comm.). Thus inbreeding depression may not be a serious issue for the Cape Vulture with its current population size and spatial distribution.

Possibly more serious is the effect of not taking any account of natural disasters. Again, the conventional wisdom is other animals' disasters are the Cape Vulture's feast (e.g. rinderpest, Foot and Mouth Disease and the Anglo-Boer War). There are avian diseases which can reach epidemic proportions in domestic stock (e.g. Newcastle disease and avian pox), and it is possible for raptors to contract some of these infectious diseases (Cooper 1978: 76-81). However, it is not known if they could spread in a population of colonial vultures. Recently, it has been noted that whole populations of dassies (the Biblical cony; Procaviidae) in southern Africa have declined to about 10% of their former numbers - whatever great catastrophe caused this went unnoticed (A.F. Boshoff pers. comm.<sup>2</sup>). Hence, it is possible that some epidemic could sweep through the Cape Vulture population and reduce it to a fraction of its current size<sup>3</sup>. It is also possible that rare weather phenomena (e.g. a hurricane) could kill many birds simultaneously. With no historical record to draw upon, it is impossible to estimate the frequency, extent or impact of such phenomena.

Problems associated with persistence and survival in small populations have been considered by a number of researchers (see the following reviews, all in the same magnificent book: Blondel 1991; Green & Hirons 1991; Lebreton & Clobert 1991; Newton 1991). Many of the issues they raise are not considered here because of a paucity of data.

It thus seems prudent to recommend a MVP much higher than the figure of 100 suggested above, and possibly for a period of 50 years or less. Also it is important to consider what minimum levels of immigration are necessary to prevent genetic decline. The way in which migration can act to ameliorate the depressive effects of demographic stochasticity will be examined in the next section.

---

2 P.J. Mundy (*in litt.*) comments "Dassies are subject to drought, we think in Zimbabwe to 'epidemics' of mange, though there is no proof. Mange is likely to be severest in drought (=food) stressed animals"

3 P.J. Mundy (*in litt.*) comments: "A good example here is the IBDV (inclusion body disease virus) of cranes that suddenly killed about 50 birds at the International Crane Foundation - see Docherty & Henning (1980) and Schuh & Yuill (1985)."

#### 7.4 Spatial-compartment models: Meta-population analysis

It is clear from the evidence presented earlier (i.e. Chapters Four to Six) that the Cape Vulture population has an age-structure (i.e. the estimates of survival and fecundity vary among the age-classes) and it also is clear that the population has a spatial structure. The notion that the population is spatially segregated has been suspected since the early 1980s (Boshoff & Vernon 1980; Mundy 1984; Vernon 1983). Two separate arguments may be presented to substantiate the hypothesis of spatial heterogeneity.

- 1) From a study of the spatial distribution of the breeding colonies it is apparent they cluster into at least four regions (see sections 3.1.1 & 3.2.1).
- 2) The Cape Vulture sightings reported to SABAP (section 3.2.5) show a disjoint distribution in South Africa, Lesotho and Swaziland (data for Botswana, Namibia and Zimbabwe were not available, but see Borello 1987 for Botswana).

Thus, although the Cape Vulture exists in about four disjoint 'patches', this does not imply that there are no movements between these patches. In fact, there is considerable evidence for movement between adjacent regions (see Chapter Six). Thus it may not be appropriate to model the sub-populations separately. The population structure may be viewed as a meta-population which is defined (Akçakaya & Ferson 1992: 1 ff.) as 'A set of populations of the same species that may exchange individuals through migration' (see also Lande 1991: 572-3). Meta-population analysis is part of a modern thrust in conservation biology to take a holistic view of a population, while acknowledging its spatial fragmentation (Newton 1991: 643; Soulé & Kohm 1989: 38).

In the analysis of meta-population dynamics it is known that frequent local extinctions and recolonization do occur in widely distributed populations (Andrewartha & Birch 1954). Local sub-populations may 'wink on and off', i.e. each patch may be short-lived. Some patches may exist as 'fountains' consistently producing excess individuals, while others exist as 'sinks' relying on immigrants to survive (Newton 1991: 641-643). As an example, electrocution has been a source of unnatural mortality acting as a sink for young Cape Vultures from many colonies, some of them exterior to the local patch, or sub-population (see Chapters Five & Six).

While there is no extensive body of evidence to suggest that Cape Vulture patches, i.e. local sub-populations, may 'wink on and off', there is some evidence to show that new sites may be colonized and old sites abandoned. Cape Vultures certainly can arrive in new areas where there is a recent supply of food (Chapter Six), and they can recolonize old breeding sites (e.g. Nootgedacht: Verdoorn & Becker 1992).

## Location of active sites within each sub-population

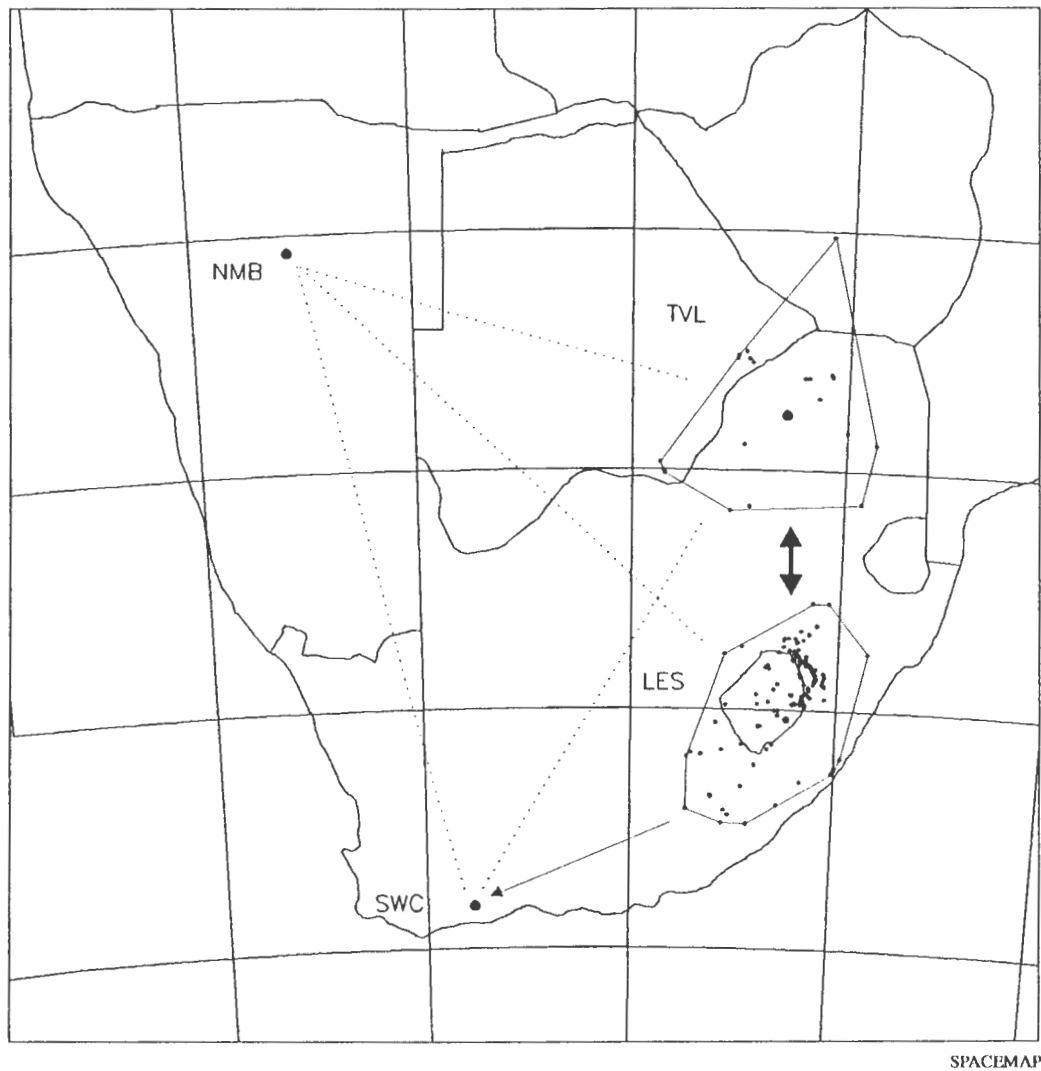


Figure 7.35 Spatial location of all active sites (i.e. roosts and colonies) shown within the sub-population boundaries used in these meta-population models. Solid lines indicate major movements, and their directions while dotted lines indicate rarer movements.

Table 7.8  
Sub-populations used in the spatial model.  
(Data from section 3.1.1)

Sub-population, $i$	Map coordinates		Initial population size, $B_i$	Carrying capacity, $K_i$
	$x_i$ mm	$y_i$ mm		
SWC	-17.56	21.00	65	65
LES	30.46	50.52	4923	5000
TVL	30.82	96.98	6825	6850
NMB	-47.04	122.26	18	50

Table 7.9  
Demographic parameters used in the spatial model.  
(Data from section 7.2)

Age-class, $i$	Stable age distribution, $A_i$	Survival, $\Phi_i$	Fecundity, $F_i$
First-years	0.181	0.53	-
Second-years	0.096	0.84	-
Third-years	0.082	0.78	-
Fourth-years	0.072	0.92	-
Fifth-years	0.064	0.92	0.32
Sixth-years	0.057	0.92	0.32
Adults	0.447	0.92	0.32
Weighted parameters		0.824276	0.181246

It is likely that many sites occupied in the Cape Province prior to the Anglo-Boer War and the rinderpest epidemic (both over by 1904), were relinquished by Cape Vultures as a result of reduced stock numbers in the early part of this century. Some were recolonized by the 1950s and 1960s, especially in the Eastern Cape because of an increase in stock numbers. In turn, many regions were vacated in the late 1960s and 1970s as a result of the sharp decline in available carcasses (Boshoff & Vernon 1980: 244-245).

#### 7.4.1 Model formulation

A model of the Cape Vulture is to be formulated which takes into account the spatial fragmentation of the population. This model is to be built using the *RAMAS/space* package to perform the simulations (Akçakaya & Ferson 1992). This package is specifically designed to handle meta-populations. Each element of the model is described, along with the methods used to estimate the demographic parameters.

*Populations.* From the maps of Chapter Three, it is clear that the population can be split into four centres which are treated as homogeneous (Table 7.8). Each centre, or patch is given a mnemonic.

- 1) SWC. Southwestern Cape comprising Potberg and the sites in the Little Karoo.
- 2) LES. All the sites in Lesotho, Natal, Transkei, OFS and Eastern Cape.
- 3) TVL. All the sites in the Transvaal and Botswana as well as Wabai Hill in Zimbabwe.
- 4) NAM. The Waterberg colony in Namibia.

For each site (Figure 7.35, Table 7.8), it is necessary to define the geometric and demographic parameters.

- 1) Centre of the distribution (X,Y). The weighted centre of gravity of each site is computed from all the sites in the region using their map coordinates ( $x_i, y_i$ ) and weighting each site by the total number of birds,  $B_i$  at that site (Table 7.8), i.e.

$$X = \{\Sigma[x_i \cdot B_i]\} / (\Sigma B_i)$$

$$Y = \{\Sigma[y_i \cdot B_i]\} / (\Sigma B_i)$$

- 2) Initial population size. The total population size of the patch,  $\Sigma B_i$ , is used as the initial population size in the simulations (Table 7.8).
- 3) Mean growth rate, R. A finite difference equation is used as the starting point for this model (Akçakaya & Ferson 1992: 10):

$$N(t+1) = R \cdot N(t)$$

where R may be a function of local density and other parameters which can vary both in space and time. The object of this simulation is to investigate how sensitive various attributes of the population are to stochastic variations in the demographic parameters. The 'base' or 'null' value of R is taken to be unity. For the special case  $R=1$ , the simulation package does not allow for density dependence. What limits should be used for R in the simulations? The rate of decrease estimated for the southwestern Cape population is about 1.6% p.a. (see section 7.2 above). The maximum growth rate so far recorded for any griffon species is +7% p.a. (Eurasian Griffons at 23 sites in northern Spain over a 20 year period; Donázar & Fernandez 1990). However, it is possible that the 7% growth included immigration in addition to natural increase (loc. cit.). The French have introduced a population of Eurasian Griffons and found that adult survival, in their highly protected population with supplementary feeding, is nearly 99% p.a. (F. Sarrazin, pers. comm, see Piper 1992). Using this estimate of adult survival in the ZPG model (see section 7.1.3) gives an estimate for R of 1.0725. It is suggested that reasonable limits on R would be 0.95 to 1.05, as long as 'unnatural' effects (e.g. electrocution) are not too large.

- 4) Standard deviation of growth rate,  $SD(R)$ . There is no *a priori* information from which values for this parameter can be estimated. However, replacing the parameter estimates in the ZPG model with random elements (values as per section 7.3), it is possible to show that the 95% confidence limits on  $R$  are about 0.89 to 1.09<sup>1</sup>. Thus using an initial value of  $SD(R)=0.10$  is conservative.
- 5) Overall survival,  $S$ . This meta-population model is based on the assumption that there is no age-structure, so that an 'average' survival needs to be estimated. The following simple scheme is suggested for computing an 'average' survival rate from the age-specific survival rates: set  $S$  equal to the weighted sum of age-specific survival rates,  $\Phi_i$  (Table 7.9), i.e.:
- $$S = \{\Sigma[\Phi_i \cdot A_i]\}/(\Sigma A_i)$$
- where  $A$  is the stable age distribution (see section 7.1.1). This yields  $S=0.824276$ .

Table 7.10  
Inter-site distances.

(i.e. between the centres of the sub-populations - mm on the map - km in parentheses)

		From Region			
		SWC	LES	TVL	NMB
To Region	SWC	- -	56.37 (846)	90.06 (1350)	105.5 (1583)
	LES	56.37 (846)	- -	46.46 (697)	105.6 (1584)
	TVL	90.06 (1350)	46.46 (697)	- -	81.86 (1228)
	NMB	105.5 (1583)	105.6 (1584)	81.86 (1228)	- -

There is a balancing equation relating survival and fecundity (Akçakaya & Ferson 1992: 25):  $R = S \cdot (1 + F)$  and this is used to compute fecundity for the simulations, i.e. from  $F = R/S - 1$  (loc. cit.). As a check on the consistency of this model the fecundity,  $F$  is estimated from the Leslie-matrix models using a weighting function (analogous to survival):

1 This is shown in a series of simulations written in Mathcad 3.0 and can be supplied on request to the interested reader.

$$F = \{\Sigma[F_i \cdot A_i]\} / (\Sigma A_i)$$

This yields  $F = 0.181246$ . Using the balancing equation it is seen that  $R = S \cdot (1 + F) = 0.824276 \cdot (1 + 0.181246) = 0.97$ . While this is slightly less than unity the agreement is adequate.

- 6) Density dependence. Previously it was seen (see section 7.2) that there is weak evidence for a negative linear relationship between nestling productivity and population size in the southwestern Cape. This suggests the use of a logistic form for density dependence (Akçakaya & Ferson 1992: 12 ff.):

$$N(t+1) = N(t) \cdot \exp\{r \cdot [K - N(t)] / K\}$$

Note that when  $N(t) = K$  the population is at equilibrium, i.e.  $N(t+1) = N(t)$ ; when  $N(t) > K$  the rate of change is negative but when  $N(t) < K$  the rate of change is positive. The maximum rate of change is as  $N(t) \rightarrow 0+$  when the multiplier  $\exp\{r \cdot [K - N(t)] / K\} \rightarrow \exp(r) = R$  {or  $r = \ln(R)$ }.

- 7) The carrying capacity,  $K$ . There is currently no known technique by which Cape Vulture numbers may be related to environmental variables. As an initial estimate, the carrying capacity,  $K$ , is set equal to the total number of individuals in the region, rounded off to a reasonable whole number (Table 7.8).

Table 7.11

An example of inter-site migration rates used in the spatial model.

		From Region			
		SWC	LES	TVL	NMB
To Region	SWC	-	.0002	.0000	.0000
	LES	.0002	-	.0009	.0000
	TVL	.0000	.0009	-	.0000
	NMB	.0000	.0000	.0000	-

*Migration (=Permanent Movement) function.* While there is good evidence to suggest that Cape Vultures, especially non-adults, move between regions, there are insufficient data from which to estimate the rate at which they move. There are four factors which are likely to influence the number of animals which move permanently from one region to another (Akçakaya & Ferson 1992: 33-39).

- 1) Distance. The rate at which animals leave one patch for another is likely to be proportional to some decreasing function of distance (Wolfenbarger 1946;

Kitching 1971). A generalized migration rate function is used in *RAMAS/space*, and this incorporates earlier models (e.g. Kitching 1971) which are just special cases:

$$m_{ij} = a \cdot \exp(-(d_{ij})^c/b)$$

where  $d_{ij}$  = distance between regions  $i$  and  $j$  (Table 7.10)

$a, b$  &  $c$  = constants  $> 0$

$m_{ij}$  = is the rate at which birds transfer, permanently from region  $i$  to  $j$

and:

$$M_{ij} = m_{ij} \cdot B_i$$

where  $M_{ij}$  = expected (= average) No. individuals moving permanently from region  $i$  to  $j$  per unit time

$B_i$  = Number of birds at site  $i$ .

There are so few data for the Cape Vulture that it is suggested that this function be simplified by putting  $a=c=1$  and choosing the parameter  $b$  such that one individual p.a. moves into the southwestern Cape sub-population from the Lesotho sub-population: this yields  $b=6.630459$ . This is to be used as the 'base line', and varied in the sensitivity analyses.

- 2) Direction. It is clear from the pattern of recoveries (see Chapter Six) that Cape Vultures are much more likely to move away from their natal colonies in some preferred directions rather than in others. It is to be noted that these directions do tend to point at, or just past, adjacent regions (see Figure 6.4)
- 3) Density. From a number of studies there is evidence to suggest that the rate of permanent movement may be a function both of the density of the area from which animals come, as well as the density of the region to which they are headed (Pokki 1981; Smith & Peacock 1990).
- 4) Stochasticity. In the real world the movement of  $n$  individual from one region to another will be a stochastic event. A suitable way of simulating the number of migrants from population  $i$  to population  $j$ ,  $M_{ij}$ , is to draw them randomly from a binomial distribution with expected value  $m_{ij} \cdot B_i$  given that there are  $B_i$  individuals in the source population (Akçakaya 1991; Akçakaya & Ferson 1992: 39; Brillinger 1986), i.e.

$$M_{ij} = \text{binomial}(m_{ij} \cdot B_i; B_i)$$

Using the above model it is possible to compute the predicted rates of transfer along the six bidirectional routes between the four regions (Figure 7.35; Table 7.11).

*Correlation function.* Do the environmental conditions vary in one region in a fashion which is completely independent of all other regions? Two problems face the modeller here. First, there is no knowledge of what constitutes a 'good season' for the Cape Vulture. By way of example, consider drought. It is probable that drought is beneficial, in the short-term, to Cape Vultures because it causes more stock losses and so generates more food (P.J. Mundy pers.

comm.). In the longer-term, drought may reduce stock levels well below their carrying capacity, so that losses may decrease and create poor times for the Cape Vulture. Secondly, because there is no knowledge of what constitutes 'environment' and how this influences Cape Vulture population dynamics, it is not possible to estimate the correlation of environmental effects as a function of distance. It is worth noting that research into the incidence of drought in southern Africa (see the extended temporal sequence of drought severity maps in Zucchini & Adamson 1984, Appendix A5) has shown that there is much spatial and temporal variation in this phenomenon, so that it is probably wrong to talk of 'South Africa is in the grip of a drought' - as if its severity were the same everywhere. There are always places in the subcontinent with above-median rainfall in the same year as other places which are in the 'grip of a drought'.

*Simulation parameters.* To run a simulation a number of parameter values needs to be specified.

- 1) Replications. From experience gained in the previous section, it is clear that the higher the number of replicated simulations the better the estimates, especially of extinction. A total of 250 replicates is used in each model.
- 2) Duration. Each simulation is run for 50 years. From preliminary analyses, it is apparent that this period is sufficient to eliminate the effects of transients. In addition, the analysis of range expansion and contraction in the Cape showed that these processes take between 10 and 50 years (Boshoff & Vernon 1980: 244).
- 3) Demographic stochasticity. All the population processes (e.g. birth, death and migration) are simulated using probabilistic methods, as this is important for investigating extinction rates in the small sub-populations.

*Baseline simulation.* A simulation is presented which is based on what are believed to be a reasonable set of demographic parameters.

- 1) Demographic parameters.  $R = 1$ ,  $SD(R) = 0.1$  and  $S = 0.824276$ , as per Table 7.9 for all sub-populations.
- 2) Spatial location, initial population size and carrying capacity as per Table 7.8.
- 3) No migration between sub-populations.
- 4) No environmental correlation between sub-population.

This simulation is to be used as a benchmark against which other simulations can be compared. The mean population size of each of the four sub-populations was approximately constant in time, but with a slowly increasing variance (Figure 7.36). The probability of extinction of the southwestern Cape sub-population was 0.008 (Figure 7.37).

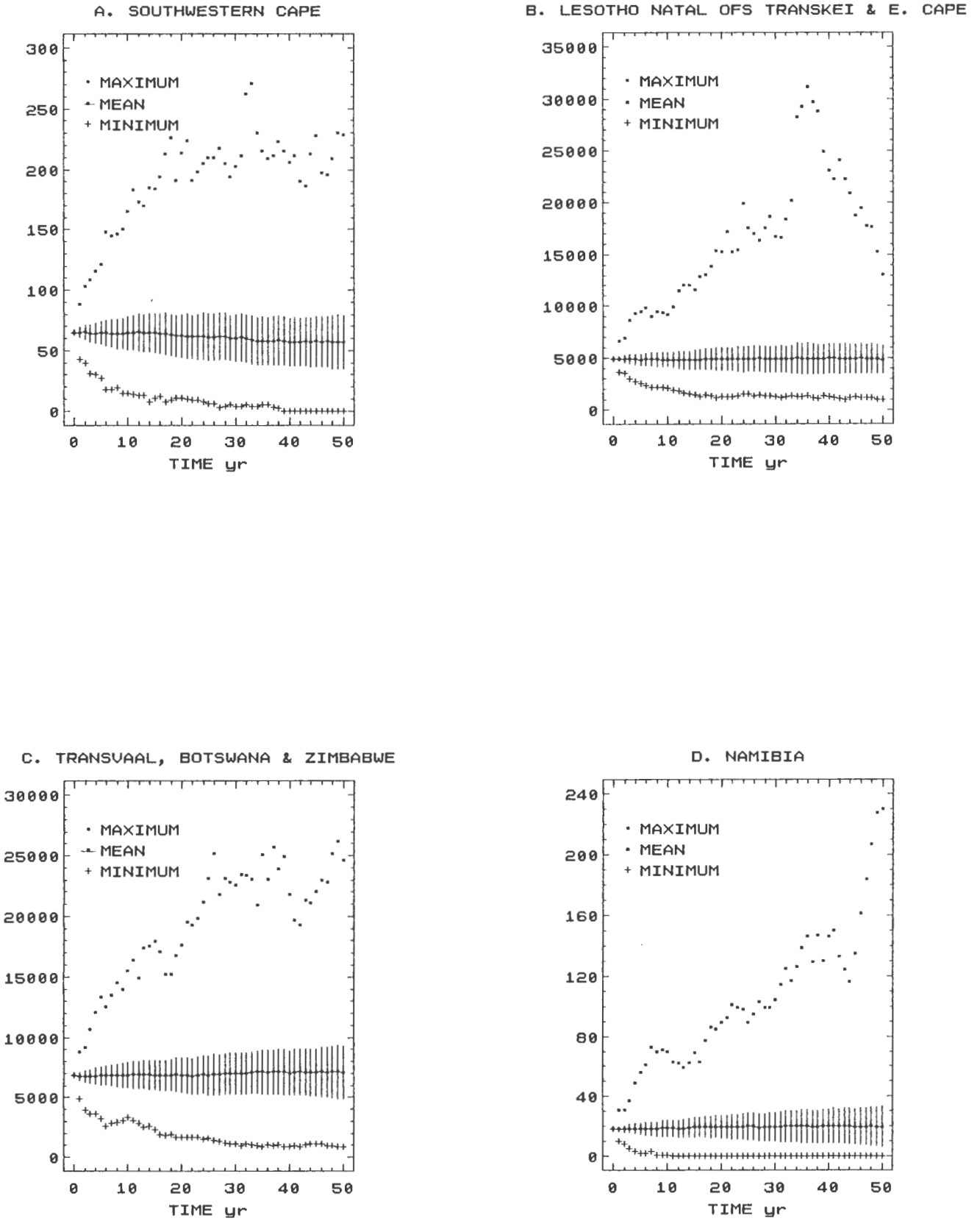


Figure 7.36 Variation in mean population size (with maximum, minimum and  $\pm$ S.D) for the four sub-populations running under the baseline parameters.

### 7.4.2 Environmental stochasticity.

The Cape Vulture is located in four separate regions (Figure 7.35), and it is likely that environmental conditions and food supply will vary regionally and temporally (see arguments above). It is possible to simulate separate and different random fluctuations in the vital rates of each region and look to see how the population varies *as a whole*. The interesting question to investigate is "what is the effect of environmental correlation"? In other words, by how much more will the population as a whole vary if there is some correlation between the regions? To investigate this, the 'baseline simulation' (described in the previous section) was varied by allowing the inter-regional correlation,  $\varphi$  (Table 7.12) to take on the values 0, 0.01, 0.25, 0.5 and 0.99. In addition, the variability of the growth rate, as measured by  $SD(R)$  was allowed to take on the values 0.01, 0.025, 0.05, 0.075, 0.1, 0.2 and 0.3. This required  $5 \times 7 = 35$  simulations. For the case of complete environmental independence (i.e.  $\varphi = 0$ ), it can be seen that the variability of the final population size (as measured using the standard deviation:  $SD(N)$ ) increases from an  $SD(N)$  of about 300 for  $SD(R) = 0.01$  to an  $SD(N)$  of about 11 000 for  $SD(R) = 0.3$  (Figure 7.38). It is also to be noted that both the overall minimum and overall maximum population sizes realized during the 250 replicates change in an approximately linear fashion with  $SD(R)$  (Figure 7.39).

Table 7.12

Correlation matrix between sub-populations for environmental stochasticity.  
(The parameter  $\varphi$  is varied between simulations)

		From Region			
		SWC	LES	TVL	NMB
To Region	SWC	1	$\varphi$	$\varphi$	$\varphi$
	LES	$\varphi$	1	$\varphi$	$\varphi$
	TVL	$\varphi$	$\varphi$	1	$\varphi$
	NMB	$\varphi$	$\varphi$	$\varphi$	1

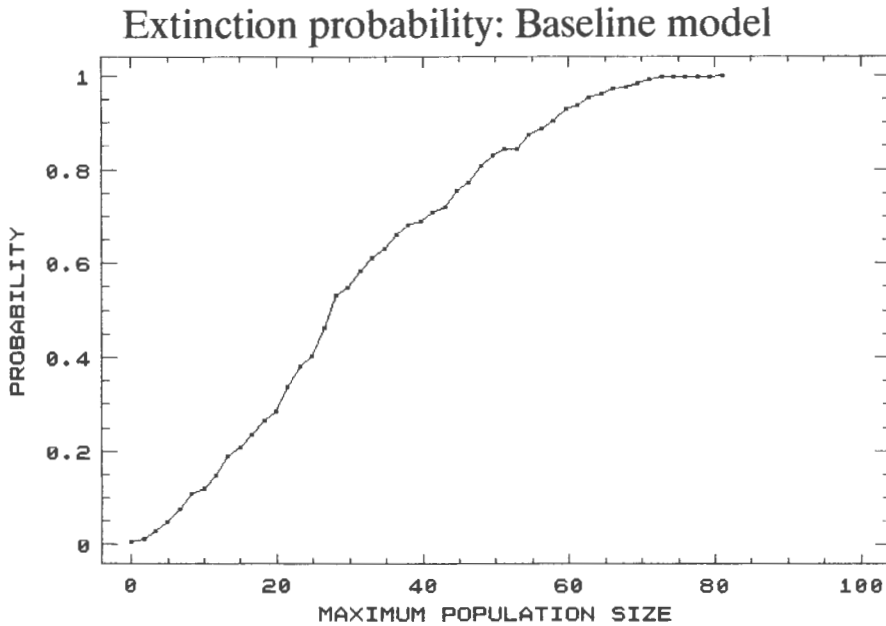


Figure 7.37. Quasi-extinction risk assessment curve for the southwestern Cape sub-population running under the baseline parameters.

In general, the higher the correlation,  $\varphi$ , the higher the variability of the population,  $SD(N)$  (Figure 7.40). This is to be expected when it is realized that the population consists of two large centres in the Transvaal (about 6825 birds) and Lesotho (about 4923 birds), which together accounting for over 99% of the population (Table 7.8). Writing these populations as T and L respectively, the variance of their total is:

$$\text{VAR}[L+T] = \text{VAR}[L] + \text{VAR}[T] + 2*\text{COV}[L,T] \quad (\text{Feller 1968: 230})$$

Given that  $L = d*T$  where  $d = 4923/6825 = 0.7213186$  it can be shown that:

$$\text{VAR}[L] = \text{VAR}[d*T] = d^2*\text{VAR}[T] \quad (\text{Feller 1968: 229})$$

The correlation coefficient,  $\varphi[L,T]$  is defined in terms of the covariance,  $\text{COV}[L,T]$  via:

$$\varphi[L,T] = \text{COV}[L,T]/\{\text{VAR}[L] * \text{VAR}[T]\}^{1/2} \quad (\text{Feller 1968: 236})$$

Thus

$$\begin{aligned} \text{COV}[L,T] &= \varphi[L,T]*\{\text{VAR}[L]*\text{VAR}[T]\}^{1/2} = \varphi[L,T]*\{d^2*\text{VAR}[T]*\text{VAR}[T]\}^{1/2} \\ &= \varphi[L,T]*d*\text{VAR}[T] \end{aligned}$$

Hence

$$\begin{aligned}
 \text{VAR}[L+T] &= d^2 \cdot \text{VAR}[T] + \text{VAR}[T] + 2 \cdot \varphi[L,T] \cdot d \cdot \text{VAR}[T] \\
 &= \text{VAR}[T] \cdot \{1 + d^2 + 2 \cdot \varphi[L,T] \cdot d\} \\
 &= F \cdot \text{VAR}[T] \text{ with } F = \{1 + d^2 + 2 \cdot \varphi[L,T] \cdot d\}
 \end{aligned}$$

The value of  $F$  will vary between approximately 1.52 for  $\varphi=0$  to approximately 2.96 for  $\varphi=1$ , i.e. by a factor of 1.95. An examination of the graph of  $\text{SD}(N)$  as a function of  $\text{SD}(R)$  and  $\varphi$  (Figure 7.40) shows that the variation due environmental correlation is small in comparison with that due to variation in growth rate. Environmental variation increases  $\text{SD}(N)$  by, at most, a factor of nearly 2 while that due to uncertainty in  $R$  is over 35 (i.e.  $\text{SD}(N)$  from about 300 to about 11 000; see Figure 7.40)

When trying to interpret the relationship between  $\text{SD}(N)$  and the variables  $\text{SD}(R)$  and  $\varphi$  (Figure 7.40) it is seen that some of the results seem to 'go the wrong way', i.e. for a high value of  $\text{SD}(R)$  the value for  $\text{SD}(N)$  is *lower* for  $\varphi=0.99$  than for  $\varphi=0$ . This is caused by the simulation noise. As a test,  $\text{SD}(N)$  was estimated for  $\varphi=0.5$  and  $\text{SD}(R)=0.1$  for 250 replications and again for two lots of 500 replications and these gave  $\text{SD}(N) = 4074, 3824.25$  and  $4111.75$  respectively, all three of which are greater than the  $\text{SD}(N)=3581.5$  realized for  $\varphi=0.25$ . There is a consistent pattern up to  $\text{SD}(R)=0.1$  but thereafter the simulation noise is greater than the effects of environmental correlation. Of course, to get greater clarity, it is possible to perform many more simulations. However, it is thought unlikely (in my opinion) that  $\text{SD}(R)$  will exceed 10% under normal conditions.

Thus it may be concluded, for the two large Cape Vulture sub-populations, that a knowledge of the degree to which environmental stochasticity is correlated is of little import when compared with the need to know the overall variation in the environment, and especially the way in which it influences the variation in the growth rate,  $\text{SD}(R)$ .

Arguing from first principles, it is readily appreciated that permanent movement between the two large sub-populations, provided it is random and in proportion to the size of the population vacated (but not related to the size of the population joined) will have an effect similar to increasing the environmental correlation. The greater the flux between two adjacent populations the more similar their fluctuations. Thus a knowledge of permanent movement for the large sub-populations is not important because environmental correlation is not important.

Variation in population size with variability in growth rate

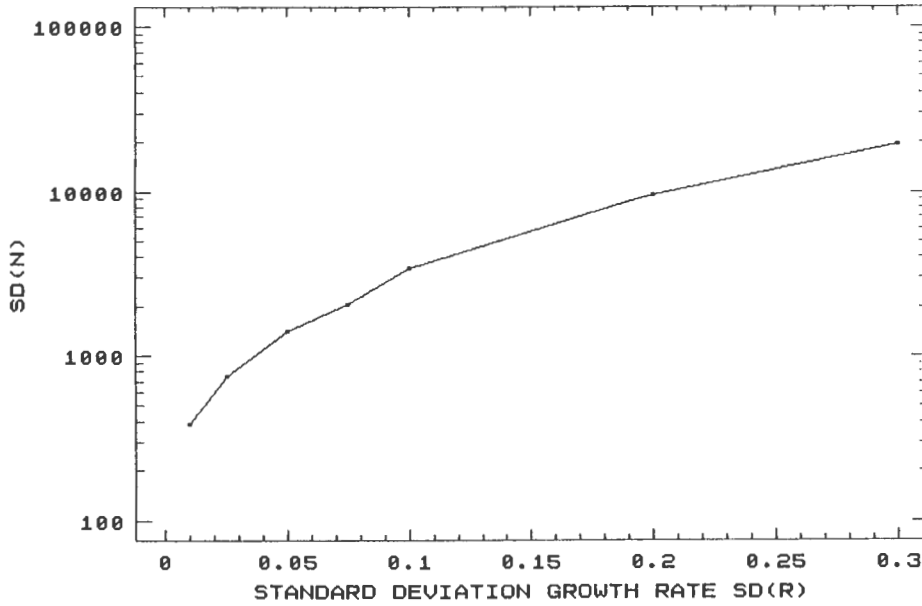


Figure 7.38 Variation in final population size as measured by SD(N) as a function of the variability of the growth rate, SD(R).

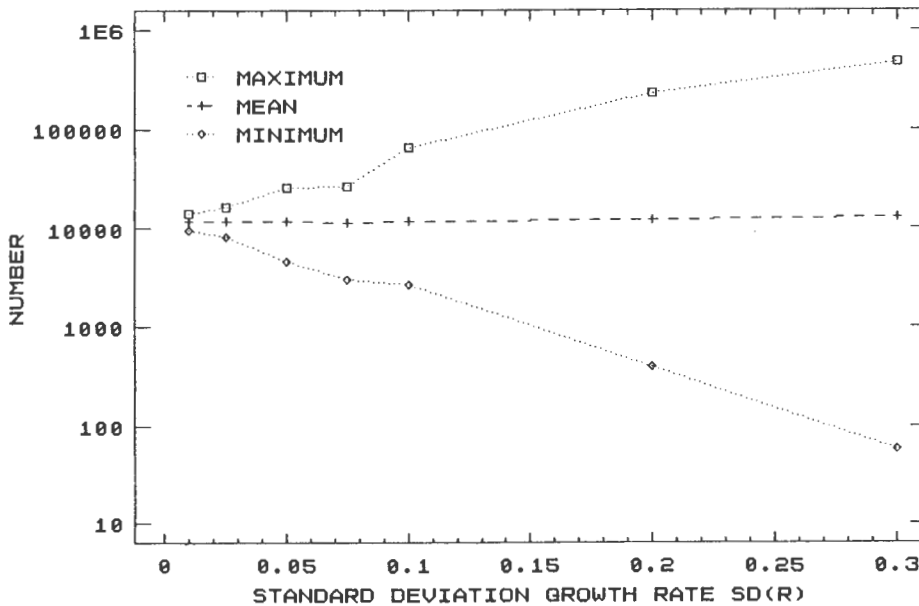


Figure 7.39 Variation in the maximum, mean and minimum population size as a function of the variability of the growth rate, SD(R).

Population size variation vs environmental correlation and growth rate

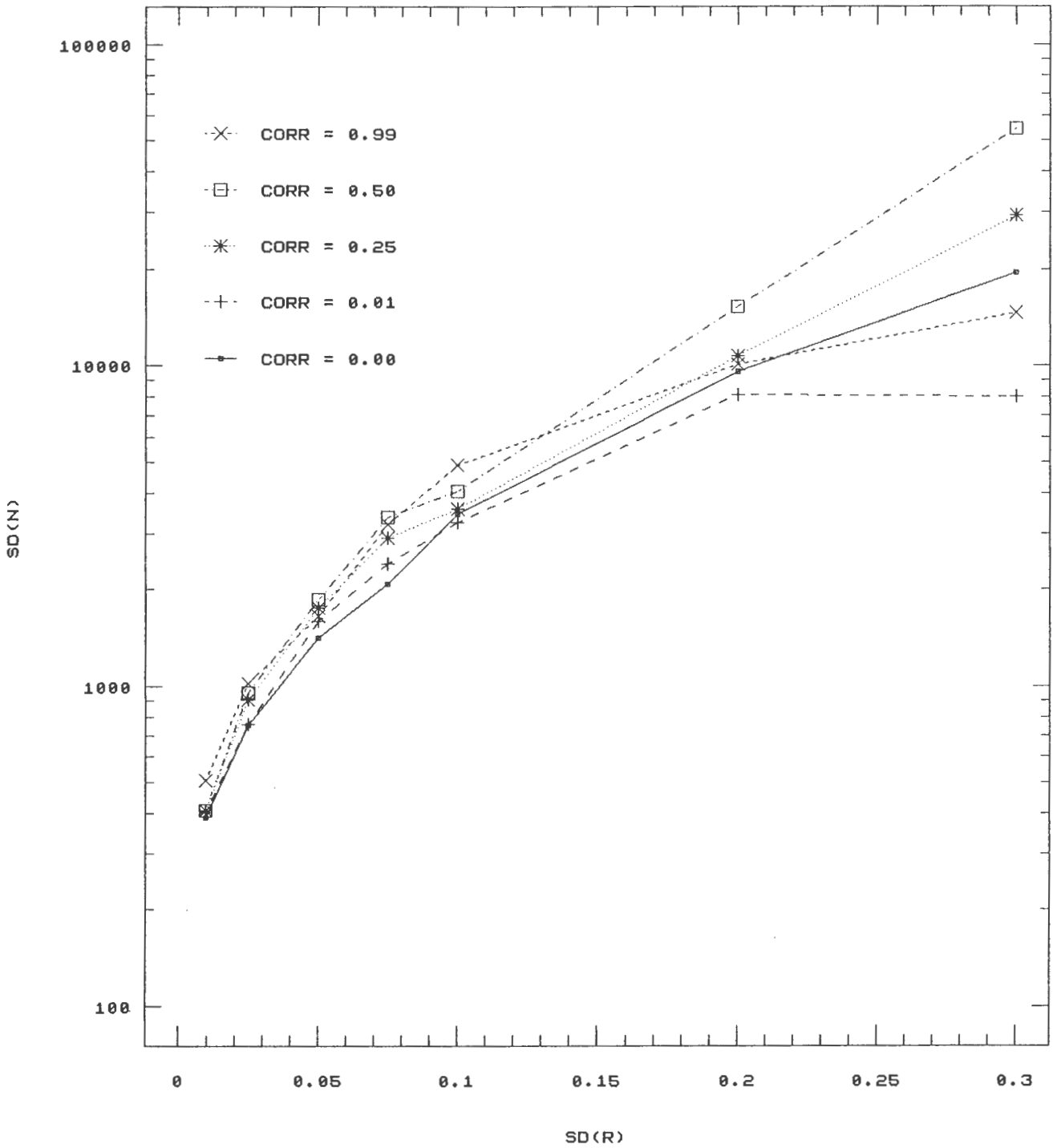


Figure 7.40 Variation in final population size as measured by  $SD(N)$  as a function of the variability of the growth rate,  $SD(R)$  and environmental correlation,  $\varphi$ .

On the other hand, the effect of permanent movement is likely to be important for a small sub-population whose nearest neighbour is a large sub-population. This is because migration will be primarily from the larger to the smaller, and it will interact with the process of demographic stochasticity. This phenomenon is investigated in the next section.

### 7.4.3 Demographic stochasticity and migration.

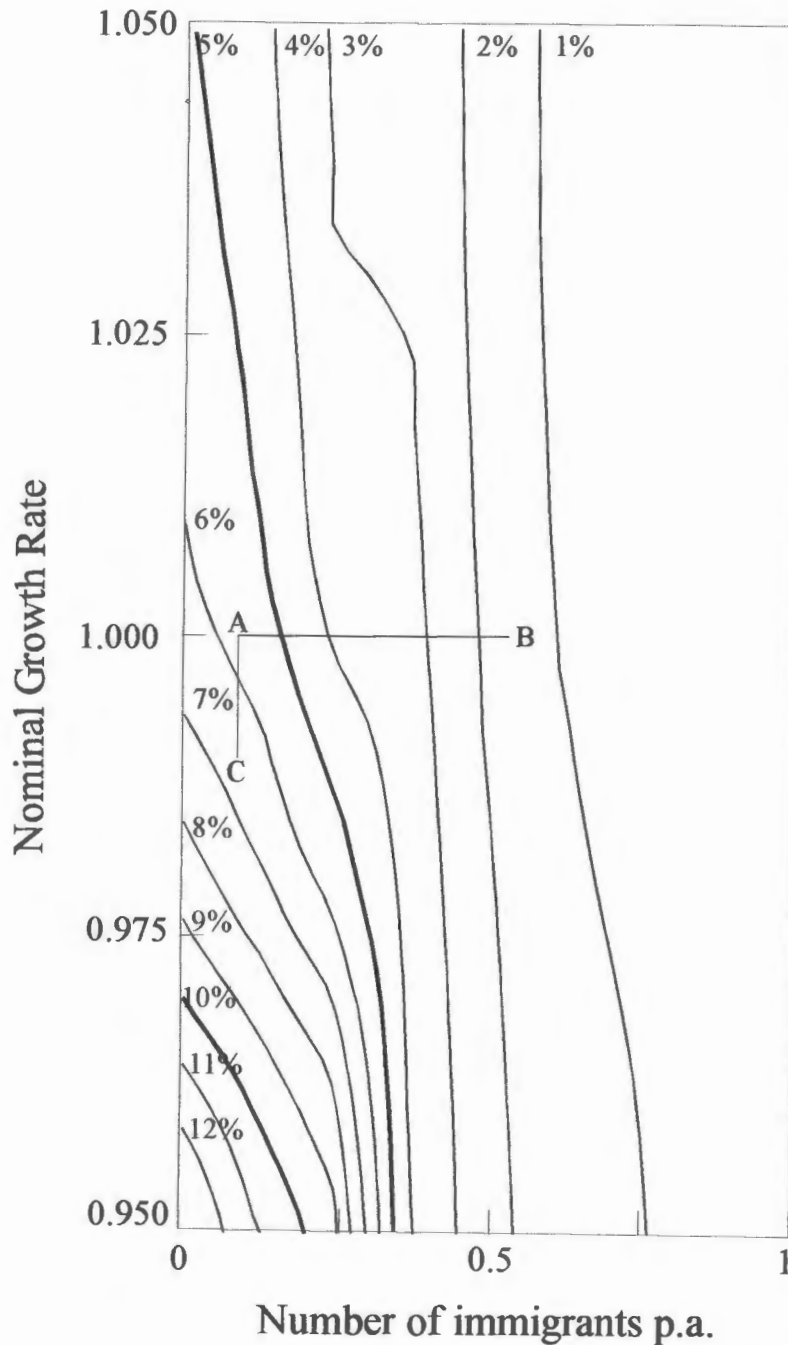
It is generally believed that the rate at which individuals leave their natal population and make a permanent move to some other population is proportional to the size of the population they leave (see arguments and references above). Thus, given the Lesotho sub-population of about 4900 and the southwestern Cape population of about 65 (Table 7.8), and assuming that the migration rate between the two is about 0.0002 per individual p.a. (Table 7.11) it follows that the transfer rate from Lesotho to southwestern Cape would be about 0.98 individuals p.a. while the reverse rate would be 0.013 individuals p.a., i.e. about one every 77 years. The permanent losses from the sub-population in the southwestern Cape will be minimal. It also needs to be noted that a single extra individual arriving in the southwestern Cape each year is equivalent to increasing the growth rate by  $1/65 = 1.53\%$  p.a., a not inconsiderable increment given that the population may be declining at about 1.6% p.a. (see section 7.2).

To investigate the effects of a net inward migration into the southwestern Cape sub-population, a series of simulations were performed.

The meta-population model was set up as per the 'baseline simulation' (section 7.4.1), but the growth rate of the southwestern Cape sub-population only,  $R$ , was allowed to take on the values 0.95, 0.975, 1, 1.025 and 1.05; all the other sub-populations had  $R = 1$ . The average number of migrants from the Lesotho sub-population to the southwestern Cape was set at 0, 0.5, 1, 1.5 or 2 individuals p.a. This required running 25 simulations of 250 replicates each. The final average population size in the southwestern Cape and its probability of extinction were recorded.

Of great interest is the influence that a constant supply of new birds has on the persistence of the sub-population as a whole (Figure 7.41). With an average recruitment of only 0.75 permanent migrants p.a. the extinction probability, over a 50 year time horizon, decreases to less than 1% - without immigration it is about 5 to 6% (Figure 7.41).

Extinction probability: southwestern Cape - including migration  
Extinction Probability



DESMES.CDR

Figure 7.41 Extinction probability of the southwestern Cape including migration from other sub-populations. Three 'example points' are shown. A: Immigration rate is 0.1 p.a.,  $\Gamma=1$  (i.e. stable population) and probability of extinction is about 5.75%. B: As with A, but with 0.6 immigrants p.a. and extinction probability has dropped to about 1.5%. C: As with A, but with  $\Gamma=0.985$  and now extinction probability has increased to 6.75%.

#### 7.4.4 Summary

A meta-population analysis is necessary because this is the only approach towards a holistic view of the entire population which is spatially disjoint. Consideration of individual sub-populations on their own is inadequate, because of the linkages caused by permanent inter-region movements. Furthermore, if the environments in the sub-populations are correlated, then the overall variability will be increased beyond that of the sum of sub-population variabilities.

The Cape Vulture is divided into two major sub-populations, namely Lesotho and Transvaal, which together account for 99% of the total population. If these two regions have environments which vary independently (in terms of their influences on Cape Vulture demography), then the overall population variability will be nearly half (i.e.  $1/1.95$ ) of that which would result from the two regions having perfect correlation. Thus, independent sub-populations fluctuating separately lead to a more stable population, overall. Because these two sub-populations are so large, they are not vulnerable to demographic stochasticity.

Much more important, however, is the need to get better estimates of the overall growth rate,  $R$  and its variability,  $SD(R)$ , for the population as a whole. Allowing  $SD(R)$  to vary from 0.01 to 0.1 causes  $SD(N)$  to vary from 300 to 1200, i.e. a fourfold increase. Further, allowing  $SD(R)$  to increase to 0.3 causes  $SD(N)$  to rise to upwards of 11 000, a more than thirty-fold increase.

The most important insight to come from of these analyses is the influence that immigrants have in stabilizing small external sub-populations. An extremely small flow of about 0.75 individuals p.a. is sufficient to prevent the southwestern Cape sub-population from declining, even when its growth rate,  $R$  is as low as 0.95. The rate at which individuals must leave the Lesotho population need only be 0.0002 per individual p.a.

This rate of 0.0002 may not be as low as it seems. First, the move to the southwestern Cape must be permanent. Secondly, it is possible that only first-years will leave their natal region. Thirdly, only adults joining the southwestern Cape population will be of any value to their breeding population. Given that recruitment to age six years is about 29% (i.e.  $0.5257 \cdot 0.8432 \cdot 0.78 \cdot 0.9115 \cdot 0.9115 = 0.28726$ ) means that one adult will be produced from every 3.5 juveniles joining the population. Given further that it is only first-years leaving the Lesotho sub-population then these are estimated to number  $4923 \cdot 0.181246 = 892.27$  p.a. (890 say). Thus the proportion needing to leave permanently for the southwestern Cape is only 0.4% (i.e.  $3.5/890$ ). This all seems so possible given the distribution of recoveries and resightings of Colleywobblers birds (see Chapter Five).

If this movement is potentially important and feasible, then steps should be taken to ensure that it can occur with minimal loss. Consideration should be given to combating the use of

poisons in the eastern and southern Cape. Consideration should also be given to reducing the incidence of drowning in stock watering troughs and farm dams in the region. However, translocation is unlikely to work given the wide distances moved by rehabilitated birds as well as their tendency to return to their natal colony (see example in Scott 1991)<sup>2</sup>.

It is known that the Cape Vulture population has expanded and contracted over vast areas of the Cape Province during recorded history (Boshoff & Vernon 1980). During the contraction phases, it is likely that small isolated sub-populations will be left behind. Provided these clumps are large (>250, say) and they tend to fluctuate nearly independently, then there will be no problems with environmental or demographic stochasticity. However, if the patches are small relicts, then they will be susceptible to catastrophes and demographic stochasticity.

As the Cape Vulture population contracts, it will either stay in a few greatly-reduced patches or it will fragment into many small patches. Either way, there will be more gaps in between the patches. From an examination of the pattern of Cape Vulture recoveries (see Chapter Six), it is seen that nearly a third of the modern (i.e. 1980s) recoveries have been found *outside* the current range of the species (as per maps of section 3.2.5). Thus the increase in 'edges' and 'gaps' is likely to mean that more young birds will die because they have lost contact with a Cape Vulture population. These edge-effects need to be investigated further.

This need to understand the implications of the spatial nature of population dynamics has been summarized by Newton (1991: 642-3):

I need hardly emphasize the need for further work on dispersal. Not only are movements between breeding sites the most neglected area of avian demography ... in nature they could often be crucial in the maintenance of local population densities ... Dispersal is central to the concept of 'source' and 'sink' areas, ... To explore these questions, we need more emphasis on spatial variations in demography, and particularly on dispersal, in population studies.

---

2 P.J. Mundy (*in litt.*) comments: "Surely translocation is likely to work, given the nomadism of juveniles, and provided they are translocated *after* their PDPF is terminated. Alternatively, large nestlings could be translocated, and a 'hacking' technique used at Potberg".

## 7.5 Summary

The 'Grand Question' was asked at the start of this chapter.

*What is the probability that the Cape Vulture will survive well into the twenty-first century as a free-flying bird?*

This was followed by a secondary question.

*What is the stability of the population in space, time and age-structure?*

The first step was to construct a Leslie matrix model of the Cape Vulture population, as a whole, using estimates of the vital rates from Chapters Four and Five. Using the current estimates of fecundity and survival it was found that, at best, the Cape Vulture population should be declining at about 16% p.a. However, from an examination of the data presented in Chapter Three it is clear that the Cape Vulture is not declining in its core areas. These analyses indicate that if the Cape Vulture population is stable, then the parameter estimate most likely to be in error is adult survival which needs to be greater than 90% p.a.

The Leslie-matrix was then used to evaluate the sensitivity of the finite rate of natural increase to the various demographic parameters. It was found that the least sensitive parameters were age-at-first-breeding, variation in breeding success with age, and maximum age of breeding (senescence is only likely to be an issue if it occurs before about 20 years of age). The important variables are the proportion of adults which breed, sub-adult survival and especially adult survival.

Using these sensitivity analyses, and setting a limit of  $\pm 2\%$  on the error in estimating the finite rate of natural increase, it was possible to devise a ringing programme which could yield parameter estimates of sufficient precision to use these models for predictive purposes.

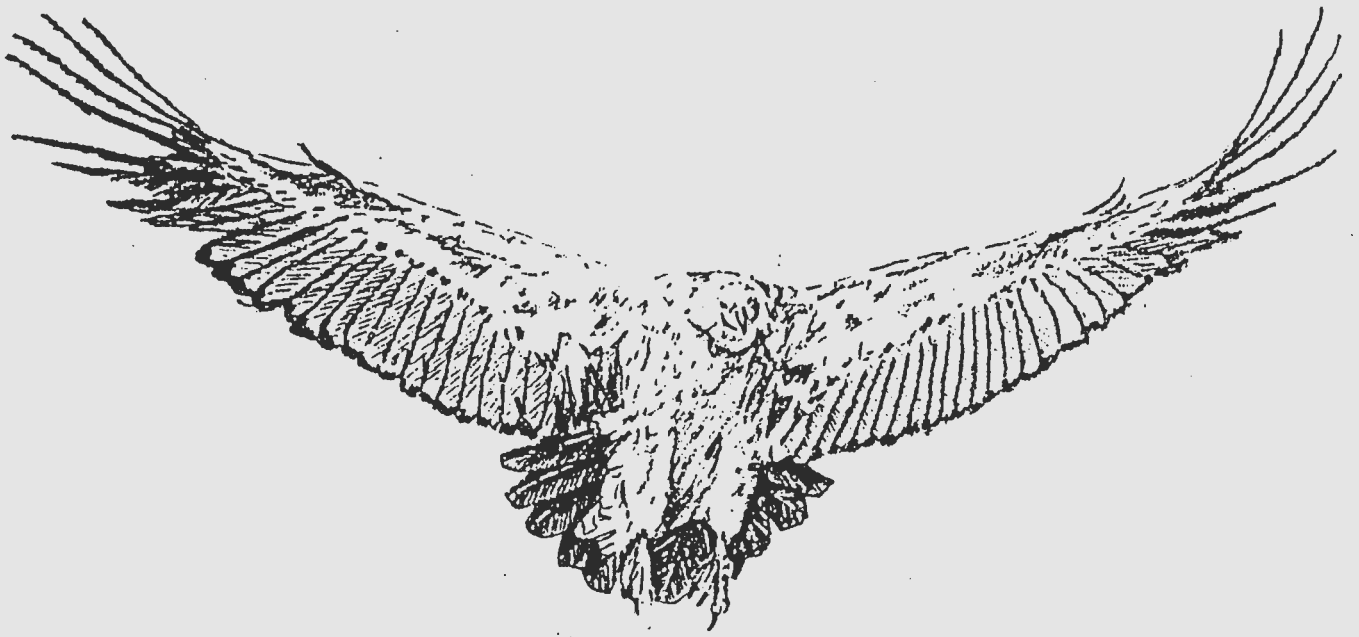
A model of the southwestern Cape sub-population was constructed using a set of finite-difference equations similar to the Leslie-matrix approach. This model gave an excellent fit to the observed time series of the number of adults in the sub-population. It also showed that an adult survival of 91% p.a. is consistent with the observations. This sub-population is suffering a slow decline of about 1.6% p.a. which is attributed to low fecundity, i.e. breeding is the critical limiting factor. This is because both the proportion of birds which attempt to breed and their breeding success is a little on the low side, in comparison with the Colleywobblers data. It is suggested that ways of increasing fecundity should be investigated.

---

A series of stochastic models were constructed using the RAMAS/age simulation package. It was found that the variation in the overall population size was most sensitive to the variations in adult survival. This serves to stress the need to have better estimates of adult survival and even to monitor it in space and time. Further application of this model showed that the minimum viable isolated population is about 100 individuals (i.e. this corresponds to a probability of extinction due to demographic stochasticity which is less than 1% for a 50 year time horizon). However, this figure of 100 individuals does not take into account the possibility of catastrophe, genetic drift and inbreeding.

Because the Cape Vulture population exists in four spatially disjoint sub-populations, it was subjected to a meta-population analysis using the RAMAS/space simulation package. Using the best possible parameter estimates available, it was found that the population, as a whole, is not sensitive to environmental stochasticity. However, small populations on the periphery are sensitive to extinction from demographic stochasticity. Probably the most exciting and important result came from an investigation of the effects of permanent movement from the central population to the peripheral isolates: an average flow of as little as 0.75 individuals p.a. is enough to reduce the risk of extinction in the currently declining southwestern Cape Vulture population of 65 individuals to less than 1% over the next 50 years.

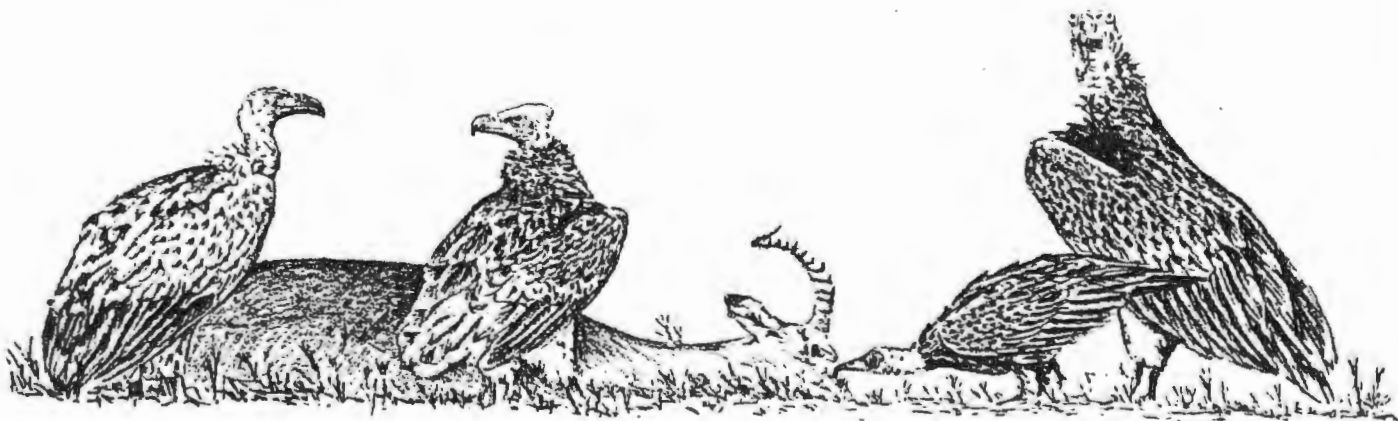
Thus it may be concluded that there is evidence, from the model of southwestern Cape sub-population, to suggest that the age-specific survival rate for adults is over 90%. If this is indeed true, then the core population is probably safe and likely to persist indefinitely under current conditions. The small peripheral sub-populations, especially those in Namibia and the southwestern Cape, are under greater threat. If the Cape Vulture population changes, it is likely to do so from peripheral losses and this will be seen as range contraction.



# Discussion, Conclusions & Recommendations

## Contents

8.1	Discussion and conclusions .....	474
8.1.1	Status .....	474
8.1.2	Population structure .....	475
8.1.3	Distribution .....	476
8.1.4	Trends at sites .....	479
8.1.5	Fecundity .....	479
8.1.6	Survival .....	480
8.1.7	Movements .....	481
8.1.8	Models .....	482
8.2	Recommendations .....	484
8.3	Summary .....	491



# Discussion, Conclusions & Recommendations

Central to these researches is the desire to understand the population dynamics of the Cape Vulture. This understanding is needed to be able to answer questions about the long-term survival of the species. This study began with a review of those aspects of the species' biology relevant to demography. Four major topics were then investigated to provide the 'baseline' parameters needed for modeling: status, fecundity, survival and movements. Using these estimates of demographic parameters and variables a series of models was built. In the following sections a brief evaluation and discussion of each part of these researches is offered.

## 8.1 Discussion and conclusions

The literature on the Cape Vulture was briefly summarized in the early 1980s (Brooke 1984: 5) and the following comment was proffered:

It will be seen that for some species such as the Jackass Penguin and the Cape Vulture there is a copious modern literature which is in great need of consolidation in one or more review papers.

In our book *The vultures of Africa* (Mundy, Butchart, Ledger & Piper 1992) most of the important papers concerning the Cape Vulture were surveyed and included in the review of the species' biology. There has yet to be a comprehensive collation of all the literature relating to the Cape Vulture, especially the large body of 'grey literature' (i.e. in Bird Club news sheets and the like). A collation, into a single document, of all the Cape Vulture references would ease greatly the work of future students of this species.

### 8.1.1 Status

Cape Vultures tend to roost repeatedly on ledges high up on cliffs and the 'whitewash' renders these sites visible from a great distance. When they breed they always use cliffs and because the breeding season is so long at least one of the adults is tied to the cliff for at least seven months of the year. It is the communal nature of their roosting and breeding which makes it feasible to count them directly (Section 3.1.1). There are nine regions in southern Africa in

which Cape Vultures have been recorded as breeding (viz. Botswana, Cape Province, Lesotho, Namibia, Natal, Orange Free State, Transkei, Transvaal and Zimbabwe) and there are two regions in which they are known to have roosted (viz. Mozambique and Swaziland).

A record has been compiled of all sites at which Cape vultures are known to have roosted or bred or are suspected of once having roosted or bred there in the past. To this compendium has been added a list of all vulture place names<sup>1</sup>. There is a total of 441 such sites. Of these 84 were in use as roost-only sites when last inspected and 83 were active breeding colonies when last subjected to a census. These sites may be grouped in two major and two minor regions. The major regions and their characteristics are listed.

- 1) Transvaal and Botswana. Mainly medium to large colonies of 100 to 1000 pairs situated far apart at some 50 to 200 km. The Cape Vultures from these colonies scavenge over the vast open plains of the highveld savannas, the lowveld bushveld and the Kalahari.
- 2) Lesotho, Natal Drakensberg, Transkei and the eastern Cape. Small to medium sized colonies of 10 to 350 pairs located close to one another to moderately far apart, i.e. 20 to 100 km. Birds from these sites search for food over the coastal plain using ocean-induced winds and around the Drakensberg massif.

There are two small isolated concentrations of breeding birds in the southwestern Cape and in Namibia.

It is estimated that there are about 12 000 Cape Vultures in the entire population which includes about 4400 breeding pairs. About 68% of these breeding pairs are in the Transvaal and Botswana while about 29% breed in Lesotho, Natal Drakensberg, Transkei and the eastern Cape. This is the first comprehensive estimate of the species' total population size and its breeding component. This is the largest estimate yet made. Unfortunately, this estimate is based on census data which are up to a decade old. This detracts from its current reliability.

There has been little effort to standardize the process of counting Cape Vultures. Most of the counts used in this thesis come from observers who made 'opportunistic' or '*ad hoc*' counts. Only a few count using techniques which are standardized and take into account the roosting behaviour of the species (e.g. B. Colahan). As yet no guidelines have been published on methods of conducting a census of a Cape Vulture roost or colony. In addition, no thought has been devoted to methods of estimating the number of birds which use power-pylons for

---

1 Recent investigations have revealed that some vulture place names of the form Aasvoelberg may in fact refer to a 'dark mountain' rather than a place inhabited by vultures - the error arises in the translation of the early Khoi and San place names into Afrikaans (C.J. Vernon, pers. comm.).

roosting. It is clear from a comparison of the spatial location of roosts and colonies with the SABAP sightings data that there are regions (e.g. Karoo and northern Cape) used by Cape Vultures for which there are no permanent cliff-based roosts. It is also clear that the estimates of population size and breeding population give a breeding proportion ( $4400 \times 2 / 12\ 000 = 73\%$ ) which is much higher than the ratio of breeding birds actually observed (i.e. about 65%). These observations suggest that the estimate of the number of non-breeding birds is negatively biased.

### 8.1.2 Population structure

There are a few counts of age-structure (section 3.1.2) and there are some counts of the proportion of non-breeding birds at colonies (section 3.1.3) and from these it is clear that there are spatial inhomogeneities in the population. The 'core' areas around the nucleus breeding colonies are dominated by breeding adults while the immatures and non-breeding adults distribute themselves around the periphery.

### 8.1.3 Distribution

It is hypothesized that vultures daily wander outwards from their colony or roost and form a 'foraging-net', watching each other all the while (Mundy, Butchart, Ledger & Piper 1992: 240-241). But, in truth, there is no factual evidence as to how this is done. It is not known if some birds prefer particular regions or search directions or if birds follow other birds which were successful on a previous day. Thus, given the geographical location of most of the colonies and roosts as well as the numbers of birds at each site, it is not possible to choose among the many 'point spread functions' devised (section 3.2.1).

The collation, by SABAP, of nearly all the field cards<sup>2,3</sup> submitted by bird watchers in southern Africa during the 1980s has provided the first comprehensive distributional data-set for the Cape Vulture (section 3.2.2). The Cape Vulture was recorded in 512 of the approximately  $1950 \frac{1}{4}^\circ$  by  $\frac{1}{4}^\circ$  grid-cells that were visited by bird watchers (section 3.2.3). The pattern that emerges from these data show that the distribution of the Cape Vulture is much more restricted than that portrayed in most standard texts.

- 
- 2 Unfortunately, no distributional data for Botswana, Namibia or Zimbabwe were extracted by SABAP for these analyses. It is to be hoped that the ornithological organizations in these three countries will give permission for these data to be extracted so as to enable the mapping process to be completed for the whole of the species' range.
  - 3 Recent correspondence with the Zimbabwe Ornithological Society indicates that permission to use their data is likely to be granted (K. Hustler in litt. 2 September 1993).

The sightings of Cape Vultures recorded in the SABAP data show no seasonal variations for any  $\frac{1}{4}^{\circ}$  by  $\frac{1}{4}^{\circ}$  grid-cell. Unfortunately, there are few  $\frac{1}{4}^{\circ}$  by  $\frac{1}{4}^{\circ}$  grid-cells for which there were enough data to test for seasonality. However, a number of observers believe that Cape Vultures are seasonal in their attendance at roosts and vulture restaurants at various localities (section 3.2.4). This problem needs to be investigated further<sup>4</sup>.

A binary presence or absence map gives, at best, a poor idea of where the highest concentration of Cape Vulture sightings occur. A much better map is provided by plotting the reporting rate (section 3.2.5). From the reporting rate map, it can be seen that the concentrations of sightings correspond broadly to the count data from the Site Register. Using the binomial kriging algorithm to smooth the reporting rate, it was found that a reporting rate of 3% or more gave a binary map which accords well with my own 'intuitive feel' for what the distribution should look like. It is suggested that this 3% binary map can be used as a standard map for field guides which wish to portray distribution in a binary format. This 3% map shows the Cape Vulture as occurring in two large concentrations.

- 1) The Transvaal and Botswana.
- 2) Lesotho, Natal, OFS, Transkei and the eastern Cape.

In addition, there are four minor regions.

- 3) The southwestern Cape.
- 4) The Karoo.
- 5) The northeastern Cape.
- 6) The Kalahari Gemsbok National Park.

The SABAP data-set contains no useful information concerning breeding and can be ignored as a tool for monitoring breeding. However, there is always the chance that the occasional record will appear which indicates a new site to be investigated or points to an old site which has been re-occupied. Thus the breeding data on the field cards should not be discarded.

There are two separate and independent data-sets yielding information on the nature of the Cape Vulture's geographical distribution: the SABAP field card sightings data and the Site Register count data. These two data-sets were compared in two ways.

---

4 Research conducted by SABAP (L.G. Underhill & J.A. Harrison, pers. comm.) has indicated that there is some small seasonality in the Eastern Cape and central Transvaal where Cape Vultures show a late summer trough and late winter peak, but the variation in reporting rate is small.

- 1) The 3% binary map generated from the binomial kriging smoothing process was overlaid with the map of all known active sites. It is seen that all the sites fall within the binary map. This indicates that there are no known sites in areas where bird watchers have never seen Cape Vultures. However, there are areas in the northern Cape, Karoo, northern Natal and eastern Transvaal where Cape Vultures sightings have been reported to SABAP, but which are much too far from the nearest known site for them to have come any extant site.
- 2) The above comparison was extended by 'spreading out' the Cape Vultures from every known site for a distance of R km and then comparing the number of predicted Cape Vultures for each  $\frac{1}{4}^\circ$  by  $\frac{1}{4}^\circ$  grid-cell with the SABAP sightings data. It is shown that the overlap of the two data-sets is between about 45% and 50%.

From these analyses, it is seen that, when the site count data are 'spread out' over a radius to give the maximum correspondence between the two data-sets, there are still many discrepancies. The following possible reasons are suggested.

- 1) The SABAP data-set from May 1991 has been improved upon, especially in the northern and northwestern Transvaal, Lesotho and Transkei. These new SABAP data show Cape Vulture records where none had been found before, largely due to the previous poor coverages in those areas (D.G. Allan pers. comm.)<sup>5</sup>.
- 2) It is likely that the way Cape Vultures spread themselves over the countryside each day in their foraging forays will differ among areas as a function of two major factors: the nature of the terrain and its atmospheric properties, and the food parcel size. Over the great open plains of the savannas characterized by thermals, the birds can ascend further into the heavens and quarter a much large area. In mountainous and hilly terrains, a major source of uplift comes from declivity winds which do not facilitate long-distance movements. In cattle ranching country the food parcels are much larger than those in smallstock areas and it is likely that cattle deaths will be less uniformly distributed in space and time. Thus Cape Vultures relying on larger carcasses will need to spread out further over the plains in bigger foraging nets. On the other hand, Cape Vultures relying on smaller carcasses will be able to congregate in small clusters foraging over shorter distances.

---

5 With the completion of the SABAP fieldwork by D.G. Allen many of these gaps have been filled in and it is now clear that some of the discontinuities in Cape Vulture distribution are real (e.g. Venda in the far northern Transvaal) and not artefacts of poor coverage (J.A. Harrison, pers. comm.).

#### 8.1.4 Trends at sites

Over a dozen sites have been monitored for long enough to enable some detection of trends to be made (section 3.3). The exact population data collected varied from site to site. Counts have been made of the total number of birds on the cliff face, the number of nests, the number of active nests, the number of immatures, and so on. Trends in the number of active breeding pairs (i.e. those pairs which build a nest and lay an egg) probably provides a better long-term monitoring tool for a colony than does a count of the number of large nestlings or the number of nestlings ringed. If the breeding colony is visited during the time when adults are on eggs then it is possible to make the most reliable counts of the number of breeding pairs because the incubating adults 'sit tight' on their eggs. Visits at other times tend to give more variable and hence less reliable estimates. Those sites in decline tend to be on the edge of the species' range, but this pattern is not clear. Only at a few sites is there some understanding of the factors causing their decline.

#### 8.1.5 Fecundity

The total productivity of the Cape Vulture population is measured as large nestlings produced p.a. and is a function of the following factors (Chapter Four).

- 1) The number of individuals in the population who are capable of forming pairs, finding a nest site and breeding. The age at which Cape Vultures can breed is somewhere between four and six years. There are no reliable estimates of the average age of first breeding for a reasonable sample of birds at a variety of sites.
- 2) The proportion of breeding pairs which actually breed in any given year. It is likely that the maximum proportion of pairs breeding in any one year is 85%. The actual proportion breeding in any one year is poorly estimated for all but a few sites.
- 3) The clutch size is one.
- 4) The breeding success from eggs laid is known for a wider range of sites and is likely to have as its upper limit an estimate of 75%.

It is estimated that there are about 4400 breeding pairs in the total Cape Vulture population, hence the maximum productivity will be  $4400 \cdot 0.85 \cdot 0.75 = 2805$  large nestlings p.a.

There are a number of issues of theoretical interest which need further investigation but it is my opinion that the current quality of the estimates of fecundity are adequate for population modelling. However, breeding still needs to be monitored rather than studied for the purposes of population monitoring.

As yet, there has been no evidence for density-dependent effects in breeding. This may be real but it could be the result of a lack of knowledge concerning the population density in the region around the breeding colony. The continued monitoring of breeding activity coupled with population monitoring could yield evidence for this effect.

### 8.1.6 Survival

The use of the ring-recovery-reporting process as the basis for estimating age-specific survival has been discredited (Chapter Five). However, it has been suggested that it may be possible to extract age-specific survival estimates from the pre-1984 Cape Vulture data-set because it is complete (i.e. all the birds that are going to die have died) and thus the reporting rate can be estimated directly (L.G. Underhill pers. comm.)<sup>6</sup>. An investigation of the ring-recovery-reporting process showed that the reporting rate varied with a number of factors (epoch, ring metal, location of ringing site, simultaneous fitting of colour-rings etc.) but that an adequate multivariate model could be constructed using a GLM. This model included time as a cubic and the presence or absence of colour rings as a dummy binary variable. It was found that fitting a bird with colour rings in addition to a metal ring increased its chance of being reported by a factor of about 1.77 (i.e. from about 3.2% to about 5.7%).

The use of observations of colour-ringed birds in the southwestern Cape revealed that survival is a function of both age and time. In addition, it must be noted that these estimates of survival have been made for the southwestern Cape population only and they may not apply to the population as a whole. These estimates were adequate for the lower age-classes but as yet, no satisfactory estimates have been made for adult survival. The estimates of survival for the first three age-classes were 17%, 61% and 74% respectively when the ring-recovery data were used in 1981; with the use of long-lasting metal rings these estimates have been increased to 42%, 61% and 64% respectively. By using the sightings of colour-ringed birds in the southwestern Cape these estimates have been improved to 52%, 84% and 78% respectively.

---

6 One of the examiners (BTJ Morgan) has suggested that new techniques developed by a student and himself could give improved and reliable estimates of survival from these Cape Vulture ring-recovery data. Prof. Morgan has offered to analyse these data. In response to his kind offer the data will be sent to him shortly.

The 'cause-of-death' reported for ringed birds found dead has been a most valuable source of information for monitoring five major categories of unnatural mortality which act on the Cape Vulture: poisons, persecution, collisions, electrocutions and drownings. It was concluded that only electrocutions have decreased - the impacts of the other four have not decreased with time.

The quality of the estimates of survival is so poor that it has not been possible to test for density-dependent effects.

### 8.1.7 Movements

*Recoveries.* From the approximately 7289 Cape Vultures ringed at 28 sites in the 21-year period 1948 to 1988 there were 597 recoveries (i.e. 8.3%) of which 192 (i.e. 2.7%) were classed as 'useful' (i.e. survived into the year after ringing and moved > 10 km). Variations in the time and location of recovery were investigated with respect to age, epoch and natal colony. The following conclusions were drawn (section 6.1).

- 1) Age effects. The elapsed distance increased with age-class until the second-year (median = 438 km) and thereafter dropped until birds were four+ years old (median = 108 km).
- 2) Temporal effects. The average distance at which birds were found dead was over 450 km in the 1950s and dropped steadily through to the 1970s when it was 232 km after which it increased again. The average age at death showed a similar trend. The proportion of recoveries found within the current distribution of the Cape Vulture was approximately 32% in the 1950s, dropped to 26% in the 1960s and thereafter rose to 69% in the 1980s. It is suggested that this is evidence for range contraction.
- 3) Natal colony. There were few differences in distances travelled as a function of colony at which the nestling was ringed. However, there were fewer recoveries in the immediate neighbourhood of the natal colony for those sites in tribal regions. The patterns of directions in which recoveries were found differed markedly among the natal colonies. There was some data to suggest that birds can move between colonies, even when they are far apart.

The geographical locations at which birds died from various unnatural causes were also investigated. It is found that deaths due to electrocutions were tightly concentrated in the southwestern Transvaal. Cape Vultures were drawn to this potential 'sink' from almost the species' entire range. On the other hand, deaths attributed to drowning occurred over a wider range than the other causes. There were no differences in the geographical distributions of deaths attributed to poison, collision or shooting (including all forms of persecution).

*Resightings.* There were 678 resightings of 267 individual birds. From an analysis of these resightings it is shown that Cape Vultures are to be seen over almost as wide a range as they are recovered. Because a resighting requires a higher level of skill and more ornithological knowledge than does a recovery, resightings tend to be made at fewer sites. Restaurants set up to feed vultures are excellent places at which to make resightings. From these observations of the resighting of colour-ringed birds, there are data to show that young birds can leave their natal colony, travel far away and then return, some years later, to their natal colony. It is also shown that birds from one colony can breed at another. The birds from the colonies and roosts in the southwestern Cape move to and fro between various sites in the region in a manner which suggests that they may be treated as a single homogeneous sub-population.

From an analysis of all the data relating to movements, the following 'word model' is suggested. Fledglings stay around their natal colony for a few months but soon start to drift away because they cannot compete with the predominantly adult population. They tend to leave at the same time, forming 'age-sets'. They find nursery areas and wander in a nomad-like fashion for a number of years. They can colonize new areas if there is sufficient food there. They eventually return to their natal colony, or some other nearby colony (if they survive that long). Once paired, they are tied to a breeding colony and do not wander far away - though nothing is known of their home range. They do not migrate.

### 8.1.8 Models

A Leslie-matrix model was constructed of the Cape Vulture population using the best estimates currently available of its demographic parameters and variables (section 7.1). The model was used to investigate the consequences of the estimates and to undertake a sensitivity analysis. From the use of the Leslie-matrix model the following conclusions were drawn.

- 1) *Age at first breeding.* There is no need to provide a better estimate of this parameter. However, monitoring this parameter as a function of population size may signal the effects of density dependence.
- 2) *Variation in breeding success with age.* No further estimates of this parameter are required.
- 3) *Proportion of adults which breed.* There is no need to improve the estimate of this parameter.
- 4) *Survival of immatures.* The estimates of survival for all non-adult classes need to be improved. Considerable effort expended in refining these estimates is justified.

- 5) *Adult survival.* It is more important to provide an accurate estimate of adult survival than of any other demographic parameter.
- 6) *Maximum age at which adults can still breed.* Provided Cape Vultures can continue to breed until their early 20s, the population will remain stable. This parameter can only be estimated if Cape Vultures are fitted with long-lasting rings.

A model was build of the Cape Vulture sub-population in the southwestern Cape using a set of finite-difference equations (section 7.2). The fit between the predicted number of free-flying birds and the actual number counted is excellent and statistically significant. There are three reasons for this.

- 1) For the southwestern Cape the number of nestlings produced each year is known exactly from direct observation.
- 2) There are reasonable estimates of survival for the first few age-classes because many nestlings were colour-ringed and subsequently resighted.
- 3) The model was found to be insensitive to the initial age-distribution.

The estimate of adult survival is 91% with approximate confidence limits of  $\pm 2\%$ . This is the first estimate of survival for adult Cape Vultures and it is accord with recent estimates for populations of Eurasian Griffons. The Cape Vulture sub-population in the south western Cape is estimated to be declining at about 1.6% p.a. It is suggested that the reasons for this decline are, that too few pairs breed each year (i.e. 70% to 80% compared with 85% at Colleywobbles) and that the breeding success of those that do breed is also too low (i.e. 71% compared with 75% at Colleywobbles).

A stochastic version of the Leslie-matrix model was constructed (section 7.3) and used to investigate the effects of environmental and demographic stochasticity. It is shown for a population with at least 50 females (and 50 males) that the probability of extinction within 50 years is less than 1%. This simulation was carried out using reasonable estimates of the Cape Vulture's demographic parameters and variables. While it is tempting to suggest that this figure of 100 individuals constitutes the minimum viable population (MVP) there are still many unknown factors which have to be investigated. Chief among these are the effects of disease, catastrophe and inbreeding.

---

A final model was constructed which took into account the fact that the population is spatially disjoint. This 'meta-population' model was used to simulate the effects of inter-regional movements on the probabilities that some of the sub-populations could go extinct as a result of demographic or environmental stochasticity. It is concluded from these simulations that the sub-population in the southwestern Cape can be stabilized, even if its growth rate is as low as 0.95 if it receives, on average, 0.75 new individuals by immigration each year.

## 8.2 Recommendations

Arising out of the above discussion a number of recommendations are made. These are presented below in the order in which they arose. It is likely that these recommendations are too ambitious (E. Danchin, pers. comm.) and so a priority listing is provided (Table 8.1)<sup>7</sup>.

- 1) **Compile and publish an Annotated Bibliography of the Cape Vulture.**  
There are just over 1000 references to the Cape Vulture, mainly in the 'grey literature'. Nearly all of these contributions could be summarized in a short abstract and, coupled with an extensive keyword index, such a compilation would be useful to future students and conservationists.
- 2) **Compile a Site Register.**  
The first step in any species-conservation programme is the compilation of an inventory. The data gathered for this thesis (i.e. Site Register - Piper, Mundy & Vernon in prep.) should be published so as to give the ornithological and conservation communities the opportunity to scrutinize and comment on the raw data and the regional summaries.
- 3) **Devise a feasible Inventory Plan.**  
The Site Register was constructed in an *ad hoc* fashion - it was not planned. Given the known distribution of the species and a reasonable knowledge of the geographical location of the major breeding concentrations, it is suggested that a plan to bring the census up to date should be devised. To be workable, this plan should take cognizance of the limitations which arise from our small community of professional and amateur ornithologists, financial constraints and the vastness of the subcontinent. To provide reliable estimates the census method should be standardized and all counters should receive some basic training before they go into the field. Their counts should be carefully scrutinized and they should be provided with rapid feedback to ensure their continued accuracy.

---

<sup>7</sup> In response to an examiner's comment (E. Danchin) extra recommendations concerning conservation have been added.

4) Devise a feasible Monitoring Plan.

To use a business analogy: the purchase of a going concern starts with a once-off inventory and then conducts regular audits in order to provide feed-back for managerial control. It is recommended that a monitoring programme be instituted with the following aims:

- A) To monitor breeding at *ALL COLONIES* which hold more than 1% of the total breeding population (i.e. 44 breeding pairs). This is analogous to the *Ramsar* Convention for water birds. This monitoring should include counts of the number of nests tenanted, the number of eggs laid and the number of large nestlings produced. Long-term monitoring of breeding coupled with population monitoring in the surrounding region could possibly yield evidence of density-dependent effects in this demographic parameter.
- B) To monitor those sites known to be under severe threat from direct persecution, the use of poison, land transformation or any other factor. These could become 'bunny-hugger' sites, i.e. sites where the direct involvement of the general public is solicited to apply social pressure against 'rogue farmers', property developers etc.

The best time to visit colonies is during the incubation period as this yields the most reliable count of the number of active breeding pairs.

5) Devise a feasible Spatial Change Detection Plan.

In addition to monitoring the population as-a-whole it is desirable to pinpoint those areas in which range contractions and expansions are taking place as well as new colonization. It is recommended that a monitoring programme be instituted with the following aims:

- A) To monitor those sites on the periphery of the population where it is suspected that range contractions and expansions can first be detected.
- B) To monitor a selection of sites which were abandoned in the recent past so as to detect any recolonization.

6) Collect data pertinent to age-structure and breeding proportion.

It is probable that young birds and non-breeders avoid competition with breeding adults by seeking out areas on the population's periphery. These areas are likely to be important conservation areas if recruitment to the breeding population is to be sustained. By monitoring the population structure these areas can be located, monitored and tracked. At the same time as other censuses are carried out it is recommended that counts be made of the number of individuals in each age-class and the proportion of birds at a site which are not breeding.

- 7) SABAP be requested to supply the Cape Vulture distributional data for Botswana, Namibia and Zimbabwe.

It is not possible to complete the Cape Vulture distribution map for the whole of southern Africa until the data for Botswana, Namibia and Zimbabwe are released. SABAP should be requested to apply to the ornithological controlling bodies of those countries for permission to release their data-sets.

- 8) SABAP be strongly encouraged to continue with the collection of field card data for southern Africa.

The data from SABAP provide the best basis for monitoring the overall distribution of the Cape Vulture. SABAP is the organisation best suited to the collation, vetting and computerization of field cards from bird watchers. The SABAP data should be used for the purposes listed below.

- A) Detecting Cape Vultures in those areas away from traditional roosts and colonies into which they may be expanding - often by using power lines as roosts.
- B) Monitoring long-term changes in distribution
- C) Accumulating enough data to carry out tests for seasonality.

- 9) Methods for detecting seasonality should be investigated.

It has been suggested (J.A. Harrison pers. comm.) that it may be possible to detect seasonality if spatial resolution is sacrificed for temporal resolution, i.e. adjacent  $\frac{1}{4}^{\circ}$  by  $\frac{1}{4}^{\circ}$  grid-cells should be combined until there are enough sightings to justify an analysis of seasonality.

- 10) A fully parametrized model relating reporting rate to density should be developed.

It is likely that the Cape Vulture is the first continental species (i.e. as opposed to marine) for which there now exist reliable spatial data of both absolute density and SABAP-type reporting rate. Using data such as these it should be possible to 'calibrate' the reporting rate. The models developed in these researches have not fully exploited this potential. A fully parametrized model of the relationship between density and reporting rate is needed. It has been suggested that the best way to tackle this, is to build a non-linear version of a GLM using ratios of polynomials for both the density and reporting rate functions (W.L. Zucchini pers. comm.). Such a model should take cognizance of the nature of the terrain and its atmospheric conditions as well as the food parcel size. This may be achieved by employing a geographic information system (GIS). Special attention should be paid to the 'gaps' in the distribution of the Cape Vulture as seen from the SABAP data. These may reveal particular habitats (natural or man-made) which Cape Vultures refuse to use.

11) Re-institute a colour-ringing programme for nestlings at a selection of sites.

It is necessary to continue to introduce nestlings into the population bearing unique rings and colour-rings for the following purposes.

- A) To provide a better estimate for the age at first breeding.
- B) To provide a continuous source of marked birds for estimating age- and time-specific survival rates from the resighting of colour-ringed birds.
- C) To monitor short- and long-range movements, philopatry and inter-colony transfers.
- D) To monitor the impacts of various sources of unnatural mortality acting on the Cape Vulture population.

It is recommended that it will be necessary to colour-ring a minimum of 1000 nestlings over a period of about five years in order provide the quality of estimates needed (section 7.1.4). Such a programme will only work if it is coupled with an intensive colour-ringing resighting programme, such as the one conducted by H.A. Scott at Potberg over a nine-year period.

12) A model to estimate age-specific survival from complete ring-recovery-reporting data-sets should be constructed.

If a ring-recovery-reporting data-set is complete then it is possible to estimate the reporting rate directly. Hence, it should be possible to build a model of age-specific survival (see also footnote 5 on page 480).

13) The model used to estimate age- and year-specific survival from observations of colour-ringed birds should be extended to include cohort-specific effects as well as the effect of supplementary feeding.

In the mid-1980s a supplementary feeding scheme was started in the southwestern Cape. It is possible that those individuals joining the population after that date have had higher survival rates (W.L. Zucchini pers. comm.). A request has been made by Dr. A.F. Boshoff (Cape Nature Conservation) that the effect of supplementary feeding on first-year survival should also be tested.

- 14) Institute a colour-ringing programme for adults at a selection of sites.  
There are no adequate estimates of survival for adult Cape Vultures. As a first attempt in providing such an estimate, it is recommended that birds in full adult plumage be caught and colour-ringed and then monitored. It is recommended that 50 adults p.a. should be caught and colour-ringed and then observed for at least five years. As with recommendation 11 above, this should be accompanied by an intensive colour-ring resighting programme.
- 15) The breeding success model of the southwestern Cape sub-population should be extended to take into account effect of the cessation of ringing.  
Nestlings were ringed each year from 1974 to 1988. Breeding success was monitored from 1974 to 1992. By comparing the 1974 to 1988 breeding success with the 1989 to 1992 breeding success there may be enough data to test for 'investigator-effects', i.e. does ringing reduce breeding success? If a preliminary analysis indicates this, then a proper randomized experiment should be designed.
- 16) Protection plans should be devised for those roosts and colonies which are vulnerable to disturbance.  
A number of colonies and roosts have suffered serious disturbance from members of the public, low-flying aircraft, egg and nestling collectors and herdsmen. Protection plans, such as the one devised for the Magaliesberg (G.H. Verdoorn) should be extended to other vulnerable sites.
- 17) Schemes to increase breeding productivity using vulture restaurants should be intensified.  
Vulture restaurants can be provisioned with poison-free meat and bone-fragments. This technique has been used successfully at a number of sites and should be extended, where possible, to colonies in decline.
- 18) Monitor ring recoveries for important sources of unnatural mortality.  
It has been shown that ring-recoveries provide the best on-going source of data for monitoring the effects of various forms of unnatural mortality (e.g. electrocution, poisoning, drowning, collision and persecution). Safring should be requested to provide a complete listing of all Cape Vulture recoveries to the Vulture Study Group once a year to maximize the usefulness of the proposed ringing programme.

19) Education campaigns for the public should be developed.

Ultimately the survival of the Cape Vulture is dependent, at least in part, on attitudes held by the public. Specific campaigns aimed at changing attitudes among the largest landholders should be devised. The target communities are the commercial farmers, subsistence farmers, Government agencies and Nature Conservancies. Their attitudes to carcass disposal, the use of poisons, the design and placements of stock watering points and persecution need to be changed. Some components of the general public have shown a change in attitude to vultures over the last 20 to 30 years and this trend needs to be encouraged and extended to all sectors of the populace in southern Africa.

20) Use captive birds to establish the usefulness and longevity of marking techniques.

There has been no systematic study of the efficacy of metal and plastic rings used on Cape Vultures. Captive birds are ideally suited to this purpose. Careful record-keeping of marked birds in animal rehabilitation centres and zoos could provide much-needed data on the longevity of rings and the colour-fastness of colour rings.

21) Determine maximum age at which Cape Vultures can breed.

It is important to know the maximum age at which Cape Vultures can breed. In the models used to date it has been assumed that they can breed up until death. If this is not so, and if in particular they can not breed after age 20 years, then the models will have to be revised.

22) Place hides at restaurants to aid resighting programmes.

A hide at a restaurant is often the best place at which to observe colour-ringed birds. When a restaurant is established a hide should be so placed as to give the best views of birds frequenting it.

23) Model home-range, foraging and food-supply.

As yet we know almost nothing of home-range and its relationship to food distribution. We do not know how vultures find their, i.e. what foraging strategy they use. It is important to know this if we are to devise supplementary feeding schemes, especially those which we hope to use to attract birds away from areas where poisoning is rife, or if we wish to attract vultures back to an area they once used.

24) Construct a suitable geographic information system for modelling the Cape Vulture population.

A geographic information system (GIS) is an ideal tool for modelling spatial processes. A GIS for southern Africa with a grid-cell size of about 2½ 5 km would be a most useful basis for both mapping and modelling the Cape Vulture, its preferred habitats and its food supply. This could then be used for both research projects and management projects.

25) Monitor 'Investigator Effects'.

When studying a population in a 'hands-on' fashion a certain amount of disturbance results (birds displaced at breeding colonies or roosts, birds interrupted at roosts by movement in a hide etc.). It is important to try and quantify and monitor these effects.

There are three constituencies with an interest in the Cape Vulture and its long-term future.

- 1) A number of academics at Universities and research institutes in southern Africa.
- 2) The Vulture Study Group, based in Johannesburg.
- 3) The Nature Conservation Administrations of the local, provincial, regional and national governments in the sub-continent.

In my opinion, the academics are best suited to undertaking intellectually difficult tasks which demand few resources beyond what the academic can personally muster. The two most important tasks are for the distribution map to be completed by incorporating the additional data for Botswana, Namibia and Zimbabwe and for the development of a model to standardize the SABAP reporting rate.

The Vulture Study Group is best at coordinating data-collection by disparate groups of people. It also serves an important role as a non-government organisation (NGO) in that it can initiate projects in conjunction with a number of other bodies, both academic and governmental. The Vulture Study Group is strongly urged to increase its efforts to initiate a long-term monitoring programme for the Cape Vulture.

The Nature Conservation Administrations have the human, technical and financial resources to monitor the major species in need of conservation in their regions and some now see the Cape Vulture as a species to be monitored and conserved (e.g. Natal - D.N. Johnson pers. comm. and the Cape - A.F. Boshoff pers. comm). The other authorities in the region are encouraged to follow their lead of these two enlightened administrations.

Table 8.1  
Summary of recommendations with suggestions of agencies responsible for their implementation.

No.	Recommendation	Academic	Priority	
			V.S.G.	Nature Conservation
1	Annotated Bibliography	Medium	Low-	-
2	Site Register	-	High	-
3	Population Inventory	-	High	High
4	Population Monitoring	-	High	High
5	Spatial Change Detection	-	Medium	Medium
6	Age- and breeding-proportion	Medium	Medium	-
7	SABAP to supply extra data	High	-	-
8	SABAP to continue mapping	-	High	-
9	Seasonality	Medium	-	-
10	Standardize reporting rate	High	-	-
11	Colour-ring nestlings	-	High	-
12	Model age-specific survival	Medium	-	-
13	Extend colour-resighting model	Medium	-	-
14	Colour-ring adults	-	High	-
15	Extend S.W. Cape model	High	-	-
16	Protection plans	-	High	High
17	Vulture restaurants	-	Medium	Medium
18	Monitor recoveries	-	High	-
19	Education campaign	-	Medium	Medium
20	Test rings	Medium	Medium	-
21	Maximum breeding age	Medium	-	-
22	Hides at restaurants	Medium	Medium	-
23	Model home-range etc.	Medium	Medium	-
24	Model home-range etc.	Medium	Medium	-
25	Model investigator effects	Medium	-	-

Note: V.S.G. = Vulture Study Group.

### 8.3 Summary

Standing back and viewing these researches from a distance allows a number of factors to stand out from the rest.

The Cape Vulture population is a single entity. Although its spatial distribution is disjoint and although there are great variations in density, it is likely that a Cape Vulture from any one sub-population can drift to any other sub-population. In addition, it is seen that the electrocution of young Cape Vultures in southwestern Transvaal drew in birds from almost

---

every sub-population. Thus it is possible for a single 'sink' of unnatural mortality to have a depressive effect on the entire population. In turn, this means that the Cape Vulture cannot be conserved in any one place, it must be conserved everywhere.

In providing estimates of the demographic parameters and variables for the process of constructing, calibrating and testing models, it has become obvious that some processes are much better studied than others. Breeding is now well understood for this species but much more effort is needed to understand survival, recruitment to the breeding population, movements and philopatry.

Nothing whatsoever is understood of the relationship between population density and the species food-base. It should not be too difficult to construct a rudimentary model of the Cape Vulture's food supply. This species feeds almost exclusively from dead domestic stock and it should be possible to get some idea of stock densities and mortalities. Southern Africa is about to undergo a massive change in land-use practices concomitant with the political changes underway. Monitoring changes in livestock may give clues as to the ways in which the Cape Vulture populations will change.

Furthermore, food is probably the most important natural limiting factor. Judging by the number of abandoned sites, it is unlikely that a lack of nest sites is limiting. The Cape Vulture has demonstrated that it is capable of finding and exploiting new sources of food. Thus it is likely that the population is still large enough to colonize new areas, or recolonize old areas.

It is not known to what extent unnatural causes of mortality (e.g. poison, persecution etc.) are acting in an additive fashion and possibly limiting recruitment to the breeding population. I would suggest that the next major study of the Cape Vulture should concern itself with an investigation of those limiting factors which constrain the population to its current size and range.

In my personal opinion, to care is not good enough. No matter how much care and effort we expend on the Cape Vulture it will slide irrevocably and relentlessly towards extinction unless we act in a 'hands-on' fashion. To understand and monitor the forces acting on the Cape Vulture and to track the species' response, it is imperative that we continue to colour-ring adults and nestlings. Without this 'hands-on' component to our research and conservation programme we do not have any way of measuring the effectiveness of our conservation actions.

---

This once beautiful and pristine continent of Africa has been despoiled by our actions. In less than four centuries it has become a wasteland filled with the ordure of our industrialized and commercialized culture. It is not a place fit for vultures. That the Cape Vulture has survived this long is a miracle - it has survived only because it has become commensal with humankind. The Cape Vulture will only survive well into the next century if we can make our environment cleaner, safer and vulture-friendly. It is my prayer that our epitaph will be 'they saved our land by becoming commensal with vultures'.



## Appendix A

### The Albers' Equal Area Map Projection<sup>1</sup>

There is a standard<sup>2</sup> 1 in 2 500 000 wall chart of southern Africa which covers the entire area inhabited by the Cape Vulture. It was decided to use this as the base-map. The map is based on the Albers' Equal Area Map Projection. At its nominal scale the map is approximately 1 m across and too big for a thesis. Thus, a scale of 1 in 15 000 000 was chosen. At this scale the map fits neatly on an A4 page leaving ample room for a page header and caption.

The Albers' Equal Area Map Projection based on a conical form and has the following properties.

- 1) The projection is equal area. Thus any two areas of the same size on the ground will map onto areas of the same size on the map. This is particularly important when displaying distributions.
- 2) Meridians map as straight lines on the map.
- 3) Parallels map as arcs of circles.
- 4) The distance and angular distortions are not large when using this map at a scale of 1 in 15 000 000 for a region the size of southern Africa.

The projection, as it is used in southern Africa, is based on the following constants.

- 1) The central meridian, running due north-south is  $dOLONG = 24^\circ E$ .
- 2) There are two standard parallels at  $dSP1 = 18^\circ S$  and  $dSP2 = 32^\circ S$ .
- 3) The Earth is assumed to be spherical of radius  $R = 6364250$  m.
- 4) The map has nominal Scale = 15 000 000 (this is user-specific).
- 5) The Earth's radius is reduced by the scale factor so that  $R_s = R/Scale$ .
- 6) The vertical offset of the map  $dOLAT = 37^\circ S$  (this is user-specific).
- 7) Constant of the cone  $n = \frac{1}{2} \cdot (dSP1 + dSP2)$ .
- 8) Radii of the standard parallels  $r_1 = R \cdot \{\cos(dSP1)\}/n$  and  $r_2 = R \cdot \{\cos(dSP2)\}/n$ .

The conversion of geographical to map coordinates proceeds in the following manner.

For any given point  $P(Lat_p; Long_p)$  the radial distance:

$$r_p = (\{r_1\}^2 + 2R^2\{\sin(dSP1) - \sin(Lat_p)\}/n)^2$$

- 
- 1 This short description is based upon a set of notes developed by Prof. H. van Gysen of the Department of Surveying and Mapping, University of Natal, Durban. He is thanked for his assistance and for his comments on other mapping problems in this thesis.
  - 2 This map projection is used as the 'standard' by a number of Surveyors-General in the region.

The angle is:

$$\Phi_p = n \cdot (\text{Long}_p - \text{dOLONG})$$

Using these polar coordinates the rectangular coordinates may be computed from:

$$y_p = r_p \cdot \cos(\Phi_p) \quad \text{and} \quad x_p = r_p \cdot \sin(\Phi_p)$$

The vertical offset may be deduced from the y coordinate:

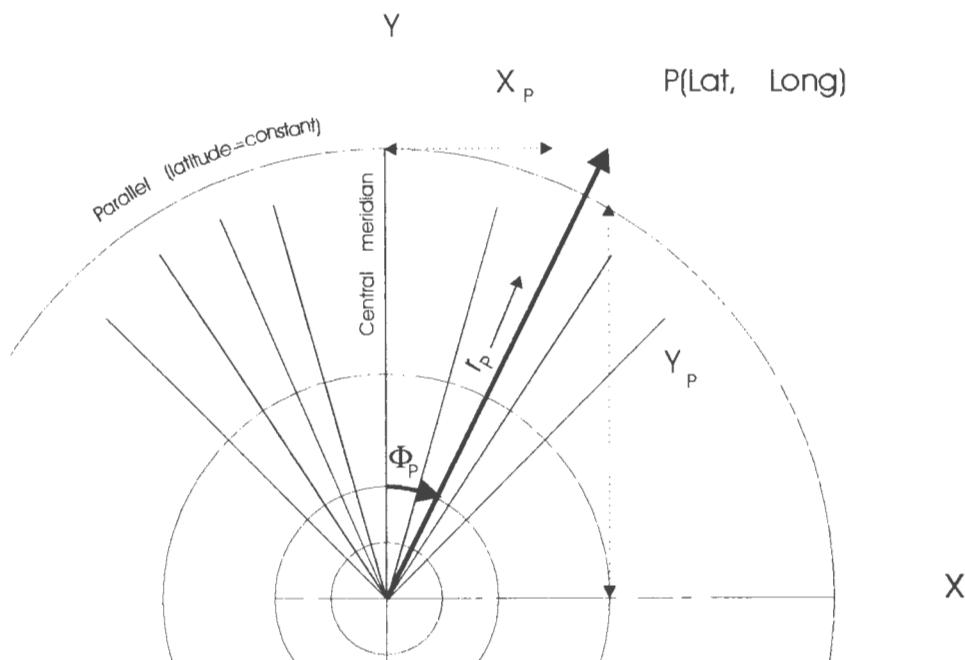
$$r_0 = (\{r_1\}^2 + 2R^2\{\sin(\text{dSP1}) - \sin(\text{dOLAT})\} / n)^2$$

The final coordinates are converted to mm for plotting:

$$Y_p = (r_p \cdot \cos(\Phi_p) - r_0 \cdot \cos(90^\circ)) \cdot 1000$$

$$X_p = x_p \cdot 1000$$

The above algorithm is implemented as a Mathcad 3.0 routine (Exhibit A.1). A reverse algorithm was also developed but is not shown here.



## Exhibit A.1 Albers' Equal Area Map Projection

Stored as E:/MCAD/AEADEC.MCAD

Computes the location of a co-ordinate pair (Long, Lat), given in decimal degrees, on the Albers' Equal Area Projection as (X,Y) in mm in the first quadrant

Constants used:

dOLAT := 37	Origin of map, degrees south
dOLONG := 24	Origin of the map, degrees east
Scale := 15000000	Scale as 1 in
dSP1 := 18	Standard parallel #1, degrees south
dSP2 := 32	Standard parallel #2, degrees east
SP1 := DEC_RAD(dSP1)	(in radians)
SP2 := DEC_RAD(dSP2)	(in radians)
OLat := DEC_RAD(dOLAT)	(in radians)
OLong := DEC_RAD(dOLONG)	(in radians)
R := 6371002.77	Earth sphere radius
$R_s := \frac{R}{\text{Scale}}$	Reduced Earth radius
$n := \frac{\sin(\text{SP1}) + \sin(\text{SP2})}{2}$	Meaned standard parallel
$C := \cos(\text{SP1})^2 + 2 \cdot n \cdot \sin(\text{SP1})$	
$r0 := \frac{R_s}{n} \cdot \sqrt{C - 2 \cdot n \cdot \sin(\text{OLat})}$	

Conversion of decimal degrees to radians

x := 22      Test value

$$\text{DEC\_RAD}(x) = x \cdot \frac{\pi}{180}$$

Exhibit A.1 (continued)

Input the data

$$M := \begin{bmatrix} 15 & 35 \\ 30 & 35 \\ 29.0167 & 28.8833 \\ 29.1 & 30.7666666 \\ 15 & 20 \\ 30 & 20 \end{bmatrix}$$

Column 0 is Longitude; Column 1 is Latitude

Determine size of input matrix

Rows := rows(M)      Cols := cols(M)

Rows = 6      Cols = 2

Now process the input matrix one row at a time

i := 0, 1.. Rows - 1

$$rp_i := \frac{Rs}{n} \cdot \sqrt{C - (2 \cdot n \cdot \sin(\text{DEC\_RAD}(M_{i,1})))}$$

Radius

$$\text{theta}_i := n \cdot (\text{DEC\_RAD}(M_{i,0}) - \text{OLong})$$

Angle

$$Xmm_i := (rp_i \cdot \sin(\text{theta}_i)) \cdot 1000$$

X in mm

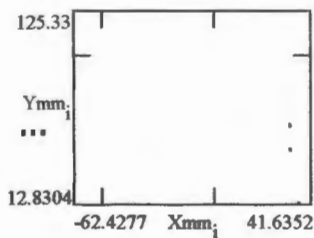
$$Ymm_i := -(r0 - rp_i \cdot \cos(\text{theta}_i)) \cdot 1000$$

Y in mm

Set up output matrix

PRNPRECISION := 2

PRNCOLWIDTH := 10

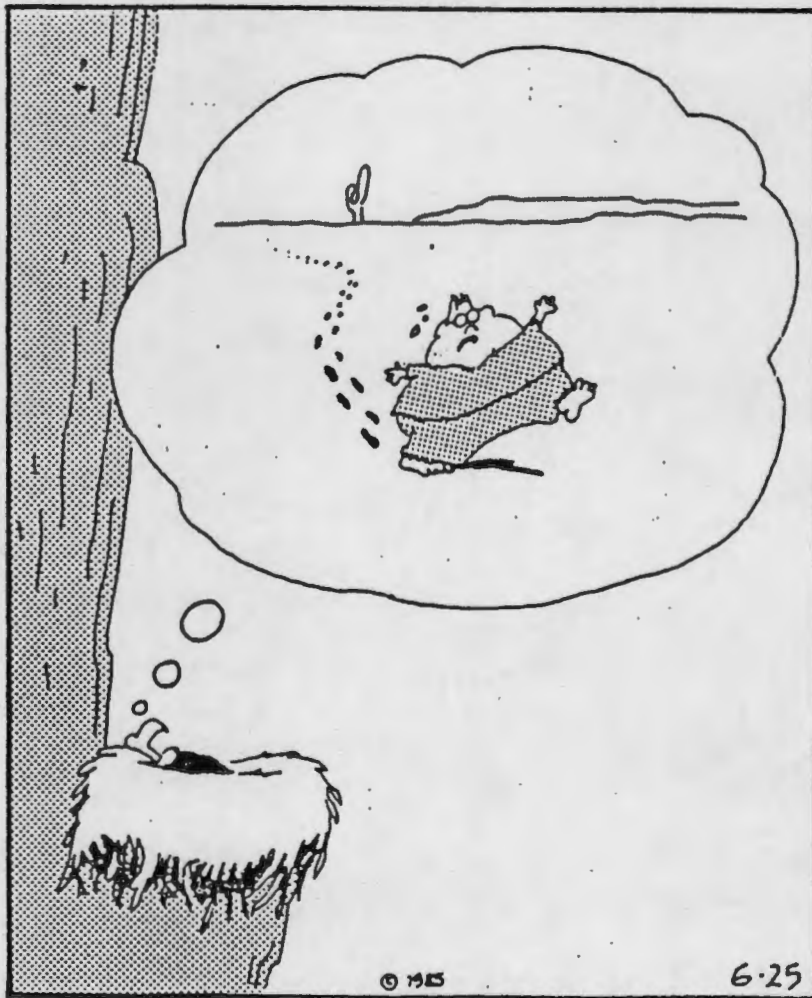


Now output the matrix

Xmm <sub>i</sub>	Ymm <sub>i</sub>	M <sub>i,0</sub>	M <sub>i,1</sub>
-55.08	12.83	15	35
36.735	13.839	30	35
32.382	59.374	29.017	28.883
32.396	45.346	29.1	30.767
-62.428	124.187	15	20
41.635	125.33	30	20

THE FAR SIDE

By Gary Larson



When vultures dream.

# References

- Abrams, R.W., Griffiths, A.M., Hajee, Y. and Schoeppe, E.** 1981. A computer-assisted plotting program for analysing the dispersion of pelagic seabirds and environmental features. *Marine Ecology* 2(4): 363-368.
- Abreu, M.V.** 1987. La dynamique des populations de nécrophages (*Gyps fulvus* et *Neophron percnopterus*) au fleuve Tejo international - 1984. Pp. 287-294 in Baccetti, N. and Spagnesi, M. (eds.): *Rapaci Mediterranei III. Suppl. Ric. Biol. Selvaggina* 12: 1-315.
- Aebischer, N.J.** 1983. Restoring the legibility of the inscriptions on abraded or corroded bird-rings. *Ringing and Migration* 4: 275-280.
- Aebischer, N.J.** 1987. Estimating time-specific survival rates when the reporting rate is constant. *Acta Ornithologica* 23(1): 35-40.
- Aebischer, N.J. and Coulson, J.C.** 1987. Lower juvenile survival rates estimated from ringing returns: reality or artefact? *Ibis* 129(1): 116-117.
- Agricultural News** 1984. Aasvoëls vrek weens vergiftiging. 15 June 1984.
- Ainley, D.G., Le Resche, R.E. and Sladen, J.C.** 1983. *Breeding biology of the Adélie Penguin*. University of California Press: Los Angeles.
- Akçakaya, H.R.** 1991. A method for simulating demographic stochasticity. *Ecological Modelling* 54: 133-136.
- Akçakaya, H.R. and Ferson, S.** 1992. *RAMAS/space. Spatially structured population models for conservation biology*. Applied Biomathematics: New York.
- Alexander, B.** 1898. Further notes on the ornithology of the Cape Verde Islands. *Ibis*, Seventh Series 4(14): 277-285.
- Allainé, D., Pontier, D., Gaillard, J.M., Lebreton, J.D., Trouvilliez, J. and Clobert, J.** 1987. The relationship between fecundity and adult body weight in Homeotherms. *Oecologia* 73: 478-480.
- Amadon, D.** 1964. The evolution of low reproductive rates in birds. *Evolution* 18: 105-110.
- Amadon, D.** 1980. Varying proportions between young and adult raptors. Pp. 327-331 in Johnson, D.N. (ed.): *Proceedings of the Fourth Pan-African Ornithological Congress*. Southern African Ornithological Society: Johannesburg.

- 
- Anderson, D.R. and Burnham, K.P.** 1980. Effect of delayed reporting of band recoveries on survival estimates. *Journal of Field Ornithology* 51(3): 244-247.
- Anderson, D.R. and Burnham, K.P.** 1987. Estimation of avian survival rates from ringing data: comments on methodology. *Acta Ornithologica* 23(1): 13-25.
- Anderson, D.R., Burnham, K.P. and White, G.C.** 1985. Problems in estimating age-specific survival rates from recovery data of birds ringed as young. *Journal of Animal Ecology* 54: 89-98.
- Anderson, D.R., Wywiałowski, A.P. and Burnham, K.P.** 1981. Tests of the assumptions underlying life table methods for estimating parameters from cohort data. *Ecology* 62: 1121-1124.
- Andrewartha, H.G. and Birch, L.C.** 1954. *The distribution and abundance of animals*. University of Chicago Press: Chicago.
- Anonymous** 1907. Habits of *Gyps Kolbii* (Common Vulture). *Journal South African Ornithologists' Union* 3(1): 137-139.
- Anonymous** 1959. Black Eagle and Cape Vultures. *Wits Bird Club News* 31: 1.
- Anonymous** 1967. Vulture flies through bus windscreen. *Bokmakierie* 19(1): 44.
- Anonymous** 1977. The Cape Vulture project. *Wits Bird Club News* 97: 10-11.
- Anonymous** 1980. Vultures poisoned in Transvaal. *Vulture News* 3: 16-17.
- Anonymous** 1981. Vulture poisoning. *African Wildlife* 35.
- Anonymous** 1988. *GENSTAT 5 Reference manual*. Clarendon Press: Oxford.
- Anthony, A.J.** 1976. The Lappet-Faced Vultures of the Gonarezhou. *Bokmakierie* 28(3): 54-57.
- Ash, J.S.** 1976. Bird-ringing in Ethiopia. Report No. TR-1, U.S. Naval Medical Research Unit Five: Addis Ababa, Ethiopia.
- Ash, J.S. and Miskell, J.E.** 1983. Birds of Somalia, their habitat, status and distribution. Ornithological Sub-committee for the East African Natural History Society: Nairobi. *SCOPUS Special Supplement* 1: 97 pp.
- Ashton, E.H.** 1957. Sixth ringing report. *Ostrich* 28(2): 98-115.

- 
- Ashton, H.** 1979. SAFRING - how it all began. *Safring News* 8(1): 3-6.
- Bailey, E.E., Woolfenden, G.E. and Robertson, W.B.** 1987. Abrasion and loss of bands from Dry Tortugas Sooty Terns. *Journal of Field Ornithology* 58: 413-424.
- Baillie, S.R. and Green, R.E.** 1987. The importance of variation in recovery rates when estimating survival rates from ringing recoveries. *Acta Ornithologica* 23(1): 41-60.
- Baker, R.R.** 1982. *Migration - paths through time and space*. Hodder & Stoughton: London.
- Baldwin, G.** 1985. Lions and vultures. *Hartebeest* 17: 25-26.
- Bands, M.** 1979. Vultures quite literally out of the blue. *Diaz Diary* 76: 5-6.
- Barnard, P. and Simmons, R.** 1985. Birds of prey of Giant's Castle Reserve. *Bokmakierie* 37: 104-107.
- Baron, S.T.** 1981. An updated list of birds of the Bontebok National Park. *Koedoe* 24: 79-98.
- Bartlett, M.S.** 1960. *Stochastic Population Models in Ecology and Epidememiology*. Wiley: New York.
- Begon, M.** 1979. *Investigating animal abundance: capture-recapture for biologists*. Edward Arnold: London.
- Benson, C.W.** 1982. Migrants in the Afrotropical region south of the equator. *Ostrich* 53: 31-49.
- Benson, P.C.** 1981. Large raptor electrocution and powerline utilization: A study in six Western States. Unpublished Ph.D. Dissertation, Brigham Young University: Provo, Utah, U.S.A.
- Benson, P.C. and Dobbs, J.C.** 1984. Causes of Cape Vulture mortality at the Kranzberg colony. Pp. 87-93 in Mendelsohn, J.M. and Sapsford, C.W. (eds.): *Proceedings, 2nd symposium on African Predatory Birds*. Natal Bird Club: Durban.
- Benson, P.C. and Dobbs, J.C.** 1985. Impacts of recreational climbing on nesting Cape Vultures. Pp. 337-338 in Bunning, L.J. (ed.): *Proceedings of Symposium on Birds and Man, Johannesburg*. Wits Bird Club: Johannesburg.
- Benson, P.C. and Dobbs, J.C.** 1985. Collisions of Cape Vultures (*Gyps coprotheres*) with towers. *Second Raptor Research Foundation Conference on Raptor Conservation Techniques*, Sacramento, California, November 9-10, 1985.

- 
- Benson, P.C., Tarboton, W.R., Allan, D.G. and Dobbs, J.C.** 1990. The breeding status of the Cape Vulture in the Transvaal during 1980-1985. *Ostrich* 61(3&4): 134-142.
- Bent, A.C.** 1937. Life histories of North American birds of prey. Part I. *Smithsonian Institution, United States National Museum Bulletin* 167: Washington.
- Bergier, P.** 1985. The breeding of the Egyptian Vulture *Neophron percnopterus* in Provence (S.E. France) from 1979 to 1983. Pp. 77-78 in Chancellor, R.D. and Meyburg, B-U. (eds.): *World Working Group on birds of Prey*. Bulletin no. 2. I.C.B.P: Berlin.
- Bergier, P. and Cheylan, G.** 1980. Statut, succes de reproduction et alimentation du Vautour Percnoptere *Neophron percnopterus* en France mediterraneenne. *Alauda* 48: 75-97.
- Berliner, D.B.** 1982. Vultures and electricity pylons. [With a comment by Ledger, J.A.] *Bokmakierie* 34(4): 79-81.
- Berliner, D.B.** 1984. The use of strychnine poison by farmers in the N.W. Transvaal and their attitudes towards vultures. *Vulture News* 12: 7-8.
- Bernardelli, H.** 1941. Population waves. *Journal of the Burma Research Society*. 31: 1-18.
- Best, P.B. and Underhill, L.G.** 1990. Estimating population size in southern right whales *Eubalaena australis* using naturally marked animals. *Rep. Int. Whal. Commn* (special issue 12).
- Birkhead, T.R., Kay, R. and Nettleship, D.N.** 1985. A new method for estimating the survival rates of the Common Murre. *Journal of Wildlife Management* 49: 496-502.
- Blakers, M., Davies, S.J.J.F. and Reilly, P.N.** 1984. *The atlas of Australian birds*. Melbourne University Press: Melbourne.
- Blondel, J.** 1991. Birds in biological isolates. In Perrins, C.M., Lebreton, J.-D. & Hiron, G.J.M. (eds.). *Bird population studies*. Oxford University Press: Oxford. pp. 45-72.
- Borello, W.D.** 1985. Poisoned vultures in Botswana: known facts. *Babbler* 9: 22-23.
- Borello, W.D.** 1987. Vulture distribution in Botswana. *Babbler* 13: 11-25.
- Borello, W.D. and Borello, R.M.** 1987. The Cape Vulture colonies in Botswana in 1985 and 1986. *Vulture News* 17: 37-42.
- Borello, W.D. and Borello, R.M.** 1992. Report on the Cape Griffon colonies in Botswana, 1987 - 1990. *Vulture News* 26: 38-47.

- 
- Boshoff, A.F.** 1980. Mobbing by Kelp Gulls *Larus dominicanus* as a possible cause of Cape Vulture *Gyps coprotheres* mortality. *Cormorant* 8(1): 15-16.
- Boshoff, A.F.** 1981. Notes on two Cape Vulture colonies in the south-western Cape Province, South Africa. *Vulture News* 5: 3-10.
- Boshoff, A.F.** 1987. Update on two Cape Vulture colonies in the southwestern Cape Province: 1981-1986. *Vulture News* 18: 37-42.
- Boshoff, A.F.** 1990. Report on the Karmelkspruit, Balloch and Dalhousie Cape Vulture colonies in the northeastern Cape Province. *Vulture News* 24: 41-45.
- Boshoff, A.F., Brooke, R.K. and Crowe, T.M.** 1978. Computerized distribution mapping scheme for vertebrates in Southern Africa. *South African Journal of Wildlife Research* 8(4): 145-149.
- Boshoff, A.F. and Currie, M.H.** 1981. Notes on the Cape Vulture colony at Potberg, Bredasdorp. *Ostrich* 52(1): 1-8.
- Boshoff, A.F. and de Kock, A.C.** 1988. Further evidence of organo-chlorine contamination in Cape Vultures. *Ostrich* 59(1): 40-1.
- Boshoff, A.F. and Robertson, A.S.** 1985. A conservation plan for the Cape Vulture colony at Potberg, De Hoop Nature Reserve, southwestern Cape Province. *Bontebok* 4: 25-31.
- Boshoff, A.F. and Robertson, A.S.** 1985. Post-nestling mortality in Cape Vultures. *Ostrich* 56: 204-207.
- Boshoff, A.F., Robertson, A.S. and Norton, P.M.** 1984. A radio-tracking study of an adult Cape Griffon Vulture *Gyps coprotheres* in the south-western Cape Province. *South African Journal of Wildlife Research* 14(3): 73-78.
- Boshoff, A.F. and Scott, H.A.** 1990. The status and breeding performance of Cape Vultures at colonies in the south-western Cape Province: 1987-1990. *Vulture News* 24: 33-40.
- Boshoff, A.F. and Vernon, C.J.** 1979. Supplementary notes on the Cape Vulture *Gyps coprotheres* in the Cape Province. Special Publication of the Cape Department of Nature and Environmental Conservation: Cape Town.
- Boshoff, A.F. and Vernon, C.J.** 1980a. The past and present distribution and status of the Cape Vulture in the Cape Province. *Ostrich* 51(4): 230-50.

- 
- Boshoff, A.F. and Vernon, C.J.** 1980b. The distribution and status of some eagles in the Cape Province. *Annals of the Cape Provincial Museums (Natural History)* 13(9): 107-132.
- Boshoff, A.F. and Vernon, C.J.** 1981. Active Cape Vulture breeding and roost sites in the Cape Province in 1979. *Vulture News* 6: 19.
- Boshoff, A.F. and Vernon, C.J.** 1984. The conservation of raptors in the Cape Province of South Africa. Pp. 559-566 in Ledger, J.A. (ed.): *Proceedings of the Fifth Pan-African Ornithological Congress*. Southern African Ornithological Society: Johannesburg.
- Boshoff, A.F. and Vernon, C.J.** 1987. The Cape Vulture colonies at Karnmelkspruit (1984-1986) and Balloch (1978-1986), north-eastern Cape Province. *Vulture News* 17: 31-36.
- Boshoff, A.F., Vernon, C.J. and Brooke, R.K.** 1983. Historical atlas of the diurnal raptors of the Cape Province (Aves: Falconiformes). *Annals of the Cape Provincial Museums (Natural History)* 14(7): 173-297.
- Bourne, W.R.P.** 1955. The birds of the Cape Verde Islands. *Ibis* 97(3): 508-556.
- Bouvet, F.** 1985. The status of the Bearded Vulture in Corsica. Pp. 129-130 in Newton, I. and Chancellor, R.D. (eds.): *Conservation Studies of Raptors*, ICBP Technical Publication No. 5, ICBP: Cambridge.
- Bowen, P.** 1970. Some observations of the Cape Vulture. *African Wildlife* 24: 125-128.
- Brillinger, D.R.** 1986. The natural variability of vital rates and associated statistics. *Biometrics* 42: 693-734.
- Brooke, R.K.** 1984a. An assessment of rare, vulnerable and endangered South African breeding birds. Pp. 567-576 in Ledger, J.A. (ed.): *Proceedings of the Fifth Pan-African Ornithological Congress*. Southern African Ornithological Society: Johannesburg.
- Brooke, R.K.** 1984b. *South African Red Data Book: Birds*. South African National Scientific Programmes Report No. 97, CSIR: Pretoria.
- Brown, C.J.** ca. 1980. *Please help us save the Cape Vulture. (English, Afrikaans and German)* Department of Agriculture and Nature Conservation: Windhoek.
- Brown, C.J.** 1985a. The status and conservation of the Cape Vulture in SWA/Namibia. *Vulture news* 14: 4-15.

- 
- Brown, C.J.** 1985b. Seminar on the use/misuse of strychnine. Unpublished Report. Namibia Nature Conservation: Windhoek.
- Brown, C.J.** 1987. The physical parameters of Cape Vultures in the Natal Drakensberg and some ideas on large size in mountain habitat. *Vulture News* 18: 22-30.
- Brown, C.J.** 1988. A study of the Bearded Vulture *Gypaetus barbatus* in southern Africa. Unpublished Ph.D. thesis, University of Natal: Pietermaritzburg.
- Brown, C.J.** 1990. An evaluation of supplementary feeding for Bearded Vultures and other avian scavengers in the Natal Drakensberg. *Lammergeyer* 41: 30-36.
- Brown, C.J. and Jones, S.J.A.** 1989. A supplementary feeding scheme in the conservation of the Cape Vulture at the Waterberg, South West Africa/Namibia. *Madoqua* 16: 111-119.
- Brown, C.J. and Piper, S.E.** 1988. Status of the Cape Vulture in the Natal Drakensberg and their cliff site selection. *Ostrich* 59: 126-36.
- Brown, L.H.** 1977. The status, population structure and breeding dates of the African Lammergeier *Gypaetus barbatus meridionalis*. *Raptor Research* 11: 49-58.
- Brown, L.H. and Pomeroy, D.E.** 1984. The age structure of populations of wild birds in tropical Africa, as demonstrated by plumage characters and marking techniques. Pp. 97-119 in Ledger, J.A. (ed.): *Proceedings of the Fifth Pan-African Ornithological Congress*. Southern African Ornithological Society: Johannesburg.
- Brown, L.H., Urban, E.K. and Newman, K.** 1982. *The birds of Africa. Vol I.* Academic Press: London.
- Brownie, C., Anderson, D.R., Burnham, K.P. and Robson, D.S.** 1978. *Statistical inference from band recovery data - a handbook (1st ed)*. Fish and Wildlife Service, Resource Publication, No.131: Washington.
- Brownie, C., Anderson, D.R., Burnham, K.P. and Robson, D.S.** 1985. *Statistical inference from band recovery data - a handbook (2nd ed.)*. Fish and Wildlife Service, Resource Publication, No.156: Washington.
- Brownie, C., Hines, J.E. and Nichols, J.D.** 1986. Constant parameter capture-recapture models. *Biometrics* 42: 561-574.
- Bryden, H.A.** 1889. *Kloof and Karroo: sport, legend, and natural history in Cape Colony, with a notice of the game birds, and of the present distribution of the antelopes and larger game*. Longmans, Green and Co.: London.

- 
- Buckelew, A.R., Hutton, E.E. and Allen, T.** 1986. Mountaintop buildings: hazards for migrating birds. *Redstart* 53: 124-130.
- Buckland, S.T.** 1980. A modified analysis of the Jolly-Seber capture-recapture model. *Biometrics* 36: 419-435.
- Buckland, S.T. and Baillie, S.R.** 1987. Estimating bird survival rates from organized mist-netting programmes. *Acta Ornithologica* 23(1): 89-100.
- Buckland, S.T., Bell, M.V. and Picozzi, N.** in Press. (eds.): *The birds of north-east Scotland*.
- Bunck, C.M.** 1987. Analysis of survival data from telemetry projects. *Journal of Raptor Research* 21: 132-134.
- Burnham, K.P.** 1989. Numerical survival rate estimation for capture-recapture models using SAS PROC NLIN. Pp. 416-435 in McDonald, L., Manly, B., Lockwood, J. and Logan, J. (eds.): *Estimation and analysis of insect populations*. Springer-Verlag: Berlin.
- Burnham, K.P. and Anderson, D.R.** 1979. The composite dynamic method as evidence for age-specific waterfowl mortality. *Journal of Wildlife Management* 43(2): 356-366.
- Burnham, K.P. and Anderson, D.R.** 1984. Tests of compensatory vs. additive hypotheses of mortality in mallards. *Ecology* 65: 105-112.
- Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C. and Pollock, K.H.** 1987. *Design and analysis methods for fish survival experiments based on release-recapture*. American Fisheries Society, Monograph 5: Bethesda (Maryland).
- Busche, G. and Staudte, A.** 1985. [Grid mapping as a basis for estimating populations of selected species.] *Vogelwelt* 106: 142-149.
- Butchart, D.** 1988. Vultures and water. *Vulture News* 19: 21-23.
- Campbell, B. and Lack, E.** 1985. (eds.): *A dictionary of birds*. A. & T.D. Poyser: Calton.
- Caswell, H.** 1989. *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer: Sunderland (Mass.).
- Celliers, D.** 1984. SABC helps protect rare Cape Vultures. *S.A.B.C. Bulletin*, July 1984.
- Chenau-Repond, R.** 1976. Birds of prey cooling themselves by standing in water. *Honeyguide* 86: 34.

- 
- Cheylan, G. and Thibault, J.C.** 1981. (eds.): *Rapaces Mediterraneens*. Centre de Recherches Ornithologiques de Provence: Aix-en-Provence.
- Chilgren, J.D.** 1979. Drowning of grassland birds in stock tanks. *Wilson Bulletin* 91(2): 345-346.
- Clinning, C.F.** 1980. Vulture study in South West Africa. *Vulture News* 3: 7-10.
- Clobert, J. and Lebreton, J.D.** 1991. Estimation of demographic parameters in bird populations. Pp. 75-104 in Perrins, C.M., Lebreton, J.-D. & Hiron, G.J.M. (eds.): *Bird Population Studies: Relevance to Conservation and Management*. Oxford University Press: Oxford.
- Clutton-Brock, T.H.** 1986. Sex ratio variation in birds. *Ibis* 128(3): 317-329.
- Cohen, G.M.** 1970. Studies on the resistance of roosters and vultures to Type A botulinum toxin. Ph.D. dissertation, Florida State University.
- Colahan, B.D.** 1988. The Cape Vulture in the Orange Free State: past and present distribution and status. Preliminary report of the O.F.S. Provincial Administration Directorate of Environmental and Nature Conservation Project N7/6/3: Bloemfontein.
- Colahan, B.D.** 1989. The Cape Vulture in the Orange Free State: past and present distribution and status. O.F.S. Provincial Administration Directorate of Nature and Environmental Conservation, Project N7/6/3/, Progress Report No. 1: Bloemfontein.
- Colclough, J.H. and Ross, G.J.B.** 1987. Colour band loss in Cape Gannets. *Safring News* 16: 35-37.
- Coleman, J.S. and Fraser, J.D.** 1983. Nesting of Black and Turkey Vultures at Gettysburg National Park, Pennsylvania. (Abstract only) U.S. Raptor Research Meeting.
- Collar, N.J. and Stuart, S.N.** 1985. (eds.): *Threatened birds of Africa and related islands. The ICBP/IUCN Red Data Book, Part I. 3rd Edition*. I.C.B.P./I.U.C.N.: Cambridge.
- Conroy, M.J.** 1983. Variation in survival and recovery rates of Ring-necked Ducks. *Journal of Wildlife Management* 47: 127-137.
- Conroy, M.J. and Hines, J.E.** 1990. Flexible models for analysing ring recovery data to estimate survival rates. *Ring* 13(1&2): 173-192.

- 
- Conroy, M.J. and Williams, B.K.** 1984. A general methodology for maximum likelihood inference from band-recovery data. *Biometrics* 40: 739-748.
- Cook, R.D. and Weisberg, S.** 1982. *Residuals and influence in regression*. Chapman and Hall: New York.
- Cooper, J.E.** 1978. *Veterinary aspects of captive birds of prey*. Standfast Press: Saul (Gloucestershire).
- Cormack, R.M.** 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51: 429-438.
- Cormack, R.M.** 1989. Log-linear models for capture-recapture. *Biometrics* 45: 395-413.
- Correia, J.M.** 1984. SABC out to protect rare Cape Vultures. *Rand Daily Mail*, 2 July 1984.
- Coulson, J.C.** 1984. The population dynamics of the Eider Duck *Somateria mollissima* and evidence of extensive non-breeding by adult ducks. *Ibis* 126(4): 525-543.
- Coulson, J.C.** 1988. Lifetime reproductive success in the Black-legged Kittiwake (*Rissa tridactyla*). *Proceedings of the International Ornithology Congress* 19: 2140-2147.
- Coulson, J.C. and Butterfield, J.** 1986. Studies on a colony of colour-ringed Herring Gulls *Larus argentatus*: I. Adult survival rates. *Bird Study* 33: 51-54.
- Craig, T.H. and Powers, L.R.** 1976. Raptor mortality due to drowning in a livestock watering tank. *Condor* 78(3): 412.
- Cramp, S. and Simmons, K.E.L.** 1980. (eds.): *The birds of the Western Palaearctic*. Vol. 2. Oxford University Press: Oxford.
- Cunningham, A.B.** 1990. Vultures and the trade in traditional medicines. *Vulture News* 24: 3-10.
- Curry-Lindahl, K.** 1981. *Bird migration in Africa*. Vol. I. Academic Press: London.
- Cyrus, D. and Robson, N.** 1980. *Bird atlas of Natal*. University of Natal Press: Pietermaritzburg.
- Daily Despatch** 1924. Reasons for decline in 1900. 30 October 1924.
- Davis, T.J.** 1989. *Tetrad atlas of the breeding birds in Devon*. The Devon Bird Watching & Preservation Society.

- 
- de Jager Jackson, A.** ca. 1920. *Manna in the desert. A revelation of the Great Karroo.* Christian Literature Depot: Johannesburg.
- Diebold, E.N.** 1992. (ed.) *North American regional studbook for Cinereous Vulture (Aegypius monachus).* 2dn. Edn. Milwaukee County Zoo: Milwaukee (WI).
- Diem, K. and Lentner, C.** 1970. (eds.) *Scientific tables.* 7th. ed. Ciba-Geigy: Basle.
- Dobbs, J.C. and Benson, P.C.** 1982. Bird-human interaction in the survival of the Cape Vulture. *National Geographic Yearbook*: 1-11.
- Dobbs, J.C. and Benson, P.C.** 1985. The effect of strychnine poisoning on the Cape Vulture (*Gyps coprotheres*). *International Vulture Symposium*, Sacramento, California, 2-3 November 1985.
- Dobson, A.P.** 1987. A comparison of seasonal and annual mortality for both sexes of fifteen species of common British birds. *Ornis Scandinavica* 18: 122-128.
- Docherty, D.E. and Henning, D.J.** 1980. The isolation of a herpesvirus for captive cranes with an inclusion body disease. *Avian Diseases.* 24: 278-283.
- Donázar, J.A. and Ceballos, O.** 1988. Alimentación y tasas reproductoras del Alimoche (*Neophron percnopterus*) en Navarra. *Ardeola* 35: 3-14.
- Donázar, J.A. and Fernandez, C.** 1990. Population trends of the Griffon Vulture *Gyps fulvus* in northern Spain between 1969 and 1989 in relation to conservation measures. *Biological Conservation* 53: 83-91.
- Donázar, S., Ceballos, J.A., Ceballos, O., Ceballos, R., Ceballos, C. and Fernandez, L.** 1987. Factors influencing the distribution and abundance of seven cliff-nesting raptors: a multivariate study. *Paper presented at 3rd World Conference on Birds of Prey*, March 1987, Eilat.
- Donnay, T.J.** 1989. Semonkong Cape Vulture colony takes a plunge. *Bokmakierie* 41(1): 19-22.
- Douglass, A.** 1881. *Ostrich farming in South Africa.* Cassell, Petter & Galpin: London.
- Draulans, D. and van Vesseem, J.** 1985. Age-related differences in the use of time and space by radio-tagged Grey Herons (*Ardea cinerea*) in winter. *Journal of Animal Ecology* 54: 771-780.

- 
- du Plessis, G.D. 1986. A review of the status and distribution of raptors in the southern part of the eastern Orange Free State. *Mirafra* 3(1): 7-16.
- E.P. Herald 1973. Eastern Province Herald, 20 January 1973.
- Earlé, R. and Grobler, N. 1987. *First atlas of bird distribution in the Orange Free State*. National Museum: Bloemfontein.
- Ebbing, B.S. and van Biezen, J.B. 1987. Estimation of annual survival rates using resightings of individually marked Barnacle Geese *Branta leucopsis*, wintering in the Netherlands and northern Germany. *Acta Ornithologica* 23(1): 101-114.
- Ebbing, B.S. and Van der Voet, H. 1990. Have all barnacle geese (*Branta leucopsis*) the same probability of being sighted? *Ring* 13(1&2): 37-44.
- Elder, W.H. and Zimmerman, D. 1983. A comparison of recapture versus resighting data in a 15-year study of survivorship of the Black-capped Chickadee. *Journal of Field Ornithology* 54(2): 138-145.
- Elgood, J.H., Fry, C.H. and Dowsett, R.J. 1973. African migrants in Nigeria. *Ibis* 115(1): 1-45, 375-411.
- Elosegi, I. 1987. *Biologie es étho-écologie du vautour fauve (Gyps fulvus Hablizl): mise au point bibliographique et recherches dans les Pyrénées occidentales*. D.E.A., Univ. de Pau.
- Feller, W. 1968. *An introduction to probability theory and its applications*. Wiley: New York.
- Ferson, S. and Akçakaya, H.R. 1990. *RAMAS/age User manual: modelling fluctuations in age-structured populations*. Applied Biomathematics: New York.
- Ferson, S. and Akçakaya, H.R. 1991. *RAMAS/age. Modelling fluctuations in age-structured populations*. Applied Biomathematics: New York.
- Ferson, S., Akçakaya, R., Ginzburg, L. and Krause, M. 1991. *Use of RAMAS to Estimate Ecological Risk: Two Fish Species Case Studies*. Technical Report EN-7176. Electric Power Research Institute: Palo Alto (California).
- Ferson, S., Ginzburg, L. and Silvers, A. 1989. Extreme event risk analysis for age-structured populations. *Ecological Modelling* 47: 175-187.
- Finch-Davies, C.G. 1920. Notes on South African Accipitres. *Ibis*, Eleventh Series 2(2): 409-39.

- 
- Flower, S.S.** 1923. *List of birds of prey, 1889-1923, with notes on their longevity*. Min. Pub. Works Egypt Zool. Surv. Publ. No. 37: Cairo.
- Flower, S.S.** 1938. Further notes on the duration of life in animals-IV Birds. *Proceedings Zoological Society*: London 108(Series A): 195-235.
- Flux, J.E.C. and Flux, M.M.** 1981. Population dynamics and age structure of Starlings (*Sturnus vulgaris*) in New Zealand. *New Zealand Journal of Ecology* 4: 65-72.
- Freeman, S.N. and Morgan, B.J.T.** 1990. Studies in the analysis of ring-recovery data. *Ring* 13(1&2): 271-288.
- Freeman, S.N. and Morgan, B.T.J.** 1992. A modelling strategy for recovery data from birds ringed as nestlings. *Biometrics* 48: 217-236.
- Freeman, S.N. and North, P.M.** 1990. Estimation of survival rates of British, Irish and French Grey Herons. *Ring* 13(1&2): 139-166.
- Fryxell, J.M.** 1986. Age-specific mortality: An alternative approach. *Ecology* 67(6): 1687-1692.
- Fuller, R.J. and Lloyd, D.** 1981. The distribution and habitats of wintering Golden Plovers in Britain, 1977-1978. *Bird Study* 28: 169-185.
- Ginzburg, L.R., Ferson, S. and Akçakaya, H.R.** 1990. Reconstruction of density dependence and the conservative assessment of extinction risks. *Conservation Biology* 4: 63-70.
- Glutz von Blotzheim, U.N., Bauer, K.M. and Bezzel, E.** 1971. *Hanbuch der vögel Mitteleuropas*. Vol. 4. Akad. Verlagsgesellschaft: Frankfurt am Main.
- Godfrey, R.** 1934. Present status of the Griffon in Eastern Cape Colony. *Blythswood Review* 11: 46-47.
- Gonzalez, R.C. and Wintz, P.** 1983. *Digital image processing*. Addison-Wesley: Massachusetts.
- Goodman, L.A.** 1967. On the age-sex composition of the population that would result from given fertility and mortality conditions. *Demography* IV: 423-441.
- Green, A.A.** 1977. New nesting records for Rüppell's Griffon *Gyps rueppellii* in West Africa. *Bulletin British Ornithologists' Club* 97(1): 9-10.

- 
- Green, P.J.** 1981. Peeling bivariate data. pp. 1-20 *In* Barnett, V. (ed.). *Interpreting multivariate data*. Wiley: Chichester.
- Green, R.E. and Hiron, G.J.M.** 1991. The relevance of population studies to the conservation of threatened birds. *In* Perrins, C.M., Lebreton, J.-D. & Hiron, G.J.M. (eds.) *Bird population studies*. Oxford University Press: Oxford. pp. 594-633.
- Grier, J.W.** 1979. Caution on using productivity or age ratios alone for population inferences. *Raptor Research* 13(1): 20-24.
- Gurney, J.H.** 1899. On the comparative ages to which birds live. *Ibis*, Seventh Series 5(17): 19-42.
- Haagner, A.K. and Ivy, R.H.** 1907. The birds of Albany division, Cape colony. *Journal South African Ornithologists' Union* 3(1): 76-116.
- Haldane, J.B.S.** 1955. The calculation of mortality rates from ringing data. Pp. 454-458 in *Proceedings of the XI International Ornithological Congress*: Basel.
- Hall, A.V.** 1989. Rare plant surveys and atlases P.148-156 in Huntly, B.J. (ed.). *Biotic Diversity in Southern Africa: concepts and conservation*. Oxford university press: Cape Town.
- Hall, B.P. and Moreau, R.E.** 1970. *An atlas of speciation in African passerine birds*. British Museum (Natural History): London.
- Halliday, T.** 1978. *Vanishing birds: their natural history and conservation*. Hutchinson: Auckland.
- Harrison, C.** 1982. *An atlas of the birds of the Western Palearctic*. Collins: London.
- Harrison, J.A.** 1991a. The value of atlassing: the seasonality of migratory birds. *Birding in Southern Africa* 43(1): 4-6.
- Harrison, J.A.** 1991b. [Book review] Lewis, A. & Pomeroy, D. 1989. *A bird atlas of Kenya*. *Ostrich* 62(1&2): 95.
- Hatch, J.J. and Nisbet, I.C.T.** 1983a. Band wear in Arctic Terns. *Journal of Field Ornithology* 54: 91.
- Hatch, J.J. and Nisbet, I.C.T.** 1983b. Band wear and band loss in Common Terns. *Journal of Field Ornithology* 54: 1-16.
- Hatch, S.A.** 1988. Testing for individual variation in breeding success. *Auk* 105: 193-194.

- 
- Heath, J., Pollard, E. and Thomas, J.A. 1984. *Atlas of butterflies in Britain and Ireland*. Viking: Harmondsworth (Middlesex).
- Heisey, D.M. and Fuller, T.K. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. *Journal of Wildlife Management* 49: 668-678.
- Hobbs, J.C.A. 1987. Bird populations not affected by collisions with power lines. *Hornbill* 11: 5-6.
- Hobbs, J.C.A. and Ledger, J.A. 1986. Powerlines, birdlife and the golden mean. *Fauna & Flora* 44: 22-27.
- Hobbs, J.C.A. and Ledger, J.A. 1986. Some environmental impacts of electricity transmission and distribution of lines. AMEU Technical Meeting, pp. 41-46.
- Hobbs, J.C.A. and Ledger, J.A. 1988. Vets, volts and vultures, Part I. *Vetmed (S. Afr. Vet. Med.)* 1: 24-27.
- Hockey, P.A.R. and Ferrar, A.A. 1985. (eds.) *Guidelines for the bird atlas of southern Africa. Ecosystems Programmes Occasional Report 2*. CSIR: Pretoria.
- Hockey, P.A.R., Underhill, L.G., Neatherway, M. and Ryan, P.G. 1989. *Atlas of the birds of the southwestern Cape*. Cape Bird Club: Cape Town.
- Holling, C.S. 1978. *Adaptive Environmental Assessment and Management*. Wiley: Chichester.
- Hoogstraal, H., Kaiser, M.N. and Kohls, G.M. 1968. The subgenus *Persicargas* (Ixodoidea, Argasidae, *Argas*). A. (P.) *zumpti*, new species, a parasite of the South African Cape Vulture. *Ann. Entomol. Soc. Am.* 61: 744-751.
- Horn, H.S. and Rubenstein, D.I. 1984. Behavioural adaptations and life history. Pp. 279-298 in Krebs, J.R. and Davies, N.B. (eds.): *Behavioural ecology. An evolutionary approach*. Blackwell: Oxford.
- Houston, D.C. 1974. Mortality of the Cape Vulture. *Ostrich* 45: 57-62.
- Houston, D.C. 1976. Breeding of the White-backed and Rüppell's Griffon Vultures, *Gyps africanus* and *Gyps rueppellii*. *Ibis* 118(1): 14-40.
- Houston, D.C. 1986. Guest editorial. Out in the cold. *Vulture News* 16: 2-4.

- 
- Houston, D.C.** 1987. Management techniques for vultures - feeding and releases. Pp. 15-29 in Hill, D.J. (ed.): *Breeding and management in birds of prey*. University of Bristol: Bristol.
- Houston, D.C. and Cooper, J.E.** 1975. The digestive tract of the Whiteback Griffon Vulture and its role in disease transmission among wild ungulates. *Journal of Wildlife Diseases* 11: 306-313.
- Humphries, C.J. and Parenti, L.R.** 1986. *Cladistic biogeography*. Clarendon Press: Oxford.
- Hustler, K. and Howells, W.W.** 1988. Breeding biology of the Hooded and Lappet-faced Vultures in the Hwange National Park. *Honeyguide* 34: 109-115.
- Hustler, K. and Howells, W.W.** 1990. The influence of primary reproduction on a raptor community in Hwange National Park, Zimbabwe. *Journal of Tropical Ecology* 6: 343-354.
- Inskipp, C. and Inskipp, T.** 1985. *A guide to the birds of Nepal*. Croom Helm: Beckenham.
- Jackson, J.A.** 1983. Nesting Phenology, nest site selection, and reproduction success of Black and Turkey Vultures. Pp. 245-270 in Wilbur, S.R. and Jackson, J.A. (eds.): *Vulture Biology and Management*. University of California Press: Berkeley and Los Angeles.
- Jarvis, M.J.F.** 1974. High tension power lines as a hazard to larger birds. *Ostrich* 45(4): 262.
- Jarvis, M.J.F., Siegfried, W.R. and Currie, M.H.** 1974. Conservation of the Cape Vulture in the Cape Province. *Journal of South African Wildlife Management Association* 4(1): 29-34.
- Johnson, P.N.** 1991. Reducing the drowning of owls and raptors in Great Britain. *Vulture News* 25: 23-24.
- Johst, G.** 1986. Einige angaben zur Zucht des Anden-Kondors (*Vultur gryphus*). *Zool. Gtn.* 56: 130-144.
- Lack, D.** 1968. *Ecological adaptations for breeding in birds*. Methuen: London.
- Lack, P.** 1986. *The atlas of wintering birds in Britain and Ireland*. T & AD Poyser: Calton.
- Lakhani, K.H.** 1990. Choice of models for estimating age-specific bird survival rates using data from ring recoveries. *Ring* 13(1&2): 23-36.

- 
- Lakhani, K.H. and Newton, I.** 1983. Estimating age-specific bird survival rates from ring recoveries - can it be done? *Journal of Animal Ecology* 52: 83-91.
- Lande, R.** 1988. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia (Berlin)* 75: 601-607.
- Larkin, R.P.** 1988. Why are migrating birds killed at tall structures? *Ill. Nat. Hist. Surv. Rep.* 277: 1-2.
- Laughlin, S.B., Kibbe, D.B. and Eagles, P.F.J.** 1982. Atlasing the distribution of the breeding birds of North America. *American Birds* 36: 6-19.
- Lebreton, J.-D.** 1977. Maximum likelihood estimations of survival rates from bird band returns: some complements to age-dependent methods. *Biométrie-Praximétrie* 17: 145-161.
- Lebreton, J.-D. and Clobert, J.** 1986. *User's manual for program Surge*, version 2.0. CEPE/CNRS: Montpellier.
- Lebreton, J.-D. and Clobert, J.** 1991. Bird population dynamics, management, and conservation: the role of mathematical modelling. Pp. 105-125 in Perrins, C.M., Lebreton, J.-L. and Hiron, G.J.M. (eds.): *Bird Population Studies: Relevance to conservation and management*. Oxford University Press: Oxford.
- Lebreton, J.-D., Hemery, G., Clobert, J. and Coquillart, H.** in Press. The estimation of age-specific breeding probabilities from recaptures or resightings in vertebrate populations.. I. Transversal models. *Biometrics* 46.
- Leconte, M.** 1985. Present status of the Griffon Vulture on the northern slopes of the western Pyrenees. Pp. 117-127 in Newton, I. and Chancellor, R.D. (eds.): *Conservation Studies of Raptors*, I.C.B.P. Technical Publication No. 5, I.C.B.P.: Cambridge.
- Ledger, J.A.** 1974. Colour-rings for vultures. *Safring News* 3(2): 23-8.
- Ledger, J.A.** 1977. Editorial. *Bokmakierie* 29(3): 58.
- Ledger, J.A.** 1978. Powerline hazards to birds in South Africa, with special reference to the Cape Vulture. P. 108 in *Proceedings of a Symposium on African Predatory Birds*, N.T.O.S.: Pretoria.
- Ledger, J.A.** 1979. Drowning of Cape Vultures in circular water tanks in South Africa. *International Symposium on the Vultures*: Santa Barbara (California).

- 
- Ledger, J.A. 1980. Plea to save Africa's birds from electrocution. *Megawatt* 63: 11-13.
- Ledger, J.A. 1982. The Vulture Study Group. *Quagga* 1: 7-11.
- Ledger, J.A. 1984. Engineering solutions to the problem of vulture electrocutions on electricity towers. *The Certificated Engineer* 57(6): 92-95.
- Ledger, J.A. 1987. Ornithological publications in southern Africa. *Bokmakierie* 39: 53-57.
- Ledger, J.A. 1988. Tackling the problem of vulture poisoning. *Bokmakierie* 40(1): 4-5.
- Ledger, J.A. 1989. Birds and transmission lines. A report to Lesotho Highlands Development Authority. Effects of phase 1A transmission lines on birds and other wildlife, and the effects of birds on the transmission lines. Report, Endangered Wildlife Trust: Johannesburg.
- Ledger, J.A. and Annegarn, H.J. 1979. Electrocution hazards to the Cape Vulture in South Africa. *International Symposium on the Vultures*: Santa Barbara (California).
- Ledger, J.A. and Annegarn, H.J. 1981. Electrocution hazards to the Cape Vulture *Gyps coprotheres* in South Africa. *Biological Conservation* 20: 15-24.
- Ledger, J.A. and Mundy, P.J. 1973. Cape Vulture ringing in southern Africa. *Safring News* 2(3): 5-11.
- Ledger, J.A. and Mundy, P.J. 1975. Research on the Cape Vulture. 1974 progress report. *Bokmakierie* 27(1): 2-7.
- Ledger, J.A. and Mundy, P.J. 1976. Cape Vulture report for 1975. *Bokmakierie* 28(1): 4-8.
- Ledger, J.A. and Mundy, P.J. 1977. Research on the rare Cape Vulture. *Fauna and Flora* 29: 12-13.
- Ledger, J.A. and Mundy, P.J. 1978. Cape Vulture recovery data. *Safring News* 7(2): 21-31.
- Leshem, Y. 1985. The rapid decline of the four vulture species in Israel. *International Vulture Symposium*: Sacramento (California). November 2-3, 1985.
- Leshem, Y. 1985. Griffon Vultures in Israel: electrocution and other reasons for a declining population. *Vulture News* 13: 14-20.
- Leshem, Y. 1985. Vultures under high tension. *Israel Land and Nature* 10(4): 149-153.

- 
- Leslie, P.H. 1945. On the use of matrices in certain population mathematics. *Biometrika* 33: 183-212.
- Leslie, P.H. 1948. Some further notes on the use of matrices in population mathematics. *Biometrika* 35: 213-245.
- Leslie, P.H. and Park, T. 1949. The intrinsic rate of natural increase of *Tribolium castaneum* Herbst. *Ecology* 30: 469-477.
- Lewis, A. and Pomeroy, D. 1989. *A bird atlas of Kenya*. Balkema: Rotterdam.
- Lexis, W. 1875. *Einleitung in die Theorie der Bevölkerungs-Statistik*. Trubner: Strasbourg.
- Leyland, J. 1866. *Adventures in the far interior of South Africa*. Routledge: London.
- Lindstedt, S.L. and Calder, W.A. 1976. Body size and longevity in birds. *Condor* 78: 91-145.
- Lint, K.C. 1960. Notes on breeding Andean Condors at San Diego Zoo. *International Zoo Year Book* 2: 82-83.
- Lotka, A.J. 1924. *Elements of Physical Biology*. Williams and Wilkins: Baltimore.
- Louwman, J.W.W. 1981. Breeding and hand-rearing the Bearded Vulture at the Wassenaar Zoo, Holland. *Avicultural Magazine* 87: 223-231.
- Lucas, J. 1970. (ed.): Longevity of birds of prey and owls in captivity. *International Zoo Yearbook* 10: 36-37.
- Ludwig, J.P. 1981. Band wear and band loss in the Great Lakes Caspian Tern population and a generalized model of band loss. *Colonial Waterbirds* 4: 174-186.
- MacArthur, R.H. and Wilson, E.O. 1967. *The theory of island biogeography*. Princeton University Press: Princeton.
- Maclean, G.L. 1985. *Roberts' birds of southern Africa. 5th edition*. John Voelcker Bird Book Fund: Cape Town.
- Mardekian, S.Z. and McDonald, L. 1981. Simultaneous analysis of band-recovery and live recapture data. *Journal of Wildlife Management* 45: 484-488.
- Mardia, K.V. 1970. *Families of bivariate distributions*. Griffon: London.
- Markus, M.B. 1972. Mortality of Vultures caused by electrocution. *Nature* 238(5361): 228.

- 
- Markus, M.B., Daly, T.J.M. and Mundy, P.J.** 1984. Host specificity of *Sarcocystis* species of wild African ungulates. *Parasitology* 89: xliii-xliv.
- Markus, M.B., Mundy, P.J. and Daly, T.J.M.** 1985. Vultures *Gyps* spp. as final hosts of *Sarcocystis* of the impala *Aepyceros melampus*. *South African Journal of Science* 81: 43.
- Martin, A.** 1890. *Home life on an ostrich farm*. George Philip: London.
- Mathiasson, S.** 1987. Parents, children and grandchildren: maturity process, reproduction strategy and migratory behaviour of three generations and two year-classes of Mute Swans *Cygnus olor*. *Acta Regiae Soc. Sci. Litt. Gothoburgensis Zool.* 14: 60-70.
- Mayr, E.** 1963. *Animal species and evolution*. Belknap: Cambridge (Mass.).
- McCullagh, P. and Nelder, J.A.** 1989. *Generalized linear models*. Chapman and Hall: London.
- McGahan, J.** 1971. The Condor, soaring spirit of the Andes. *National Geographic* 139(5): 684-709.
- McGahan, J.** 1972. *Behaviour and ecology of the Andean Condor. Parts 1, 2 and 3*. University of Wisconsin, University Microfilms: Ann Arbor.
- McNeill, L.** 1991. Interpolation and smoothing of binomial data for the Southern African Bird Atlas Project. *South African Statistical Journal* 25: 129-136.
- Mearns, R. and Newton, I.** 1984. Turnover and dispersal in a Perigrine population. *Ibis* 126: 347-355.
- Mendelssohn, H. and Leshem, Y.** 1983. Observations on reproduction and growth of old world vultures. Pp. 214-241 in Wilbur, S.R. and Jackson, J.A. (eds.): *Vulture Biology and Management*. University of California Press: Berkeley and Los Angeles.
- Mendelssohn, H. and Marder, U.** 1989. Reproduction of *Torgos tracheliotus negevensis* in captivity. *Vulture News* 22: 28-33.
- Mertz, D.B.** 1971. The mathematical demography of the California Condor population. *American Naturalist* 105(945): 437-453.
- Mills, J.A.** 1989. Red-billed Gull. Pp. 387-404 in Newton, I (ed.): *Lifetime Reproduction in Birds* Academic Press: London.

- 
- Minnemann, D. and Busse, H.** 1984. Longevity of birds of prey and owls at East Berlin Zoo. Pp. 108-110 in Olney, P.J.S. (ed.): *1983 International Zoo Yearbook*. 23. Zoological Society: London.
- Miquet, A.** 1990. Mortality in Black Grouse *Tetrao tetrix* due to elevated cables. *Biological Conservation* 54: 349-355.
- Moorcroft, E.** 1984. Letter to the editor. *Diaz Diary* 125: 3-4.
- Moore, C.P., Pickett, J.P. and Beehler, B.** 1985. Extracapsular extraction of senile cataract in an Andean Condor. *Journal of the American Veterinary and Medical Association* 187: 1211-1213.
- Morgan, B.J.T.** 1984. *Elements of simulation*. Chapman & Hall: London.
- Morgan, B.T.J. and Freeman, S.N.** 1989. A model with first-year variation for ring-recovery data. *Biometrics* 45: 1087-1102.
- Morris, A. and Mundy, P.J.** 1981. Incidents of poisoning vultures in Zimbabwe. *Zimbabwe Science News* 15(5): 127-9.
- Muir, B.** 1983. A new view. *Blue Jay* 41: 118-119.
- Mundy, P.J.** 1973. On the Cape and White-backed Vultures. *Honeyguide* 76: 10-17.
- Mundy, P.J.** 1974. Review. *Safring News* 3(3): 37-38.
- Mundy, P.J.** 1982. *The comparative biology of southern African vultures*. Vulture Study Group: Johannesburg.
- Mundy, P.J.** 1983. The conservation of the Cape Griffon Vulture of southern Africa. In *Vulture Biology and Management* (Wilbur, S.R. and Jackson, J.A., eds.). University of California Press: Berkeley and Los Angeles: 57-74.
- Mundy, P.J.** 1984. Vultures are Forever. Pp. 105-117 in Mundy, P.J. (ed.): *The Extinction Alternative*. Endangered Wildlife Trust: Johannesburg.
- Mundy, P.J.** 1985. (ed.): The biology of vultures: A summary of the workshop proceedings. Pp. 457-482 in Newton, I. and Chancellor, R.D. (eds.): *Conservation Studies of Raptors*, I.C.B.P. Technical Publication No. 5, I.C.B.P.: Cambridge.
- Mundy, P.J., Butchart, D., Ledger, J.A. and Piper, S.E.** 1992. *The vultures of Africa*. Acorn Books & Russel Friedman Books: Johannesburg.

- 
- Mundy, P.J., Grant, K.I., Tannock, J. and Wessels, C.L. 1982. Pesticide residues and eggshell thickness of Griffon Vulture Eggs in southern Africa. *Journal of Wildlife Management* 46(3): 769-773.
- Mundy, P.J. and Ledger, J.A. 1975. The effects of fire on a Cape Vulture colony. *South African Journal of Science* 71: 217.
- Mundy, P.J. and Ledger, J.A. 1980. Vultures poisoned in Zimbabwe-Rhodesia and Transvaal. *Vulture News* 3: 16-17.
- Mundy, P.J., Ledger, J.A. and Friedman, R. 1980. The Cape Vulture project in 1977 and 1978. *Bokmakierie* 32(1): 2-8.
- Mundy, P.J., Ledger, J.A., Friedman, R. and Butchart, D. 1989. *Vulture restaurants and other aspects of the conservation and management of Cape Vultures in the Magaliesberg 1981-1984*. Final project report to S.A. Nature Foundation. V.S.G.: Johannesburg.
- Mundy, P.J. and Marais, E. 1981. Vultures in captivity in southern Africa. *Avicultural Magazine* 87(4): 215-222.
- Mundy, P.J., Robertson, A.S., Komen, J. and O'Connor, T.G. 1986. Attacks by Black Eagles on vultures. *Raptor Research* 20(2): 61-64.
- Mundy, P.J. and Steyn, P. 1977. To breed or not to breed. *Bokmakierie* 29(1): 5-7.
- Nelson, J.B. and Powell, D. 1986. The breeding ecology of Abbott's Booby *Sula abbotti*. *Emu* 86: 33-46.
- Nelson, L.J., Anderson, D.R. and Burnham, K.P. 1980. The effect of band loss on estimates of annual survival. *Journal of Field Ornithology* 51(1): 30-38.
- Newman, K.B. 1988. *Birds of southern Africa*. Southern Book Publisher: Johannesburg.
- Newton, I. 1979. *Population ecology of raptors*. A. & T.D. Poyser: Berkhamsted.
- Newton, I. 1985. Lifetime reproductive output of female sparrowhawks. *Journal of Animal Ecology* 54: 241-253.
- Newton, I. 1989. (ed.): *Lifetime Reproduction in Birds*. Academic Press: London.
- Newton, I. 1989. Synthesis Pp.441-469 in Newton, I (ed.): *Lifetime Reproductions in Birds*. Academic Press: London.

- 
- Newton, I.** 1989. Population limitation in raptors. Pp. 3-12 in *Proceedings of the northeast raptor management symposium and workshop*. Natl. Wildlife Fed. Dci. Tech. Ser. 13.
- Newton, I.** 1991. Population limitation in birds of prey: a comparative approach. p. 3-21 *In* Perrins, C.M., Lebreton, J.-D. and Hiron, G.J.M. *Bird population studies. Relevance to conservation and management*. Oxford University Press: Oxford.
- Newton, I., Davis, P.E. and Davis, J.E.** 1989. Age of first breeding, dispersal and survival of Read Kites *Milvus milvus* in Wales. *Ibis* 131: 16-21.
- Newton, I., Marquiss, M. and Rothery, P.** 1983. Age structure and survival in a sparrowhawk population. *Journal of Animal Ecology* 52: 591-602.
- Nikolaus, G.** 1984. Large numbers of birds killed by electric power line. *Scopus* 8: 42.
- Nikolaus, G.** 1987. Distribution atlas of Sudan's birds with notes on habitat and status. *Bonn. Zool. Monograph* No. 25.
- Nisbet, I.C.T. and Hatch, J.J.** 1983. Band wear and band loss in Roseate Terns. *Journal of Field Ornithology* 54: 90.
- Norman, J.L.** 1982. The Coweta TV tower kill. *Bulletin Oklahoma Ornithological Society* 15: 19-22.
- Norman, J.L.** 1987. Synopsis of birds killed at the Coweta, Oklahoma, TV tower, 1974-1984. *Bulletin Oklahoma Ornithol. Soc.* 20: 17-22.
- North, P.M.** 1987. Ring recovery analytical methods: a brief review. *Acta Ornithologica* 23(1): 7-12.
- North, P.M.** 1990. Analysis of avian ring recovery and live recapture data: where have we come from Wageningen to Sempach? *Ring* 13(1&2): 11-22.
- North, P.M. and Morgan, B.J.T.** 1979. Modelling Heron survival using weather data. *Biometrics* 35: 667-681.
- Ogden, J.C., Barbour, D.B., Bloom, P.H., Grantham, J. and Riopelle, L.** 1983. First year results from Radio Tracking the California Condor (*Gymnogyps californianus*). *U.S. Raptor Research Symposium*.
- Olendorff, R.R., Miller, A.D. and Lehman, R.N.** 1981. Suggested practices for raptor protection on power lines - the state of the art in 1981. *Raptor Research Foundation Report* No. 4.

- 
- Ollason, J.C. and Dunnet, G.M.** 1988. Variations in breeding success in Fulmars. Pp. 263-278 in Clutton-Brock, T.H. (ed.): *Reproductive Success*. University of Chicago Press: Chicago.
- Palmer, R.S.** 1988. (ed.): *Handbook of North American birds. Volume 4: Diurnal raptors (Part 1)*. Yale University Press: London.
- Parker Rabenold, P.** 1985. Identifying causes of population decline in Black or Turkey Vultures in the U.S.A. *Vulture News* 14: 16-18.
- Parker Rabenold, P.** 1986. Family association in communally roosting Black Vultures. *Auk* 103(1): 32-41.
- Partridge, L.** 1989. Lifetime Reproductive Success and Life-history Evolution. p. 421-440 In Newton, I. (ed.) *Lifetime reproduction in birds*. Academic Press: London.
- Patel, J.K., Kapadia, C.H. and Owen, D.B.** 1976. *Handbook of statistical distributions*. Marcel Dekker: New York.
- Peach, W.J., Buckland, S.T. and Baillie, S.R.** 1990. Estimating survival rates using mark-recapture data from multiple ringing sites. *Ring* 13(1&2): 87-102.
- Pennycuik, C.J.** 1972. Soaring behaviour and performance of some East African birds observed from a motor glider. *Ibis* 114: 178-218.
- Pennycuik, C.J.** 1976. Breeding of the lappet-faced and white-headed vultures (*Torgos tracheliotus* Forster and *Trigonoceps occipitalis* Burchell) on the Serengeti Plains, Tanzania. *East African Wildlife Journal* 14: 67-84.
- Pennycuik, C.J.** 1983. Effective nest density of Ruppell's Griffon Vulture in the Serengeti-Rift Valley area of Northern Tanzania. Pp. 172-184 in Wilbur, S.R. and Jackson, J.A. (eds.): *Vulture Biology and Management*. University of California Press: Berkeley and Los Angeles.
- Perrins, C.M.** 1991. Constraints on the demographic parameters of bird populations. p. 190-206 In Perrins, C.M., Lebreton, J.D. and Hiron, G.J.M. *Bird population studies. Relevance to conservation and management*. Oxford University Press: Oxford.
- Petit Bois, G.** 1961. *Tables of indefinite integrals*. Dover: New York.
- Pielou, E.C.** 1969. *An introduction to mathematical ecology*. Wiley: New York.

- 
- Piper, S.E.** 1985. Observations on the Cape Vulture at Umtamvuna, Natal. *Bokmakierie* 37(2): 35-37.
- Piper, S.E.** 1992. François Sarrazin and the re-introduction of the Eurasian Griffon *Gyps fulvus* in France. *Vulture News* 27: 28-29.
- Piper, S.E., Mundy, P.J. and Ledger, J.A.** 1981. Estimates of survival in the Cape Vulture, *Gyps coprotheres*. *Journal of Animal Ecology* 50: 815-825.
- Piper, S.E., Mundy, P.J. and Mundy, V.S.** in Prep. *Marked Cape Vultures Gyps coprotheres: all birds handled to 1990*. Scientific Report. Vulture Study Group: Johannesburg.
- Piper, S.E., Mundy, P.J. and Vernon, C.J.** 1989. An ageing guide for the Cape Vulture. *Madoqua* 16(2): 105-110.
- Piper, S.E. and Ruddle, P.** 1986. An initial evaluation of the Cape Vulture colonies at Mkambati, Transkei. *Vulture News* 15: 7-12.
- Plunkett, R.L.** 1978. Integrated management of endangered birds. A review. In *Endangered birds. Management techniques for preserving threatened species* (Temple, S.A. ed.). University of Wisconsin Press: Madison: 387-396.
- Pokki, J.** 1981. Distribution, demography and dispersal of the field vole *Microtu agrestis*(L.) in the Tvärminne archipelago, Finland. *Acta Zoologica Fennica* 164: 1-48.
- Pollock, K.H.** 1981. Capture-recapture models allowing for age-dependent survival and capture rates. *Biometrics* 37: 521-529.
- Pollock, K.H. and Raveling, D.G.** 1982. Assumptions of modern band-recovery models, with emphasis on heterogeneous survival rates. *Journal of Wildlife Management* 46: 88-98.
- Pollock, K.H., Winterstein, S.R. and Conroy, M.J.** 1989. Estimation and analysis of survival distributions for radio-tagged animals. *Biometrics* 45: 99-109.
- Pomeroy, D.E.** 1977. Marabous associated with vulture parties in East Africa. *Scopus* 1(4): 103-106.
- Pomeroy, D.E. and Lewis, A.D.** 1983. Estimating the number of species likely to occur in Kenya bird atlas squares. *Scopus* 7(2): 40-43.

- 
- Postupalsky, S.** 1989. Osprey. Pp. 297-296 in Newton, I (ed.): *Lifetime Reproduction in Birds*. Academic Press: London.
- Pradel, R., Clobert, J. and Lebreton, J.D.** 1990. Recent developments for the analysis of multiple capture-recapture data sets. An example concerning two Blue Tit populations. *Ring* 13(1&2): 193-204.
- Pringle, V.L.** 1974. The Bashee vulture colony. *Eastern Cape Naturalist* 53: 7.
- Purroy, F.J.** 1981. (ed.): Primer censo de buitreras (1979) [First general survey of Griffon Vulture breeding colonies in the Iberian Peninsula, 1979.] *Ardeola* 26-27: 165-312.
- Quickelberge, C.D.** 1989. *Birds of the Transkei*. Durban Natural History Museum: Durban.
- Reinert, S.E.** 1984. Use of introduced perches by raptors: experimental results and management implications. *Raptor Research* 18(1): 25-29.
- Richardson, P.R.K.** 1984. The scavenging behaviour of vultures in southern Africa. Pp. 331-353 in Ledger, J.A. (ed.): *Proceedings of the Fifth Pan-African Ornithological Congress*. Southern African Ornithological Society: Johannesburg.
- Richford, A.S. and Platt, J.M.** 1982. Status of the Black Vulture in Mallorca in 1982. *Vulture News* 8: 11-18.
- Rinne, J., Lokki, H. and Saurola, P.** 1990. Survival estimates of nestling recoveries: forbidden fruits of ringing? *Ring* 13(1&2): 255-270.
- Robertson, A.S.** 1982. Vulnerable vultures: a case study of the Potberg colony. *Vulture News* 7: 3-4.
- Robertson, A.S.** 1983. The feeding ecology and breeding biology of a Cape Vulture colony in the southwestern Cape province. Unpublished M.Sc. Dissertation, Witwatersrand University: Johannesburg.
- Robertson, A.S.** 1984. Aspects of the population dynamics of Cape Vultures in the Cape province. *Ostrich* 55(4): 196-206.
- Robertson, A.S.** 1984. Post fledging dependence periods of Cape Vultures at the Potberg colony. P. 59 in Mendelsohn, J.M. and Sapsford, C.W. (eds.): *Proceedings, second symposium on African predatory birds*. Natal Bird Club: Durban.
- Robertson, A.S.** 1985. Observations on the post-fledging dependence period of Cape Vultures. *Ostrich* 56: 58-66.

- 
- Robertson, A.S.** 1986. Notes on the breeding cycle of Cape Vultures (*Gyps coprotheres*). *Raptor Research* 20(2): 51-60.
- Robertson, A.S.** 1986. Copulations throughout breeding in a colonial accipitrid vulture. *Condor* 88(4): 535-539.
- Robertson, A.S. and Boshoff, A.F.** 1986. The feeding ecology of Cape Vultures *Gyps coprotheres* in a stock-farming area. *Biological Conservation* 35: 63-86.
- Robertson, A.S. and Butchart, D.** 1990. Vulture conservation in Thabazimbi. *Vulture News* 23: 26.
- Robertson, A.S. and February, E.** 1986. Towards an historical perspective of Cape Vultures and domestic stock: a view from the southwestern Cape. *Vulture News* 15: 4-6.
- Roos, L. and Roos, M.** 1988. A possible case of vulture poisoning in the OFS. *Mirafra* 5(2): 30-32.
- Rothery, P. and Prince, P.A.** 1990. Survival and breeding frequency in albatrosses. *Ring* 13(1&2): 61-74.
- Samour, H.J., Olney, P.J.S., Herbert, D., Smith, F., White, J. and Wood, D.** 1984. Breeding and hand-rearing the Andean Condor *Vultur gryphus* at London Zoo. Pp. 7-11 in Olney, P.J.S. (ed.): *1983 International Zoo Yearbook* 23. Zoological Society: London.
- Sarker, S.U.** 1984. Young vulture hatched. *Vulture News* 11: 21.
- Sauer, E.G.F.** 1973. Notes on the behaviour of Lappet-faced Vultures and Cape Vultures in the Namib Desert of South West Africa. *Madoqua* Series II, 2: 43-62.
- Saurola, P.** 1989. Ural Owl. Pp. 327-345 in Newton, I. (ed.): *Lifetime Reproduction in Birds*. Academic Press: London.
- Schenk, H., Aresu, M. and Serra, G.** 1987. Sull'ecologia e sulla conservazione del grifone (*Gyps fulvus*) nella Sardegna nord-occidentale, 1971-1984. Pp. 217-233 in Baccetti, N. and Spagnesi, M. (eds.): *Rapaci Mediterranei III. Suppl. Ric. Biol. Selvaggina* 12: 1-315.
- Schlatter, R., Reinhardt, G. and Burchard, L.** 1978. Estudio del jote (*Coragyps atratus foetens* Lichenstein) en Valdivia: etologia carronera y rol en diseminacion de agentes patogenos. *Arch. Med. Vet.* 10: 111-127.

- Schreiber, R.W. and Schreiber, E.A.** 1983. Use of age-classes in monitoring population stability of Brown Pelicans. *Journal of Wildlife Management* 47: 105-111.
- Schuh, J.C.L. and Yuill, T.M.** 1985. Persistence of inclusion body disease of cranes virus. *Journal of Wildlife Diseases* 21: 111-119.
- Scott, H.A.** 1991. A 'miracle' Cape Griffon? *Vulture News* 25: 17-20.
- Seber, G.A.F.** 1982. Estimation of animal abundance and related parameters. 2nd. ed. Charles Griffin: London.
- Seber, G.A.F.** 1986. A review of estimating animal abundance. *Biometrics* 42: 267-292.
- Sharrock, J.T.R.** 1976. (ed.): *The atlas of breeding birds in Britain and Ireland*. T. & T.D. Poyser: Berkhamsted.
- Shedden, C.B., Monaghan, P., Ensor, K. and Metcalfe, N.B.** 1985. The influence of colour-rings on recovery rates of Herring and Lesser Black-backed Gulls. *Ringing and Migration* 6: 52-54.
- Shields, W.M.** 1984. Optimal inbreeding and the evolution of philopatry. In Swingland I.R. & Greenwood, P.J. eds. *The ecology of animal movement*. Clarendon Press: Oxford. p. 132-159.
- Siegfried, W.R.** 1984. Red data books: bibles for protectionists, Aunt Sallies for conservationists. In *The extinction alternative* (Mundy P.J., ed.). Endangered Wildlife Trust, Johannesburg: 119-26.
- Siegfried, W.R., Frost, P.G.H., Cooper, J. and Kemp, A.C.** 1976. Rare and Vulnerable Birds in South Africa. *Biological Conservation* 10: 83-93.
- Simberloff, D.** 1980. A succession of paradigms in ecology: essentialism to materialism and probabilism. In Saarinen, E. (ed.). *Conceptual issues in Ecology*. Reidel.
- Sinclair, A.R.E.** 1984. The function of distance movements in vertebrates. In Swingland, I.R. & Greenwood, P.J. (eds.). *The ecology of animal movement*. pp. 240-258. Oxford University Press: Oxford.
- Smith, A.T. and Peacock, M.M.** 1990. Conspecific attraction and the determination of metapopulation colonization rates. *Conservation Biology*. 4: 320-323.

- 
- Smith, J.N.M., Arcese, P. and Hochachka, W.** 1991. *In* Perrins, C.M., Lebreton, J.-D. & Hiron, G.J.M. (eds.). *Bird population studies*. Oxford University Press: Oxford. pp. 148-167.
- Snow, D.W.** 1978. (ed.): *Atlas of speciation in African non-passerine birds*. British Museum (Natural History): London.
- Snyder, N.F.R.** 1983. California Condor reproduction, past and present. *Bird Conservation* 1: 67-86.
- Snyder, N.F.R.** 1985. Multiple-clutching of wild California Condors (*Gymnogyps californianus*). *International Vulture Symposium*. Sacramento (California). 2-3 November 1985.
- Snyder, N.F.R.** 1988. California Condor. Pp. 43-66 in Palmer, R.S. (ed.). *Handbook of North American birds*, vol. 4. Yale University Press: New Haven (Conn.).
- Snyder, N.F.R., Snyder, H.A., Hamber, J.A. and Cox, C.** 1985. California Condor (*Gymnogyps californianus*) breeding biology. *International Vulture Symposium*, Sacramento (California). 2-3 November 1985.
- Sokal, R.R. and Sneath, P.H.A.** 1963. *Principles of numerical taxonomy*. Freeman: San Francisco.
- Soulé, M.E. and Kohm, K.** 1989. *Research priorities for conservation biology*. Island Press: Washington (DC).
- Spiker, C.J.** 1936. Turkey Vultures possible victims of an automobile. *Auk* 53: 76-77.
- Sprunt, Jr, A.** 1937. Turkey Vultures killed by automobiles. *Auk* 54: 383-384.
- Starfield, A.M. and Bleloch, A.L.** 1986. *Building models for conservation and wildlife management*. MacMillan: Basingstoke (Hants.).
- Stewart, P.A.** 1977. Migratory movements and mortality rate of Turkey Vultures. *Bird Banding* 48(2): 122-124.
- Stewart, P.A.** 1983. The biology and communal behaviour of American Black Vultures. *Vulture News* 9/10: 14-36.
- Steyn, P.** 1982. *Birds of prey of southern Africa*. David Philip: Cape Town.

- 
- Stuart, C.T., Macdonald, I.A.W. and Mills, M.G.L.** 1985. History, current status and conservation of large mammalian predators in Cape Province, Republic of South Africa. *Biological Conservation* 31: 7-19.
- Tarboton, W.R.** 1968. *Checklist of the birds of the south central Transvaal*. Wits Bird Club: Johannesburg.
- Tarboton, W.R. and Allan, D.G.** 1984. The status and conservation of birds of prey in the Transvaal. *Transvaal Museum Monograph* No. 3: Pretoria.
- Tarboton, W.R., Allan, D.G. and Benson, P.C.** 1984. Aerial censusing of Cape Vulture colonies project TN 6/4/4/9: a threatened Transvaal bird species. Report of Transvaal Provincial Administration, Nature Conservation Division: Pretoria.
- Tarboton, W.R., Kemp, M.I. and Kemp, A.C.** 1987. *Birds of the Transvaal*. Transvaal Museum: Pretoria.
- Taylor, C.H. and Bucknill, J.A.** 1907. Notes on a collection of birds made in the Amsterdam district upon the Transvaal-Swaziland border between the months of June and October, 1906. *Journal South African Ornithologists' Union* 3(1): 12-42.
- Temple, S.A.** 1985. Status and recovery efforts for the California Condor. *Bird Conservation* 2: 162-165.
- Temple, S.A. and Wallace, M.P.** 1989. Survivorship patterns in a population of Andean Condors *Vultur gryphus*. Pp. 247-251 in Meyburg, B.-U. and Chancellor, R.D. (eds.): *Raptors in the modern world*. World Working Group on Birds of Prey and Owls: Berlin.
- Terrasse, J.-F.** 1977. Maturité sexuelle du Vautour Fauve, premières données obtenues dans la nature. *Oiseau* 47: 214-218.
- Thiollay, J.-M.** 1975. Migrations de rapaces africains en Ouganda et au Rwanda. *Oiseau RFO* 45: 192-194.
- Thiollay, J.-M.** 1976. Les rapaces d'une zone de contact savane-foret en Cote-d'Ivoire: modalités en succes de la reproduction. *Alauda* 44(3): 275-300.
- Thiollay, J.-M.** 1977. Distribution saisoniere des rapaces diurnes en Afrique occidentale. *Oiseau* 47(3): 253-294.
- Thomas, G.B.** 1960. *Calculus and analytic geometry*. Addison-Wesley: Reading (Mass.).

- Toone, C.K. and Toone, W.D.** 1985. Techniques for captive rearing of California Condors (*Gymnogyps californianus*) from eggs removed from the wild. *Symposium on Raptor Rehabilitation and Captive Breeding*. Sacramento (California). 2-3 November 1985.
- Torres, J.A., Jordano, P. and Villasants, J.** 1980. Estructura y dinamica temporal de una colonia de Buitre Negro, *Aegypius monachus* en Sierra Morena Central (Cordoba). *Bol. Est. Centr. Ecol.* 9(17): 67-72.
- Tukey, J.W.** 1977. *Exploratory Data Analysis*. Addison-Wesley: Reading (Mass.).
- Udvardy, M.D.F.** 1969. *Dynamic zoogeography*. Reinhold: London.
- Underhill, L.G., Oatley, T.B. and Harrison, J.A.** 1991. The role of large-scale data collection projects in the study of southern African birds. *Ostrich* 62(3&4): 124-148.
- Upton, G.J.G., Fingleton, and B** 1989. *Spatial data analysis by example*. Vol. 2. *Categorical and directional data*. Wiley: Chichester.
- Utschick, H.** 1984. Rasterkartierung von Sommervogelbeständen zur Nutzung der Bioindikation häufiger Vogelarten. *Journal für Ornithologie* 125: 39-57.
- van der Byl, R.** 1987. Letters. *Vulture News* 17: 56.
- van Heerden, J.** 1980. Report on the Cape Vultures at Merrimetsi in the Excelsior district, Orange Free State. *Vulture News* 4: 13-14.
- van Jaarsveld, J.** 1987. Population also loses poisoned vultures' chicks or eggs. *Custos* 16(7): 18-19.
- Verdoorn, G.H. and Becker, I.** 1992. Cape Griffons of the Magaliesberg: 1991 census of nestlings and first breeding record at Nooitgedacht since 1964. *Vulture News* 27: 19-25.
- Verdoorn, G.H., Becker, I. and Branfield, A.S.** 1992. Annual census of Cape Griffon nestlings in the Magaliesberg - 1990 results. *Vulture News* 26: 22-29.
- Verner, J.** 1978. California Condors: Status of the recovery effort. General Technical Report PSW-28: Berkeley (California).
- Vernon, C.J.** 1975. Seventeenth ringing effort for southern Africa. *Ostrich* 46(2): 125-128.
- Vernon, C.J.** 1978. Change in the reporting locality of the Cape Vultures ringed in the Transvaal in the period, 1953-1975. *Safring News* 7(2): 17-19.

- 
- Vernon, C.J.** 1982. Bawa Falls revisited - the Cape Vulture colony of the Gcuwa River, Transkei. *Vulture News* 8: 33.
- Vernon, C.J.** 1983. Notes from the border - 11. *Bee-Eater* Supplement No. 10.
- Vernon, C.J.** 1984. The poisoner or the poisoned? A variant of the singer or the song theme, with vultures in the major role on a farming stage. *Pelea* 3: 56-60.
- Vernon, C.J.** 1984. The Cape Vulture colony at Karnmelkspruit, Cape Province in 1982/83. *Vulture News* 12: 18-21.
- Vernon, C.J.** 1987. More vultures poisoned in the Eastern Cape. *Vulture News* 17: 16-18.
- Vernon, C.J., Boshoff, A.F. and Robertson, A.S.** 1983. The Cape Vulture colony at Karnmelkspruit, Cape Province in 1981. *Vulture News* 9/10: 42-43.
- Vernon, C.J. and Piper, S.E.** 1984. The Cape Vulture colony at Colleywobbles, Transkei, in 1983. *Vulture News* 12: 25-28.
- Vernon, C.J. and Piper, S.E.** 1986. The Cape Vulture colony at Colleywobbles, Transkei, in 1984 and 1985. *Vulture News* 15: 27-28.
- Vernon, C.J. and Piper, S.E.** 1986. Cape Vulture twins. *Vulture News* 16: 5-6.
- Vernon, C.J. and Piper, S.E.** 1988. The Cape Vulture colony at Colleywobbles, Transkei in 1986 and 1987. *Vulture News* 19: 24-26.
- Vernon, C.J. and Piper, S.E.** 1991. Observations of Cape Vulture *Gyps coprotheres* nest occupancy (1980 to 1989) at Colleywobbles, Transkei. *Scientific Report* No.1 Vulture Study Group: Johannesburg.
- Vernon, C.J., Piper, S.E. and Schultz, D.M.** 1980. The breeding success of the Cape Vulture at Colleywobbles, Transkei, in 1980. *Vulture News* 4: 21-22.
- Vernon, C.J., Piper, S.E. and Schultz, D.M.** 1982. The breeding success of the Cape Vultures at Colleywobbles, Transkei in 1981. *Vulture News* 8: 26-29.
- Vernon, C.J., Piper, S.E. and Schultz, D.M.** 1983. The Cape Vulture at Colleywobbles Transkei in 1982. *Vulture News* 9/10: 11-13.

- Vernon, C.J., Piper, S.E. and Schultz, D.M. 1984. Reproductive performance of the Cape Vulture at Collywobbles, Transkei. Pp. 109-124 in Mendelsohn, J.M. and Sapsford, C.W. (eds.): *Proceedings Second Symposium on African Predatory Birds*. Natal Bird Club: Durban.
- Vernon, C.J. and Robertson, A.S. 1982. A discussion of the factors regulating breeding in the Cape Vulture *Gyps coprotheres*. *Vulture News* 7: 10-13.
- Wallace, M.P. and Temple, S.A. 1983. "El Niño" and the breeding cycle of Andean Condors in Peru. U.S. Raptor Research Meeting.
- Walton, C. 1984. (ed.): *Atlas of southern Africa*. Reader's Digest: Cape Town.
- Weaver, P. 1981. *The Bird-Watchers Dictionary*. T & AD Poyser: Calton
- Weimerskirch, H. and Jouventin, P. 1987. Population dynamics of the Wandering Albatross, *Diomedea exulans*, of the Crozet Islands: causes and consequences of the population decline. *Oikos* 49: 315-322.
- White, G.C. 1983. Numerical estimation of survival rates from band-recovery and biotelemetry data. *Journal of Wildlife Management* 47(3): 716-728.
- Wiemeyer, S.N., Hill, E.F., Carpenter, J.W. and Krynitsky, A.J. 1986. Acute oral toxicity of sodium cyanide in birds. *Journal of Wildlife Diseases* 22: 538-546.
- Wilkie, D. 1983. Rayleigh test for randomness of circular data. *Applied Statistics* 32: 311-312.
- Wolfenbarger, D.O. 1949. Dispersion of small organisms. *American Midland Naturalist*. 35: 1-152.
- Woods, R.W. 1975. *The birds of the Falkland Islands*. Nelson: Oswestry.
- Wooller, R.D., Bradley, J.S., Skira, I.J. and Serventy, D.L. 1989. Short-tailer Shearwater. Pp. 405-417 in Newton, I. (ed.): *Lifetime Reproduction in Birds*. Academic Press: London.
- Wooller, R.D. and Coulson, J.C. 1977. Factors affecting the age of first breeding of the Kittwake *Rissa tridactyla*. *Ibis* 119: 339-349.
- Wooller, R.D., Skira, I.J. and Serventy, D.L. 1985. Band wear on Short-tailed Shearwaters *Puffinus tenuirostris*. *Corella* 9: 121-122.
- World Bank 1991. *The World Bank atlas 1991*. World Bank: Washington (D.C.).

- 
- Zmud, M.E. 1985. Marking of the Redshank *Tringa totanus* in the Northwestern Pricernomorije. *Ring* 122/123: 7-15.
- Zu-Aretz, S. and Leshem, Y. 1980. [The sea - A trap for gliding birds.] *Torgos* 1(1): 14-20.
- Zucchini, W. and Adamson, P.T. 1984. *The occurrence and severity of droughts in South Africa*. WRC Report No. 91/1/84. Water Research Commision: Pretoria.

